Vegetation Response to Disturbance: Implications for Range Recovery for the Little Smoky and A la Peche Caribou Herds

FINAL REPORT

Prepared for:
Caribou Landscape Management Association

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LETTER OF TRANSMITTAL

January 8, 2008

Mr. Wayne Thorp
Managing Director
Box 7352
Peace River, Alberta T8S 1S9

Dear Mr. Thorp:

Re: Vegetation Response to Disturbance: Implications for Range Recovery for the A La Peche and Little Smoky Caribou Herds

At your request, Fiera Biological Consulting Ltd. has completed a report examining the response of vegetation to disturbance in west central Alberta; this information is meant to serve as base for developing caribou habitat management recommendations (in an adaptive management framework), as well as manage ungulate browse in the same landbase. Meta-analysis results are presented for vegetation functional group response to a number of predictor variables (e.g. stand age, forest type, topographic variables). A synthesis of results and a literature review is provided. Knowledge gaps and recommendations for future work are also identified.

If you have any questions or comments regarding this report please contact our office at your convenience.

Sincerely,
Fiera Biological Consulting Ltd.

Katherine Maxcy, M.Sc.
Sr. Wildlife Biologist

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Executive Summary

Through the Caribou Landscape Management Association (CLMA), a network of forest and oil and gas companies are working together to minimize their industrial footprint within the winter ranges of the Little Smoky and A La Peche caribou herds. While the A La Peche herd is one of the few herds in Alberta considered to be stable, the Little Smoky Herd is in rapid decline and is thought to be at “immediate risk of extirpation” (AWCRT 2005). The proximate causes for caribou declines are unknown, and research is currently on-going throughout Alberta and British Columbia examining various aspects of caribou ecology and predator-prey relationships to determine the cause(s) of the declines. The purpose of this report is to examine the response of vegetation functional groups, in a meta-analysis approach, to a number of predictor variables (e.g. stand age, forest type, disturbance type) in the CLMA Planning Area, and to determine the implications of this response on the management of caribou winter range habitat and ungulate browse in the CLMA plan area on the Little Smoky and A la Peche caribou herds.

The percent cover of five vegetation functional groups (shrubs, dwarf shrubs, forbs, grasses, mosses) as well as terrestrial and arboreal lichen were obtained from a variety of data sources (e.g. on-line biological index databases, PhD and Master’s theses, unpublished data) to include in the meta-analysis. Data were obtained from 19 sources including: 12 sources and 1168 percent cover estimates for all vegetation functional groups, 13 data sources and 224 percent cover estimates for terrestrial lichen, and 4 data sources and 90 biomass estimates for arboreal lichen. A Classification and Regression Tree (CART) analysis was used to analyze the relationship between vegetation and lichen functional group abundance (either percent cover or biomass) and a number of potential explanatory variables.

Predictor variables that commonly explained variation in the functional groups included: natural subregion, seral stage (or stand age), dominant tree, elevation, aspect, and slope. Of these predictor variables, results were not consistent among functional groups, nor were relationships between predictor variables and functional groups. In general, the predictor variables included in the CART analysis explained a large amount of the variation observed in the abundance patterns of mosses and dwarf shrubs (i.e. >50%), a moderate amount for grasses and terrestrial lichen (i.e. >30%), and a relatively small amount for forbs, shrubs, and arboreal lichen (i.e. <25%). Site specific information was generally lacking on soil moisture and nutrient regimes for most studies; this information would likely have increased the variation explained for all functional groups, but particularly for shrubs and forbs. Further, for all vegetation functional groups (with the exception of mosses), the relationship between stand age and vegetation cover could not be adequately addressed because of the lack of records in early-successional stands, specifically anthropogenically disturbed stands. As a result, the question of when cutblocks stop providing forage for alternate prey species and begin to function as caribou foraging habitat could not be answered directly in this meta-analysis. In spite of this, some general patterns emerged that were consistent with results observed elsewhere, particularly for lodgepole pine-dominated stands. Therefore, these results may serve as a base for developing caribou habitat management recommendations (in an adaptive management framework), while also highlighting information needs and priorities for research.

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1.0 Introduction

The management of woodland caribou and their habitats in Alberta has become a focus of governments and industries that operate within caribou range. Alberta is home to the Boreal and Southern Mountain populations of woodland caribou (*Rangifer tarandus caribou)*, and both these populations are listed as Threatened under Schedule 1 of the *Species At Risk Act* (SARA). Provincially, Alberta has recognized the need to protect caribou populations, and as a result, woodland caribou are listed as At Risk under the Species at Risk Program, and are considered Threatened under Alberta's *Wildlife Act*.

The Caribou Landscape Management Association (CLMA) Planning Area is home to both the A la Peche (mountain ecotype) and the Little Smoky (boreal ecotype) caribou herds. While the A La Peche herd is one of the few herds in Alberta considered to be stable, the Little Smoky Herd is in rapid decline and is thought to be at "immediate risk of extirpation" (AWCRT 2005). The proximate causes for caribou declines are unknown, and research is currently on-going throughout Alberta and British Columbia examining various aspects of caribou ecology and predator-prey relationships to determine the cause(s) of the declines.

Habitat loss and alteration have both been cited as factors potentially affecting woodland caribou success in Alberta, and it is currently unclear when regenerating stands begin to function as caribou habitat following disturbance (Dzus 2001). Information is also lacking on whether there are any important differences between naturally and anthropogenically disturbed stands in their regeneration times, and in particular, when these stands begin to function as caribou habitat. This information is important from a management perspective in order to determine how to provide caribou habitat as quickly and efficiently as possible following disturbance. Foraging information is also required on alternate prey species occurring in the area, as increased ungulate densities may have negative impacts on caribou due to altered predator-prey interactions. Therefore, the purpose of this report is to examine the response of vegetation functional groups to a number of predictor variables in the CLMA Planning Area, and to determine the implications of this response on the management of the Little Smoky and A la Peche caribou herds.

2.0 Methods

2.1 Data Sources

We searched for studies that measured the percent cover of five vegetation functional groups (shrubs, dwarf shrubs, forbs, grasses, mosses) as well as terrestrial and arboreal lichen to include in the meta-analysis. We assembled and reviewed potential vegetation data sources from: on-line biological index databases, PhD and Master's theses available on-line, government publications available on-line, and on-line searches of large forestry-related sites. We also reviewed existing forestry vegetation databases from FMA and quota holders (e.g. PSP, ARIS, FGYA) for potential data. Finally, we contacted people with unpublished datasets to try and obtain permission to use these data sources in this meta-analysis.

Data was included in the vegetation and lichen meta-analysis if:

- Data was collected in the Foothills and Rocky Mountain Natural Regions of Alberta to minimize variability in the dataset due to difference in geographic location of data collection. The arboreal lichen dataset did include data from British Columbia because of the lack of data sources in west central Alberta.

- For vegetation and terrestrial lichen, data was presented as percent cover for either individual species or as a total for functional groups. Studies that presented vegetation data in a derived form (e.g. multivariate analyses) could not be used, nor could studies that reported abundance as biomass (kg/ha) because of the lack of comparable information.
- For arboreal lichen, abundance was presented in biomass (kg/ha) or in a form that could be converted to kg/ha; studies that measured abundance in units that could not be converted to kg/ha were excluded.
- Data sets were mostly complete i.e. percent cover of most individual species was presented. If cover information was only included for common species or for species with a significant difference in abundance between treatments, these data were not included in the meta-analysis.
- Data points had an associated stand age, either numeric age or a categorical estimate (e.g. mature, old).
- There was information on the forest type in which the data was collected.

The percent cover for each functional group was directly extracted from the data source when possible. When percent cover for individual species was presented, total percent cover was calculated for each functional group by first classifying each species into a functional group and then adding percent covers for species within a particular functional group (e.g. shrubs) to get an estimate of total percent cover.

In addition to percent cover of each function group, we also recorded information on potential predictor variables of vegetation abundance (Table 1). Dominant tree species for a stand was determined by the most abundant species in a stand if there were more than one tree present. Spruce stands, including white spruce (Sw) and Engelmann spruce (Se) were combined into one category labeled “Sx”. Additional explanatory variables (e.g. ecosite, soil moisture/nutrient regime) were not included in the meta-analysis because this information was generally unavailable for most studies.

Table 1. Description of explanatory variables examined in the vegetation and lichen meta-analysis. Under variable type: N = numeric, C = categorical. For dominant tree: Fa = subalpine fir, La = alpine larch, Lt = larch, Mix = mixedwood (coniferous and deciduous), Pb = whitebark pine, Pl = lodgepole pine, Sb = black spruce, shrub = shrub-dominated stand, Sx = white spruce and/or Engelmann spruce, Ta = trembling aspen.

Variable	Type	Values
Percent Cover	N	0-100% (occasionally percent covers >100% were recorded and included in the data set)
Natural Region	C	Foothills, Rocky Mountains
Natural Subregion	C	Lower Foothills, Upper Foothills, Montane, Subalpine, Alpine (occasional combinations were recorded e.g. Montane and Subalpine)
Dominant tree	C	Fa, La, Lt, Mix, Pb, Pl, Sb, shrub, Sx, Ta
Openness	C	Open vs. Closed canopy forest
Elevation	N	500 to 2500 m
Aspect	N	0 to 359 degrees
Slope	N	0 to 90 degrees
Disturbance type	C	Natural vs. Anthropogenic
Stand Treatment	C	Unmanaged, Clearcut, Burned
Site Preparation	C	Scarified vs. Unscarified
Seral Stage	C	Early seral (0-10 years), Young (>10 to 25 years), Immature (>25 to 50 years), Mature (>50 to 80 years), Mature/Old (>80 to 120 years), Old (>120 years)
Stand Age	N	0 to 500+ years

2.2 Statistical Analysis

2.2.1 Classification and Regression Trees (CARTs)

Classification and Regression Tree (CART) was the statistical analysis selected to conduct the meta-analysis of vegetation functional group response to predictor variables. CARTs are a regression technique with a strong theoretical foundation (Breiman et al. 1984; Venables and Ripley 1994) that allows the use of categorical and continuous data, and which can also handle non-linear relationships, data skew, and missing values in order to explain variation in a single response variable as a function of multiple explanatory variables. An important characteristic of CARTs is that they implicitly include complex interactions among predictor variables (Faraway 2006), particularly within complex data sets (De'ath and Fabricius 2000; Crawley 2002). In this case, CART analysis was used to analyze the relationship between vegetation and lichen functional group abundance (either percent cover or biomass) and a number of potential explanatory variables (Table 1).

CARTs (hereafter referred to as “trees”) are created using recursive partitioning to separate the response observations into increasingly homogenous subsets of data. Each split (node) in the tree is based on a threshold value of the predictor variable that produces the greatest within-group similarity for the response variable by minimizing the within-group sums-of-squares. The entire dataset may be partitioned until each observation is explained or according to pre-specified stopping criteria. The optimal tree size (i.e. number of nodes) is a balance between explanatory ability and generality to other datasets. In this analysis, the optimal tree size is obtained through a k-folds cross-validation pruning procedure (Venables and Ripley 1994; De'ath and Fabricius 2000; Faraway 2006).

2.2.1 Modeling Vegetation and Lichen Functional Group Abundance

Regression trees (CARTs; Breiman et al. 1984) were used to model the percent cover of several plant and lichen functional groups as a function of several independent variables (Table 1). Because the data for this analysis were taken from several studies, each with differing numbers of plots used to estimate percent cover, the CART analysis was weighted by $\sqrt{n}$, where n is the number of replicates for a given study. We determined the optimal tree size through a k-folds cross-validation pruning procedure as described by Faraway (2006). All analysis was performed using the R software package (R Development Core Team 2007).

3.0 Results

Data were obtained from 19 sources (Table 2) including: 12 sources and 1168 percent cover estimates for all vegetation functional groups, 13 data sources and 224 percent cover estimates for terrestrial lichen, and 4 data sources and 90 biomass estimates for arboreal lichen. The percent of variation explained from each tree ranges from a low of 15.9% for shrubs to a high of 59.7% for dwarf shrubs. Variables that commonly explained variation in the functional groups included: natural subregion, seral stage (or stand age), dominant tree, elevation, aspect, and slope. Responses of each functional group to the main predictor variables are presented below.

Table 2. Summary of data sources for vegetation functional groups (shrubs, dwarf shrubs, forbs, grasses, and mosses), terrestrial lichen and arboreal lichen.

Functional group	**Data Source**
Vegetation, Terrestrial Lichen	Alberta Conservation Association raw data
Terrestrial Lichen	Albright and Kranrod (2001)
Vegetation, Terrestrial Lichen	National Park Land Classification raw data
Vegetation, Terrestrial Lichen	Bortoff (2001)
Vegetation, Terrestrial Lichen	Corns and Roi (1976)
Terrestrial Lichen	Corns (1978)
Vegetation	Edmonds and Bloomfield (1984)
Terrestrial Lichen	Fiera Biological raw data
Vegetation, Terrestrial Lichen	Kranrod (1996)
Vegetation	Roi et al. (1988)
Vegetation, Terrestrial Lichen	Sachro et al. (2005)
Arboreal Lichen	Serrouya raw data (Summarized results in Serrouya et al. 2007)
Terrestrial and Arboreal Lichen	Shephard raw data (Summarized results in Shephard 2006)
Vegetation, Terrestrial Lichen	Snyder and Woodard (1992)
Arboreal Lichen	Snyder (1987)
Vegetation, Terrestrial Lichen	Stelfox et al. (1998)
Vegetation, Terrestrial Lichen	Strong (2002)
Arboreal Lichen	Terry et al. (2000)
Vegetation	West Fraser PSP raw data

3.1 Shrubs

The classification and regression tree for shrubs identified two variables as important determinants of shrub abundance in west central Alberta, including: seral stage (early seral, young, immature, mature, mature/old, old) and slope (Figure 1). This tree only explained 15.9% of the variation in the percent cover of shrubs. The majority of the variance explained by the tree was at the first split where seral stage was the main explanatory variable; shrub cover was lower in early seral, young, and mature/old stands (20.5% ± 2.0) compared to immature, mature, and old stands (47.6% ± 2.1). Within both these seral stage groupings, shrub cover was lower on shallower slopes. Overall, the highest percent cover of shrubs was recorded in immature, mature, and old stands with slopes >3.5^0; 77% of these stands were old i.e. >120 years.

3.2 Dwarf Shrubs

The classification and regression tree for dwarf shrubs identified the following four variables as important determinants of dwarf shrub abundance in west central Alberta, including (Figure 2): dominant tree, slope, natural vs. anthropogenic disturbance, and natural subregion. This tree explained 59.7% of the variation observed in the percent cover of dwarf shrubs. The left node is strongly homogenous and is not further subdivided; the lowest percent cover (mean ± SE) of dwarf shrubs are observed in forested stands dominated by subalpine fir, larch, mixedwood (conifer and deciduous), and spruce (8.1% ± 1.6) (Figure 2). The remaining data points occurred in lodgepole pine-dominated or black spruce-dominated stands where dwarf shrubs (mean ± SE) were more abundant (40.8 % ± 4.4). Of these pine or black spruce stands, dwarf shrubs were more abundant in stands with slopes ≤14.5, that were naturally disturbed (as opposed to clearcut), and that occurred in the following natural subregions: upper foothills, montane, or subalpine. Dominant tree reentered the tree at the lowest branch with lodgepole pine-dominated stands recording higher percent cover of dwarf shrubs compared to black spruce stands.

3.3 Forbs

The forb classification and regression tree identified only one important explanatory variable of forb abundance i.e. subregion, which explained 23.4% of the variation observed in percent cover of forbs (Figure 3). The percent cover of forbs (mean ± SE) was highest in the Upper Foothills subregion (38.7% ± 4.5) compared to the remaining subregions (Lower Foothills, Montane, Subalpine) in which percent cover was only 11.7 % (± 4.5).

3.4 Grasses

The grass classification and regression tree identified two important explanatory variables, subregion and seral stage, which explained 37.7% of the variation observed in percent cover of grasses (Figure 4). The right node, predicted by the Lower Foothills and Montane subregions, is not further sub-divided forming a terminal node with a mean percent cover (± SE) of 28.4% (± 4.5); this node may be the result of observer bias as 23 of the 26 data points (88%) were from one study with one replicate each. The data points to the left of the tree were generally classified into Upper Foothills and Subalpine subregions (but also included missing values and Foothills) and were further subdivided by seral stage with grasses (mean ± SE) most abundant in stands <80 years old (12.1% ± 4.5) compared to stands >80 years of age (5.3% ± 0.7).

3.5 Moss

The classification and regression tree for percent cover of moss identified the following four variables as important determinants of abundance in west central Alberta, including (Figure 5): stand age, dominant tree, elevation, and aspect. This tree explained 50% of the variation observed in the percent cover of moss. The percent cover of moss (mean ± SE) is relatively low in stands <61 year of age (13.6% ± 2.1) (Figure 5); this left node is strongly homogenous and is not further subdivided. The remaining data points occurred in stands >61 years of age. Of these stands, moss abundance was highest in lodgepole pine and spruce stands occurring at lower elevations (<2034 m) and on more south-facing aspects. Stand age and elevation re-entered the tree at the lowest branches. Stands >105.5 years of age and stands <105.5 years of age at elevations below 1378 m had the highest observed mean percent covers (±SE) of moss with 66.6% (± 2.1) and 71.5% (± 5.2) respectively.

3.6 Terrestrial Lichen

The classification and regression tree for percent cover of terrestrial lichen identified the following five variables as important determinants of abundance in west central Alberta, including (Figure 6): elevation, dominant tree, subregion, seral stage, and aspect. This tree explained 30.8% of the variation observed in the percent cover of terrestrial lichen. At elevations below 1848 m, terrestrial lichen cover (mean ± SE) was highest in lodgepole pine stands (6.0% ± 0.8) compared to all other stands combined (2.4% ± 0.4). Terrestrial lichen cover appears to be more abundant in the Subalpine subregion compared to the remaining subregions and in early seral, young, and old seral stages but this section of the tree appears to be strongly affected by one particular study. At elevations >1848 m, the subdivisions in the data again appear to be due to observer bias as data was primarily divided into the Subalpine subregion and the Montane and Subalpine subregion based on two data sources. However, at higher elevations, terrestrial lichen is more abundant on more south-facing aspects.

3.7 Arboreal Lichen

The arboreal lichen classification and regression tree identified only one important explanatory variable of arboreal lichen biomass i.e. slope, which explained 17.2% of the variation observed in biomass of arboreal lichen (Figure 7). The mean (± SE) biomass (kg/ha) of arboreal lichen was highest on slopes less than 7.5^0 with 48.1 (± 11.4) kg/ha compared to the slopes $\geq 7.5^0$ where biomass was 13.4 (± 1.8) kg/ha.

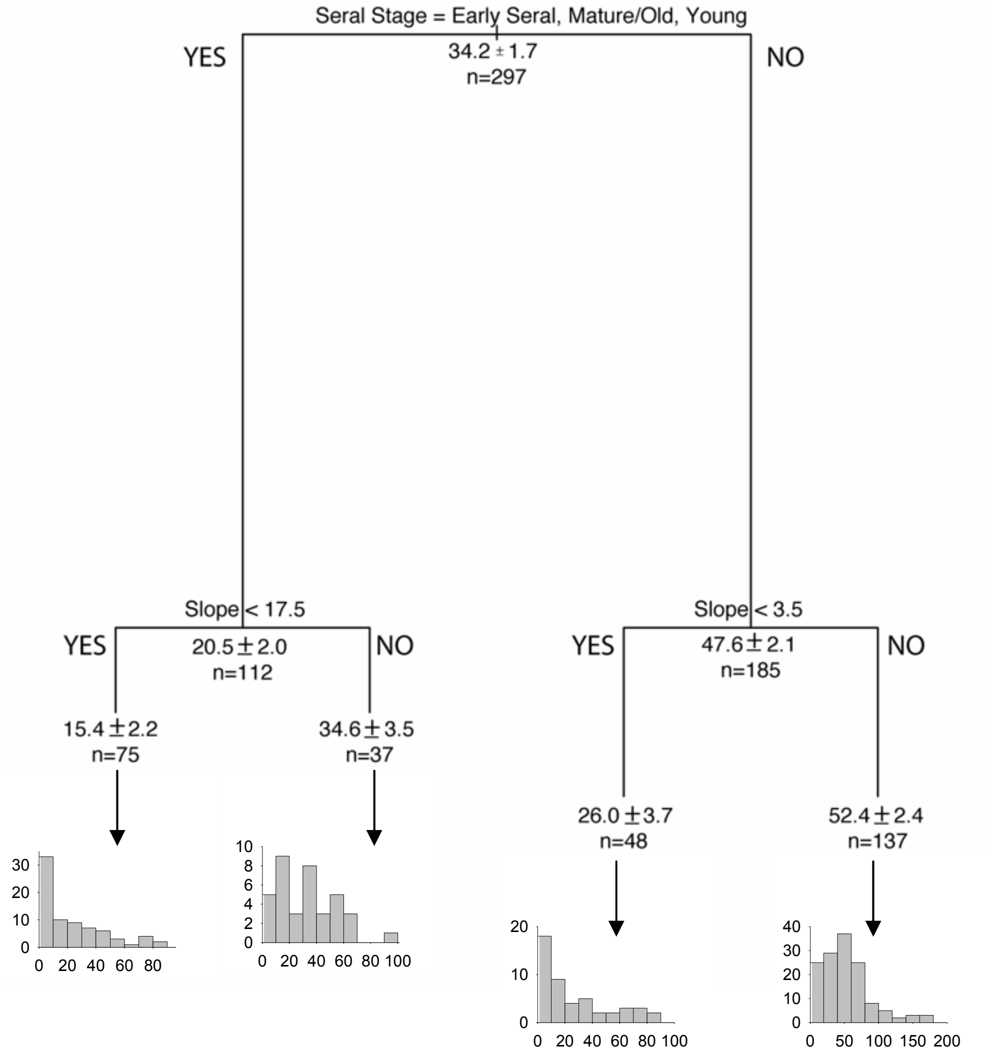

Figure 1. Regression tree analysis of the percent cover (± standard error) of shrubs. The main explanatory variables for shrub abundance were seral stage (early seral, young, immature, mature, mature/old, old), and slope. The predictor variable and threshold value are presented for each split (node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the four leaves (terminal nodes), the distribution of observed percent cover values of shrubs is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 16% of the variation observed in percent cover of shrubs with the vertical line length proportional to the amount of deviance explained by the preceding node.

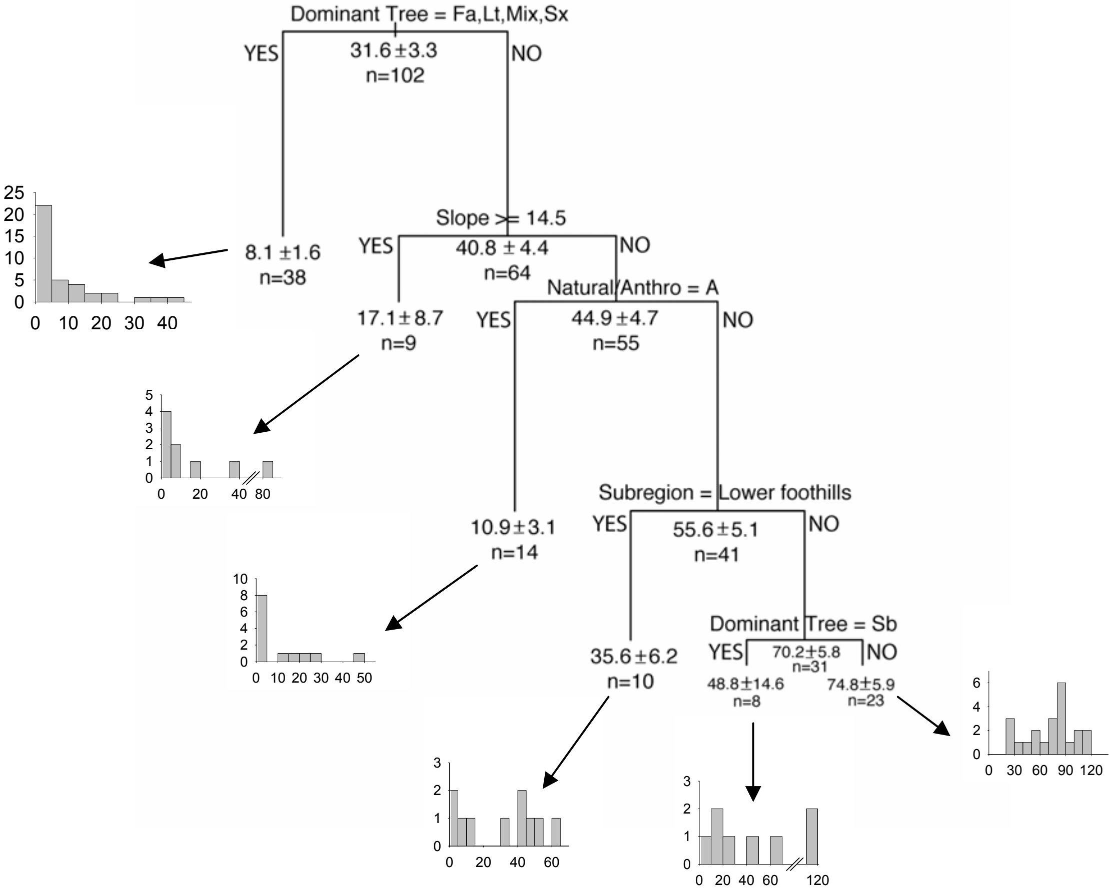

Figure 2. Regression tree analysis of the percent cover (± standard error) of dwarf shrubs. The explanatory variables were dominant tree (Fa, Lt, Mix, Sb, Sx, and Pl), slope, natural vs anthropogenically disturbed (clearcut) stands, natural subregion (Lower Foothills and unclassified), and dominant tree (Sb, Pl). The predictor variable and threshold value are presented for each split (node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For each of the six leaves (terminal nodes), the distribution of observed percent cover values of dwarf shrubs is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 60% of the variation observed in percent cover of dwarf shrubs with the vertical line length proportional to the amount of deviance explained by the preceding node.

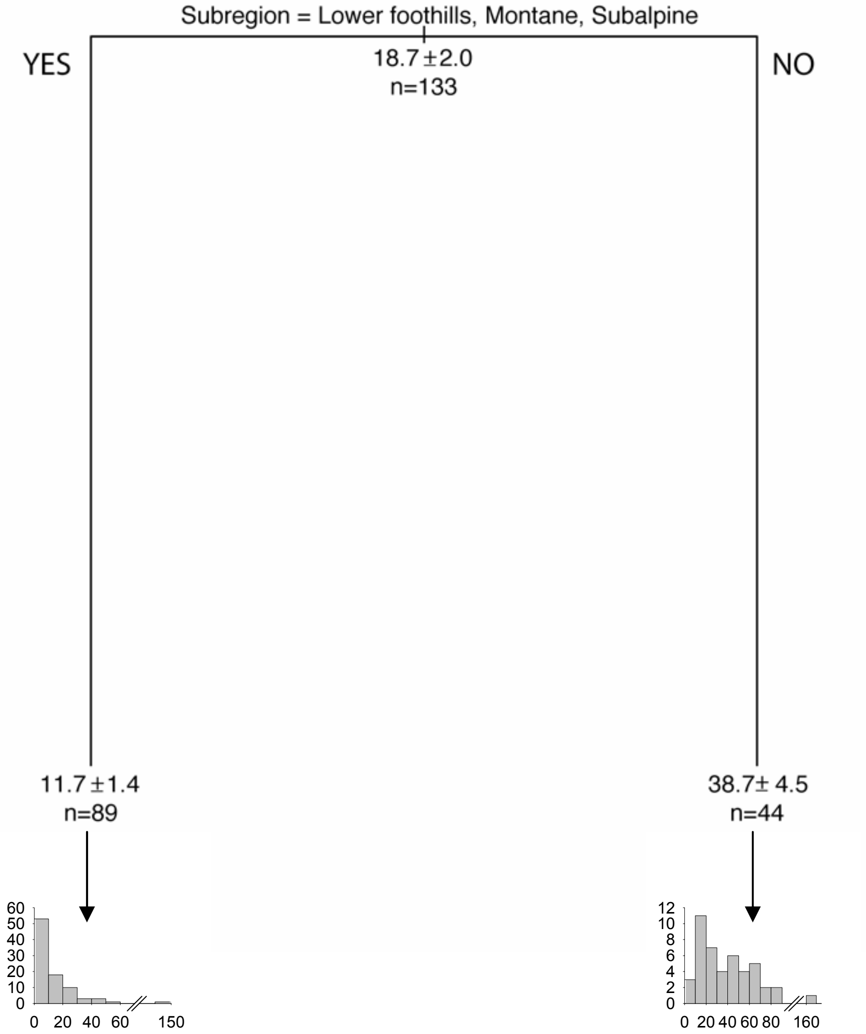

Figure 3. Regression tree analysis of the percent cover (± standard error) of forbs. The main explanatory variable for forb abundance was subregion (lower foothills, upper foothills, montane, and subalpine). The predictor variable and threshold value are presented for each split (node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the two leaves (terminal nodes), the distribution of observed percent cover values of forbs is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 23% of the variation observed in percent cover of forbs with the vertical line length proportional to the amount of deviance explained by the preceding node.

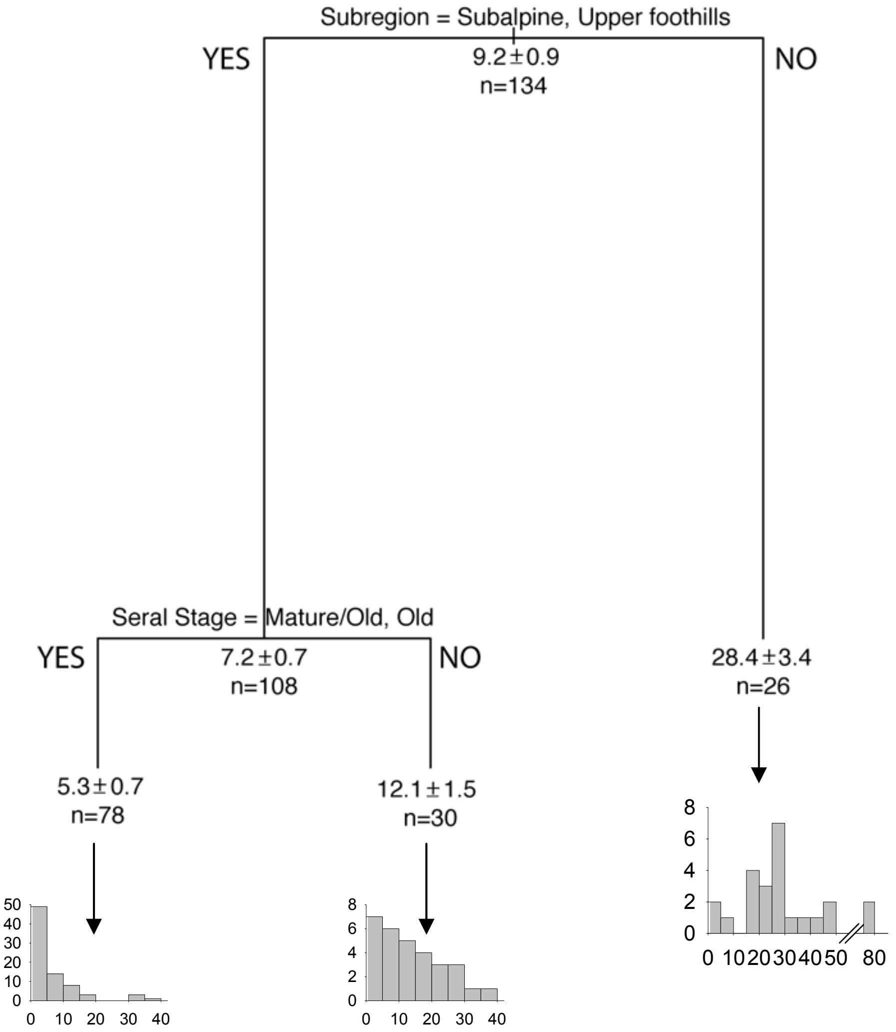

Figure 4. Regression tree analysis of the percent cover (± standard error) of grasses. The main explanatory variables for grass abundance were subregion (lower foothills, upper foothills, montane, and subalpine) and seral stage (early seral, young, immature, mature, mature/old, and old). The predictor variable and threshold value are presented for each split (nonterminal node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the three leaves (terminal nodes), the distribution of observed percent cover values of grasses is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 38% of the variation observed in percent cover of grasses with the vertical line length proportional to the amount of deviance explained by the preceding node.

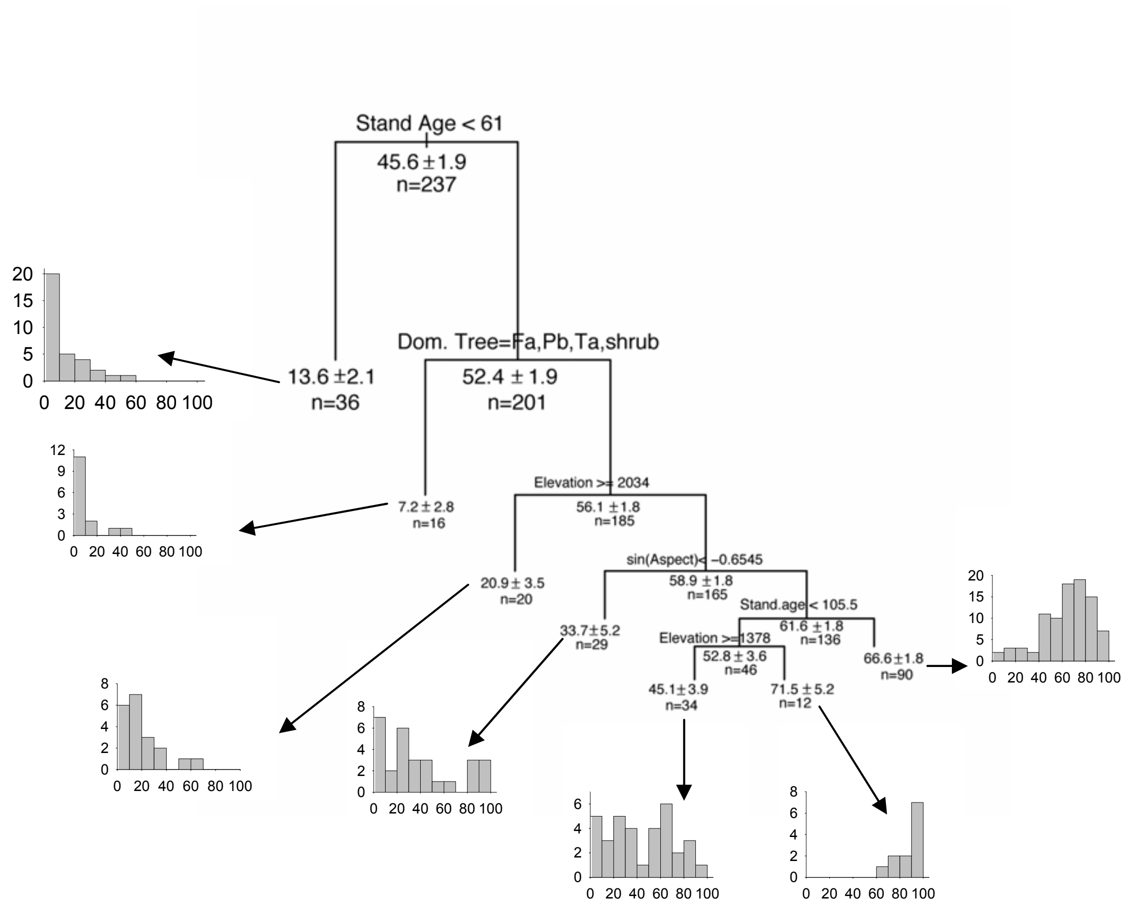

Figure 5. Regression tree analysis of the percent cover (± standard error) of mosses. The main explanatory variables for moss abundance were stand age, dominant tree, elevation, and aspect. The predictor variable and threshold value are presented for each split (nonterminal node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the seven leaves (terminal nodes), the distribution of observed percent cover values of mosses is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 50% of the variation observed in percent cover of mosses with the vertical line length proportional to the amount of deviance explained by the preceding node.

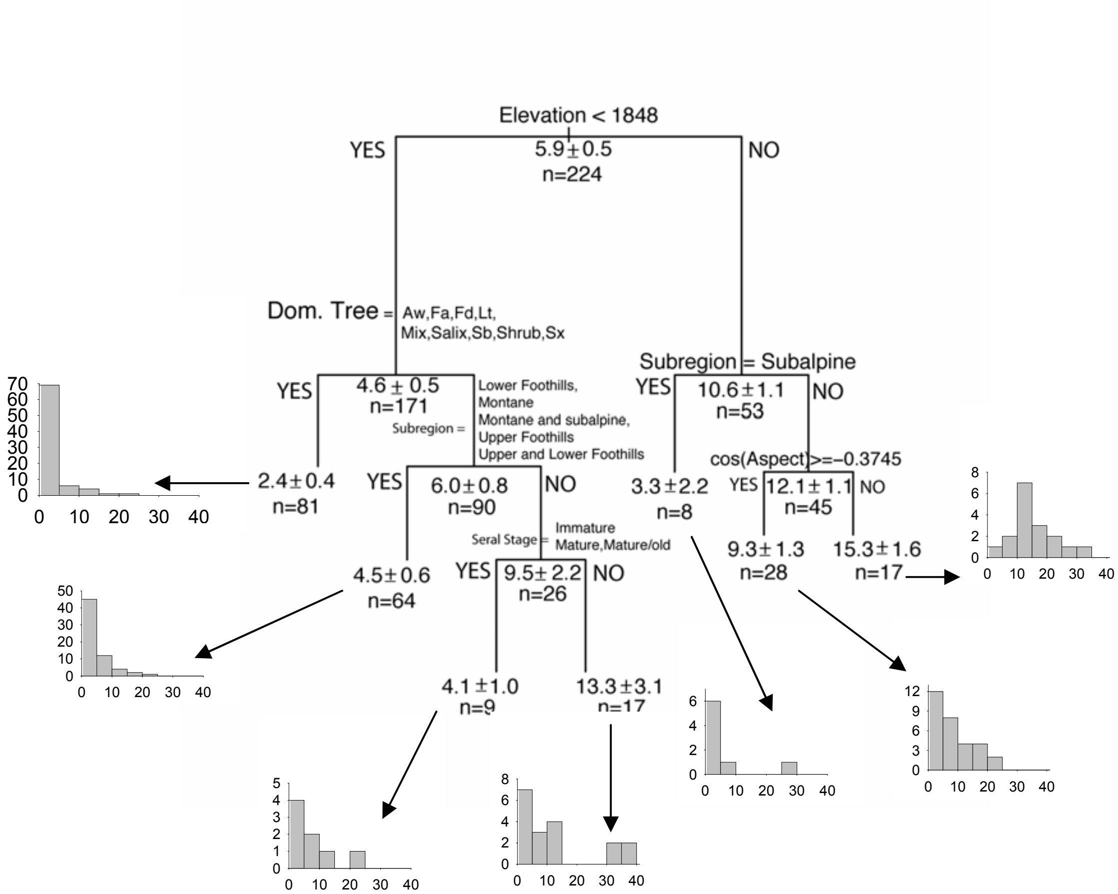

Figure 6. Regression tree analysis of the percent cover (± standard error) of terrestrial lichen. The main explanatory variables for lichen abundance were elevation, dominant tree, subregion, seral stage, and aspect. The predictor variable and threshold value are presented for each split (nonterminal node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the seven leaves (terminal nodes), the distribution of observed percent cover values of terrestrial lichen is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 31% of the variation observed in percent cover of terrestrial lichen with the vertical line length proportional to the amount of deviance explained by the preceding node.

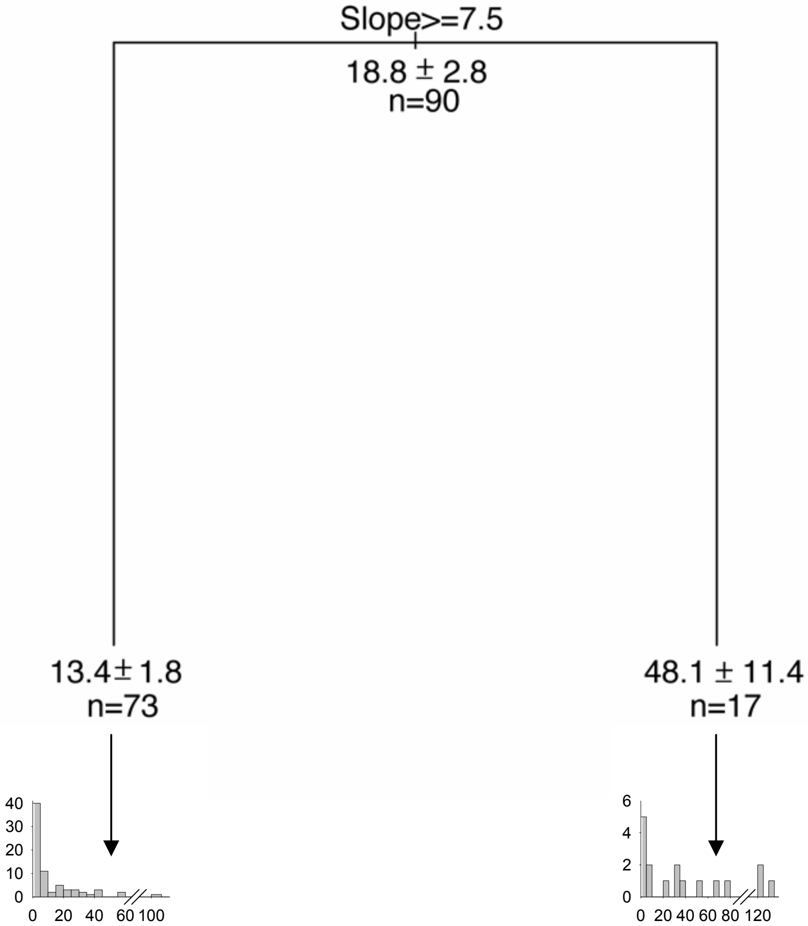

Figure 7. Regression tree analysis of the percent cover (± standard error) of arboreal lichen. The main explanatory variable for arboreal lichen abundance was slope. The predictor variable and threshold value are presented for each split (nonterminal node) in the tree, along with the mean percent cover, standard error, and number of data points (n). Subsets of observations agreeing with the threshold value ('YES') are to the left of each node. For the two leaves (terminal nodes), the distribution of observed percent cover values of arboreal lichen is shown in a histogram with percent cover along the x-axis and frequency along the y-axis. This tree explained 17.2% of the variation observed in percent cover of arboreal lichen with the vertical line length proportional to the amount of deviance explained by the preceding node.

4.0 Discussion

There were several predictor variables that commonly explained variation in percent cover of vegetation functional groups examined in this meta-analysis, including: natural subregion, seral stage (or stand age), dominant tree, elevation, aspect, and slope. Of these predictor variables, results were not consistent among functional groups, nor were relationships between predictor variables and functional groups. In general, the predictor variables included in the CART analysis explained a large amount of the variation observed in the abundance patterns of mosses and dwarf shrubs, a moderate amount for grasses and terrestrial lichen, and a relatively small amount for forbs, shrubs, and arboreal lichen. Further, for all vegetation functional groups (with the exception of mosses), the relationship between stand age and vegetation cover could not be adequately addressed because of the lack of records in early-successional stands, and specifically anthropogenically disturbed stands. As a result, the question of when cutblocks stop providing forage for alternate prey species and begin to function as caribou foraging habitat could not be answered directly in this meta-analysis. In spite of this, some general patterns emerged that were consistent with results observed elsewhere, particularly for lodgepole pine-dominated stands. Therefore, these results may serve as a base for developing caribou habitat management recommendations (in an adaptive management framework), while also highlighting information needs and priorities for research.

4.1 Understory Vegetation Responses

4.1.1 Shrubs

Seral stage and slope were the two main predictor variables useful for explaining the variation in shrub abundance in this meta-analysis. Most variation was explained by seral stage as shrubs were most abundant in stands that were immature (25 to 50 years old), mature (50 to 80 years old), and old stands (>120 years old), compared to young stand (<25 years old) and mature/old stands (80 to 120 years old). This result may seem unexpected given that shrubs generally respond quickly to increased light availability found in recently disturbed (e.g. burned, clearcut) stands and can be very abundant in these young stands. However, this meta-analysis had relatively few observations for young stands (<25 years) compared to older stands, with 85 of the 112 records included in the early seral-young-mature/old CART grouping from the mature/old category (Figure 1). Therefore, patterns of shrub abundance in the youngest seral stages were not adequately represented in the meta-analysis, and the results obtained here, at least for the young seral stages, may not be considered representative of shrub development with age. The higher cover of shrubs in old seral stages (i.e. >120 years) seen in this study is not unexpected; variability in canopy structure and light availability as a result of small scale disturbances such as windthrow and insect outbreaks create canopy gaps where shrubs may be abundant (Bainbridge and Strong 2005; Hart and Chen 2006). Again, while the immature, mature, and old seral stages were grouped together in the CART analysis, most of these observations occurred in old forest, suggesting that immature and mature seral stages were not adequately represented in this meta-analysis. In general the cover and biomass of shrubs is expected to be highest in early successional stands, peaking within the first 20 to 30 years post-fire, and then declining during the closed canopy phase of stand development, until, in older stands, cover fluctuates depending on stand conditions (Bainbridge and Strong 2005; Hart and Chen 2006).

Some of the variation in the percent cover of shrubs was also explained by slope; shrub cover was higher on sites with increased slope. Shrubs may be more abundant on steeper slopes because there is increased light availability, more suitable edaphic conditions, and/or less competition for available resources. Regardless of the mechanism, moderate slopes may provide optimal growing conditions for shrubs.

Overall, only 16% of the variation in shrub cover abundance was explained by the CART analysis, indicating there are a number of other factors that were not considered in this analysis that could explain shrub distribution, in particular, light availability, soil moisture, and nutrient availability (Nadeau and Corns 2002; Hart and Chen 2006). Certainly, including these factors in the CART analysis would likely have increased the variation explained in shrub cover distribution between stands.

4.1.2 Dwarf Shrubs

In contrast to shrubs, almost 60% of the variation in dwarf shrub cover was explained by four main predictor variables, including: dominant tree, slope, natural vs. anthropogenic disturbance, and natural subregion. Dwarf shrubs do well in lodgepole pine forests located in higher elevation natural subregions (e.g. montane, upper foothills, subalpine) that have not been anthropogenically disturbed. The close association of dwarf shrubs with lodgepole pine forests type suggests conditions in this forest type are also generally favoured by dwarf shrubs, which puts them in direct competition with terrestrial lichen for resources. Given optimal soil moisture and nutrient regimes and abundant light, dwarf shrubs may successfully outcompete terrestrial lichen in these forests which may be an important consideration for caribou foraging habitat management (Williston et al. 2006)

4.1.3 Forbs

Natural subregion explained 23% of the variation in forb abundance in west central Alberta and was the only predictor variable that explained variation in forb percent cover; forbs were most abundant in the Upper Foothills natural subregion. Like shrubs, the low amount of variation explained indicates there are several other factors not included in the CART analysis, such as light, soil moisture, and nutrient regimes, that may better explain forb abundance patterns. While stand age was not important in explaining variation in forb abundance, forbs are expected to follow a similar successional pathway as shrubs, increasing in early successional stands to a peak at 20 to 30 years post-fire, followed by a decline during stem-exclusion, finally showing fluctuations in abundance depending on stand conditions in older seral stages (Bainbridge and Strong 2005; Hart and Chen 2006). Degree of tree canopy shading may primarily control the successional development of shrubs and forbs, with forbs declining in response to increased canopy closure as opposed to forest age (Bainbridge and Strong 2005).

4.1.4 Grasses

Natural subregion and seral stage were the two predictor variables important in explaining variation in the percent cover of grasses. Grasses are most abundant in the Lower Foothills and Montane Natural Subregions as compared to the Upper Foothills and Subalpine Natural Subregions. Within the Upper Foothills and Subalpine Natural Subregions, grasses are most abundant in younger forests (i.e. < 80 years old). Grasses can be common in early successional environments; therefore, this higher abundance of grass in younger forests is not unexpected, nor is the abundance of grass in lower elevation subregions, as grass and shrub habitat were historically common in lower valley areas in the Rocky Mountains (Sachro et al. 2005).

4.1.5 Mosses

Stand age, dominant tree, elevation, and aspect were all important predictor variables of moss, explaining 50% of the variation in west central Alberta. Moss is more abundant in older stands, particularly lodgepole pine stands that are greater than 105 years in age. Other studies have also observed a positive association between moss cover and stand age (Harris 1992; Snyder and Woodard 1992; Coxson and Marsh 2001), as dispersal ability and limited environmental tolerances generally restrict the abundance of mosses in early successional stands. Re-establishment of bryophyte communities, particularly in lodgepole pine forests, depends on the proximity of source populations as well as the development of suitable microclimatic conditions (i.e. cool and humid) which may take upwards of 100 years (Williston et al. 2006) as seen by the relationship with moss and stand age in this meta-analysis.

4.1.6 Terrestrial Lichen

Terrestrial lichen abundance was explained by elevation, dominant tree, natural subregion, seral stage, and aspect. The prediction of percent lichen cover by these predictor variables appears to be partly biologically based, and partly due to observer bias among the different data sources. At elevations below 1848 m, lichen was most abundant in lodgepole pine stands, particularly in the Subalpine Natural Subregion. The abundance of lichen in lodgepole pine forests observed in this analysis is not an unexpected result. Pine-lichen woodlands occur commonly across western Canada, and are characterized by dry, nutrient-poor conditions with coarse, well-drained soils (Ahti 1977; Bennett et al. 1983; Snyder 1987). The successional pathway of these forests results in a reindeer lichen (*Cladina*-dominated) phase that exists from approximately 50 to 150 years of age when feathermoss (*Pleurozium schreberi*) often becomes the dominant ground cover (Ahti 1977; Snyder 1987; Harris 1992; Pharo and Vitt 2000; Coxson and Marsh 2001; Sulyma 2002; Bainbridge and Strong 2005). There is variation around this pattern of lichen succession depending on local nutrient and moisture conditions with lichen displacement occurring more rapidly in more mesic stands (Sulyma 2003; Williston et al. 2006).

Stand age does not appear to be an important predictor of terrestrial lichen abundance in this analysis as observer bias is likely responsible for the one stand age terminal node observed; however, lichen cover appears to follow the expected trajectory as that discussed above with cover increasing with forest age to a peak at approximately 100 years of age in old lodgepole pine stands before declining in older forests (Figure 8). At elevations greater than 1848 m, 45 of 53 observations originate from one data source (Shephard raw data) which provides less certainty that the results can be generalized across west central Alberta. However, at these higher elevations, terrestrial lichen is actually less abundant in the Subalpine Natural Subregion (in contrast to lower elevation sites), and more abundant on south-facing aspects.

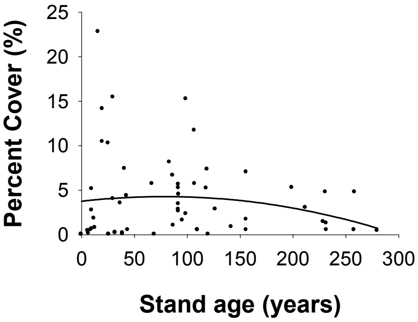

Figure 8. Scatter plot of percent cover of terrestrial lichen as a function of stand age in lodgepole-pine stands at elevations <1848 m.

4.1.7 Arboreal Lichen

Slope was the only factor that explained a significant source of variation in the abundance of arboreal lichen; arboreal lichen biomass was more than three times greater on slopes ≥7.5, compared to shallower slopes. However, the amount of variation explained in arboreal lichen biomass was low, suggesting other factors not included in this meta-analysis are better predictors of lichen biomass. There are a number of factors that affect the biomass of arboreal lichen within a stand including: tree density, snag density, and tree size (Serrouya et al. 2007) as well as stand soil type (Campbell and Fredeen 2007). These factors were not included in the meta-analysis as predictor variables but likely would have improved the amount of variation explained in arboreal lichen biomass.

Unlike terrestrial lichen which is expected to peak in abundance in mid-successional nutrient-poor pine forests, arboreal lichen is expected to be more abundant in older (>130 years) mesic, non-pine forests at higher elevations which are characterized by cooler, more moist conditions (Bennett et al. 1983; Snyder 1987; Shephard 2006). Stand age was not identified as an important predictor of arboreal lichen biomass; however, over 90% of the observations were in forests older than 60 years old, and over half of these in stands greater than 120 years old. Therefore, the relationship of arboreal lichen development in forested stands under different disturbance regimes could not be examined.

4.2 Literature Review and Synthesis of Results

Understory vegetation communities are the result of several factors that interact in complex ways to produce patterns of composition, distribution, and abundance of communities across the landscape. These factors include environmental tolerances, variable light, moisture and nutrient regimes, precipitation and topography, past disturbance events, and biotic interactions (e.g. inter/intra-specific competition; Small and McCarthy 2005; Hart and Chen 2006). In particular, light is often the most limiting resource affecting understory vegetation development (Bainbridge and Strong 2005; Hart and Chen 2006), with soil nutrient and moisture status also important (Nadeau and Corns 2002). However, in this meta-analysis, while these factors were certainly affecting the distribution and abundance of vegetation functional groups, these factors could not be analyzed explicitly because studies generally lacked site specific information on light, soil moisture, and nutrient regimes. Therefore, the abundance of some vegetation functional groups (e.g. shrubs, forbs) was not well explained by predictor variables. Further, biotic factors such as dispersal and competitive ability were not accounted for in this analysis despite that fact that these factors can also be very important in explaining the distribution of particular functional groups (e.g. terrestrial lichen). Finally, while stand age is expected to be a better predictor of the distribution and abundance of many of the functional groups, it did not perform well at explaining variation in percent cover for most of the functional groups, except moss. This lack of relationship with stand age, may in part, be due to the lack of data from early successional stands and lack of data from anthropogenically disturbed stands in particular. Despite these limitations of the meta-analysis, some patterns did emerge that are consistent with literature expectations of successional pathways, particularly for lodgepole pine-dominated stands.

4.2.1 Vegetation Succession

Vegetation development in early seral stages varies with site moisture and nutrient regimes making it difficult to construct a single model of vegetation development (Bainbridge and Strong 2005). However, cover and biomass of vascular plants is generally highest in early successional stands, peaking within the first 20 to 30 years post-fire before declining during the stem-exclusion phase of forest development. As stands age, gap-phase dynamics opens the canopy, resulting in the fluctuation of vegetation cover and biomass depending on stand conditions (Bainbridge and Strong 2005; Hart and Chen 2006).

Typically, bryophyte and lichen species are not a large component of vegetation communities during the early stages of post-fire succession because of their inability to exploit increased resources following disturbances and their poor competitive ability; this result appears to be reflected by the meta-analysis, specifically for moss. This pattern may be especially evident in more mesic stands with high site productivity; under these conditions, poor competitors such as lichen species would be expected to occur in low abundance, particularly when population sources have been destroyed by fire (Williston et al. 2006). While terrestrial lichens occur in low abundance early in stand succession, they reappear as the forest matures (Snyder 1987), as reindeer lichens are generally most abundant in lodgepole pine stands between 50 and 150 year old years of age (Harris 1992; Coxson and Marsh 2001; Sulyma 2002). Beyond 150 years, seral development has varying outcomes depending on the region and stand characteristics (e.g. increasing crown closure; Coxson and Marsh 2001; Sulyma and Coxson 2001; Sulyma 2002). The lichen community chronosequence often culminates in a plant community dominated by feather moss mats that require some form of disturbance on the landscape to promote the rejuvenation of terrestrial lichen communities. Fire was formerly the main disturbance resetting this successional pathway; however, forest harvesting has replaced fire as the predominant disturbance in west central Alberta.

Harvesting affects forest floor vegetation in two ways: mechanical damage (impacting source populations) and physiological responses to altered light, temperature, and moisture conditions (Williston et al. 2006). As a result, forest harvesting has generally been assumed to negatively influence terrestrial lichen communities. However, the ecological processes that govern the regeneration of pine-lichen forests after harvesting may differ in several ways from those initiated by wildfire; consequently, forest harvest may actually promote lichen regeneration, particularly if specific harvesting strategies are used (Harris 1992; Coxson and Marsh 2001; Sulyma 2002). For example, Sulyma (2002) found terrestrial lichen declined in abundance from 0 to 12 years following harvest, but recovered to levels more typical of 70 to 100 year old lodgepole pine stands by the time stands reached 30 years of age; Coxson and Marsh (2001) observed a similar lichen recovery in harvested stands. Unlike fire which completely destroys lichens, logging leaves much of the lichen biomass intact which may accelerate the recovery of the lichen crop

(Harris 1992; Sulyma 2002). Sites with specific edaphic conditions (e.g. nutrient-poor, coarse-textured soil) may be particularly favourable for the recovery of lichen communities (Harris 1992; Sulyma 2002).

Silvicultural strategies that minimize ground disturbance may also positively affect the recovery of terrestrial lichen after harvest. Winter harvest with minimal ground disturbance reduces short-term impacts on lichen abundance compared to summer harvesting and/or harvested stands that are scarified (Kranrod 1996; Coxson and Marsh 2001). Scarification may be particularly bad for lichen recovery in the short term, as this technique disturbs the ground surface, exposes large amounts of mineral soil, and severely damages vegetation and residual lichen remaining in the cutblock (Snyder and Woodard 1992; Kranrod 1996). However, in the long-term, scarification may lead to an increase in lichen abundance provided that sufficient residual lichen cover remains in the cutblock to provide a source population for colonization (Harris 1992; Snyder and Woodard 1992). Finally, silvicultural systems with residual trees may also benefit terrestrial lichen communities by minimizing mechanical disturbance while maintaining suitable microclimatic conditions for lichen growth (Harris 1992; Snyder and Woodard 1992; Williston et al. 2006).

Like fire, clearcutting substantially increases the amount of light relative to uncut stands, which in turn increases the abundance of vascular plants and shrubs which are palatable to a number of ungulate species (Visscher et al. 2006). Further, mesic, nutrient-rich sites provide optimal growing conditions for shrubs and forbs allowing them to grow quickly and dominate a harvested site for many years after disturbance, particularly on sites that have been mechanically logged with consequent disruption of the surface vegetation (Brumelis and Carleton 1989). Scarification techniques that cause greater disruption to the forest floor may produce favorable conditions for more early-seral species (e.g. alder, willow) to colonize and allow these species to persist for longer, perhaps prolonging the availability of ungulate forage in these stands (Haeussler et al. 1999). Minimizing site disturbance and the maintenance of infertility on the forest floor are two potential means of reducing the dominance of shrubs and forbs on a harvested site (Brumelis and Carleton 1989). Degree of shading can also inhibit the development of understory vegetation (Bainbridge and Strong 2005).

In general, mesic, productive sites are favoured by vascular plants (Brumelis and Carleton 1989; Hart and Chen 2006), while lichen performs well under dry, nutrient-poor conditions with ample light (Ahti 1977; Snyder 1987; Coxson and Marsh 2001; Sulyma 2002; Botting and Fredeen 2006). Highly productive sites which produce an abundance of forage for ungulate species, particularly in young forest age classes, are likely not the same sites that will produce high quality foraging habitat for caribou. Therefore, it is the juxtaposition of these habitats that may be the primary concern when managing for caribou forage as well as minimizing the spatial overlap with other ungulates to minimize caribou predation risk. Of course, for both ungulates and caribou, although forage production may be enhanced under certain site conditions or silvicultural techniques, the use of the stands particularly in the winter still needs to be determined. High food availability does not necessarily equal high quality habitat because the energetic costs associated with getting to the food may outweigh the benefits of increased forage abundance in certain stands in the winter when snow may limit the accessibility of forage (Morrison et al. 2003). As a result, the animal may select an area that has less overall food, but which is easier to obtain, and therefore has a greater net energetic benefit.

While terrestrial lichen is preferred for caribou in west central Alberta, arboreal lichen may become very important in years of heavy snowfall when access to terrestrial lichen is limited (Snyder 1987). Arboreal lichen can be present in young stands (e.g. 60 years) as indicated by this study and others (Goward and Campbell 2005). However, arboreal biomass appears to peak in stands between 150 and 200 years of age in stands in west central Alberta (Snyder 1987). Further, forests that support high abundances of arboreal lichen (i.e. old seral, high elevation, non-lodgepole pine stands) are not the same stands that support the highest abundances of terrestrial lichen (i.e. nutrient-poor, dry, lodgepole pine stands). Therefore, management of caribou winter range must also consider the abundance and spatial distribution of arboreal lichen-supporting forest types to ensure caribou have adequate resources during more extreme winters. There is currently very little information examining the response of arboreal lichen to different silvicultural systems (e.g. partial harvesting) which may provide some management direction for these forests.

5.0 Recommendations for Further Research

During the process of the meta-analysis and literature review, several gaps in our understanding of vegetation response to disturbance were identified. Consequently, these is a need for further research that would help fill these critical knowledge gaps, such that land managers may be able to focus and prioritize the management of caribou foraging habitat while at the same time minimizing caribou predation risk.

Ecosystems occurring in the Foothills and Rocky Mountains of west central Alberta are disturbance-adapted ecosystems; however, information on understory development (including lichen) on post-harvest stands, and in particular for mid-seral stages (e.g. >30 to approximately 80 years of age) under different soil moisture and nutrient regimes is generally lacking. It seems likely that functional group response will vary with stand conditions (e.g. soil, nutrients, moisture), thereby driving conditions for recovery of ungulate forage species and terrestrial lichen communities. Therefore, understanding stand conditions that are beneficial to browse regeneration and lichen regeneration, and how these conditions may differ for these functional groups, is an important step towards developing strategies and prioritizing areas for managing lichen caribou winter range.

Research priorities include:

- Developing a resource selection function model (e.g. Saher and Schmiegelow 2004) for the CLMA area that identifies areas that are high value caribou winter range (i.e. dry, nutrient-poor, lodgepole-pine and black spruce leading stands) in addition to areas predicted to be high value foraging habitat for other ungulate species (i.e. productive sites with high abundance of shrubs/forbs). This could be done using groupings of ecosites (based on similar tree species, dominant vegetation, and moisture/nutrient regime) or some other measure of site productivity. Based on GIS modeling results, stands would then be field-tested to determine if the model is classifying optimal pine-lichen forests with a high degree of certainty. Based on the distribution of optimal foraging habitat, areas surrounding high value caribou foraging habitat could then be prioritized for potential vegetation (browse) management in ecosystems/stand ages where browse is expected to occur in high abundance. This spatial analysis would also identify anthropogenic features in the landbase that may require additional management action (e.g. browse reduction) to minimize the spatial overlap of other ungulates with caribou.

- Using a chronosequence approach, stratify the landbase by ecosystem type (as identified above) as well as by elevation (Natural Subregion), and age class, focusing on anthropogenically-disturbed stands from 10 to 80 years old. Sample a replicate number of stands within each stratum to improve understanding of vegetation functional group response to forest age in different ecosystem types. This information would: 1) identify ecosystem types that provide an abundance of browse for ungulates other than caribou, 2) establish how long these stands remain attractive habitat for these ungulates, and 3) identify stands that may function as optimal caribou foraging habitat. Management priorities could then be established to manage ecosystems with high browse production that are in close proximity to caribou foraging habitat. This approach could also include identifying stands of different ages with residual retention to determine the benefits of different silvicultural practices in maintaining terrestrial lichen.

- While examining the relationship between forest age and lichen development is important, it is also important to document caribou use of previously logged stands through telemetry locations or snow tracking. While lichen production may be enhanced by certain silvicultural practices, caribou may not use these stands for other reasons. Similarly for ungulates, increased forage abundance may not translate into increased use of a stand during the winter unless the forage is relatively accessible and/or there is suitable forest cover nearby. Winter habitat use of other ungulates also needs to be determined.

- While not specifically addressed in the meta-analysis, the impact of mountain pine beetle on caribou foraging habitat is quickly becoming a management priority in west central Alberta. Like forestry, the effects of mountain pine beetle on caribou and caribou habitat is not well understood, making it difficult to develop management prescriptions that minimize impacts to caribou. Recent research in British Columbia indicates that pine-beetle infestations in pine stands cause changes in growing conditions at the forest floor, resulting in a corresponding shift in the dominance of ground cover species from terrestrial lichen to low-growing shrub species (Williston et al. 2006). Therefore, an adaptive management approach to managing caribou winter foraging habitat may be warranted, including targeting some lichen-producing pine stands for partial harvesting before the pine beetle attack these stands. These partially harvested stands could then be compared to unharvested stands attacked by pine beetle to determine which approach is better for maintaining lichen communities.

- There are a number of datasets currently being collected by the FMA holders within the CLMA boundary (e.g. PSP data) that are not being collected in a consistent manner. Coordination among FMA holders to collect the same type of data in the same way with an increased emphasis on understory characteristics (including lichen) could be very useful to future research in the area.

6.0 Summary

This report examined the response of vegetation functional groups, in a meta-analysis approach, to a number of predictor variables (e.g. stand age, forest type, disturbance type) in the CLMA Planning Area in order to provide direction for the management of caribou winter range habitat and ungulate browse in the Little Smoky and A la Peche caribou herd ranges. Predictor variables that commonly explained variation in the functional groups included: natural subregion, seral stage (or stand age), dominant tree, elevation, aspect, and slope. Of these predictor variables, results were not consistent among functional groups, nor were relationships between predictor variables and functional groups. In general, the predictor variables included in the CART analysis explained a large amount of the variation observed in the abundance patterns of mosses and dwarf shrubs (i.e. >50%), a moderate amount for grasses and terrestrial lichen (i.e. >30%), and a relatively small amount for forbs, shrubs, and arboreal lichen (i.e. <25%). Site specific information was generally lacking on soil moisture and nutrient regimes for most studies; this information would likely have increased the variation explained for all functional groups, but particularly shrubs and forbs. Further, for all vegetation functional groups (with the exception of mosses), the relationship between stand age and vegetation cover could not be adequately addressed because of the lack of records in early-successional stands, specifically anthropogenically disturbed stands. As a result, the question of when cutblocks stop providing forage for alternate prey species and begin to function as caribou foraging habitat could not be answered directly in this meta-analysis. In spite of this, some general patterns emerged that were consistent with results observed elsewhere, particularly for lodgepole pine-dominated stands. Therefore, these results may serve as a base for developing caribou habitat management recommendations (in an adaptive management framework), while also highlighting information needs and priorities for research.

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