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FACTORS INFLUENCING EPIPHYTIC LICHEN COMMUNITIES IN ASPEN-ASSOCIATED FORESTS OF THE BEAR RIVER RANGE, IDAHO AND UTAH

by

Paul C. Rogers

A dissertation submitted in partial fulfillment
of the requirement for the degree

of

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in

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Approved:

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ABSTRACT

Factors Influencing Epiphytic Lichen Communities in Aspen Forests of the Bear River Range, Idaho and Utah

by

Paul C. Rogers, Doctor of Philosophy

Utah State University, 2007

Major Professor: Dr. Ronald J. Ryel
Department: Wildland Resources

In western North America, quaking aspen (Populus tremuloides Michx.) is the most common hardwood in montane landscapes. Fire suppression, grazing, wildlife management practices, and climate patterns of the past century are some of the threats to aspen coverage in this region. Researchers are concerned that aspen-dependent species may be losing habitat, thereby threatening their long-term local and regional viability. Though lichens have a rich history as air pollution indicators, I believe that they may also be useful as a metric of community diversity associated with habitat change. To date, few studies have specifically examined the status of aspen's epiphytic lichen community in the Rocky Mountains. A preliminary study was conducted using 10 transect-based plots to assess lichen species substrate preferences between aspen and various conifer species and to gain basic knowledge of species diversity. Following this work, I established 47 plots in the Bear River Range of northern Utah and southern Idaho to evaluate the effects of forest succession on epiphytic macrolichen communities. Plots were located in a narrow elevational belt (2,134-2,438 m) to minimize the known covariant effects of elevation and moisture on lichen communities. Results show increasing lichen diversity and a decrease in aspen-dependent species as aspen forests succeed to conifer cover types. The interactive roles of stand aspect, basal area and cover of dominant trees, stand age, aspen bark scars, and recent tree damage were examined in relation to these trends. An aspen index score was developed based on lichens showing an affinity for aspen habitat. I present a landscape-level multivariate analysis of short- and long-term factors influencing epiphytic lichen communities in aspen forests. Nonmetric multidimensional scaling (NMS) ordination stressed the importance of succession and local air pollution sources in shaping lichen communities. I also investigated the role of historic human intrusions and climate on aspen forests and aspen-dependent epiphytic lichens at the landscape-level. Implications of this work include 1) realization of nitrogen impacts on ecosystems, 2) the potential for using lichens as bioindicators for monitoring aspen stand health, and 3) suggestions for working with natural disturbance regimes to minimize human impacts on aspen and associated species.

(177 pages)

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The U.S.D.A. Forest Service, Rocky Mountain Research Station, provided numerous resources which made the research possible. Utah State University facilitated storage and cataloguing of lichen voucher samples. John Lowry, Utah State University GIS/Remote Sensing Lab, was very helpful with geographic data acquisition and numerous technical pointers in using GIS software. The staff at Utah State University library, Special Collections, and Scott Bushman, USDA Forest Service, Logan Range District, provided invaluable service related to locating pertinent historical documents. Dr. Henrik Hedenås, of Umeå University (Sweden), Department of Ecology and Environmental Sciences, was an important tutor regarding lichen and European aspen interactions. Dr. Bruce McCune, Oregon State University, introduced me to lichen ecology and provided helpful direction in setting up the preliminary study design.

My friends and colleagues in the Logan area provided moral support throughout this process. I had the unflagging support of many family members of Rogers, Hedrich, and related clans. My greatest teachers are those nearest at hand; my family – Emmon

Hedrich Rogers, Leidy Hedrich Rogers, and Anne Elizabeth Hedrich – gave freely of their wisdom, compassion, and love that, in sum, comprise my motivation and my *raison d'être*.

Paul C. Rogers

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CHAPTER 1

INTRODUCTION

My fundamental interest in ecology is measuring and assessing anthropogenic impact on vegetative systems. Humans alter ecosystems at levels relative to their population and ability to exploit technology. The technology of today moves faster, covers larger areas, and affects more resources quicker than that of a century or millennium ago. Population and technology, developing exponentially, have ever increasing impacts not only in developed areas, but in more remote ecosystems. In the western United States, vast tracts of public land provide challenges to monitoring widely dispersed human impacts, such as those associated with long-term management policies (i.e., grazing, logging, fire suppression) or air- or water-borne pollutants. Biomonitoring—using plant or animal surrogates to assess change—is an inexpensive and efficient alternative of monitoring with remote instrumentation. Additionally, biomonitoring is attractive to ecologists because it involves direct impacts to ecosystem components (i.e., plants and animals). In contrast, monitoring devices often require calibration to levels of ecosystem impact; adding potential for error in interpretation.

The goal of this dissertation is to conduct a series of landscape-level experiments to assess change in epiphytic lichen communities associated with a range of aspen conditions. The study area encompasses mid-elevation aspen (*Populus tremuloides* Michx.) forests of the Bear River Range of Idaho and Utah. This dissertation is comprised of six chapters, four of which will be submitted as independent publications. Chapter submissions to journals are specified, along with the authors and status of publication, in the "Chapter preview" section below. Note that chapters submitted for journal publication are printed here in the respective journal formats, thus the dissertation contains inherent format variability.

While some environmental factors affect an aspen over story directly (e.g., management or natural disturbance), and over time their dependent lichen species, other influences may have direct impacts on the lichens themselves (e.g., micro-substrate availability, animal foraging, air quality). As we examine this line of inquiry, factors affecting change in these communities multiply quickly. Thus, to narrow the range of contributing factors, a brief review of aspen and lichen ecology is required prior to outlining the components (i.e., chapters) of this study.

Study background

Aspen ecosystems

In many Rocky Mountain forests quaking aspen is the sole hardwood tree among a variety of conifer species. Though aspen is the most widespread tree species in North America (Preston, 1976), it often comprises only a moderate portion of forests for a given region (Rogers et al., 2001). Even in Colorado and Utah, where coverage is relatively high, aspen makes up only 16 and 9 percent of total forest area, respectively (Rogers et al., 1998; Keyes et al., 2001). Many believe that aspen is steadily declining due to human intrusions of the last century (Kay, 1997; Bartos and Campbell, 1998; Rogers, 2002; Di Orio et al., 2005), while others have challenged this assertion with contrary findings (Manier and Laven, 2002; Elliott and Baker, 2004; Kulakowski et al., 2004). It is likely that new explanations of aspen trends will emerge where biogeographic, climatic, and social factors play a larger role in detailing unique local pathways fostered by these factors (Romme, 2004).

Beyond the aspen decline debate, there is strong support for the notion of aspen's unique contribution to regional biodiversity (DeByle, 1985; Mueggler, 1988; Matson, 2000; Ripple et al., 2001; Shepperd et al., 2006). Of course, biodiversity has many components. A sample of past research describes diversity in aspen ecosystems measured by avifauna (Flack, 1976; Turchi et al., 1995), wildlife in general (DeByle, 1985; Scott and Crouch, 1988), and understory vegetation (Mueggler, 1988; Potter, 1998). Where aspen plays a minor role in forest composition in the dry Interior West, its importance to the survival of many wildlife species may be elevated as aspen stands act as oases of relative moisture (Shepperd et al., 2006). As such, some have highlighted aspen forests as a "keystone" type — denoting an amplified role of aspen in supporting entire ecosystems (Manley et al., 2000; Campbell and Bartos, 2001).

Whether we accept this designation or not, interest throughout the West is high among managers and researchers alike for developing efficient methods for monitoring aspen conditions. One approach to evaluating complex systems, such as aspen forests, is to designate efficiently sampled indicator species as meaningful barometers of larger community conditions (Nash and Wirth, 1988; White and Stevens, 1990; Riitters et al., 1992; National Research Council, 2000).

Lichen communities

Lichens are an important component of terrestrial biota because they provide an "early warning" of potentially damaging agents to plant communities. Lichens communities provide a direct measure of air pollution impacts on lichens, but they also suggest air pollution impacts to whole forests that are not readily observable in "higher" plant forms, such as trees. Sensitivity of lichens to anthropogenic alteration of the atmosphere results from their lack of a cuticle, stomata, or epidermis and therefore near-total reliance on atmospheric sources of nutrition (Brodo et al., 2001). Lichens also do not readily excrete toxins, thereby accumulating pollutants over time. In contrast, multiple factors influence vascular plant growth (i.e., soil condition, moisture regime, canopy and position, diseases, insects, physical injuries, excretion of secondary compounds, and others) so that even chronic air pollution may not be readily observable at the individual organism level, much less the community level.

Though lichens have been used to monitor air quality for some time (Nash and Wirth, 1988; Richardson, 1992; Stolte et al., 1993) their utility as indicators of community diversity is less well known (Neitlich and McCune, 1997; Rogers et al., 1998). In this study, the aspen-related macrolichen community is the proposed indicator of species diversity at-large, though its utility as an air quality indicator is interwoven with my evaluation. In addition to detecting urban pollutants, recent research from California has stressed the ability of lichens to detect a signal of agricultural toxins, such as ammonia (Jovan and McCune, 2005, 2006). Similar high levels of ammonia in Cache Valley may be affecting plants in northern Utah's forests (personal comm., Randy Martin, Atmospheric Scientist, Utah State University).

Studies addressing epiphytic lichen communities in aspen are limited. The landmark publication *Aspen: ecology and management in the western United States* (DeByle and Winokur, 1985) makes no mention of lichen communities in its extensive review of aspen research in the United States. A similar review of aspen-related topics in Canada also features no lichen studies (Peterson and Peterson, 1992). Apparently, these large-scale reviews have overlooked the importance of the lichen community in increasing aspen-related diversity in North America (Case, 1977; Buckley, 2002a, 2002b). Research on European aspen (*Populus tremula*) has more closely tracked the value of lichens in aspen forest types (Lipnicki, 1998; Hedenås and Ericson, 2000, 2004). Two studies by Hedenås and Ericson (2000, 2004) focus on the unique macrolichens found in European aspen communities and the effects of human alterations of those systems. However, greater climatic moisture in northern Scandinavia allows for a richer lichen flora than the relatively dry forests of the Bear River Range.

In the Interior West, I know of two published works examining lichens in quaking aspen. In Colorado, Carmer (1975) inventoried lichen communities on 10 riparian hardwoods, including aspen, in the Front Range. She found 23 species on aspen, about half being macrolichens (fruticose and foliose) and the rest being microlichens (crustose). This study only examined aspen within 50 meters of stream beds, so conclusions are somewhat limited to riparian (i.e., relative high moisture) systems. Nonetheless, this study concluded that aspen was second only to narrowleaf cottonwood (*Populus angustifolia*) in terms of lichen species richness for riparian hardwoods (Carmer, 1975).

Martin and Novak (1999) compared the lichen flora of aspen stems in Idaho with those of adjacent Douglas-fir (*Pseudotsuga menziesii*) in upland sites. Their work highlights the greater diversity of all lichen species (not just macrolichens) on Douglas-fir and points to several factors (tree age, trunk moisture gradients, bark pH, bark texture, and air pollutants) that may influence this difference. They also note a distinct lichen flora between the species. This final conclusion (no overlap between aspen and conifer lichen species) conflicts with my informal observations of aspen lichen flora locally. In the Bear River Range, I have previously witnessed a minimum of 3-5 species in pure aspen types alone and a wide range—up to 18 species—in mixed hardwood/softwood stands. Their data also show only a single macrolichen species on aspen throughout two study sites (Martin and Novak, 1999), which leads me to speculate that a more thorough study (more plots/more lichen species)—though having different and broader objectives—may lead to alternate conclusions regarding the nature of macrolichen diversity in Interior West aspen communities.

None of the above works has applied the dual factors of succession and air quality to lichen communities on aspen. A study design, as described in further detail in Chapter 3, focusing on forest succession and attempting to account for moisture and pollution gradients, makes unique contributions in both the ecological literature of aspen and epiphytic lichens.

Chapter previews

Chapter 2: Aspen indicator species in lichen communities in the Bear River Range of Idaho and Utah

Authors: Paul C. Rogers, Roger Rosentreter, and Ronald J. Ryel.

Journal: Evansia 6, 2007.

This study represents the first phase of research to track aspen conditions using epiphytic macrolichens as bioindicators. Our goal was to establish lichen preference for aspen and associated conifers. Specifically, three questions are addressed in this preliminary study: 1) are there geographic differences in lichen communities in aspen-associated stands among three broad zones from north to south in the study area? 2) do different lichen species live on aspen versus conifers? and 3) if certain lichens show preference for aspen, can we determine a ranking of aspen "faithfulness" among these species? In addition to answering these questions, we hoped to gain an initial feel for community-wide lichen composition across the study area.

If we can determine a set of lichen indicator species of aspen communities for the Rocky Mountains, then perhaps these species may be used as a barometer of aspen community conditions. If local or regional aspen populations are dwindling (or stabilizing) we would expect to see concurrent patterns in lichen associates. This work contributes to our basic ecological knowledge about lichen preferences for aspen substrates and may be useful to managers in further aspen monitoring efforts.

Chapter 3: Lichen community change in response to succession in aspen forests of the southern Rocky Mountains

Authors: Paul C. Rogers, and Ronald J. Ryel.

Journal: Forest Ecology and Management (in review).

The purpose of this research is to evaluate how macrolichen communities change with advancing succession in aspen forests. The study design involves a systematic landscape-level survey of aspen forests — from pure to remnant stands — between 2,134 and 2,438 m elevation in the Bear River Range, Idaho and Utah. We surveyed approximately 50 systematically distributed plots for location, stand structure, and lichen community data. Various plot-level attributes were analyzed using Analysis of Variance

(ANOVA) to assess differences between pure, invaded, declining, and remnant aspen stands. We were interested in differentiating between total lichen diversity and diversity associated with aspen dependent species. A byproduct of this research is the development and evaluation of an "aspen index score" based on the diversity and abundance of species showing affinity for aspen stems and forests using Indicator Species Analysis (Dufrêne and Legendre, 1997). Aspen dependency at the tree-level was determined from Chapter 1 work, while aspen dependency at the stand-level was examined here. Specifically, we had three goals: 1) to determine the diversity of lichens associated with aspen forests in the study area; 2) to assess trends in lichen communities as forests advance in succession from pure aspen to conifer-dominated stands; and 3) to evaluate the importance of specific successional stages on lichen community development.

A secondary theme of this research was to investigate epiphytic lichens as bioindicators of habitat change. Since little research has been conducted specifically related to aspen forests, there is a high potential for increased basic knowledge of lichen species presence, as well as more complex relationships with forest change. We are unaware of previous studies in western North America examining the interface between aspen dynamics and lichen communities. Thus, we anticipate these findings providing further insight to ecological change associated with succession, as well as applications to forest management and monitoring.

Chapter 4: Aspen succession and nitrogen loading: a case for epiphytic lichens as bioindicators in changing forests

Authors: Paul C. Rogers, Ronald J. Ryel, and Kori D. Moore.

Journal: Ecosystems (in review).

This study originated as an extension of Chapter 3 work, using Analysis of Covariance (ANCOVA) to isolate other factors, in addition to forest succession, that contribute to lichen diversity in aspen stands. The same basic methods and data sets were used as in Chapter 3, although we added ammonia sensor data previously collected from urban and agricultural settings in the adjacent Cache Valley. After ANCOVA testing, we implemented non-metric multidimensional scaling (NMS) ordination to compare univariate to multivariate approaches to explain community variance lichens among sample locations. NMS allows testing of numerous variables, such as succession stage, stand age, canopy cover by tree types, amount of aspen bole scarring, various pollution variables (i.e., nitrophilous lichen assemblages, distance to peak ammonia sources, distance to population centers), and presence/absence of certain lichen species. Results of NMS are presented as *r* values per explanatory axis in a table, or graphically as ordination joint plots.

The beauty of NMS is being able to "view" multiple potential explanatory variables in relation to each other, as well as in lichen "species space" as determined using Sørensen distance measures (McCune et al., 2002). Based on previous work we believed that certain nitrophilous (i.e., nitrogen "loving") lichens could be used to construct indices of N-affinity (van Herk, 1999; van Haluwyn and van Herk, 2002; Jovan and McCune, 2005, 2006). The Bear River Range and adjacent Cache Valley, Utah and Idaho, present an ideal landscape-level experiment for testing transport of ammonia (NH_3) and its air-borne derivative ammonium (NH_4) as there are numerous local sources of NH_3 related to agriculture and urban activities. Results from Chapter 3 and ANCOVA, allowed us to test the predictive ability of our aspen index score in relation to several other variables and along an expected succession gradient. We suspected that level and type of aspen bole scarring and lichen colonization may not be adequately tested using only analysis of variance statistics and may benefit from this multivariate approach. There is also the possibility that additional stand structure variables will emerge as predictive candidates in NMS analysis.

Chapter 5: Historical patterns determining lichen community composition in aspen-associated forest of the Rocky Mountains, USA

Authors: Paul C. Rogers, Ronald J. Ryel, and Dale L. Bartos.

Journal: Journal of Biogeography (in review).

The aim of this chapter is to synthesize the entire project around broader themes and to focus on the element of historical change in both aspen and lichen systems. Themes of interest, but not yet discussed in earlier more focused chapters, include disturbance ecology, long-term human influences, climatic change, and management implications. In addition to widening our view of aspen and lichen interactions, we hope to incorporate new data sources, such as climate data available from the National Oceanic and Atmospheric Administration (NOAA) (Cook et al., 2004) and available local historic (Utah State University, Special Collections Library) and agency (Wasatch-Cache National Forest) information, with our stand structure and lichen data sets.

Specifically, we built a chronology of climate and human impacts on aspen forests since Euro-American settlement, and then related these influences to associated epiphytic lichen communities. In as much as we have linked lichens as dependent species of various aspen stand types (Chapters 3 & 4), we think there may be lessons for other aspen-dependent flora and fauna. Both climate and historical records will significantly aid our ability to make long-term suppositions regarding lichen communities. Bridging these diverse sources, we believe, lends itself to constructing a more complete picture of landscape and community evolution during a period of dynamic change. By examining broad-scale climate patterns of the past, this approach may allow applications for addressing future climate scenarios. Insights from this synthetic approach may be instructive to contemporary forest managers, lichen specialists, and aspen ecologists.

Chapter 6: Summary and implications

In North America, aspen and epiphytic lichen interactions have heretofore been little explored. Broad-scale lichen monitoring from the western United States (McCune et al., 1998; Neitlich et al., 2003; Jovan and McCune, 2005, 2006) in combination with aspen and lichen related studies from northern Europe (Esseen et al., 1996; Hedenås and Ericson, 2000; Pykälä, 2004) provided an impetus for the current work here in the Rocky Mountains. In comparison to this previous work, our montane study area is relatively dry and therefore less conducive to great macrolichen diversity. My hope through this dissertation is to make a unique contribution to aspen ecology by using lichens as bioindicators of larger trends. The summary relates the results of each chapter, talks about trends revealed, and explores future questions spawned by this work.

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CHAPTER 2

ASPEN INDICATOR SPECIES IN LICHEN COMMUNITIES IN THE BEAR RIVER RANGE OF IDAHO AND UTAH [1]

Introduction

Quaking aspen (*Populus tremuloides*) is the most widespread and dominant hardwood in the Rocky Mountain region of the U.S. Aspen is a seral species that is short-lived compared to most of its conifer cohorts. Following disturbance, aspen normally dominate a site for 40-80 years, after which they succumb to natural thinning from disease, aging, and increasing succession (shading) by competing conifers (Mueggler 1985; Rogers 2002). Aspen is a minor commercial species, but is highly valued for its wildlife habitat and aesthetic appeal, most notably as autumn leaves change to a bright yellow among a sea of conifers. It is also widely believed that aspen are declining on a regional scale (Bartos and Campbell 1998; Di Orio et al. 2005; Rogers 2002), although contrary results have been documented (Barnett and Stohlgren 2001; Kulakowski et al. 2004; Manier and Laven 2002).

Studies addressing epiphytic lichen communities in North American aspen are limited. Research on European aspen (*Populus tremula*) has more closely tracked the value of lichens in aspen forest types (Hedenås and Ericson 2000; Hedenås and Ericson 2004; Lipnicki 1998). In Canada, lichens in aspen forests play a significant role in increasing overall forest diversity (Buckley 2002; Case 1977). In the Colorado Rocky Mountains, Carmer (1975) examined lichen diversity on riparian hardwoods, one of

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[1] Coauthored by Paul C. Rogers, Roger Rosentreter, and Ronald J. Ryel.

which was aspen. He found that aspen stems were second only to narrowleaf cottonwood (*Populus angustifolia*) in terms of epiphytic lichen diversity. Finally, Martin and Novak (1999) compared the lichen flora of aspen stems in Idaho to those of adjacent Douglas-fir (*Pseudotsuga menziesii*) in upland sites. Their work highlights the greater diversity of lichen species on Douglas-fir (compared to aspen) and points to several factors (tree age, trunk moisture gradients, bark pH, bark texture, and air pollutants) that may explain this difference (Martin and Novak 1999).

The concept of ecological indicators – a single measure or index representing greater ecosystem conditions – is central to contemporary monitoring methodology (National Research Council 2000; Riitters et al. 1992; Wickham et al. 1999). Though lichens have been used to monitor air quality for some time (Nash and Wirth 1988; Richardson 1992; Stolte et al. 1993), their utility as indicators of community diversity is less well known (Jovan and McCune 2005; Neitlich et al. 2003; Rogers et al. 1998). This study represents the first phase of an effort to specifically track aspen community "health" by using epiphytic macrolichens as bioindicators. In order to accomplish that goal it is important to establish community composition and, more critically, presence of aspen "indicator species" (i.e., species unique to aspen as a substrate). If we can determine a set of lichen indicator species of aspen communities for the Rocky Mountains then perhaps these species can be used in conjunction with a larger lichen monitoring effort, as a barometer of aspen community conditions. If local or regional aspen populations are dwindling (or stabilizing) we would expect to see concurrent patterns in lichen associates. Further, if specific pollutants, such as excess nitrogen or ammonia (Jovan and McCune 2006; Rosentreter 1990), are affecting aspen forests lichen communities may provide an early warning of potential forest-wide effects. Additionally, lichen monitoring in these communities may prove to be a cost-effective surrogate for total animal and plant enumeration given the high faunal and floral diversity of aspen forests (Mueggler 1988; Shepperd et al. 2006).

Study site

The Bear River Range is a north-south trending block fault uplift consisting primarily of limestone from 1,370 – 3,040 meters elevation. The range is approximately 20 kilometers in width by 70 kilometers in length. Moisture comes predominantly from the west in the form of winter precipitation, though short-duration summer thunderstorms are not uncommon. The Bear River Range is too far north to be influenced by summer monsoonal precipitation common to the southwest U.S.

Lichen communities are likely influenced by the increasing precipitation associated with elevation (Marsh and Nash 1979). To moderate this and other environmental influences, we sampled only in a mid-elevation belt comprising aspen's optimum growth zone in the Bear River Range. Dominant trees at this elevation are aspen, subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*).

Methods

Ten mixed aspen-conifer plots were randomly selected in the north (Idaho) and central and south (Utah) portions of the Bear River Range near Logan, Utah, respectively (Figure 2.1). Plots were limited to those 2,134 – 2,438 meters in elevation, at least 30 meters from a road, and greater than 25 percent basal area in either aspen or conifer stems. All sample plots were located at least one kilometer apart. At each location trees were selected along a north-trending transect, alternating between conifer and aspen sample trees, at 20 meter intervals until 10 trees were sampled (5 in each tree group). If conditions changed from the basic stand selection criteria (e.g., forest opening, species composition change, or road is encountered), a new transect was begun from the plot center at the next cardinal direction (east), and the procedure was repeated along primary transects (south, west, northeast, etc.) until 10 trees were sampled. At each tree, presence of all macrolichens (i.e., foliose and fruticose) between 0.5 and 2.5 meters, on branches and boles, was noted. Lower boles (below .5 meters) were not sampled to limit the influence of ground-dwelling lichen communities that occasionally inhabit tree bases. Only mature standing trees (at least 12.7 centimeters d.b.h.), both live and dead, were sampled for this study. Raw field score for each sample unit consists of a value (0-5) denoting the presence/absence of a given lichen species for each of five potential trees at each site/species combination.

Multivariate statistics were used for all tests in this study because the nature of lichen community data does not lend itself to normal distributions and equal variances. The analysis centered on two primary questions: 1) Is there a difference in lichen communities living on aspen versus those living on associated conifers?; 2) If these epiphytic communities differ, what are the species that most faithfully represent aspen dependence? Prior to examining these questions we assessed possible differences associated with geographic location within the Bear River Range. Using Multi-response Permutation Procedures (MRPP) we tested for differences between north, central, and south plot groups (McCune et al. 2002). A blocked MRPP (MRBP) was used to test for group differences between aspen and conifer lichen communities. The MRBP is a statistical test for assessing difference between groups within blocks (Biondini et al. 1988; McCune et al. 2002).

Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) in the PC-ORD software (McCune and Mefford 1999) provides a compliment to MRBP in that it further elucidates exactly which species are unique to groups with significant differences in community composition (McCune et al. 2002). More succinctly, ISA is used here for evaluating lichen species "faithfulness" to aspen in aspen/conifer mixed forests. The ISA calculation is composed of computations of relative abundance and relative frequency of each lichen species by group (aspen or conifer), then multiplying those scores to give a final indicator value. The statistical significance of the highest indicator value for each species is tested by 5,000 runs of a Monte Carlo randomization procedure. The resulting p-value represents the probability that the calculated indicator value for any species is greater than that found by chance.

Results

Fifteen lichen species were sampled on all plots in our study area with two samples unidentifiable beyond the genus level (Table 2.1). Of these, four species were encountered only one time (*Bryoria fuscescens*, *Candelaria concolor*, *Imshaugia aleurites*, and *Physciella chloantha*). The most cosmopolitan species, *Physcia adscendens*, was sampled at every location on both aspen and conifers. The theoretical distribution for total lichen tally ranges from100 (total trees examined) to presence of a species on one tree. Though lichen abundance (i.e., quantity of cover, as opposed to presence/absence of species on individual trees) was not specifically sampled, the total tally column gives the reader some idea of relative abundance of the species listed throughout the study area, by tree types.

Given the great distance between sample locations in the Bear River Range (Figure 2.1), there was concern that community sampling might reflect gross environmental differences rather than differences in lichen communities between tree species substrates. Geographic groups were arbitrarily defined by broad sub regions to force a geographic sampling spread within the study area. Three plots were located in the north, four in the central, and three in the south group. Results of the MRPP show no significant difference ($A = 0.018$, $p = 0.225$) between lichen communities in these three broad zones. The chance-corrected within-group agreement describes the measure of agreement (A) between groups; where $A = 1$ is perfect agreement and $A = 0$ means that there is no more agreement between groups than is expected by chance.

The present study was designed around the establishment of equal sample groups (aspen and conifer) in 10 blocks (plots). Each sample unit consists of a unique combination of groups and blocks. MRBP to test for differences between lichen communities found on aspen versus conifers in mixed stands showed a significant difference ($A = 0.292$, $p = 0.001$). Because distributions here are assumed to be non-normal, a simple Euclidean distance measure was used in the MRBP. McCune et al. (2002) suggest that, as a benchmark, $A > 0.3$ is a high score for ecological studies using multi-response permutation methods. Using that benchmark, a relatively strong separation of lichen communities between aspen and conifers was found in this study.

Given that MRPB established a statistical difference in lichen communities we then turned to ISA to pinpoint which species are responsible for the unique aspen lichen community composition in mixed stands. Table 2.2 provides a summary of ISA statistics for the 10 plots in our study area. The three species showing the best results (i.e., faithfulness) as indicators of aspen-specific lichen communities are *Phaeophyscia nigricans* ($p = 0.001$), *Xanthomendoza galericulata* ($p = 0.001$), and *Xanthomendoza fulva* ($p = 0.039$). Three species showed more exclusive preference for conifers over aspen: *Melanelia exasperatula* ($p = 0.004$), *Melanelia subolivacea* ($p = 0.007$), and *Xanthomendoza montana* ($p = 0.0006$).

Discussion

Martin and Novak (1999) found a limited set of species growing on Douglas-fir and aspen stems in southwestern Idaho (just five macrolichen species on Douglas-fir and only one on aspen). While the present study documents a more robust lichen flora at similar elevations, we can only speculate that their southwest Idaho sites were located in somewhat drier habitats. In the Bear River Range, we looked at a greater variety of substrates, over a larger area, and with more sample locations. Moreover, the sampling method here highlights lichen communities in the same stands, alternating between aspen and conifer stems in our transect layout, to emphasize similarities and differences among stand cohorts. Knowing we were somewhat limited by small sample size, when we tested for differences in geographic groups across the sub regions of the range we found no statistical difference in lichen communities on aspen and conifers. This tells us, at a gross scale, that there are not large differences in lichen communities within our mid-elevation sampling belt based on latitude.

One element not tested in this study, but which was readily apparent in the sampling procedure, was that the location of lichen species on trees differed between aspen and conifers. Lichen species on conifers were sampled from tree stems, main branches, and twigs within the 0.5 to 2.5 meter vertical sampling area. On aspen, lichens were principally on main stems and rarely on branches. Further, epiphytic lichens are confined almost exclusively to stem scars from old branches, various physical wounds, and canker and conk scaring. Most of the typical aspen stem, the smooth white surface, is not conducive to macrolichen colonization (Martin and Novak 1999).

As stated earlier, we were most interested in demonstrable differences in the lichens present on aspen substrates versus those on conifers. The results of MRBP here ($A = 0.273$, $p = 0.001$) describe two distinct communities in these forests; one found primarily on conifers and the other on aspen stems, though significant overlap in species is acknowledged and expected. This result should not be surprising given that these species groups have different bark morphology and pH, and that previous researchers have shown sharp differences between hardwood and softwood trees in terms of lichen species assemblages (Hedenås and Ericson 2000; Martin and Novak 1999; Neitlich and McCune 1997). The value of this information is nonetheless important to furthering our understanding of the role this particular hardwood plays in the Rocky Mountains, where it is often the only hardwood present softwood-dominated landscapes. Further study in this region may need to explore the contribution of other minor hardwoods to the total lichen diversity equation. We have made the assumption here that aspen is either the sole or dominant hardwood in most mid-elevation Rocky Mountain forests. This assumption may reasonably be challenged at some locales, most notably in riparian corridors or lower elevations. At any rate, the successful establishment of unique communities between aspen and conifers using MRBP makes the further testing for indicator species a logical next step.

The second goal of this study was to determine which species, if any, were unique to aspen and therefore might represent 'species of concern' should aspen populations become altered significantly. We tested for indicator species of aspen communities using ISA and found that the three species most faithfully representative of aspen ramets were *Phaeophyscia nigricans*, *Xanthomendoza galericulata,* and *Xanthomendoza fulva* (Table 2.2). While some species reflected the opposite (i.e., most faithful to conifers) further study would be needed to partition which conifer species provide the best substrates for particular lichen species for this information to be useful. Of course, the emphasis here is faithfulness to aspen in lichen indicator species; thus we have no further need to discuss conifer preference by lichens in our area. Rather, we may further use of the three aspen indicator species developed here to evaluate lichen habitat in aspen stands.

An aspen indicator score can be assigned to any lichen sampling plot that is suitable for aspen growth (i.e., presently having either live or dead aspen on site). The intent of the score is to place emphasis on communities where aspen and aspen-dependent lichens may be threatened. The most straightforward approach to scoring aspen plots based on these species is to grade the quality of lichen-surveyed aspen stands based on the combination of species presence and abundance scores. A standard system of lichen abundance rating has been adopted from National Forest Health monitoring protocols (McCune 2000; Will-Wolf 2002) and applied to a larger set of systematically surveyed plots in the Bear River Range (Rogers, study in progress). One caution is that our findings confirm those of Lindbloom (1997) that there are common morphological overlaps between *Xanthomendoza galericulata* and *Xanthomendoza fulva* that may make absolute field identification, as indicator species, more difficult. For this reason it may be prudent to focus on presence of *Phaeophyscia nigricans* as the most dependable indicator of unique aspen habitat where aspen is competing with conifers. Bear in mind that our study addresses forest habitat where aspen is primarily the sole hardwood species. In settings where other hardwoods may co-exist with aspen, then additional habitat for these three lichens may be present, although we did not specifically test hardwood-to-hardwood competition here.

Based on results of this study, three macrolichens appear dependent on aspen substrates for existence in the central Rocky Mountains of northern Utah and southeast Idaho. As tree populations, such as aspen, fluctuate based on human and environmental influences we would expect that dependent species would display concurrent fluxes. In this way, we may use indicator species as a means of monitoring availability of ample habitat for maintaining viable aspen-dependent species populations. Similar analysis could be performed for other tree species of local and regional concern. As a barometer of community health, lichen monitoring for species diversity may be just as important as for air quality. Better still, the combination of both values may provide an important component for both large-scale and local forest monitoring efforts.

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Table 2.1 Tally of lichen species on aspen, conifers, and species totals for 10 mixed aspen/conifer plots in the Bear River Range, Idaho and Utah.

Species	**Tally on aspen**	**Tally on conifer**	**Total**
Bryoria Fuscescens		1	1
Candelaria concolor	1		1
Imshaugia aleurites		1	1
Letharia vulpina		4	4
Melanelia elegantula	9	32	41
Melanelia exasperatula	5	31	36
Melanelia subolivacea	1	27	28
Phaeophyscia nigricans	23		23
Physcia adscendens	45	39	84
Physcia spp.	1	1	2
Physciella chloantha	1		1
Usnea spp.		2	2
Usnea lapponica		4	4
Xanthomendoza fallax	25	26	51
Xanthomendoza fulva	22	6	28
Xanthomendoza montana	12	42	54
Xanthomendoza galericulata	29		29
Total tally	174	216	390

Table 2.2 Indicator Species Analysis values for all species tallied by maximum score group (1 = aspen, 2 = conifer). Significant p-values are in bold type.

Species	**Maximum score group**	**Indicator value**	**Mean**	**Standard deviation**	**p**
Bryoria Fuscescens	2	10.0	10.0	0.14	1.0000
Candelaria concolor	1	10.0	10.0	0.14	1.0000
Imshaugia aleurites	2	10.0	10.0	0.14	1.0000
Letharia vulpina	2	10.0	10.0	0.14	1.0000
Melanelia elegantula	2	62.4	42.8	8.33	0.0296
Melanelia exasperatula	2	86.1	41.3	9.15	**0.0006**
Melanelia subolivacea	2	67.5	31.0	9.34	**0.0074**
Phaeophyscia nigricans	1	80.0	30.8	9.21	**0.0012**
Physcia adscendens	1	53.6	52.4	1.94	0.3518
Physcia spp.	1	5.0	12.1	7.49	1.0000
Physciella chloantha	1	10.0	10.0	0.14	1.0000
Usnea spp.	2	20.0	12.3	7.50	0.4842
Usnea lapponica	2	20.0	13.3	6.24	0.4634
Xanthomendoza fallax	2	40.8	48.8	6.99	0.9846
Xanthomendoza fulva	1	62.9	43.2	8.72	**0.0398**
Xanthomendoza montana	2	77.8	48.6	6.80	**0.0006**
Xanthomendoza galericulata	1	80.0	30.8	9.18	**0.0010**

Figure 1

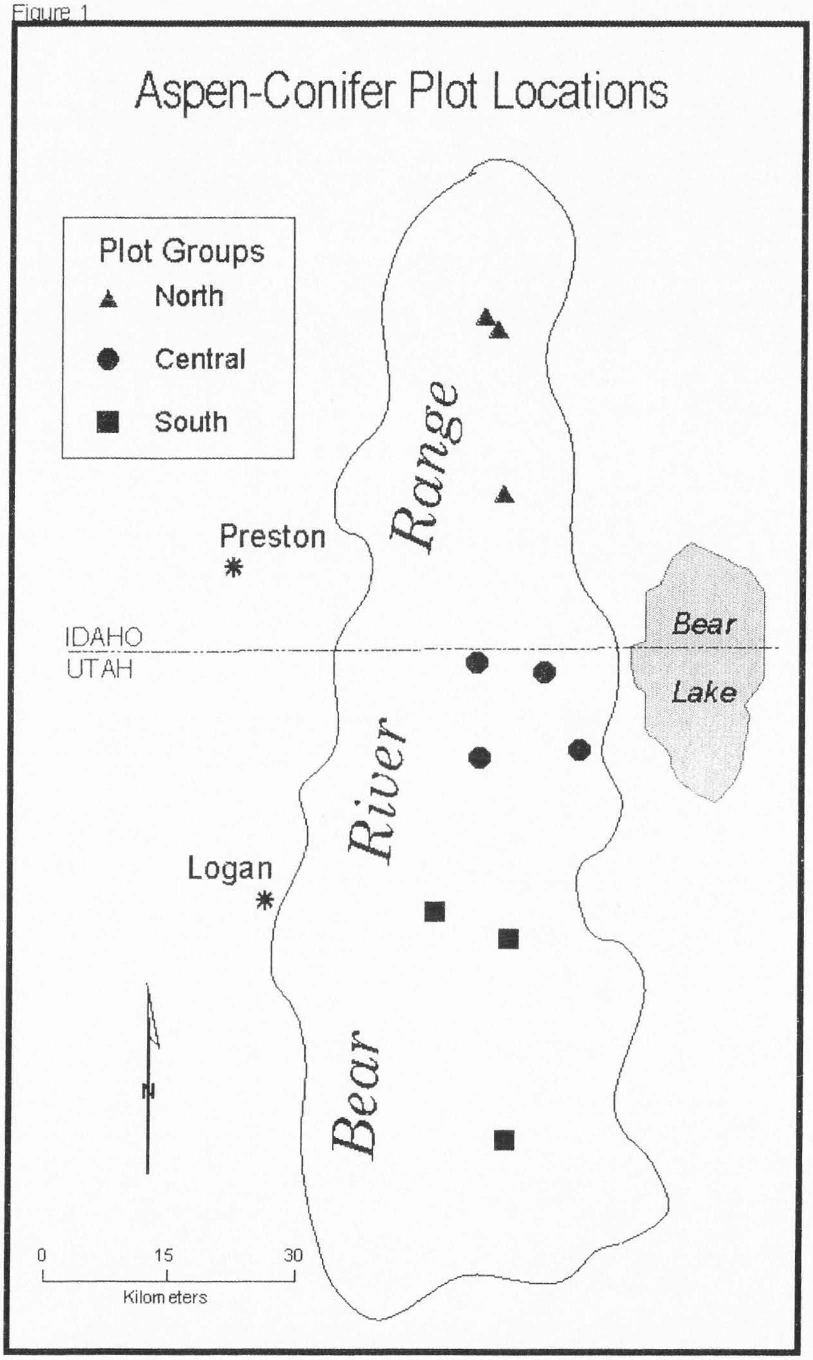

Figure 2.1 Map of randomly selected plot sites.

CHAPTER 3

LICHEN COMMUNITY CHANGE IN RESPONSE TO SUCCESSION IN ASPEN FORESTS OF THE SOUTHERN ROCKY MOUNTAINS[2]

Introduction

Quaking aspen (*Populus tremuloides*), the most widespread and plentiful hardwood of the southern Rocky Mountains, USA, is purportedly in regional decline. Explanatory factors contributing to aspen change are fire suppression, climate change, impacts of European settlement, and effects of browsing by wildlife and livestock (Shepperd et al., 2006). Numerous studies have addressed the status of aspen forests in the region, with some showing declining coverage (Bartos and Campbell, 1998; Rogers, 2002; Gallant et al., 2003; Brown et al., 2006) and others describing aspen expansion (Manier and Laven, 2002; Kulakowski et al., 2004). Researchers agree that aspen succumb to conifer invasion where seral stands are devoid of recent disturbance. While some aspen display long-term stability, conifers eventually invade most stands and convert them to other forest types in the absence of disturbance (Mueggler, 1988). From this perspective succession in aspen communities plays a crucial role not only in the development and potential conversion of aspen to other types, but as a catalyst for change in associated species. There is strong support for the notion of aspen's unique contribution to biodiversity of western North American landscapes (DeByle, 1985; Mueggler, 1988; Ripple et al., 2001; Shepperd et al., 2006) and some have highlighted

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aspen as a "keystone" type, denoting their amplified role in supporting entire ecosystems (Campbell and Bartos, 2001; Manley et al., 2000).

Lichen community reaction to aspen-to-conifer succession is poorly understood in the Rocky Mountain region. A review of landmark publications on aspen ecology in both the U.S.A. and Canada makes no mention of lichens (DeByle and Winokur, 1985; Peterson and Peterson, 1992) and overlooks the importance of the lichen communities' role in increasing aspen-related diversity in North America (Buckley, 2002; Case, 1977). In contrast, research and subsequent management actions in European forests have elevated the profile of aspen (*Populus tremula*) as a landscape element and found that aspen promotes species diversity including lichens (Hedenås and Ericson, 2000; Hedenås and Ericson, 2004; Lipnicki, 1998).

In the United States, we know of two published works examining lichens specifically in quaking aspen. In the Colorado Front Range, lichen communities were inventoried on 10 riparian hardwood species, including aspen (Carmer, 1975). The author found 23 species on aspen, about half being macrolichens (i.e., foliose and fruticose forms) and the rest being microlichens (i.e., crustose) species. This study concluded that aspen was second only to narrowleaf cottonwood (*Populus angustifolia*) in terms of lichen species richness for riparian hardwoods (Carmer, 1975). Also, Martin and Novak (1999) compared the lichen flora of aspen stems in Idaho to those of adjacent Douglas-fir (*Pseudotsuga menziesii*) and noted a distinct lichen flora between tree substrates. Their work also highlighted the importance of tree age, trunk moisture gradients, bark pH, bark texture, and air pollutants on lichen species diversity in these forest communities. The importance of bark scarring in providing habitat for epiphytic lichens has been noted in a number of studies (Case, 1977; Martin and Novak, 1999; Rogers et al., 2007a). Since the bole of North American aspen is predominantly smooth white bark, a correlation may occur between scars on aspen boles originating as cankers, conks, physical wounds, and branch stubs and lichen diversity and abundance at the stand-level.

This paper focuses on change in epiphytic lichen communities associated with succession in aspen forests. Specifically, we have three objectives: 1) to determine the diversity of lichens associated with aspen forests in the Southern Rockies Ecoregion; 2) to assess trends in lichen communities as forests change from pure aspen to conifer-dominated stands; and 3) to evaluate the importance of specific successional stages on lichen community development. In conjunction with this final objective, we hope to gain specific understanding of how lichens exclusive to aspen substrates react to conifer encroachment.

An underlying theme of this work is to test the ability of epiphytic lichens to act as bioindicators of forest change. Since little research has been conducted on this subject in our geographic region, there is significant potential for increased basic knowledge on lichen species presence, as well as interactions related to forest change. We are unaware of previous studies in western North America examining the interface between aspen dynamics and lichen communities. We anticipate that these findings will provide further insight to ecological change associated succession, as well as applications to forest management and monitoring.

Study area

The Bear River Range is a north-south trending block fault range straddling the Utah and Idaho border (Figure 3.1). These mountains lie in the Southern Rocky Mountains Ecoregion Province between 1,370 and 3,040 m elevation, and receive between 51 and 102 cm of precipitation per year (Bailey, 1995). Most precipitation comes in the form of winter snowfall. The northern portion of the Southern Rocky Mountains experiences summer drought with occasional brief thunderstorms. Dry lightning storms provide the prime ignition source for fire-prone forests of the area (Bailey, 1995).

Aspen forests comprise the primary hardwood element of mid- and upper-elevations in the Southern Rockies Ecoregion (Rogers, 2002). In the Bear River Range, aspen's conifer cohorts are subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and to a lesser degree Engelmann spruce (*Picea engelmannii*), Rocky Mountain juniper (*Juniperus scopulorum*), and limber pine (*Pinus flexilis*). Subalpine fir is the dominant conifer in this study area. Minor hardwoods of the area include bigtooth maple (*Acer grandidentatum*), Scouler willow (*Salix scouleriana*), western serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and mountain mahogany (*Cercocarpus ledifolius*). The remaining vegetation cover of this range is made up of big sagebrush (*Artemisia tridentata* var. *vaseyana*) and subalpine meadow openings. Understory vegetation in aspen stands ranges from lush stands of diverse forb and grass groups, to shrubby cover dominated by snowberry

(*Symphoricarpos spp.*), to sagebrush, and mixed assemblages of each of these groups (Mueggler, 1988).

A fire history in the Bear River Range concluded that during the settlement era (c.1850-1900) fire frequencies increased due to amplified human fire ignitions related to extractive activities (i.e., logging, grazing, mining, hunting), while during the 20th century fire suppression and decreased grazing led to longer fire intervals. This general pattern has favored shade-tolerant fir and spruce at the expense of fire-dependent aspen and lodgepole pine (Wadleigh and Jenkins, 1996). Additionally, a relatively moist 20th century in this region, excepting the 1930's drought, probably served to augment fire suppression efforts in terms of favoring shade-tolerant conifer species (Gray et al., 2004).

Methods

The goal of plot selection was to attain at least 10 sample plots in each of four qualitative succession groups evenly distributed across the study area. An underlying assumption of this work is that all stands sampled could potentially succeed to conifer types. For this reason, dry south-facing aspects were avoided because they are the most unlikely to be invaded by conifers at mid elevations. Seral aspen stands (the subject of this study) are most commonly encountered on cooler, moist aspects where conifers thrive (Mueggler, 1988). The initial screening was made from a set of 422 potential aspen plots located between 2,134 and 2,438 m elevation and selected from a 500 m grid overlay of Utah and Idaho digital vegetation maps (USGS, 2004; USGS, 2005). Using ArcMap® geographic information system software (ESRI Corp. Redlands, CA), we randomly selected 25 % of potential aspen plots throughout the range for field sampling.

These plots were appointed stand type labels of 1 – 4 corresponding to "pure," "invaded," "declining," and "remnant" aspen populations. The 52 selected plots were adjusted before field sampling to move them into adjacent stands estimated from aerial photographs to meet the stand type qualifications (Table 3.1). Upon field sampling, plot centers were located using the same aerial photos, then either placed at the actual grid point intersections (unadjusted) or by chaining into stands (adjusted) a predetermined distance to allow for measuring the entire plot within the same type. Sixteen field plots were located on privately owned land. Five of these plots were dropped from the survey where owners denied access. A total of 47 field locations distributed in the four aspen cover categories are shown in Table 3.1 and Figure 3.1.

Field measurements encompassed two broad categories: stand characterization composed of site descriptors and mensuration variables, and lichen sampling by species tally, voucher collection, and abundance estimation. Location descriptors include a plot identifier, GPS readings, slope, aspect, stand type, percent aspen cover, percent conifer cover, stand age, and aspen age. Five cover estimates for mature aspen and conifers were taken at the plot center and 2 m inside the lichen plot perimeter (33 m radius) at the four cardinal directions, respectively. Stand ages were based on at least two cored aspen trees (stand types 1 and 2) and an additional two cores of dominant conifer species (stand types 3 and 4). We cored the nearest healthy co-dominant trees to the plot center fore age determination. Stand ages were calculated by adding five years to the breast height average of aspen cored and 10 years to average conifer ages to account for the growth period between ground level and breast height.

Forest mensuration variables were collected on a single fixed-area subplot 7.3 m in radius and centered in the 0.378 ha lichen survey plot (Will-Wolf, 2002). Tree species, diameter at breast height (dbh = 1.3 m), size class, and status (live/dead) were collected on all trees 12.7 cm diameter and greater. Additionally, on aspen we tallied damage type and severity, plus percent of the main stem with bark scarring, lichen colonization of scars, and lichen colonization of smooth bark. Scarring and colonization variables consisted of percent area of stems from 1-2 m above the ground. Finally, we counted tree seedlings (> 0.3 m < 1.3 m height) and saplings (≥ 1.3 m height < 12.7 cm dbh) within the subplot by species to estimate per hectare regeneration levels. When referring to "seedlings" in our field protocol we mean all tree species meeting the size qualifications above; including aspen whose regeneration is vegetative and not from seed.

Lichen sampling was modeled after the procedure used in the USDA Forest Service, Forest Health Monitoring program (McCune, 2000; Will-Wolf, 2002). In short, a 0.378 ha plot was systematically examined for presence of epiphytic macrolichens 0.5 m above the forest floor for up to two hours. Lichens were not sampled below 0.5 m to avoid overlap with terricolous and saxicolous species and their accompanying forest floor influences (i.e., soil type, moisture, leaf litter, vascular plant abundance). The method allowed workers to examine fresh litter fall as surrogate for upper canopy lichens. At least 40 minutes was spent traversing the area, the last 10 minutes without new species tally, before the survey was terminated. On average, 60 – 75 minutes were needed for the survey. After completion of lichen tally, each species was assigned an abundance class score for the entire area: 1= 1-3 individuals (distinct thalli); 2= 3-10 individuals; 3= between 10 individuals and occurrence on half of all trees/shrubs on the plot; 4= greater than half of all woody substrates on the plot exhibited the lichen. Previous research found that for sparsely populated vegetation in large sample areas, visual abundance classes were preferable to continuous cover measures because accuracy was comparable while efficiency was greatly increased (McCune and Lesica, 1992). Unknown species were collected as vouchers for later verification under a dissecting scope and, when needed, by other lichen experts. One modification of the standard protocol was that we noted tree substrate groups on which lichens were tallied.

After data compilation and error checking, several derived variables were calculated for tree and lichen data at the plot level. Aspen and subalpine fir seedlings and saplings were tabulated on a per hectare basis. Though seedlings of other species were tallied, there were not enough individuals for meaningful analysis. Likewise, we calculated per hectare basal area for aspen, conifer, and dead trees. For all plots with live aspen present we computed average percent bole scarring, lichen colonization of scars, and colonization of smooth bark. Stand level aspen damage was determined by the proportion of bole-damaged versus undamaged live aspen stems tallied. For lichens, the two primary plot-level variables were species richness (number of distinct species) and total species abundance (cumulative abundance class scores).

Analyses were conducted to quantify lichen diversity in each of the four stand types that corresponded to different stages of conifer encroachment. Prior to analyses, the following statistics were generated to assess community diversity: gamma diversity (γ), the total number of distinct species identified in the study; alpha diversity (α), the mean species richness per sample plot; and beta diversity (β), γ/α, which yields an estimate of "community turnover." We conducted simple Pearson correlations (SAS proc

CORR) for all plot level variables to identify initial relationships. Analysis of variance (ANOVA; SAS proc GLM) was the primary analytical tool (SAS Institute, 2005). Response variables were lichen species richness and abundance. These variables were further scrutinized for normality of distribution (SAS proc UNIVARIATE) and equality of variance using Brown and Forsythe's test (SAS proc GLM, hovtest= bf welch).

To pinpoint individual species reactions to succession from aspen to conifer forests we used Indicator Species Analysis (ISA), a multivariate approach to testing for no difference between *a priori* groups (i.e., stand type) regarding individual species affinity, or faithfulness, based on species abundance scores in particular groups (Dufrêne and Legendre, 1997; McCune et al., 2002). Perfect "faithfulness" is defined as always being present in the identified group and being exclusive to that group (McCune et al., 2002). The ISA calculation is composed of PC-ORD© (McCune and Mefford, 1999) computations of relative abundance and a relative frequency of each lichen species by group, then multiplying those scores to give a final indicator value. The statistical significance of the maximum indicator value for each species is tested by 5,000 runs of a Monte Carlo randomization procedure. The resulting p-value represents the probability that the calculated indicator value for any species is greater than that found by chance. Output includes the group for which the maximum indicator value is found, the indicator score for that group, and the associated p-value for each species. Results were considered significant for ISA where $p < 0.05$.

Finally, we combined lichen species showing preference for aspen substrates (*Xanthomendoza fulva, X. galericulata, Phaeophyscia nigricans*) using ISA (Dufrêne and Legendre, 1997) in previous work (Rogers et al., 2007a) with *Physcia tenella*, which was only found on aspen in the present study, into an "aspen index score" using the following formula:

$$\text{Aspen index score} = 100(S_{asp}/S)$$

where S_{asp} is the sum of plot abundances for the four indicator species and S equals the total of all abundance scores for each plot. The aspen score had a minimum of zero, indicating none of these species was present, and a maximum of 100, indicating that only these species were present and all in the highest abundance category. Index scores could be useful as a metric of aspen community health as we track aspen-dependent species through successional stages. If the index is successful, it should produce declining scores with advancing conifer succession. We tested this assumption using a one-way ANOVA test for differences in the effect of succession classes on aspen index scores.

Results

Stand characteristics

We stratified our sample into broad succession groups based on estimation of aerial coverage of aspen prior to field visits. Field measures fell within the group cover parameters (Table 3.1) 70 % of the time. However, where cover estimates appeared to be inaccurate for the stand type, basal area measurements did comply with our stand types. This offsetting of objective measures (cover and BA) led us to maintain the original groupings based on the assumption that cover measures near heterogeneous stand edges had produced erroneous results (when compared to aerial photo estimates and plot-center BA) in about 30 % of plots.

Overall, we believe our groupings adequately capture successional trends in basal area, tree cover, and regeneration. Aspen cover (ANOVA, F = 26.77, $p < 0.0001$) and aspen basal area declined (ANOVA, F = 5.13, $p = 0.004$), while conifer cover (ANOVA, F = 28.81, $p < 0.0001$) increased with stand type progression (Figure 3.2a-c). Total basal area (Figure 3.2d) also increased from pure through remnant aspen stands (ANOVA, F = 5.80, $p = 0.002$). These figures illustrate the largest differences between invaded and declining stands (stand types 2 and 3) are more evident in cover estimates than basal area measures. Both seedlings and saplings reflect the same basic trend, although most relationships are statistically weaker. The number of aspen seedlings tallied was not correlated with conifer cover (r = -0.16, $p = 0.28$), but was positively correlated with subalpine fir seedling counts (r = 0.55, $p < 0.0001$). The strongest correlation among regeneration measures was between conifer cover and aspen saplings (r = -0.52, $p = 0.0002$), indicating a marked decrease in aspen sapling survival as conifers invade and eventually dominate stands.

Sample plots were located on slopes from 3-55 %, with the average slope being 24 % (13°). Mean plot slopes increased with stand type, meaning remnant aspen stands were more likely to be on steeper slopes than pure aspen. The average slope was 30 % for remnant stands and 20 % for pure aspen; invaded and declining stands averaged 24 % and 25 %, respectively. As stated earlier, we chose sample locations from all aspects except the south (135-225°). Of the 47 sample plots, most stands were on north aspects (22), followed by west (15), and east (10). Pure aspen were predominantly found on east and west aspects (5 each), while declining and remnant stands were found mostly on north aspects (9 and 7, respectively) and fewer on west slopes (2 and 5, respectively). Invaded stands were evenly distributed among north (4), east (4), and west aspects (3).

Stand age was not associated with stand type (ANOVA, $F = 0.24$, $p = 0.87$), lichen species richness (ANOVA, $F = 1.16$, $p = 0.29$), or total lichen abundance (ANOVA, $F = 0.43$, $p = 0.52$). However, if we remove three old-age outliers in the pure (stand age 156) and invaded (stand ages 132, 127 years) aspen and substitute conifer cover for stand type relationships improve, but are still not statistically significant (ANOVA, $F = 3.59$, $p = 0.06$). Stand type means with the modified stand age data set (i.e., outliers removed) are pure 82, invaded 85, declining 86, and remnant 90 years.

Lichen species diversity and abundance

Twenty-four lichen species (γ diversity) and a single specimen identifiable to genus only were tallied on the 47 plots in our study. Additional diversity statistics are $\alpha = 10.66$ (sd = 2.38) and $\beta = 2.5$. Most species were either cosmopolitan (multiple substrates) or found only on associated conifer species (Table 3.2). Fifty-four percent ($n = 13$) of lichen species found were on aspen substrates, though most of these were also found on adjacent conifers. Two species were confined to aspen substrates and a single occurrence of *Physconia isidiigera* was found on the upland willow, *Salix scouleriana*. Three species (*Physcia adscendens, Xanthomendoza montana, X. galericulata*) were sampled on every plot (N = 47) in our study area, and two others, *Melanelia elegantula* (N = 45) and *Xanthomendoza fulva* (N = 45), were located on most plots. The minimum number of lichen species sampled on a plot was six and the maximum was 16. Species abundance class score averaged 27.45 (sd = 5.25) for all plots, with a minimum score of 16 and a maximum of 38.

Lichen species richness (ANOVA, $F = 17.31$, $p < 0.0001$) and abundance (ANOVA, $F = 16.18$, $p < 0.0001$) increased from pure aspen through remnant stands (Figure 3.3a, b). The aspen index declined (ANOVA, $F = 14.32$, $p < 0.0001$) from pure to remnant aspen stands. Correlations between conifer cover and species richness ($r = 0.70$, $p < 0.0001$), total abundance ($r = 0.73$, $p < 0.0001$), and aspen index score ($r = -0.61$, $p < 0.0001$) were all strong. Relations between stand type and conifer cover so closely parallel each other (Table 3.3, $r = 0.81$, $p < 0.0001$) that further analysis focuses on stand type groups, though conifer cover (and aspen cover conversely) describe the same trends. Because of concern that the aspen index score was overly influenced by fewer species in pure aspen stands and washed out by greater diversity in conifer forest types, we ran an additional ANOVA test on absolute abundances for the four index species against stand types. Again we found significant declines in combined abundances of these species with increasing succession classes ($F = 4.12$, $p = 0.0118$).

Table 3.4 presents the results of ISA for those species tallied on more than a single plot in our study area. Only five species were significant as "indicator species" for particular succession groups based on corresponding maximum indicator groups and *p-values*. Of these, *Xanthomendoza galericulata* is the only lichen that displayed faithfulness to aspen forest types (either group, pure or invaded). The other four species showed preference for declining (*Melanelia exasperatula* and *Usnea lapponica*) or remnant (*Bryoria fuscescens* and *Letharia vulpina*) stands (Table 3.4, Figure 3.4). Three of four of these species preferring advanced succession forest types were fruticose, while no fruticose species were tallied throughout the study on aspen stems and therefore none exhibited faithfulness for aspen forest types. Of the remaining three species used in calculation of aspen index scores, *Phaeophyscia nigricans*, *X. fulva*, and *Physcia tenella*, none displayed significant preference for a particular aspen type (Table 3.4). Figure 3.4 describes trends across stands types for each species that occurred more than once in the study area. Though these line graphs do not carry the statistical rigor of ISA (Table 3.4), they do provide an overview of species high and low points as succession advances. For example, we see that *P. nigricans* and *X. fulva* appear to drop in remnant aspen forests and several species begin with relatively low presence in pure stands, then level off as conifers appear (Figure 3.4).

Lichen colonization of aspen

Both casual observation and measurement results suggest that most lichen colonization of aspen takes place on scars found on primary stems and branches. Only 0.24 % of lichens on aspen were located on smooth bark. Our prediction was that increasing damage may lead to further bole scarring, resulting in greater lichen habitat on aspen at the stand-level. We tested whether there was a relationship between amount of aspen stem damage and stand age and succession classes. While we found no relationship between stand age and stand type (see above), or between percent of aspen damage and stand type ($F = 0.38$, $p = 0.76$), we found moderately strong correlations between percent of the aspen bole scarred and stand age ($r = 0.31$, $p = .04$) and percent of scars colonized and stand type ($F = 3.37$, $p = 0.03$). This suggests that stem scarring and level of scar colonization increase with stand age, although our measures of recent detectable damage do not provide a strong cause and effect relation. Lichen species richness was not correlated with percent damage (r = -0.13, p = 0.42) and percent of aspen bole scarring (r = 0.11, p = 0.47). Moderately strong correlations were found between total lichen abundance and level of lichen colonization of scars (r = 0.32, p = 0.04) and smooth bark (r = 0.33, p = 0.03). However, smooth bark colonization, at 0.24 %, was very low overall compared to bark scar colonization levels (15 %).

Discussion

Successional trends from aspen to conifer cover

Due to a dry climate, epiphytic lichen diversity is relatively low in the Southern Rockies Ecoregion as compared to other U.S. regions (Ambrose et al., 2005). Even within Idaho, the Southern Rockies Ecoregion averages only 7.3 epiphytic lichens in forest stands, while monitoring sites in the moister Central and Northern Rockies average 8.1 and 12.2 species, respectively (Neitlich et al., 2003). Similar results were found for the Utah portion of the Southern Rockies (Keyes et al., 2001), though data in that study was not averaged at the plot level as was done in Idaho (Neitlich et al., 2003). Summaries at regional scales may be incomplete, however. Lichen diversity is highly influenced by both macro- and micro-scale moisture gradients. Locally, elevation presents the most obvious moisture gradient, so we expect lichen diversity to parallel increased precipitation and decreased evapotranspiration patterns normally associated with increasing elevation. By design, the current study limited elevational variability in order to focus specifically on aspen stand dynamics.

The Bear River Range is centrally located in the western United States and is generally characteristic of aspen conditions found throughout the Rocky Mountains. Without disturbance, aspen stands in this area are generally susceptible to increased encroachment by fir, spruce, Douglas-fir, and lodgepole pine (Mueggler, 1988). The mid-elevation belt sampled here was believed to comprise a locally optimum zone of aspen growth and, as southern aspects were excluded, a landscape prone to invasion by competing conifers. Areas at moisture, elevation, or geographic limits of aspen would be expected to display atypical successional patterns and perhaps support uncharacteristic lichen communities.

Pure, invaded, declining, and remnant aspen groups in this study mimic classic forest succession patterns. Aspen basal area and cover declined with increasing conifer invasion. The largest differences in aspen cover were found between invaded and declining stand types (Figure 3.2), which also constitute the difference between changes in forest types (i.e., plurality of tree cover). The theme of a "tipping point" between aspen and conifer forest types was explored in previous work conducted at a regional scale by Rogers (2002). He concluded that condition and presence of other species regenerating in aspen stands was the strongest factor in predicting change to conifer types. Though not measured specifically, it was apparent that tree species diversity in our study also increased along the successional gradient. A telling pattern here was the decline in aspen sapling survival with increasing conifer invasion. While aspen sprouts may continue to emerge with even the smallest available canopy openings, the proliferation and survival of those sprouts becomes increasingly limited without greater disturbance. Survival of aspen sprouts in conifer-dominated stands is low due to resource limitations and the well documented impacts of ungulate browsing (Baker et al., 1997; Hessl and Graumlich, 2002; Kay and Bartos, 2000; Ripple et al., 2001). Moreover, reduced aspen cover results in limited viability of the root system for sprouting: the fewer healthy trees above ground, the less likely new sprouts will emerge either on a continuous basis or in a flush following disturbance (Shepperd et al., 2006).

The lichen community in aspen forests

In this study in northern Utah and southern Idaho, we documented 24 epiphytic macrolichen species (γ diversity). Four of these species occurred only once in our survey (Table 3.2). Lichens that occurred rarely were of little value in terms of analysis, though it is useful to note their presence at this time as a record for future comparison. A mean species richness per plot (α diversity) of 10.66 was greater than found in a statewide inventory of Idaho (9.2) (Neitlich et al., 2003), but community turnover (β diversity) was much higher in their work (8.2) than in this study (2.2). Our work, covering a much smaller geographic area, would be expected to have lower β diversity due to relative limitations in distance, elevation, and substrates. For comparison, the Idaho-wide study yielded a γ diversity of 75 epiphytic macrolichens (Neitlich et al., 2003).

One species that was not collected in our previous tree-level survey (Rogers et al., 2007a), but was common here, is *Physcia tenella*. It is possible we missed this species due to potential confusion with the ubiquitous *P. adscendens* (McCune and Geiser, 1997). Because this species was only located on aspen substrates it was added to the list of species shown to be consistent indicators of aspen communities (Rogers et al., 2007a) and used as a component of the aspen index score.

This summation of lichens tallied here stands in contrast to the species diversity documented by a study of aspen and Douglas-fir in southwestern Idaho (Martin and Novak, 1999). They found a total of six macrolichens in their study, and only one species (*Xanthoria ulophyllodes*) exclusive to aspen. Work on European aspen (*Populus tremula*) in Sweden describes a much broader lichen community, consisting of a wide variety of foliose, fruticose, crustose, and cyanolichens species (Hedenås and Ericson, 2000). It is difficult to make comparisons of lichen communities where large-scale climate differences have such an influence. One would expect to find these differences between continents, but within the same region there apparently is enough contrast in moisture conditions to facilitate large differences in lichen communities (i.e., southwest Idaho to northern Utah), as well. Martin and Novak's (1999) study sites were in the same elevation range as those found here, but although they do not give precipitation data they do refer to both of their study locations as being "dry, rocky soil supporting *Artemisia tridentata*" – a nominal moisture distinction from our predominantly moister mollisol, forb, and non- *A. tridentata* stands. Two sites with the fewest lichen species (6), both pure aspen stands, in our study equal their total diversity of macrolichens in mixed Douglas-fir aspen stands.

Another trend found in the composition of lichen species in this study is the clear preference for conifers by fruticose species (*Bryoria, Letharia, Usnea*). No fruticose species were noted on aspen substrates here, or by Novak and Martin (1999) in southwest Idaho. In addition to their use by wildlife for food and nesting (Rosentreter, 1995), fruticose lichens are among the most sensitive to air pollution in our region (Neitlich et al., 2003). In contrast, genera common on aspen substrates, like *Physcia* and

Xanthomendoza, appear to react favorably to nitrogen-based pollutants and air-borne dust particles (Rosentreter, 1990; Jovan and McCune, 2006). The presence of both pollution intolerant and tolerant species in aspen forests suggests linkages to local air quality patterns. Qualitatively, we note a paucity of pollution sensitive lichens and an abundance of several tolerant "cosmopolitan" species.

The effects of stand age and damage on lichen habitat

One of our objectives was to better understand the relationship between aging stands, stem scarring, and lichen richness and abundance. First we needed to examine the cause, amount, and percent lichen colonization of aspen stem scars in relation to stand age. Our data showed a nearly exclusive lichen preference for scarred portions of aspen stems versus the dominant smooth bark. Percent of aspen damage was not only lower in our study (31 %) than statewide levels (45 %) (Keyes et al., 2001), but could not be directly related to the age of stands. We found that stand age was positively correlated to percent of bole scarring, and that there was a moderate positive relationship between conifer encroachment and the percent area of scars on aspen that have been colonized by lichens. Additionally, our results indicate no relationship between species richness and scarring, but a moderately strong correlation to total abundance. While these results are informative, they may be confounded by the significant presence of lichen species that occur only on conifers.

We conclude there is sufficient scarring on aspen, regardless of amounts and types of damage, to allow for the level of lichen colonization recorded. Many stem scars originate at former branch junctions. Aspen branches in the lower crown, now long since shed, die from upper crown shading or weather damage. Other sources of stem scarring are healed over cankers (Hinds, 1985) and animal browsing and rubbing (Hinds and Krebill, 1975) that were not recorded as active damages here. Hinds and Krebill (1975) attribute most of this scarring to foraging by elk (*Cervus elaphus*) and moose (*Alces alces*), plus wounds initiated under the winter snow pack, which may reach three meters, by chewing of voles (*Microtus longicaudus*). Aspen are also frequently scarred by humans near recreation sites (Shepperd et al., 2006). Finally, very old aspen may have fissured or roughed bark that accumulates under normal conditions in the largest diameter ramets. Though aspen accumulation of lichens seems to be associated with aging trees and their accumulated scars, we were unsuccessful in linking this trend to specific damage agents.

Lichen community change over time

Forest succession groups may be viewed as a surrogate for temporal change in aspen-associated landscapes. Progression from a singular overstory composition to a more diverse cover via succession appears to increase epiphytic lichen community diversity. This seems a likely outcome: diversity of substrate-dependent species is contingent on substrate diversity. When the presence of that substrate decreases then dependent species are also expected to decline. Aspen basal area per hectare does indeed decrease as we progress through the succession types in our study (Figure 3.2c). With this trend we would expect to see concomitant decrease in the aspen index score, assuming that there is simply less total substrate for specialists to colonize. In fact, aspen index score decreased significantly from pure to remnant stands (Figure 3.3c). This suggests a strong parallel relationship between aspen basal area per hectare and presence of aspen lichen specialists. However, as discussed earlier, confounding factors like scarring levels and colonization densities point to a more complex explanation.

Overall, aspen provides only a marginal substrate for lichens compared to its conifer cohorts (Table 3.2). We suspect this difference is primarily related to the abundance of smooth bark, compared to conifer stems and twigs, which is less hospitable to lichen colonization. We are aware, however, that other physiological factors not explored here, such as bark pH, bark peeling, texture, or aspect, may also play a role in colonization and persistence (Martin and Novak, 1999). For example, European aspen generally possesses a rougher bark and a more diverse lichen flora (Hedenås and Ericson, 2000). In an earlier study, we used ISA to assess differences in lichen faithfulness to aspen and conifer substrates in the Bear River Range (Rogers et al., 2007a). Three species, *Phaeophyscia nigricans*, *Xanthomendoza fulva*, and *X. galericulata*, were found to have statistically significant preference for aspen. In the present study we found that only *X. galericulata* displayed exclusive preference for aspen forest types. The difference between these two studies is that Rogers et al. (2007a) examined individual tree faithfulness to lichens, while this study focuses on whole communities as qualitative succession classes. While Rogers et al. (2007a) were confined by individual stems along a transect, the present study samples a greater diversity on tree species, tree forms, and microhabitats within a larger plot area. The end product is that ISA results at the community level reflect a larger number of factors and samples so we are not surprised to see fewer indicators of whole stand conditions versus targeted tree stems and species.

We developed an aspen index score comprised of species favoring aspen substrates to test in a one-way ANOVA for differences in succession classes (i.e., change over time). A clear trend depicting declining aspen index score with advancing succession (Figure 3.3c) contrasts with overall species diversity (Figure 3.3a) and abundance (Figure 3.3b) increases. We cannot attribute this pattern solely to concurrent declines of total aspen ramets with advancing succession, as scarring on individual stems increased over the same general sequence. It appears lichen habitat remains available in conifer-encroached forests and the density of colonization appears to increase, but fewer aspen specialists proliferate. Perhaps there is an unknown mechanism at work here that exercises a 'carrying capacity' for generally sparsely colonized aspen. Whatever that process, it is clear that the surrounding forest community is simultaneously attracting greater overall lichen diversity while limiting conditions for aspen specialists. Thus, a broader theme emerges: a caution against using total species richness as a sole metric in changing landscapes where particular habitat specialists may provide a better index of target communities.

Lichens as indicators of community change

Ecologists have long debated the notion of keystone species. Recently this term has been applied to aspen in the western U.S. (Campbell and Bartos, 2001; Manley et al., 2000). Ripple et al. (2001) trace the important trophic interactions of wolves, elk, and aspen survival in Yellowstone National Park emphasizing the critical nature of carnivores in regulating large ungulates that browse on aspen regeneration. Without regeneration following large-scale disturbance, future aspen forests, dependent on vegetative sprouting to persist, will dwindle in the landscape. In this paper we have discussed the dependence of species, namely epiphytic lichens, on aspen forests: effectively another trophic level dependent on aspen as a vegetative cover type. We believe that aspen are critical to the survival of many floral and faunal species and that widespread human activities, such as fire suppression, game and livestock regulation, and climate warming, have and will drastically continue to alter these communities (Logan et al., 2007; Rogers et al., 2007b). Further, we feel that lichen communities, including metrics such as an aspen index score, may be used as a means of monitoring community conditions at large.

In the successional gradient from pure aspen to conifer, vascular plant diversity and abundance decreases as conifer encroachment advances (Mueggler, 1985). Yet it is difficult to track the large number of understory plants (versus macrolichens) dependent on aspen cover, as well as those favoring shaded conifer environments. Epiphytic lichens appear to increase with succession; unless we focus on the aspen-dependent species comprising the index score (Figure 3). If we look at all species in terms of succession classes, some lichens favor succession endpoints, while others (e.g., *Candelaria concolor, Melanelia exasperatula, M. subolivacea, Physcia tenella, Usnea lapponica*) show preference for aspen-conifer transition stages (Figure 3.4, stand types 2 & 3).

A generalized model depicting aspen forest change over time is shown in Figure 3.5. Numerous biotic factors influence stand development over time and are prominent during different successional periods (Shepperd et al., 2006). We have shown here that along with successional trajectories, aspen-dependent lichen species will decline in tandem with the overstory. Likewise, we expect old growth-, conifer-, or shade-dependent species to follow a similar trajectory as the conifer canopy. If we wish to manage for particular aspen conditions we can expect to influence lichen species populations favoring particular stages (Table 3.4, Figures 3.4 and 3.5). We me may also utilize natural biotic factors, or management surrogates, appropriate for successional stages (Figure 3.5) to achieve desired overstory and epiphyte goals.

This generalized successional model (Figure 3.5) provides a way to forecast the trajectory of aspen-dependent species in stands at various stages and across mosaics of aspen and conifer forests. Key elements that correspond to succession stages outlined above are preservation of natural disturbance cycles (stand types 3 and 4), reduction of livestock and wildlife browsing on aspen suckers (stand types 1 and 2), and maintenance of an adequate growing environment (all stand types). This final point argues for balance in successional stages, while avoiding exclusive management toward the extremes of pure and remnant stands. Preservation of ecosystem functions, such as historical disturbance regimes and native browsing levels, is important to maintaining balance across large forest mosaics (Rogers et al., 2007b). Management implications of these ideas are addressed in greater detail by Shepperd et al. (2006). Our purpose here is to point out changes in epiphytic lichens associated with conifer encroachment in the southern Rocky Mountains. The pattern described here for aspen index species (Figure 3c) may apply equally to other aspen-dependent plants and animals. For example, aspen dependence by particular birds (Turchi et al., 1995), mammals (DeByle, 1985), and vascular communities (Mueggler, 1988) have already been demonstrated and deleterious effects from advancing succession on these species are commonly implied.

In a broader context, we see that many factors affect the aspen community on which lichens depend. Recent history and climatic factors have often conspired against aspen proliferation in the form of reduced wildfire, herbivory, human interventions, and moist climates (Rogers et al., 2007b). Furthermore, future climate warming scenarios predict dire consequences for quaking aspen if exotic species such as gypsy moth (*Lymantria dispar*) are able to penetrate montane environments (Logan et al., 2007). Though these factors are not universally prevalent, when they combine in our region we may expect parallel declines in aspen-dependent species. Questions of species loss are difficult to assess at single locations or by stand-level studies. The condition of the wider forest mosaic, occurring at many successional stages in the case of aspen, gives us the clearest picture of individual species or functional group (e.g., aspen indicator species) conditions. We feel a focus on preserving forest structure (i.e., succession stages) and ecosystem function (i.e., disturbance regimes) will provide the greatest flexibility for the future of aspen and its community of dependent species.

Conclusion

Landscape-level studies are needed to capture the breadth of species variations relating to environmental conditions and cover changes. In this paper we have described how epiphytic lichen communities change with advancing succession of aspen forests in the relatively dry southern Rocky Mountains. We found 24 epiphytic macrolichens in mid-elevation aspen-associated forests of the Bear River Range. General trends show increased lichen diversity and abundance, while simultaneously tracking a decrease in those species dependent on aspen. Indicator species analysis determined *Xanthomendoza galericulata* as being the most aspen-dependent species at the stand level, though previous research based on tree-level analysis found two additional species that favored aspen substrates (Rogers et al., 2007a). We presented an aspen index score based on dependent lichen species and suggest its further utility for monitoring and post-treatment recovery efforts as a surrogate for greater community diversity and health. Simple species richness measures may not provide the most useful method for assessing landscape health, most notably where systems are dependent on seral cover types such as those found in aspen communities.

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Table 3.1 Stand type codes, cover values, and plots sampled by stand type categories. Cover values are used for stratification of aspen stands for plot selection based on aerial photograph estimation.

	Stand Types			
	Pure	Invaded	Declining	Remnant
Stand type code	1	2	3	4
% aspen tree cover	> 90	50-90	49-10	< 10
Plots sampled	12	11	12	12

Table 3.2 Occurrence of epiphytic lichen species, by primary tree substrate groups, in the Bear River Range, Idaho, and Utah. Multiple substrates include lichen species found on two or more of the substrate groups as shown. Minor substrate species include (in order of prominence): *Acer grandidentatum, Salix scouleriana, Amelanchier alnifolia, Prunus virginiana, Cercocarpus ledifolius,* and *Juniperus scopulorum.* Infrequent occurrence (< 10% of total frequency) on minor substrates did not remove species from their major group affiliations (i.e., conifer or aspen). Numbers in parentheses represent total frequencies of species on all plots ($N = 47$).

Multiple substrates*	**Conifer**	**Aspen**	**Minor substrates**
Melanelia elegantula (45)	*Bryoria fuscescens* (13)	*Phaeophyscia nigricans* (38)	*Physconia isidiigera* (1)
Melanelia exasperatula (33)	*Candelaria concolor* (12)	*Physcia tenella* (24)	
Melanelia subolivacea (39)	*Imshaugia aleurites* (1)		
Physcia adscendens (47)	*Letharia columbiana* (4)		
Physcia biziana (10)	*Letharia vulpina* (14)		
Physcia dimidiata (8)	*Parmelia sulcata* (1)		
Physciella chloantha (13)	*Parmeliopsis ambigua* (3)		
Xanthomendoza fallax (32)	*Phaeophyscia orbicularis* (1)		
Xanthomendoza fulva (42)	*Usnea hirta* (1)		

Table 3.3 Pearson correlation coefficients (*r*) for key variables describing relationships between lichen communities and succession in aspen forests.

N = 47 plots. All correlations were significant with p <0.0001.

	Aspen cover	Conifer cover	Stand type	Species richness	Total species abundance	Aspen index score
Aspen cover	------	-0.7168	-0.7773	-0.6757	-0.6609	0.6203
Conifer cover		------	0.8140	0.7031	0.7277	-0.6142
Stand type			------	0.7147	0.6945	-0.7051
Species richness				------	0.9565	-0.6731
Total abundance					------	-0.6345

Table 3.4 Indicator Species Analysis values for species tallied by maximum score group (Stand Types: 1 = pure aspen, 2 = invaded, 3= declining, 4 =remnant). Single-occurrence species have no value as indicators; therefore, they are not shown here. Significant *p*-values are shown in bold type, denoting lichen species preference for particular stand type groups.

			Indicator values from randomization		
Species	**Maximum score group**	**Indicator value**	**Mean**	**Standard deviation**	***p***
Bryoria fuscescens	4	46.3	16.5	5.83	**0.0010**
Candelaria concolor	3	17.5	15.8	5.70	0.3340

Letharia columbiana	4	9.8	10.1	5.35	0.5574
Letharia vulpina	4	30.6	16.9	5.64	**0.0246**
Melanelia elegantula	4	27.4	27.0	0.92	0.3020
Melanelia exasperatula	3	33.9	25.5	3.82	**0.0276**
Melanelia subolivacea	2	30.3	26.8	2.63	0.1722
Parmeliopsis ambigua	4	11.1	8.7	5.57	0.4598
Phaeophyscia nigricans	3	22.7	27.1	3.24	0.9536
Physcia adscendens	3	26.4	26.0	0.64	0.2414
Physcia biziana	4	12.6	14.5	5.80	0.6158
Physcia dimidiata	4	11.1	13.2	5.83	0.6394
Physcia tenella	2	19.2	22.1	5.13	0.6952
Physciella chloantha	2	11.6	16.4	5.76	0.7870
Usnea lapponica	3	38.7	21.9	4.96	**0.0042**
Xanthomendoza fallax	4	24.6	25.1	4.04	0.5104
Xanthomendoza fulva	1	28.5	27.2	1.98	0.3050
Xanthomendoza montana	3	26.0	26.2	0.65	0.8210
Xanthomendoza galericulata	1	27.8	26.2	0.68	**0.0150**

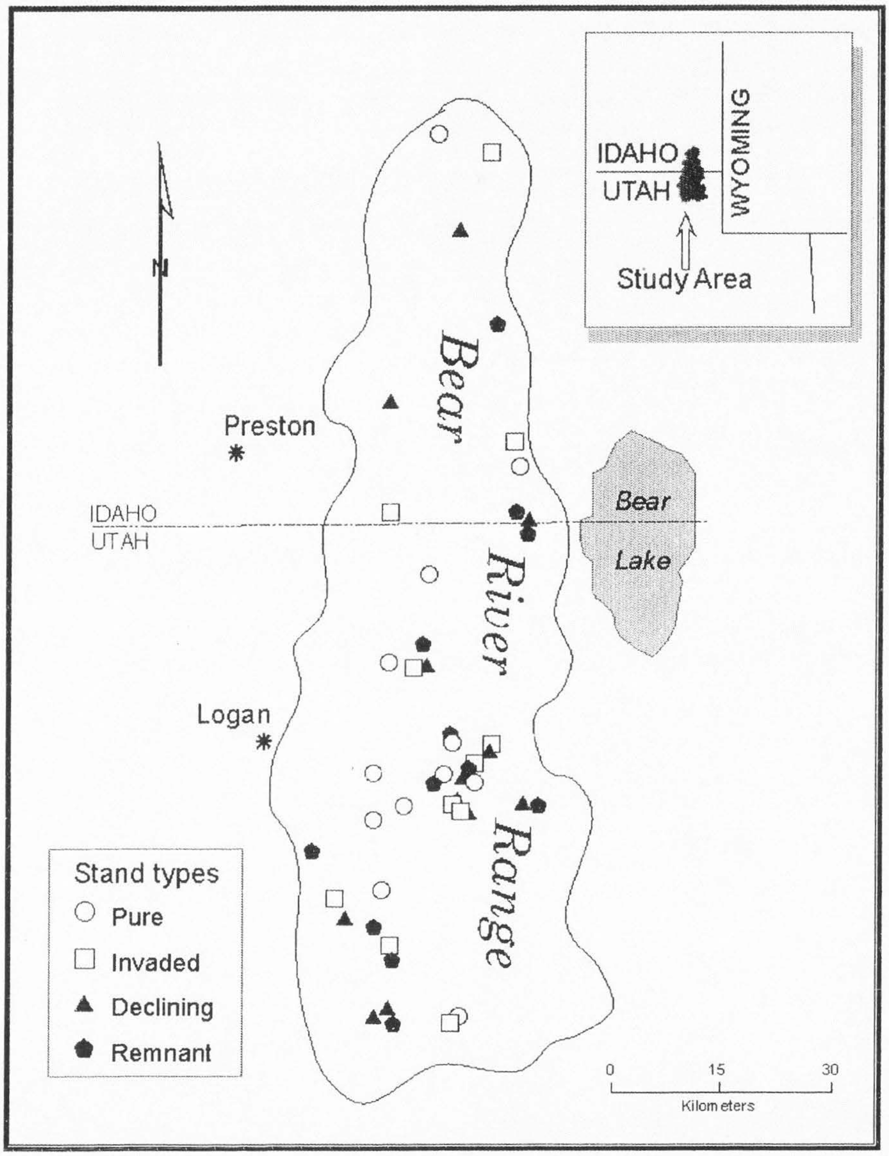
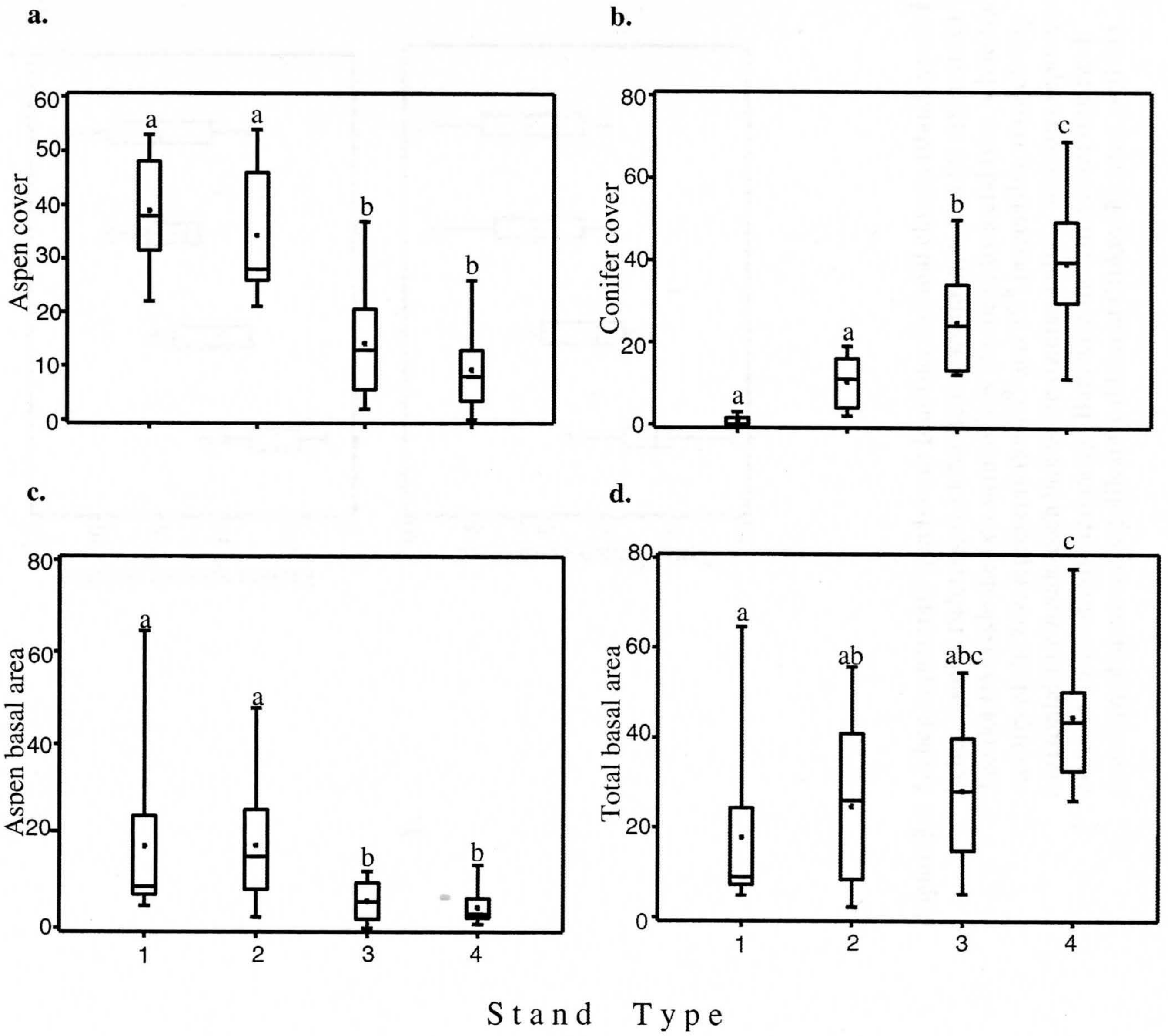


Figure 3.1 Location of study area and plots in the Bear River Range of Idaho and Utah.

Figure 3.2 Stand structure trends over four successional classes (stand types) for: (a) aspen cover, (b) conifer cover, (c) aspen basal area (m^2), and (d) total basal area (m^2). The dot (•) inside the box symbolizes the mean by stand type, while bottom and top of the box represents the 25th and 75th percentiles, respectively. The horizontal line inside each box is the median value. Whiskers represent extreme observations (variance). Bars with the same letter represent quantities that are not significantly different (Tukey-Kramer, $p<0.05$).


a.
b.
c.
d.
Aspen cover
0
10
20
30
40
50
60
a
a
b
b
Conifer cover
0
20
40
60
80
a
a
b
c
Aspen basal area
0
20
40
60
80
a
a
b
b
Total basal area
0
20
40
60
80
a
ab
abc
c
1
2
3
4
Stand Type

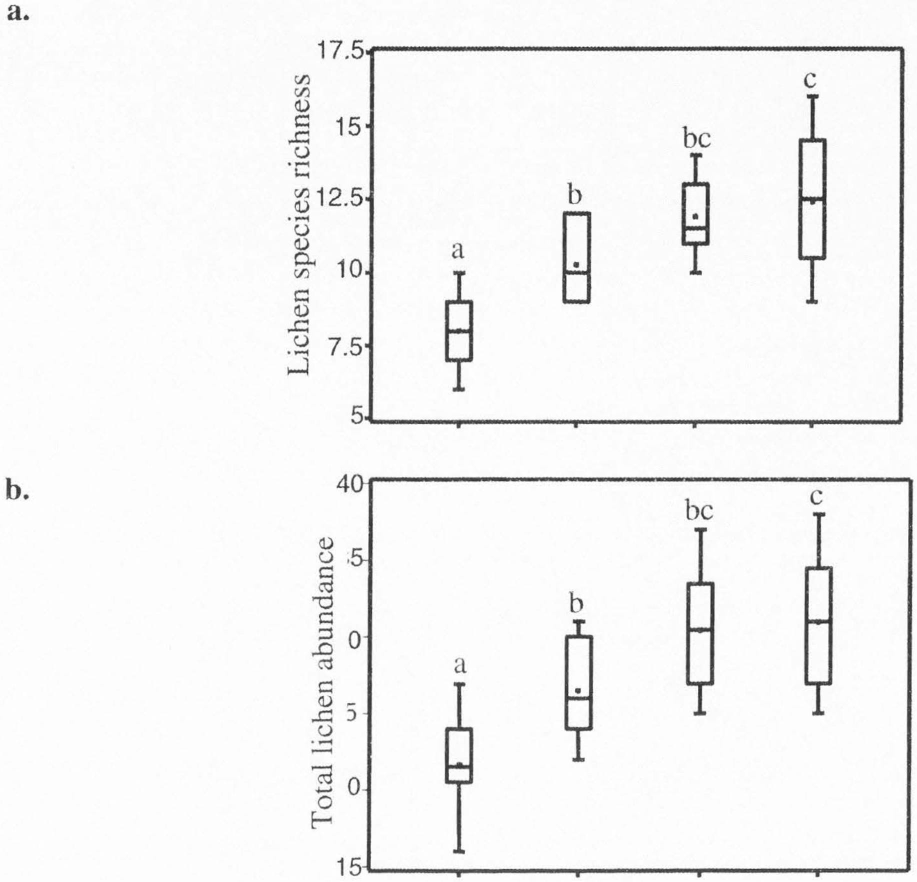
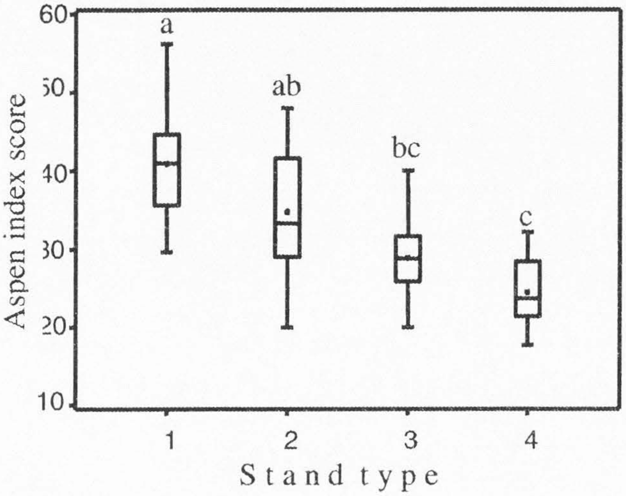


Figure 3.3 Lichen community trends over four successional classes (stand types) for: (a) lichen species richness, (b) total lichen abundance, and (c) aspen index score. The dot (•) inside the box symbolizes the mean by stand type, while bottom and top of the box represents the 25th and 75th percentiles, respectively. The horizontal line inside each box is the median value. Whiskers represent extreme observations (variance). Bars with the same letter represent quantities that are not significantly different (Tukey-Kramer, $p<0.05$).

c.



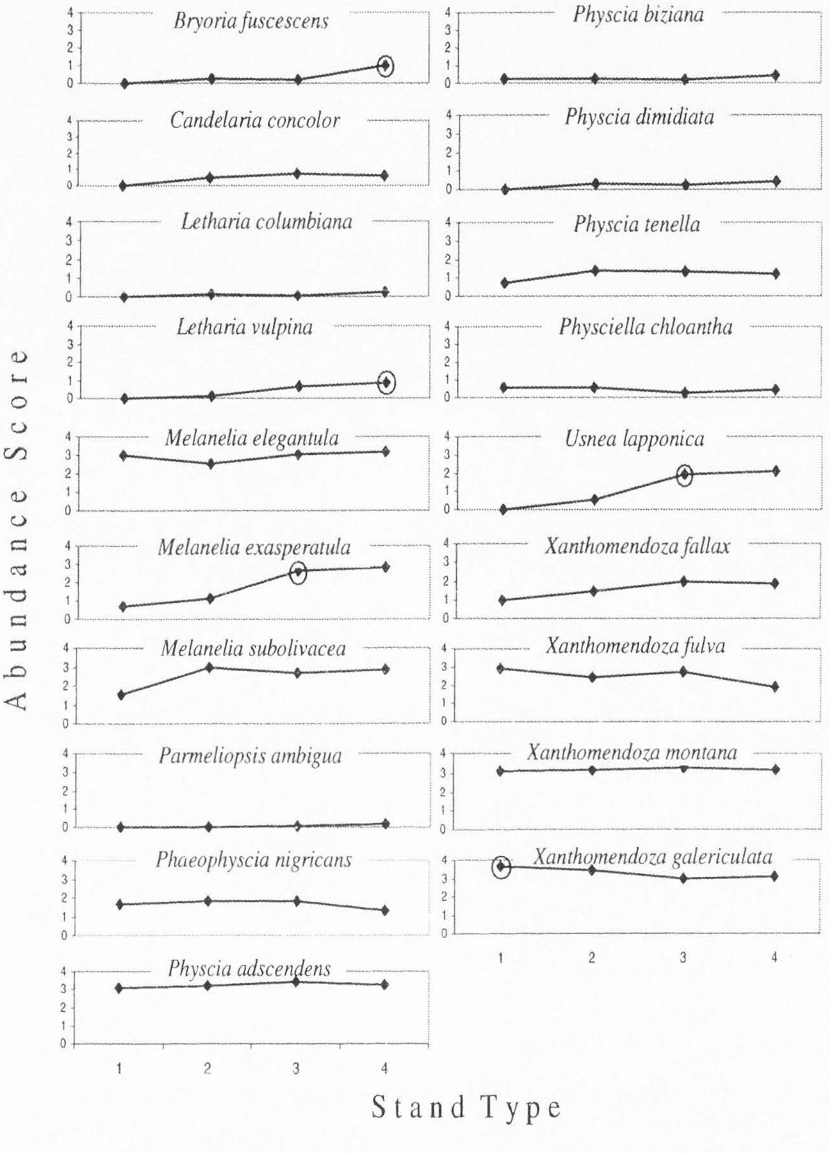


Figure 3.4 Line charts of lichen species occurring multiple times in the study area. Nodes are average abundance scores for species by stand type. Circles around individual nodes denote significant ($p < 0.05$) preference for specific stand types in Indicator Species Analysis (see Table 3.4).

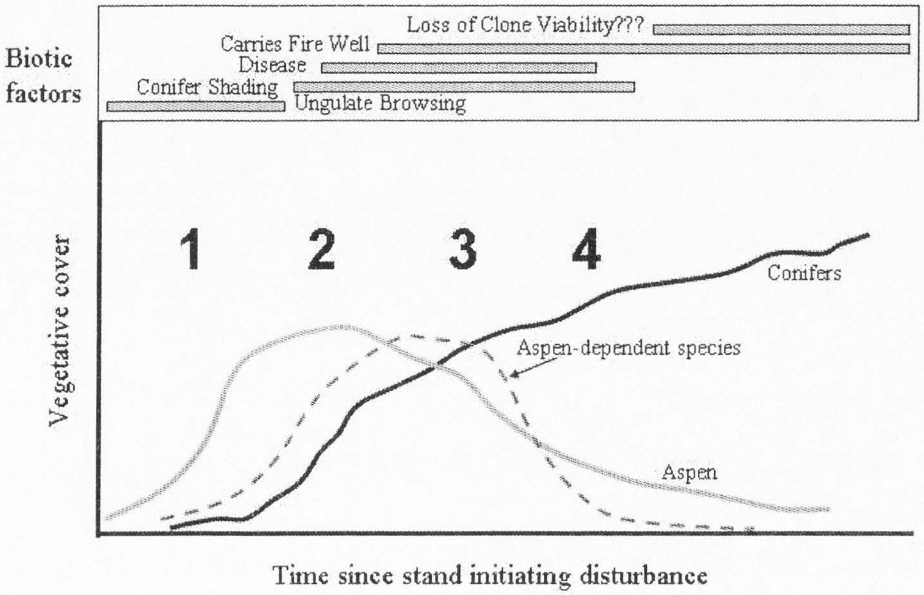


Figure 3.5 A generalized model of aspen succession in forests prone to conifer encroachment in the southern Rocky Mountains. Several factors affect stand development at various stages in the life cycle of aspen. Numbers 1 - 4 represent how stand types addressed in this study fit into the time sequence presented. The dashed line, representing the hypothesized trajectory of aspen-dependent species such as epiphytic lichens, peaks after pure aspen stands are established and plunges prior to mortality of remnant aspen. The transition period from aspen to conifer overstory dominance—between stand types 2 and 3—depicts a "tipping point" for predominant disturbances (biotic factors) and aspen-dependent species.

CHAPTER 4

ASPEN SUCCESSION AND NITROGEN LOADING: A CASE FOR EPIPHYTIC LICHENS AS BIOINDICATORS IN CHANGING FORESTS[3]

Introduction

Human-induced change in ecosystems may be obvious or subtle, often depending on the particular scale or perspective of observation. For example, retrospective examinations of quaking aspen (*Populus tremuloides*) cover in western North America commonly describe dramatic landscape-level change. As the premier montane hardwood, aspen is threatened by livestock grazing, wild ungulate browsing, fire suppression (Gallant and others 2003; Di Orio and others 2005; Shepperd and others 2006), and potentially climate warming (Logan and others 2007). Quantification of change has been controversial, however, as numerous authors have documented landscape-level losses (Bartos and Campbell 1998; Gallant and others 2003; Di Orio and others 2005) as well as gains (Barnett and Stohlgren 2001; Manier and Laven 2002; Kulakowski and others 2004) in aspen coverage over recent decades. Both conclusions implicate the primacy of anthropomorphic factors, but for the most part studies have neglected the impacts of change on aspen-dependent species.

Changes in smaller-scale vegetation (e.g., epiphytic lichens) may appear slight, although proportionally their alteration may be equal to dominant landscape elements such as trees. Moreover, minute ecosystem components may act as bioindicators of

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[3] Coauthored by Paul C. Rogers, Ronald J. Ryel, and Kori D. Moore.

various human impacts, but may be overlooked in landscape analysis. Lichens have been used to monitor human-induced change for nearly 150 years (Hawksworth 2002). Numerous studies have investigated the impacts of various air pollutants on lichens (Barkman 1958; Richardson 1992). More recent work has tracked decreases in airborne sulfur dioxide (SO_2) and increases in ammonia (NH_3) initiated nitrogen (N) loading (van Herk 1999; Nimis and others 2002; Jovan and McCune 2005, 2006). In addition to air quality studies, lichen communities have been linked to habitat change (Neitlich and McCune 1997; Rogers and Ryel 2007), wildlife concerns (Rosso and Rosentreter 1999), and biological diversity (Will-Wolf and others 2002a; Hedenås and Ericson 2004).

Recent investigations have explored the impact of changing aspen forests on epiphytic macrolichen communities in the Interior West, U.S.A. (Rogers and Ryel 2007; Rogers and others 2007b). Here we wish to take a wider view of factors, including temporal aspen change, affecting lichen abundance and composition in these forests. In terms of epiphytic lichens, forest succession represents a long-term change at decade- or century-scales, while other factors of interest (i.e., tree pathogens, bole scarring, air quality, nitrogen loading) denote shorter-scale change. As with most landscape-level studies there are multiple influences—some environmental and some anthropogenic—that affect plant community development. We hope to address causality by integrating a network of montane aspen plots where lichen communities have been sampled with up-wind ammonia monitoring stations near local population and agricultural centers.

Community analysis involves assessing plant species groups as they are affected by environmental conditions (van Haluwyn and van Herk 2002; McCune and others 2002). In taking a community approach we hope to answer the following primary questions: 1) What role do changing aspen forests play in increasing or decreasing lichen diversity and abundance? 2) Are local pollution sources generally, and NH_3 specifically, affecting lichen communities in these forests? and 3) If N loading is taking place, how might we expect changing aspen forests and associated epiphytes to react? In answering these questions we hope to shed light on some subtleties found in contemporary ecosystems that may be harbingers for more apparent changes to come.

Methods

Field Experiments

The Bear River Range has a north-south orientation straddling the Utah and Idaho border and is about 135 km long and 30 km wide (Figure 4.1). These mountains lie in the Southern Rocky Mountains Ecoregion Province between 1,370 and 3,040 m elevation, and receive between 51 and 102 cm of precipitation per year (Bailey 1995). Moisture arrives primarily in the form of winter snowfall. This area experiences summer drought with sporadic brief thunderstorms. Lightning occasionally provides an ignition source for fire-prone forests (Bailey 1995). Circulation and storm patterns normally pass through this region from west to east. Cache Valley, comprised of a small urban center (Logan), numerous small primarily agricultural towns, and a state university that total approximately 100,000 people, lies to the west of the Bear River Range.

The Bear River Range is a mosaic of conifers, a few hardwoods, and subalpine meadows. Aspen is the primary hardwood of mid and upper elevations in the Southern Rockies Ecoregion (Rogers 2002). At this elevation, it coexists with subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), limber pine (*Pinus flexilis*), and Rocky Mountain juniper (*Juniperus scopulorum*). Minor hardwoods include bigtooth maple (*Acer grandidentatum*), Scouler willow (*Salix scouleriana*), western serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and mountain mahogany (*Cercocarpus ledifolius*). The remaining vegetation consists of forest openings of big sagebrush (*Artemisia tridentata* var. *vaseyana*) and meadows. The understory of aspen ranges from lush stands of diverse forb and grass groups, to shrubby cover dominated by snowberry (*Symphoricarpos spp.*), to sagebrush, and mixed assemblages of these groups (Mueggler 1988).

Field methods

We randomly selected 47 field locations from a pool of 422 potential plots range-wide falling in aspen forest types on Utah and Idaho digital vegetation maps (USGS 2004; USGS 2005). These locations covered all land ownerships, except where private landowners denied access to sites. All plots were between 2,134 and 2,438 m elevation and we excluded south-facing slopes from our survey to best meet the assumption that all plots should be susceptible to conifer invasion. Plots were stratified based on aerial photographic interpretation into four broad succession groups: pure aspen, invaded, declining, and remnant (see Table 4.1 for group criteria; Figure 4.1). Further detail of the plot selection procedure may be found in Rogers and Ryel (2007).

An independent network of ammonia (NH_3) monitoring sites was located throughout the adjacent (upwind) Cache Valley, Utah and Idaho, west of the study area (Figure 4.1). During June and July of 2006 20 gas-phase ammonia samplers, Ogawa

Model 3300 (Ogawa USA, Inc., Pompano Beach, FL, USA), were loaded with pads pre-coated with a citric acid solution and were deployed to yield a spatially resolved representation of ambient ammonia concentrations. Five additional samplers were deployed near locations expected to be strong sources of NH_3 (i.e., concentrated agriculture and urban sites). Samplers were deployed for 4 to 7 days per sample period; once in June and twice in July. After exposure, the pads were eluted with deionized water that had been passed through a 0.45 μm filter and analyzed via ion chromatography. Ambient concentrations were calculated using diffusion equations given by Roadman and others (2003). For each location, mean values were calculated combining the three sample periods representing summer NH_3 conditions. A detailed description and validation of the Ogawa passive sampler for scientific studies was provided by Roadman and others (2003). Distances from each montane sample plot to nearest NH_3 site, the nearest edge of the adjacent Cache Valley, and to the local urban center (Logan) were used as surrogates for air quality.

Aspen plot measurements were of two broad types: stand characterization consisting of location descriptors and tree measures, and lichen sampling by species tally, voucher collection, and abundance estimation. Tree mensuration was conducted on a 0.016 ha (7.3 m radius) circular subplot, which was centrally embedded in a 0.378 ha lichen survey and plot descriptor circle. Collectively, the entire sample area is heretofore referred to as the "plot." Plot descriptors included GPS readings, slope, aspect, stand type, percent aspen cover, percent conifer cover, stand age, and aspen age. Five cover estimates for aspen and conifers > 2 m in height were taken at the plot center and 2 m inside the lichen plot perimeter (33 m radius) at the four cardinal directions. Stand ages were based on at least two cored aspen trees (stand types 1 and 2) and an additional two cores of dominant conifer species (stand types 3 and 4). Stand ages were calculated by adding five years to the breast height average of aspen cored and 10 years to average conifer ages to account for the growth period between ground level and breast height.

Lichen sampling was modeled after the procedure used in the USDA Forest Service, Forest Inventory and Analysis/Forest Health Monitoring program (McCune 2000; Will-Wolf and others 2002b). Briefly, the entire plot area was systematically examined for presence of epiphytic macrolichens 0.5 m above the forest floor for up to two hours. Lichens were not sampled below 0.5 m to avoid overlap with terricolous and saxicolous species and their accompanying forest floor influences (i.e., soil type, moisture, leaf litter, vascular plant abundance). The method allows examination of fresh litter fall as surrogate for upper canopy lichens. At least 40 minutes was spent traversing the area, the last 10 minutes without new species tally, before the survey was terminated. We found that an average of 60 – 75 minutes was required for the survey. After completion of lichen tally, each species was assigned a qualitative abundance class for the entire area: 1 = 1-3 individuals (distinct thalli); 2 = 3-10 individuals; 3 = between 10 individuals and occurrence on half of all trees/shrubs on the plot; 4 = greater than half of all woody substrates on the plot exhibited the lichen. Previous work found that for sparsely populated vegetation in large sample areas, visual abundance classes were preferable to continuous cover measures because accuracy was comparable while efficiency was greatly increased (McCune and Lesica 1992).

Unknown species were collected as vouchers for later verification under a dissecting scope and, when needed, by other lichen experts. We also noted on which tree substrate groups, or occasional minor woody species, lichens were tallied. Vouchers of lichen specimens were archived at the Utah State University herbarium. Nomenclature follows Brodo and others (2001) for most species, though *Xanthomendoza* (formerly *Xanthoria*) follows Lindblom (2004, 2006) and McCune (key online, Table 4.2 footnote).

Derived Variables

In addition to field-collected variables, the following values were derived post-field: aspen and subalpine fir seedlings and saplings per hectare; basal area of aspen, conifer, and dead trees per hectare; for live aspen trees, average percent bole scarring, lichen colonization of scars, and colonization of smooth bark per plot; proportion of boles damaged versus undamaged for all live aspen per plot; and plot-level lichen species richness (number of distinct species) and total species abundance (cumulative abundance scores). Additionally, we summed, at the plot-level, the abundance values of nitrophilous (nitrogen-loving) lichens, calculated their species richness, and derived their proportion (percent) in relation to all species. These measures were originally used by Jovan and McCune (2005), while designation of nitrophilous lichens follows van Herk (1999) and Jovan and McCune (2005) (Table 4.2).

Analytical methods

Analysis of variance (ANOVA) was used to make an initial assessment of the hypothesis that there was no difference in lichen communities between succession groups (proc GLM, SAS Institute 2005). This stage involved further analysis of covariance (ANCOVA) to assess the added role, if any, of a covariate in determining lichen community composition. The covariate, representing a hypothesized influence of air quality on lichen communities, was the continuous variable distance to urban area (i.e., Logan, Utah), a clear population center and therefore presumed peak of automobile emissions in the valley. The independent variable in ANCOVA tests was stand type (Table 4.1), though we tested other succession variables based on cover and basal area to find the best representation of succession for our final model. Response variables were lichen species richness, total abundance, and an aspen index value. The index value consists of the sum of abundance scores for aspen indicator species (*Phaeophyscia nigricans*, *Physcia tenella, Xanthomendoza fulva*, and *X. galericulata*) as a proportion of total abundance of all lichens at a sample plot (Rogers and Ryel 2007).

Multivariate analysis was used to explore statistical causality among several variables, including those not meeting normality and variance requirements, simultaneously. Our prime areas of concern, based on previous work (Rogers and others 2007b; Rogers and Ryel 2007), were forest succession from aspen to conifer, age and basal area of stands, air quality (distance to sources), nitrophilous lichens, and amount of aspen damage related to the level of stem scarring. We used PC-ORD software version 5.0 (McCune and Mefford 2006) to run nonmetric multidimensional scaling (NMS, Kruskal 1964; McCune and others 2002) on a primary matrix of plots by species and a secondary matrix of plots by derived environmental variables. Only species recorded on at least 5% of field plots were used in the NMS analysis. The outlier analysis module in PC-ORD was used to eliminate plots with greater than 2 standard deviations from the mean Sørensen distance. Data were subjected to 500 iterations per run using a relative Sørensen distance measure and a random number start. The solution with the lowest stress was derived from 250 runs using real data. "Stress" is quantitative assessment final solution monotonicity; or a measure of how well the real data fit the ordination (McCune and others 2002). The lowest stress solution was then subjected to 250 randomized runs using a Monte Carlo test to evaluate the probability of final NMS patterns being greater than chance occurrence. Orthogonal rotation of the resulting NMS solution was used to maximize correlation between the strongest environmental variables (i.e., *r* value) and prime axes. The lowest number of dimensions (axes) was selected when adding another dimension decreased the final stress by < 5 (McCune and others 2002).

Results

Twenty-four lichen species were tallied on 47 plots in four aspen succession groups in the Bear River Range (Table 4.2). Five species were tallied only a single time and one specimen was unidentifiable beyond the genus level (*Usnea spp.*) because of its stunted growth form or young age. Eleven species were tallied on more than half of our plots, though their abundance varied greatly by sample site. Five fruticose species were tallied, though only one species, *Usnea lapponica*, was found on more than half of sample sites (Table 4.2). *Physcia adscendens, Xanthomendoza galericulata,* and *Xanthomendoza montan*a were found on every plot.

The total species tally (24) represents our sample gamma diversity (γ). Alpha diversity (α), 10.66 (SD = 2.38), is the mean species richness per plot. Thus, our beta diversity (β), a measure of community turnover, is 2.5 (β = γ/α). Mean lichen species richness progressed with aspen stand types from pure (8.00), to invaded (10.27), to declining (11.92), to remnant (12.42). Species abundance averaged 27.45 (SD = 5.25) for all plots, with a minimum score of 16 and a maximum of 38. Fifty-four percent (*n* =13) of lichen species were on aspen substrates, though most of these were also found on adjacent conifers. Two species were confined to aspen substrates and a single occurrence of *Physconia isidiigera* was found only on the upland willow, *Salix scouleriana*.

Both ANOVA and ANCOVA were used to test for differences between groups. We were interested in determining other prominent factors contributing to lichen variance; specifically how much the air quality surrogate variable "distance to urban area," as the covariate in the ANCOVA test, added to the variance explanation. All lichen response variables showed significant differences between stand types (i.e., succession levels); however, only the aspen index score remained significant ($p = 0.01$) with the addition of the covariate (Table 4.3). This covariate also resulted in the reduction in the error factor from 42.96 to 38.15 for aspen index score (Table 4.3).

Ambient NH_3 samplers recorded a summer average high of 92.2 $\mu m\ m^{-3}$ near a poultry processing plant and a low of 7.3 $\mu m\ m^{-3}$ in a rural town on the west side of Cache Valley. Mean summer average for all sites was 22.8 $\mu m\ m^{-3}$ (SD = 20.8). Twenty-two of the 25 NH_3 sample sites fell in the lowest two quintiles (bottom 40%) of the data (Figure 4.1). In addition to the poultry facility, a second peak site was located at a lagoon-based municipal wastewater treatment facility (68.8 $\mu m\ m^{-3}$). A final ammonia sample site, recorded as just below our peak site cutoff (58.2 $\mu m\ m^{-3}$), was adjacent to a beef processing plant feedlot in the southern part of Cache Valley.

NMS analysis was run on a matrix of 19 species by 46 plots, with a secondary matrix of 20 environmental variables (Table 4.4) by 46 plots. A single plot was eliminated in outlier analysis (PC-ORD, v.5, McCune and Mefford 2006). Five species were eliminated from the analysis due to their sparse (< 5%) occurrence on plots (Table 4.2). The NMS ordination resulted in a 3-axes solution where the final stress and instability were 17.53 and 0.002, respectively. We assessed stability by plotting a graph of stress versus number of iterations (PC-ORD, v.5, McCune and Mefford 2006). Stability was reached at approximately 40 iterations from a maximum of 500 iterations. Monte Carlo test results indicate that this three-dimensional solution using real data was less than would be expected by chance ($p < 0.01$). A scree plot tracks the relationship between stress and dimensionality contrasting real data with the randomized data set (Figure 4.2). The scree plot shows little improvement with more than three axes and that the real data set is predominantly less than the random data set. The three axes explain the majority of variability in our lichen community data set (axis 1: $r^2 = 0.19$; axis 2: $r^2 = 0.48$; axis 3: $r^2 = 0.10$; total $r^2 = 0.78$). Because of the relatively small contribution of the third axis and its unclear relation to environmental variables we will not discuss it further.

An ordination joint plot and the categorical variable stand type are overlaid on the results of the NMS (Figure 4.3). The centroid of the graph is determined by the total tally of *all* species and their abundances in relation to all other species (i.e., "species space"). Environmental variables, presented as direction and strength vectors, are superimposed upon the centroid of the species ordination. Coefficient of determination (r) values between environmental variables and axes 1 and 2 were calculated (Table 4.4). Environmental variables with than $r > 0.50$ (Table 4.4) for either principal axis were considered important contributors to species distributions (Figure 4.3). Overall, axis 2 describes the stronger of the two ordination relationships corresponding to aspen succession and lichen species richness and abundance. This is verified by the overall ordination and the *r* values for vectors corresponding to axis 2 versus axis 1 (Table 4.4). Generally, declining and remnant plots correlate positively with increased conifer cover and lichen species diversity and abundance in the upper half of the graphic (Figure 4.3, Table 4.4). In contrast, stands closer to pure aspen (stand type 1) are negatively correlated with axis 2 and strongly associated with the aspen canopy cover and aspen index score (Figure 4.3, Table 4.4). Percent nitrogen abundance is closely correlated (r = -0.78) with indicators of pure aspen stands. All measures of basal area and aspen damage/scarring correlated poorly with axis 2 (Table 4.4).

Axis 1 describes a significant gradient of nitrophilous lichen abundance and distance from both urban and peak NH_3 centers (Figure 4.3). The unrelativized variable nitrogen abundance decreased ($r = -0.59$) with increasing distance from the local urban center ($r = 0.51$) and areas of NH_3 concentration ($r = 0.52$).

Figure 4.4 shows the same NMS ordination (i.e., exact orthogonal rotation) as Figure 4.3 with an alternate background display of all lichens surveyed in species space. We have included some of the same environmental variables for orientation purposes and plotted significant ($r = < -0.5$ or > 0.5) species vectors. This view points out which lichen species may be useful indicators of particular gradient trends (Figure 4.4). *Bryoria fuscescens* ($r = 0.55$), *Letharia vulpina* ($r = 0.65$), *Melanelia exasperatula* ($r = 0.75$), and *Usnea lapponica* ($r = 0.83$), correlate positively with axis 2 and conifer cover, while *Xanthomendoza galericulata* ($r = -0.62$) correlates with aspen canopy cover (and aspen index score, Figure 4.3). Axis 1, a gradient of nitrogen loading related to distance from sources, revealed a strong link between abundance of nitrophilous species and *Phaeophyscia nigricans* ($r = -0.77$).

Other "clean air" lichens, such as *Usnea, Bryoria, and Letharia* (Neitlich and others 2003), display a stronger correlation to axis 2, although *Melanelia exasperatula* and *Letharia vulpina* exhibit a positive tendency toward clean air metrics (axis 1) both having *r* values of 0.48 (Figure 4.4). Similarly, *Xanthomendoza fallax* related equally strongly in a positive direction with conifer cover (axis 2) and negatively to distance to pollution sources.

Discussion

Our study was designed to emphasize favorable local conditions for aspen growth and the potential for encroachment by shade-tolerant tree species. By limiting sample plots to a 300 meter mid-elevation belt and avoiding south-facing aspects we also restricted moisture differences known to strongly influence lichen community composition (Marsh and Nash 1979; McCune and others 1998). Sampling conducted at moisture, elevation, or geographic limits of aspen would be expected to display atypical successional patterns and likely support uncharacteristic lichen communities. Because of these design restrictions and the relatively dry climate of the Southern Rocky Mountains Ecoregion, lichen diversity statistics ($\gamma = 24$, $\alpha = 10.66$) do not seem unreasonable compared to previous work in the region (Keyes and others 2001; Neitlich and others 2003). Beta diversity ($\beta = 2.5$), however, is lower than recorded in a statewide survey of Idaho lichens ($\beta = 8.5$), covering multiple physiographic provinces (Neitlich and others 2003). We attribute this considerable difference in community turnover to disparities between the study designs and breadth of geographic coverage.

Uncommon lichens species tallied in our survey were those found at only a single sample location (Table 4.2). While these species have little value for the ecological analysis conducted here, and were subsequently removed for multivariate analysis, they do document species presence for future comparisons.

Because our study design required the presence of at least some aspen on each plot we feel compelled to address how aspen alone affects the lichen community. First, previous work in our study area using Indicator Species Analysis (Dufrêne and Legendre 1997) determined a host of cosmopolitan lichens and a few species showing preference for either conifers or aspen (Rogers and others 2007b). Only two species, *Phaeophyscia nigricans* and *Physcia tenella*, were exclusive to aspen forest types (i.e., a plurality of aspen stems, or stand types 1 and 2). Because we attempted to sample each stand type (Table 4.1) equally we do not feel particular forest types or tree species were favored. However, if advancing succession due to climate or fire suppression continues, we may witness a gradual loss of lichen species favoring aspen stands.

Second, even though we did not measure bark pH, previous research has addressed lichen preferences based on pH differences between hardwoods and softwoods (Barkman 1958; Martin and Novak 1999; Jovan and McCune 2006). Hardwood bark is generally more alkaline than conifer bark and may therefore be expected to attract nitrophilous species (Jovan and McCune 2006). In fact, the species included in our aspen index score (*Phaeophyscia nigricans, Physcia tenella, Xanthomendoza fulva*, *X. galericulata*) are all considered to be nitrophilous (Table 4.2). This potential conflict may explain some of the apparent weakness of linear ANCOVA tests and, by contrast, the efficacy of multivariate analysis conducted here. In short, ANCOVA results were unable to distinguish between multiple factors corresponding to lichen diversity and abundance, except when the aspen index score was used as the response variable (Table 4.3). NMS output parsimoniously assessed correspondence between nitrogen loading and aspen-to-conifer succession (Figure 4.3, Figure 4.4, and Table 4.4). Thus, though bark pH variability likely contributes added noise to the question of species use of substrate, these results suggest a stronger (or additional) ability to favor air borne nutrients beyond natural substrate pH.

Axis 2: Lichen community change with succession

Changing epiphytic lichen communities with advancing succession from aspen- to conifer-dominated stands was addressed in detail in a previous study (Rogers and Ryel 2007). Similar results - increasing lichen diversity/abundance and decreasing aspen index scores with advancing conifer encroachment - resulted from the present ANCOVA and multivariate analysis (Table 4.3, Table 4.4, Figure 4.3, and Figure 4.4). Further, the aspen index score in all of these tests was the most consistent response variable to community change with succession. Species affinities as they correspond to primary gradients and a few significant environmental variables are indicated in Figure 4.4 (see Figure 4.3 for significant environmental variables using the same orthogonal rotation). Lichens favoring aspen forest types (i.e., aspen indicators) are located below, albeit only just, the midpoint of the successional gradient (axis 2), while several species positively correlated with succession are located near the upper end of the gradient. Fruticose species in our study are exclusively associated with conifers, and more so with remnant aspen stands; thus they are located furthest from the centroid on the successional gradient. No species display as strong a negative correlation to axis 2, signaling as clear a preference for pure aspen stands (Figure 4.4).

Axis 1: Relating valley ammonia monitoring to montane lichen communities

In lieu of a locally established lichen-based gradient (Will-Wolf and others 2002b; Jovan and McCune 2005), we tested the distance from each plot to urban and NH_3 sources (Figure 4.1) as independent variables in a natural gradient based on location within a mid-elevation montane landscape. Our initial attempt to account for linear covariation (ANCOVA) with distance from a pollution center was only marginally successful with the greatest reduction in error occurring with the response variable aspen index score (Table 4.3). The addition of more potential explanatory variables, including metrics of nitrophilous lichens, and the incorporation of non-linear relations in NMS ordination, yielded a clearer picture of environmental influences on aspen's epiphytic lichens (Table 4.4, Figure 4.3, and Figure 4.4).

Axis 1 shows a clear relation to nitrophilous lichen species and distance from NH_3 sources. Distance to urban center implies a general air quality gradient, but admittedly a less clear relationship (Figure 4.3). Abundance of nitrophilous lichen species in our survey is negatively correlated to axis 1 and *Phaeophyscia nigricans* stands out as a strong indicator of nitrogen deposition (Figure 4.4). As distance increases from peak NH_3 sources *P. nigricans* decreases in epiphytic lichen communities regardless of successional stage. Earlier work in the Bear River Range found that *P. nigricans* was the strongest indicator species displaying affinity for individual aspen tree stems versus conifers (Rogers and others 2007b), though the preference for aspen did not hold up in whole forest stand environments (Rogers and Ryel 2007). At the stand-level, only *Xanthomendoza galericulata* stood out as a significant indicator of pure aspen forests.

Melanelia exasperatula and *Letharia vulpina* seemed to show some promise as clean air indicators (positively correlated to axis 1), though their primary relation was to axis 2. It may be that other traditional clean air species, such as *Bryoria* and some *Usnea* species, are either better represented in the third access of our ordination or that these groups are already largely depleted from the landscape and giving only a weak pollution signal in our analysis.

Percent nitrogen abundance is strongly negatively correlated with axis 2, acting more like an indicator of aspen forest types than a metric of nitrogen deposition (Figure 4.3). As stated earlier, all species comprising the aspen index score are also nitrophytes. When abundance scores of nitrophilous species were relativized to all species tallied, their importance became inflated where fewer total lichen species were present (i.e., in pure aspen stands). For this reason, a straight abundance sum of nitrophilous lichens yielded a more equitable picture of nitrophytes across all plots, regardless of total diversity or affinity to aspen-dominated stands. Jovan and McCune (2005, 2006) probably had more success with a proportional nitrophyte metric because of their much larger gamma diversity, thus minimizing the effect we encountered here where lower species richness in aspen-dominated stand types (pure and invaded) amplified relative nitrophyte abundances overall.

Axis 1 also addresses air pollution generally versus specific NH_3 sources. Distances from each montane sample plot to the nearest edge of the adjacent Cache Valley and the local urban center acted as surrogates for general measures of air quality.

While ANOVA results showed a relationship between aspen index and distance to urban center (Table 4.3), the broader measure of Cache Valley pollution (D_cache) was statistically insignificant in NMS (Table 4.4). Comparison of values between the distance to urban center and that of NH_3 sources showed a very close relation statistically and in orientation to major gradients (Figure 4.3). We note that one of the two NH_3 peak areas in Cache Valley is geographically near the urban center, so this may partially explain the correlation of these two measures. Also, other authors have pointed out that automobile exhaust, assumed to peak in population centers, is also a source of atmospheric NH_3 (Fenn and others 2003a; Jovan and McCune 2005, 2006). However, we show marked differences from NH_3 monitors in close proximity to our local urban center (Figure 4.1). Two sites within the city of Logan have much lower readings (22.7 and 11.4 $\mu g\ m^{-3}$) than those of the upwind wastewater treatment facility (68.8 $\mu g\ m^{-3}$). The distances between NH_3 sites near Logan (~ 5 km) is much less than to even the nearest sample plots (~ 13 km), which are also a minimum of 760 meters higher in elevation. We expect that NH_3 will not remain in the air given its high deposition velocity (Fenn and others 2003a), though longer range transport of the pollutant is likely a result of NH_3 conversion to other forms of atmospheric N.

Ammonium (NH_4) wet deposition is believed to have impacts on plant communities between 100 – 1000 km from its NH_3 origin, while dry deposition NH_3 has a much higher deposition velocity (van Herk and others 2003). These authors found NH_3, with an airborne distance limit of perhaps 50 km, is responsible for increases in nitrophilous lichens, while NH_4 wet deposition at much lower levels may deplete regional-scale communities of 'acidophytes'. Acidophytes are lichen species known to show preference for acid bark (van Herk and others 2003), and three species found in our study (*Bryoia fuscescens, Imshaugia aleurites, Usnea hirta*) were shown to be sensitive to long-range transport of N in European forests. A key difference in the two study areas may be the strong orographic effect of precipitation in the Southern Rockies Ecoregion. As precipitation increases with elevation N deposition rates also increase (Williams and Tonnessen 2000), potentially accounting for the increase in nitrophilous lichen species found here at montane sites nearer NH_3 sources. Further, though NH_3 dry deposition is known to chemically alter tree bark, it is believed that long-range deposition of NH_3 in the form of NH_4 will not alter bark pH, but is absorbed directly into lichen thalli via precipitation (van Herk and others 2003). NH_4 wet deposition, because of the distance from sources in the present study, is believed to be at least partially responsible for elevated nitrophytes and reduced acidophytes. Based on our limited tally of acidophytic lichens, depletion of these species may already be underway where wet NH_4 deposition is occurring over mid- and long-distances from sources enhanced by steep elevational gradients.

Effects of nitrogen loading on aspen ecosystems

Nitrogen loading in the U.S. and globally has been increasing in recent decades (Fenn and others 2003a; van Herk 1999; Tillman and others 2001). At least one study has linked nitrogen deposition related to urban pollution to aspen expansion in Alberta's parklands (Köchy and Wilson 2001). We do not know how nitrogen inputs affect aspen in competitive montane forests, as opposed to expansion into prairie biomes, given its status in our region as a predominantly seral tree species. Jovan and McCune (2005,

2006) documented a clear gradient of NH_3 effects on lichen communities at a regional scale in California. While it appears the same phenomenon is occurring at a landscape scale in the present study, an evolving aspen environment, inserts an added dimension to our epiphytic considerations. Where nitrophytes are assumed to favor NH_3 saturated forests, we wonder how that effect is manifested in lichen species with limited or declining primary substrates.

If present trends continue, a lack of predators to limit and harass browsing ungulates combined with aggressive fire suppression (Ripple and others 2001; Rogers and others 2007a) will likely lead to local aspen decline. A cooler and wetter 20th century (Gray and others 2004) may have supplemented suppression efforts, further favoring conifer advancement. Moreover, expected warming trends may impart devastating effects on regional aspen forests if exotic invertebrates are allowed to expand into higher elevational zones (Logan and others 2007). All of these factors potentially favor declines in lichen species dependent on montane hardwoods; a designation dominated by aspen in the Southern Rockies Ecoregion. So, while aspen may directly expand in other biomes due to nitrogen deposition, we believe that in the highly competitive realm of mid-elevation mixed conifer and aspen forests, barring sizable disturbance and protection from ungulates, aspen will decrease leaving limited substrates for hardwood-dependent lichens. And where nitrophilous lichens may increase in reaction to N influx, species requiring alkaline woody substrates may be limited to the remaining sparse assemblage of montane hardwoods in conifer-dominated ecosystems.

Application of research findings

Forest succession and nitrogen deposition related to local NH_3 sources explain most of the variation in lichen communities in our Southern Rockies Ecoregion aspen forests. Epiphytic lichen communities may be used as an effective monitoring tool for biodiversity in forests generally, and aspen communities specifically, and as bioindicators of N loading. Further, as NH_3 recording devices are expensive and concentrated in urban and agricultural systems, an efficient alternative for remote locations is to implement biomonitoring methods such as those employed here.

As managers contemplate monitoring to measure baseline and post-management activities in aspen forests, they should consider targeted assessments of macrolichens as an indicator of system health for both short- and long-term scenarios. Past work points to the importance of each successional stage in promoting the totality of lichen diversity in our area, so we should be cautious about active management which favors pure or remnant stands to the detriment of intermediate phases (Rogers and Ryel 2007). Likewise, ecosystem managers should be cognizant of recent causality (i.e., N loading) affecting aspen-dependent species while addressing long-term problems targeting successional stages and trajectories.

Lichen diversity research aimed at specific tree species, such as aspen, is in its infancy in the western U.S. In Europe, more work has been done on epiphytic contributions of aspen (*Populus tremula*) to larger forest systems, resulting in an elevated status of this forest type in conservation efforts (Lipnicki 1998; van Herk 1999; Hedenås and Ericson 2004). Further research is needed in our area concentrating on connections to landscape- and stand-scales, as well as regional ties. For example, though local sources of nitrogen have produced an audible signal in the present study, we wonder about the role of large regional sources of NH_3 (Fenn and others 2003b). These authors have modeled very high concentrations of nitrogen deposition 100 – 200 km west of our study area. Is there a mechanism to differentiate between local and regional NH_3 sources and their impacts on ecosystems? Likewise, can we determine how short-range dust, livestock waste, and small combustion engines affect adjacent aspen/lichen systems? Though further work is needed, this study has provided some initial tools, such as lichen indicator species of N loading and an aspen index score based on lichen communities, for monitoring changing aspen ecosystems over time. We believe these basic methods can be applied to other forest communities where concern for seral or threatened species may have cascading effects on dependent flora.

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Table 4.1 Study site stratification by succession groups and cover requirements

	Succession groups			
	Pure	Invaded	Declining	Remnant
Group code	1	2	3	4
Percent aspen tree cover	> 90	50-90	49-10	< 10
Field plots sampled	12	11	12	12

Table 4.2 Summation of epiphytic macrolichens recorded on aspen plots (*n* = 47) in the Bear River Range, Utah and Idaho. Codes** are used in Figure 3 and 4.

Species*	Code**	Freq.	% Freq.	Sensitivity***
Bryoria fuscescens	BRFU60	13	27.7	S
Candelaria concolor	CACO64	12	25.5	N
Imshaugia aleurites	IMAL60	1	2.1	U
Letharia columbiana	LECO26	4	8.5	S
Letharia vulpina	LEVU2	14	29.8	S
Melanelia elegantula	MEEL5	45	95.7	U
Melanelia exasperatula	MEEX60	33	70.2	I
Melanelia subolivacea	MESU61	39	83.0	I/T
Parmelia sulcata	PASU63	1	2.1	T
Parmeliopsis ambigua	PAAM60	3	6.4	I
Phaeophyscia nigricans	PHNI5	38	80.9	N
Phaeophyscia orbicularis	PHOR60	1	2.1	N
Physcia adscendens	PHAD60	47	100.0	N
Physcia biziana	PHBI6	10	21.3	T
Physcia dimidiata	PHDI12	8	17.0	N
Physcia tenella	PHTE60	24	51.1	N
Physciella chloantha	PHCH4	13	27.7	U
Physconia isidiigera	PHIS2	1	2.1	T
Usnea hirta	USHI60	1	2.1	S/I
Usnea lapponica	USLA60	24	51.1	S/I
Usnea spp.	USSSP	1	2.1	S/I
Xanthomendoza fallax	XAFA	32	68.1	N
Xanthomendoza fulva	XAFU	42	89.4	N
Xanthomendoza galericulata	XAGA	47	100.0	N
Xanthomendoza montana	XAMO60	47	100.0	N

* Nomenclature follows Brodo et al. (2001), except for recent revisions of *Xanthomendoza* (formerly *Xanthoria*) by McCune (unpubl. key at: http://oregonstate.edu/~mccuneb/Xanthoria.PDF), who is following Lindblom (2004, 2006).

** Codes are derived from the USDA Natural Resource Conservation Service, PLANTS database (http://www.plants.usda.gov/).

*** Sensitivity ratings: N = nitrophyllus, S = sensitive, I = intermediate, T = tolerant, U = unknown. Sources: McCune and Geiser (1997); McCune and Jovan (2005); van Herk (1999); and Neitlich et al. (2003).

Table 4.3 ANOVA and ANCOVA scores for lichen response variables and the covariate Distance to Urban Center by stand types. Aspen index score is the summation of abundance values for four species showing preference for aspen versus conifer forest types (Rogers and Ryel 2007). The covariate for ANCOVA is "distance to urban area." Results shown in bold type are considered significant where *p*-values are < 0.05.

	ANOVA			ANCOVA				
	F	*p*	error	F	*p*	error	Dist. Urban F	Dist. Urban *p*
Species richness	**17.31**	<0.0001	2.74	**12.89**	<0.0001	2.78	0.38	0.5436
Total abundance	**16.18**	<0.0001	13.87	**12.01**	<0.0001	14.10	0.30	0.5889
Aspen index score	**14.32**	<0.0001	42.96	**13.70**	<0.0001	38.15	**6.42**	0.0151

Table 4.4 Coefficients of determination for correlations between environmental variables and ordination axes. Abbreviations are used in Figure 3 and 4.

		r value	
Variables*	Abbreviation	Axis 1	Axis 2
Aspect		-0.006	0.074
Aspen basal area per hectare	aspBA h	-0.454	-0.427
Aspen cover	**aspcov**	-0.121	**-0.752**
Aspen index score	**aspscore**	-0.471	**-0.865**
Basal area per hectare	BA h	-0.277	0.392
Conifer cover	**concov**	0.031	**0.684**
Dead basal area per hectare	deadBA h	-0.107	0.377
Distance to urban (Logan)	**D_logan**	**0.509**	0.139
Distance to peak NH3	**D_pkNH3**	**0.523**	0.113
Distance to valley (Cache)	D_cache	0.237	0.111
Lichen species richness	**sprich**	-0.062	**0.783**
Nitrogen abundance	**N_abund**	**-0.586**	0.140
Nitrogen richness	N_rich	-0.366	0.376
Percent aspen damage	paspdam	0.136	0.092
Percent aspen scars colonized	pscarcol	-0.102	0.135
Percent aspen bole scarring	pbolescar	0.065	0.074
Percent nitrogen abundance	**P_Nabund**	-0.444	**-0.781**
Slope		0.106	0.054
Stand age	stdage	-0.402	-0.033
Total lichen abundance	**totabund**	-0.134	**0.746**

* Variables in boldface have r values > 0.5 or < -0.5.

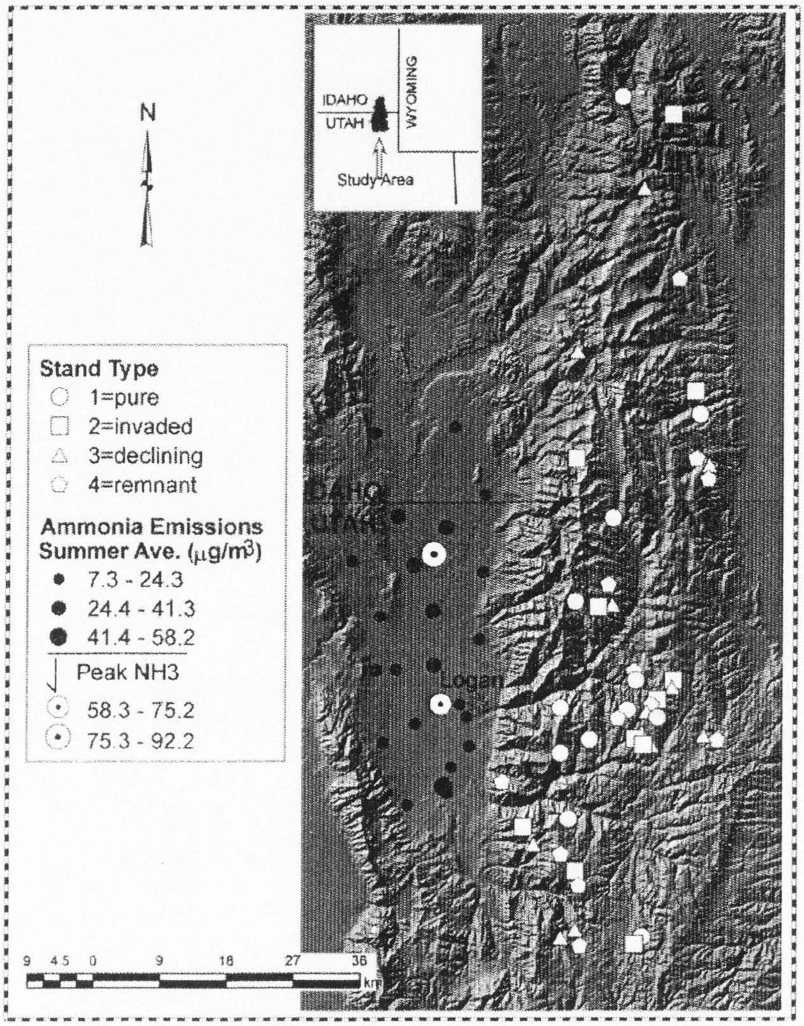

Figure 4.1 Study area including location of lichen sampling plots, their stand type designations, ammonia (NH_3) monitoring stations, and the local urban center, Logan, Utah. Stand types represent categories of aspen cover in a successional continuum (see Table 1). Symbology used to represent peak passive air monitoring NH_3 sites were derived from the two highest quintiles (equal interval) of readings averaged over three one-week summer data collection periods.

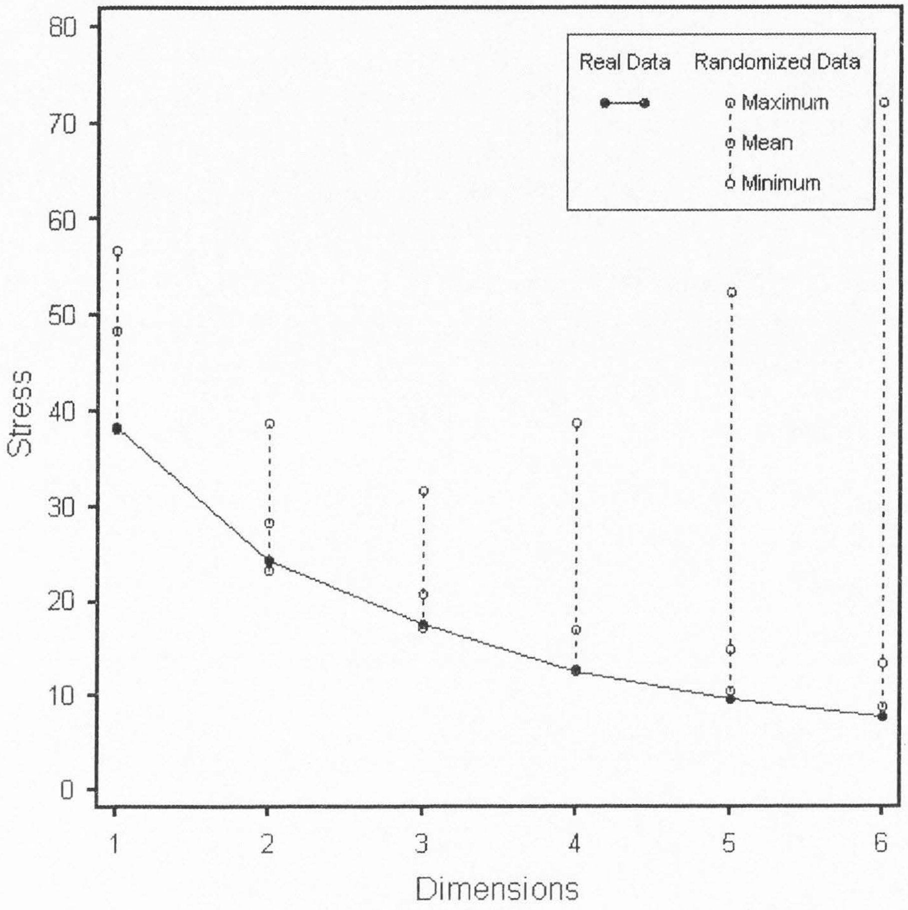

Figure 4.2 Scree plot graphs stress versus dimensionality from nonmetric multidimensional scaling (NMS) results and contrasts the study data set and 249 random configuration runs (Monte Carlo test) of the data set.

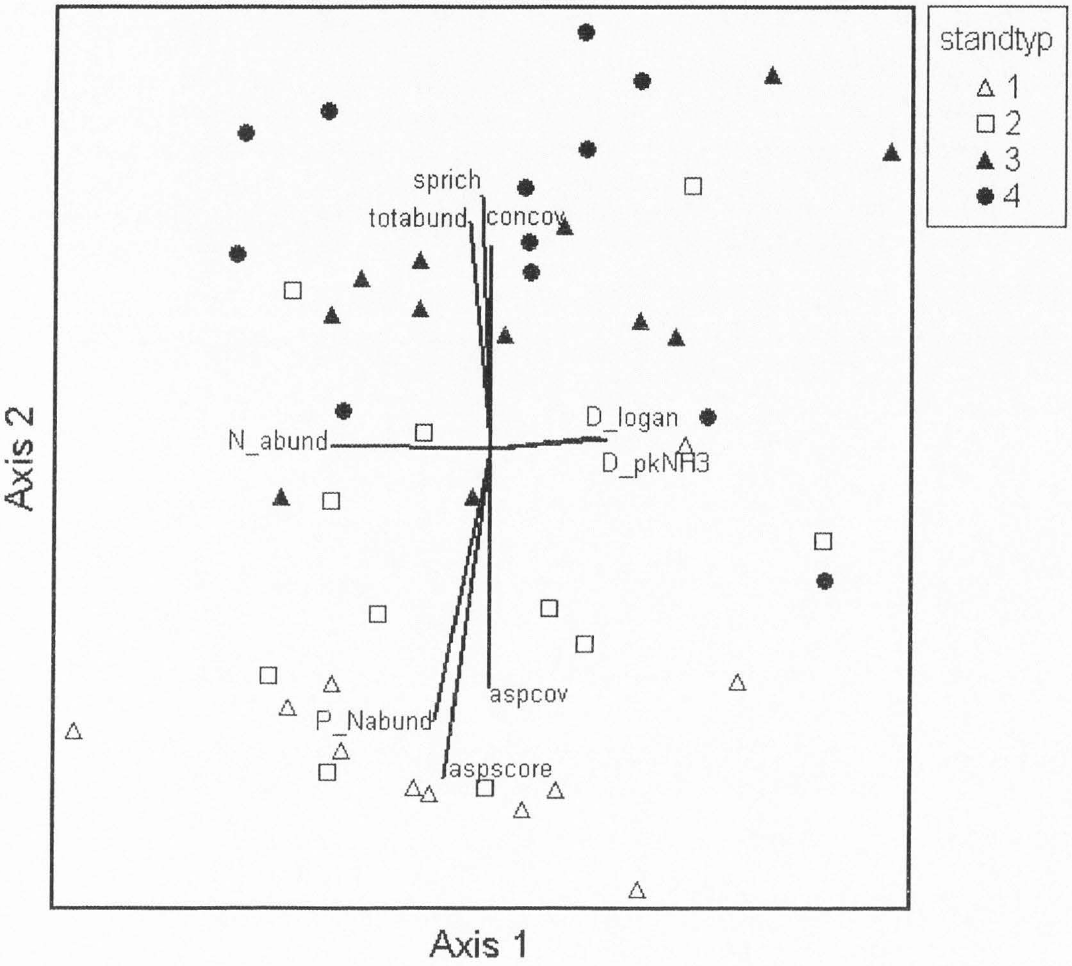

Figure 4.3 Ordination joint plots from nonmetric multidimensional scaling (NMS) with environmental variables plotted as vectors. Stand types correspond to stratification by successional groups (Table 4.1). Vector directions and lengths designate correlations with the ordination. All environmental variables with r < -0.5 or > 0.5 are shown (see Table 4.4). A key to abbreviations for environmental variables are found in Table 4.4.

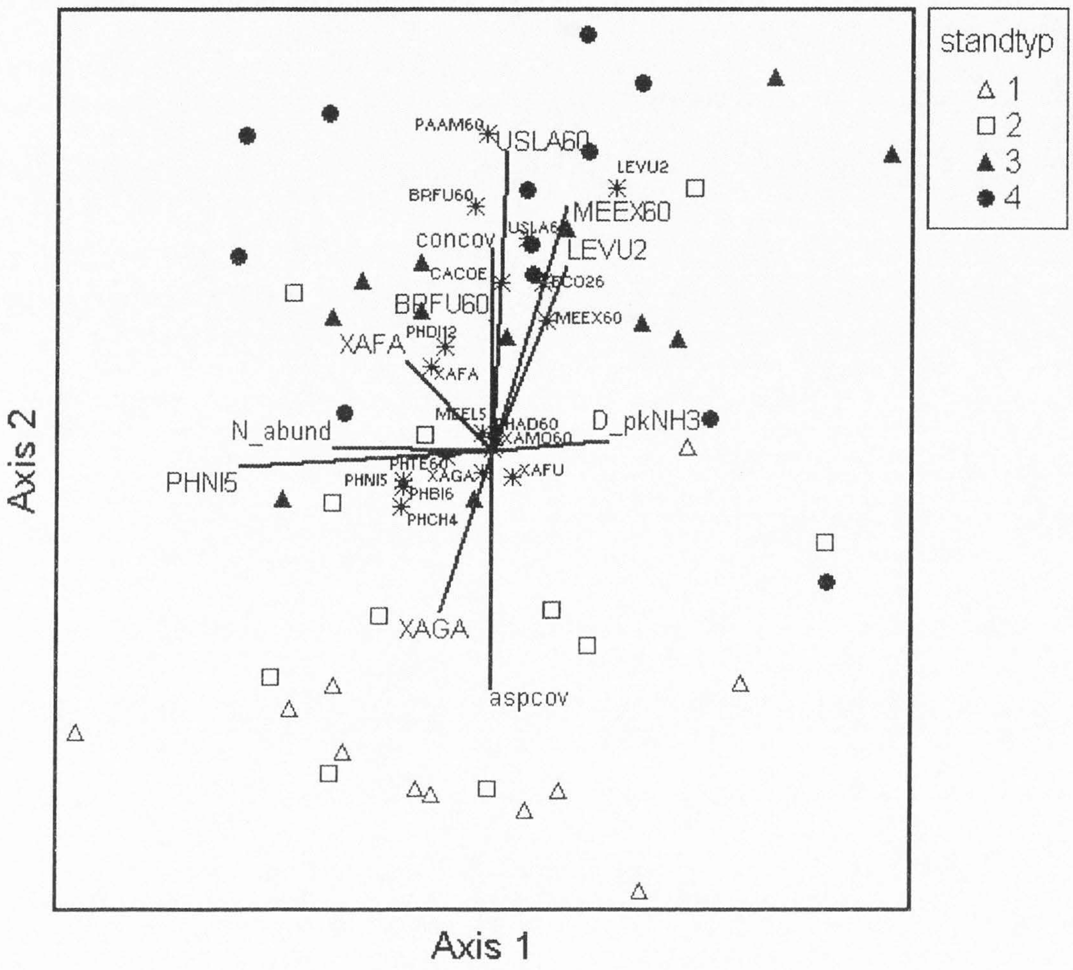

Figure 4.4 Ordination joint plot from nonmetric multidimensional scaling (NMS) with lichen species above our threshold (r < -0.5 or > 0.5) plotted as vectors and all species locations in the ordination shown as asterisks (*). Vector directions and lengths designate correlations with the ordination. Large font species codes (Table 4.2) correspond to vectors; smaller font codes (Table 4.2) are associated with asterisks representing location in relation to all other species (i.e., "species space"). The exact orthogonal rotation is used here as in Figure 4.3. Four environmental variables (concov, aspcov, N_abund, D_pkNH3 – see Table 4.4 for abbreviations) from Figure 4.3 are included for orientation. Stand type symbols correspond to stratification by successional groups (Table 4.1).

CHAPTER 5

HISTORICAL PATTERNS INFLUENCING ASPEN AND EPIPHYTIC LICHENS IN THE ROCKY MOUNTAINS, USA[4]

Introduction

How have forests changed over time in response to interactions of climate and various human intrusions? This is a common question of biogeographical investigation. Numerous authors have applied these concerns to western USA quaking aspen (*Populus tremuloides* Michx.) forests (Elliot & Baker, 2004; Kulakowski *et al.*, 2004; Shepperd *et al.*, 2006; Brown *et al.*, 2006; Rogers *et al.*, 2007a). While these studies place a premium on aspen dynamics through time and across landscapes, we wonder how aspen-dependent species will be affected by changing tree cover.

Our previous work has concentrated on elucidating preference of epiphytic lichens for tree species and forest types and assessing factors affecting change in lichen community composition (Rogers *et al.*, 2007b; Rogers & Ryel, 2007; Rogers *et al.*, 2007c). Lichen communities have long been used as indicators of air quality (Barkman, 1958; Richardson, 1992; Hawksworth, 2002), and more recently of wildlife habitat (Rosentreter, 1995) and general forest conditions (Neitlich & McCune, 1997; McCune, 2000; Pykälä, 2004). Lichen work specifically related to aspen communities in Sweden has highlighted the importance of this tree in greater epiphytic diversity (Esseen *et al.*, 1996; Hedenås & Ericson, 2000). North American research highlighting aspen's epiphytic contributions to forest diversity have lagged behind European efforts. We are

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unaware of work linking past landscape disturbance to lichen species and community preferences.

While other fauna and flora may be somewhat dependent on aspen as a "keystone species" (Campbell & Bartos, 2001), epiphytic lichens, by their very nature, are highly dependent on arboreal substrates. Further, it is not uncommon among lichens to have specific preferences (e.g., bark texture, bark pH, moisture, etc.) that confine them to certain tree species within a stand. A common division is among hardwood- and softwood-preferring lichens. In mid- to upper-elevation Rocky Mountain forests aspen is the primary, and often the only, hardwood present among landscapes dominated by softwood species.

Our objective is to build a chronology of climate and human impacts on aspen forests over the past 150 years, and further relate these influences to associated epiphytic lichen communities. In this way, we hope to gain further understanding for numerous other species that are either partly or wholly dependent on aspen ecosystems and provide a climate-based approach for addressing future management scenarios. Our chief sources will include a landscape survey of aspen forest structure, a lichen community inventory, an ammonia monitoring network for the adjacent valley, climate reconstructions, fire records, and historical accounts since Euro-American settlement. Bridging these diverse sources, we believe, lends itself to constructing a more complete picture of landscape and community dynamics during a period of robust change. Insights from this synthetic approach may be informative to lichen specialists, aspen ecologists, and land managers alike and provide valuable information for addressing future climate scenarios.

Methods

Study area

Our study area encompasses the Bear River Range in northern Utah and southern Idaho (Figure 5.1). These mountains are of block fault origin and trend in a north-south direction, approximately 120 by 30 kilometers, with a total area of about 3,300 square kilometers. The range lies in the Southern Rocky Mountains Ecoregion Province between 1,370 and 3,040 m elevation, and receives between 51 and 102 cm of precipitation per year (Bailey, 1995). Most precipitation arrives as winter snowfall. The northern western portion of this ecoregion experiences summer drought without a seasonal southern moisture flow. Dry lightning storms provide the prime ignition source for fire-prone forests of the area (Bailey, 1995).

Aspen forests comprise the primary hardwood element of mid- and upper-elevations in the Southern Rockies Ecoregion (Rogers, 2002). In the Bear River Range, aspen coexist with subalpine fir (*Abies lasiocarpa* Nutt.), Douglas-fir (*Pseudotsuga menziesii* Franco), lodgepole pine (*Pinus contorta* Dougl. ex Loudon), and to a lesser degree Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and limber pine (*Pinus flexilis* James). Minor hardwoods of the area include bigtooth maple (*Acer grandidentatum* Nutt.), Scouler willow (*Salix scouleriana* Barratt in Hook.), western serviceberry (*Amelanchier alnifolia* Nutt.), chokecherry (*Prunus virginiana* L.), and mountain mahogany (*Cercocarpus ledifolius* Nutt.). The remaining vegetation cover of this range is made up of mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* Rydb.) and subalpine meadow openings. Understory vegetation in aspen stands ranges from lush stands of diverse forb and grass groups, to shrubby cover dominated by snowberry (*Symphoricarpos spp.*), to sagebrush, and mixed assemblages of each of these groups (Mueggler, 1988).

Landscape aspen and lichen survey

We selected 47 field plots stratified by four successional cover classes (stand types) of aspen using Utah and Idaho vegetation cover maps (USGS, 2004, 2005). Sample sites were selected from all aspects except south-facing slopes where potential conifer invasion – a central requirement of this study – was least likely. All plots were between 2,134 and 2,438 m elevation. Plots were stratified based on aerial photographic interpretation into four broad successional groups: pure, invaded, declining, and remnant aspen (see Table 5.1 for group criteria; Figure 5.1). Further detail of the plot selection procedure may be found in Rogers & Ryel (2007).

An independent set of ammonia (NH_3) monitoring sites were located throughout the Cache Valley, Utah and Idaho (Figure 5.1). During June and July of 2006, 25 gas-phase ammonia samplers, Ogawa Model 3300 (Ogawa USA, Inc., Pompano Beach, FL, USA), were loaded with pads pre-coated with a citric acid solution and were deployed to yield a spatially resolved representation of ambient ammonia concentrations. Three sets of samples were taken for 4 to 7 days each during June and July. After exposure, the pads were eluted with deionized water that had been passed through a 0.45 μm filter and analyzed via ion chromatography (Rogers *et al.*, 2007c). Ambient concentrations were calculated using diffusion equations given by Roadman *et al.* (2003). For each location, mean values were calculated combining the three sample periods representing summer

NH_3 conditions. A detailed description and validation of the Ogawa passive sampler for scientific studies was provided by Roadman *et al.* (2003).

Aspen plot measurements were of two broad types: stand characterization consisting of location descriptors and tree measures, and lichen sampling by species tally, voucher collection, and abundance estimation. Tree mensuration was conducted on a 0.016 ha (7.3 m radius) circular subplot, which was centrally located in a 0.378 ha lichen survey and plot descriptor circle. Collectively, the entire sample area is heretofore referred to as the "plot." Plot descriptors included GPS readings, slope, aspect, stand type, percent aspen cover, percent conifer cover, stand age, and aspen age. Five cover estimates for aspen and conifers > 2 m in height were taken at the plot center and 2 m inside the lichen plot perimeter (33 m radius) at the four cardinal directions. Stand ages were based on at least two cored aspen trees (stand types 1 and 2) and an additional two cores of dominant conifer species (stand types 3 and 4). Stand ages were calculated by adding five years to the breast height (bh) average of aspen cored and 10 years to average conifer ages to account for the average growth period between ground level and bh. After data collection basal area was calculated for standing dead trees and by tree cover types. We also determined type and percent of tree damage and level of aspen scar colonization by lichens, as previous research has indicated scarring of smooth-bark aspen is an important habitat requirement for epiphytes (Martin & Novak, 1999).

Lichen sampling was adopted from the procedure used by the U.S. Forest Service, Forest Health Monitoring program (McCune, 2000; Will-Wolf, 2002). Briefly, the entire plot area was systematically examined for presence of epiphytic macrolichens 0.5 m above the forest floor for up to two hours. Lichens were not sampled below 0.5 m to avoid overlap with the ground dwelling lichen community. This method allows examination of fresh litter fall as a surrogate for upper canopy lichens. At least 40 minutes must be spent traversing the area before the survey is terminated. The survey ends when the minimum search time has elapsed and no new species have been found within the preceding ten minute period. We found an average of 60 – 75 minutes were required for the survey in our area. After completion of lichen sampling, each species was assigned a qualitative abundance class for the plot: 1 = 1-3 individuals (distinct lichens, i.e., thalli); 2 = 3-10 individuals; 3 = between 10 individuals and occurrence on half of all trees/shrubs on the plot; 4 = greater than half of all woody substrates on the plot exhibiting the lichen. Previous work showed that for sparsely populated vegetation in large sample areas, visual abundance classes were more efficient with comparable accuracy to continuous area measures (McCune & Lesica, 1992). Unknown species were collected as vouchers for later identification under a dissecting scope and, when needed, by other lichen experts. Lichen nomenclature followed Brodo *et al.* (2001) for all species except recent revisions of *Xanthomendoza spp.* (formerly *Xanthoria*) by Lindblom (2004, 2006). Lichen vouchers were collected and stored at the Utah State University Herbarium.

Several derived variables related to the lichen survey were determined following data collection. We measured the distance from each plot to peak NH_3 sources, the local human population center, and edge of dispersed rural population/pollution sources using ArcMap® GIS software. Nitrogen abundance is the sum of abundance scores for each nitrophilous species (Table 5.2) per plot. Nitrogen richness is simply a count of those same species for each plot. Percent nitrogen abundance is a relative score indicating the percent of total abundance found in nitrophilous species at the plot level (Jovan & McCune, 2006).

Climate and historical sources

Climate reconstructions are based on models linking the dendrochronological record to past weather data (Cook *et al.*, 1999). We obtained Palmer Drought Severity Index (PDSI) data from the National Climate Data Center (Cook *et al.*, 2004) at four continental grid points surrounding our study area. The reconstruction index and a 20-year smoothing of the index were averaged over the four grid points (grid points 85, 86, 101, 102; Cook *et al.*, 2004).

Historical sources include published reports and journals, plus wildfire records of the 20th century. A combination of these sources was used to gain an understanding of human-caused disturbances to forested ecosystems in the study area. Information prior to 1900 was largely anecdotal; however, general trends may be discerned after corroborating multiple sources (i.e., aspen stand ages, PDSI reconstructions, historical accounts). After 1903, with the establishment of a federal forest reserve, more detailed descriptions of conditions and fire events could be found in agency records.

Analysis of lichen communities

Multivariate analysis was used to discriminate lichen species preferences for stand types and to assess causal factors contributing to lichen composition and abundance. Indicator Species Analysis (ISA) is a multivariate approach to testing for no difference between *a priori* groups (i.e., stand types) regarding individual species affinity, or faithfulness, based on species abundance scores in particular groups (Dufrêne &

Legendre, 1997; McCune *et al.*, 2002). Perfect "faithfulness" is defined as always being present in the identified group and being exclusive to that group (McCune *et al.*, 2002). The ISA calculation is composed of PC-ORD© (McCune & Mefford, 2006) computations of relative abundance and a relative frequency of each lichen species by group, then multiplying these scores to give a final indicator value. The statistical significance of the maximum indicator value for each species is tested by 5,000 runs of a Monte Carlo randomization procedure. The resulting p-value represents the probability that the calculated indicator value for any species is greater than that found by chance. Output includes the group for which the maximum indicator value is found, the indicator score for that group, and the associated p-value for each species. Results were considered significant for ISA where $p < .05$.

Multivariate analysis was used to explore statistical causality among several variables potentially contributing to lichen community diversity and abundance in aspen forests. Our prime areas of concern, based on previous work (Rogers *et al.*, 2007c; Rogers & Ryel, 2007), were 1) forest succession from aspen to conifer, 2) stand structure (age and basal area), 3) air quality (distance to sources), 4) presence and abundance of nitrophilous lichens, and 5) amount of aspen damage related to the level of stem scarring. We used PC-ORD© software (McCune & Mefford, 2006) to run nonmetric multidimensional scaling (NMS, Kruskal, 1964; McCune *et al.*, 2002) on a primary matrix of plots by species and a secondary matrix of plots by environmental variables. Only lichen species recorded on at least 5% of field plots were used in the NMS analysis. The outlier analysis module in PC-ORD was used to eliminate plots with greater than 2 standard deviations from the mean Sørensen distance. Sørensen distance is a measure of abundance score dissimilarity in relation to all other species in an ordination. Data were subjected to 500 iterations per run using a relative Sørensen distance measure and a random number start. The solution with the lowest stress was derived from 250 runs using real data. "Stress" is a quantitative assessment final solution monotonicity; or a measure of how well the real data fit the ordination (McCune *et al.*, 2002). The lowest stress solution was then subjected to 250 randomized runs using a Monte Carlo test to evaluate the probability of final NMS patterns being greater than by chance. Orthogonal rotation of the resulting NMS solution was used to maximize correlation between the strongest environmental variables (i.e., *r* value) and prime axes. The lowest number of dimensions (axes) was selected when adding another dimension decreased the final stress by < 5 (McCune *et al.*, 2002).

Results

Historic sources and Euro-American impacts

The settlement period in Cache Valley Utah and Idaho (c. 1856 – 1900) followed a half-century of sporadic use by Euro-American fur trappers and explorers. According to Peterson (1997), only small Native American bands, subsisting mainly on fish, settled the area due to relatively harsh winter conditions. Aboriginal use of mountain terrain was therefore limited to seasonal hunting parties from various tribes in the region (Hovey, 1956; Peterson, 1997). This assessment supports a broader geographic analysis asserting modest aboriginal impacts, particularly where Native populations were sparse, at higher elevations in the Rocky Mountains (Baker, 2002). Euro-American fur trappers, although mostly transitory by nature, nearly extirpated native beaver (*Castor canadensis* Kuhl) populations (Hovey, 1956), which probably relieved aspen stands of a common herbivore for at least two decades (c. 1820 – 1840 AD), but it is unknown what longer term impacts this may have had.

Mormon pioneers established homesteads in 1856 and immediately began to tap surrounding uplands for construction materials and fuel wood. From settlement until the 1870's resource extraction was minor and consisted of easily accessible wood products. Many of the early homes were made of products other than wood (e.g., adobe) due to the lack of available lumber (Arrington, 1956). After 1870, forest cutting accelerated to provide for a rapidly expanding population and to supply ties for a northern spur of the Union Pacific railroad. In the 1880's and 1890's sheep herding became the primary use of montane forests and parks as accessible timber was depleted and lumber imports from the West Coast became more economical (Peterson, 1997). Potter (1902) estimated that 150,000 sheep had been grazing in the Bear River Range where the sustainable capacity was closer to 50,000. Both logging and sheep herding were commonly followed by intentional burning by settlers region-wide and locally (Potter, 1902; Hoxie, 1910; Bird, 1964; Cermak, 2005), which accounts for measurable reductions in fire intervals in the Bear River Range of the late 19th century (Wadleigh & Jenkins, 1996). Historical sources also confirm the exacerbating effect of regional drought on an overly taxed mountain ecosystem (Johnson, 2006). Potter's (1902) diary refers repeatedly to the "aspen thickets" that covered ridgelines and burned over areas of the range.

An era of forest conservation was ushered in with the new century and with the establishment of the Bear River National Forest (later Cache National Forest) in 1905 (Johnson, 2006). Originally there was heated debate over the benefits of prescribed burning (Hoxie, 1910), although by 1920 agency policy turned to fire suppression (Cermak, 2005). Little mention is made in Wasatch-Cache National Forest fire records indicating elevated fire activity throughout the early 20th century. Peterson (1997) refers to conservation corps field crews battling numerous small fires and actually being responsible for inadvertently igniting a fire in 1933. Fire records show increased activity in the 1950s and 1990s on the National Forest (Wasatch-Cache National Forest, unpublished records).

Stand structure and climate data

Results of ANOVA describe a marked decrease in both aspen cover and basal area with advancing stand types (Figure 5.2). Aspen cover (ANOVA, F = 26.77, $p <$ 0.0001) and aspen basal area declined (ANOVA, F = 5.13, $p = 0.004$), while conifer cover (ANOVA, F = 28.81, $p < 0.0001$) increased with stand type progression. However, stand ages were not consistently correlated with stand types (ANOVA, $F = 0.24$, $p =$ 0.87), lichen species richness (ANOVA, $F = 1.16$, $p = 0.29$), or total lichen abundance (ANOVA, $F = 0.43$, $p = 0.52$) as we thought might be the case.

In addition to testing overall stand age linkages to stand structure and lichen variables, we wanted to determine if there was an association between climate and the ages of the aspen cohort within each stand. We found aspen stand ages to be closely related to PDSI reconstructions. Figure 5.3a is a histogram of all plots tallied by their aspen stand ages. Stand ages are represented as initiation year classes in 10 year increments for all 47 plots measured in our survey. We have aligned PDSI reconstructions vertically with the stand age histogram by year for the 120 year span of aspen stand ages in the study (Figure 5.3b). Droughts are represented by sustained periods of the PDSI below the zero line and moist periods are those above zero. Stand initiating events are closely related to droughts followed by periods of above average moisture. Magnitude of the fluctuations also seems to correspond to the frequency of new aspen stands created. A 1000-year PDSI reconstruction presents context for comparison to weather extremes since settlement (Figure 5.3c). This figure indicates the early 20th century is among the wettest periods of the last millennium.

Lichen community analysis

Indicator Species Analysis results suggest significant preferences by lichen species for specific levels of aspen coverage (Rogers & Ryel, 2007). Table 5.3 provides the results of ISA for the 19 lichen species found in our four stand types. Five species were significant as "indicator species" for particular succession groups based on corresponding maximum indicator groups and *p-values*. *Xanthomendoza galericulata* is the only lichen that displayed faithfulness to aspen forest types (either pure or invaded). The other four species showed preference for declining (*Melanelia exasperatula* and *Usnea lapponica*) or remnant (*Bryoria fuscescens* and *Letharia vulpina*) stands. Three of four of these species preferring advanced succession forest types were of fruticose morphology, while no fruticose species were tallied on aspen stems and therefore none exhibited faithfulness for aspen forest types. Additionally, we saw that species trends differ as they progress through aspen succession classes (Figure 5.4). Transitional stand types (i.e., invaded and declining) appear to provide optimal habitat for some species, while successional endpoints favor other lichens. For example, *Bryoria fuscescens* is most associated with remnant stands and *Xanthomendoza galericulata* favors pure aspen, while *Usnea lapponica* shows a preference for declining stands over other classes. *Melanelia subolivacea* and *Physcia tenella* appear to peak in invaded aspen stand types, then level off as succession progresses (Figure 5.4).

Results of NMS ordination found three primary axes explained 78 % of epiphytic lichen variability in our study area. NMS analysis was run on a matrix of 19 species by 46 plots, with a secondary matrix of 20 environmental variables by 46 plots. A single plot was eliminated in outlier analysis due to its combined diversity and abundance values lying more than two standard deviations (Sorensen distance) from the grand mean (McCune & Mefford, 2006). Five lichen species were eliminated from the analysis due to their sparse (< 5%) occurrence on plots. The NMS ordination resulted in a 3-axes solution where the final stress and instability were 17.53 and 0.002, respectively. We assessed stability by plotting a graph of stress versus number of iterations (McCune & Mefford, 2006 PC-ORD). Stability was reached at approximately 40 iterations from a maximum of 500 iterations. Monte Carlo test results show that this 3-dimensional solution using real data was less than would be expected by chance ($p = 0.01$). The three axes explain the majority of variability in our lichen community data set: axis 1 $r^2 = 0.19$, axis 2 $r^2 = 0.48$, axis 3 $r^2 = 0.10$, and total $r^2 = 0.78$. Because of the relatively small contribution of the third axis and its unclear relation to environmental variables we will focus discussion on the two primary axes. Greater detail of these test results are found in Rogers *et al.* (2007c).

An ordination joint plot is overlaid upon the categorical variable stand type and features the results of the NMS highlighting species relationships and key environmental variables (Figure 5.5). The centroid of the graph is determined by the total tally of *all* lichen species and their abundances in relation to all other species (i.e., "species space"). Environmental variables and significant species are presented as direction and strength vectors emanating from the ordination centroid. Coefficient of determination (r) values for all environmental variables and lichen species in relation to axes 1 and 2 are listed in Table 5.4. Labeled vectors shown in Figure 5.5 are those with $r = < -0.5$ or > 0.5 in Table 5.4 for either principal axis. Generally, vector lengths and r values show that axis 2 describes the stronger of the two ordination relationships corresponding to aspen succession and lichen species richness and abundance. As expected stand type 3 and 4 plots correlate positively with increased conifer cover, but also with lichen species diversity and abundance in the upper half of the graph (Figure 5.5). In contrast, stands closer to pure aspen (stand type 1) are negatively correlated with axis 2 and strongly associated with aspen canopy cover and the aspen index score (Figure 5.5, Table 5.4).

Axis 1 describes a significant gradient of nitrophilous lichen abundance and distance from both urban and peak NH_3 centers (Figure 5.5). The unrelativized variable nitrogen abundance decreased ($r = -0.586$) with increasing distance from the local urban center ($r = 0.509$) and areas of NH_3 concentration ($r = 0.523$).

Lichen species react differently to prominent environmental gradients (Figure 5.5). *Bryoria fuscescens* ($r = 0.561$), *Letharia vulpina* ($r = 0.634$), *Melanelia exasperatula* ($r = 0.734$), and *Usnea lapponica* ($r = 0.830$), correlate positively with axis 2 and conifer cover, while *Xanthomendoza galericulata* ($r = -0.599$) correlates with increasing aspen canopy cover (Figure 5.5). Axis 1, a gradient of nitrogen loading related to distance from sources, revealed a strong link between abundance of nitrophilous species (Table 5.2) and *Phaeophyscia nigricans* ($r = -0.771$). No species had > 0.5 *r*-value for axis 1, however both *L. vulpina* ($r = 0.476$) and *M. exasperatula* ($r = 0.478$) showed moderate positive relationships with distance from pollution sources (Figure 5.5), indicating their aversion to elevated air pollution levels.

Discussion

History, climate, and aspen forest development

Our combined evidence suggests that climate and related disturbance exert the greatest influence on local forest succession, with the exception of the brief, but significant, settlement period. By extension, these successional influences have most strongly affected substrate-dependent species, such as epiphytic lichens favoring aspen. While local impacts to the forest resource began slowly after 1856, by the 1870s timber extraction increased. Peterson (1997) and Arrington (1956) both attest to the pioneer frustration with the lack of available timber, and subsequent use of alternative construction materials such as adobe to satisfy growing housing needs. "By the time adequate roads penetrated the steep canyons to the east, railroads brought other material into the valley, so local lumber was the primary Cache County building material for only a very brief time" (Peterson, 1997). Still, local impacts from timber extraction and intentionally setting fires probably increased the establishment rate of aspen stands in conjunction with the documented increase in fire occurrence (Figure 5.3a, b) (Wadleigh & Jenkins, 1996). This trend was greatly increased, however, where devastating levels of sheep grazing followed by autumn range burning coincided with severe drought conditions of the later part of the century (Figure 5.3; Gray *et al.*, 2004). While we have heretofore assumed that pioneer aspen stands arose from vegetative sprouting, periods of extensive fire followed by unusually moist spring conditions presented potential opportunities for establishment by seed (Barnes, 1966; McDonough, 1979), assuming subsequent browsing by native and domestic ungulates were kept in check. Evidence of aspen seedling establishment in alpine areas during the same general time period as shown in this study (1900-1920) focused on facilitating effects of an extended moist period following drought (Elliot & Baker, 2004). Based on PDSI reconstructions used here (Figure 5.3c), the early 20th century moist period is among the wettest periods of the last millennium for our study area. A similar pattern of drought, crown fire, and moist spring conditions characterized the noted establishment of aspen seedlings following the Yellowstone National Park fires of 1988 (Romme *et al.*, 1997), though in this instance subsequent elk (*Cervus elaphus* Linnaeus) browsing has severely diminished survival rates except where seedlings were protected from herbivores (Romme & Turner, 2004). Though empirical evidence for seedling establishment is absent here, climatic and cultural impacts in our study area around 1900 offer a likely scenario for increasing genetic diversity of local aspen.

Following establishment of the bulk of our aspen stands, there was a climate shift toward higher moisture for most of the 20th century regionally (Gray *et al.*, 2004; Millar *et al.*, 2004) and locally (Figure 5.3). We note corresponding drops in aspen establishment during this century; most prominently during the infamous 1930s drought (Figure 5.3a, b). As moisture returns there are parallel rises in aspen establishment. Dry climates favor frequent fires and vegetative reproduction, leading to aspen stand expansion, as opposed to new stand initiation from seed (Elliot & Baker, 2004). In this way, prominent past climate epochs, such as the Warm Medieval Period (Figure 5.3c), may provide useful analogues for current warming and drying trends of the early 21st century (Rogers *et al.*, 2007a).

Chronology of influences for aspen-dependent lichens

We do not know the abundance and diversity of lichens that thrived in historic aspen communities. Our results do show, however, that the four broad successional stages tested here are each important to community preservation. Combining lichen preferences for particular aspen states with knowledge of historical environmental change in the area, we can begin to reconstruct past conditions and communities. A generalized timeline of environmental and human impacts on aspen forests and aspen-dependent lichens in presented in Figure 5.6. Certainly spatial and temporal variance within these broad groupings took place. Our objective in presenting this model, however, is not to pinpoint specific conditions at a point in time, but rather to illustrate general disturbance patterns and their impact on dependent species. Further, we believe this approach will be useful in forecasting effects on aspen and the many species that depend on the unique habitat that aspen spawns.

Earlier discussion has shown dramatic historical changes in the type and amount of impacts wrought by humans over the past two centuries. A historically abrupt transformation from subsistence- to industrial-level human impacts resulted in far-reaching ecological repercussions (Rogers, 1996). We have also examined the interaction between Euro-American impacts and climatic moisture. The pre-settlement era marks the end of the Little Ice Age (c.1400-1850), a period noted not only for wetter, but also for cooler conditions (Millar & Woolfenden, 1999). Under these circumstances, aspen would be most influenced by infrequent mixed- to high-severity wildfires (Rogers *et al.*, 2007a). Coincident with a changing climatic pattern in the mid-19th century pioneers began to settle the Bear River region. Climatically, this period can be characterized as transitional between two longer trends of cool-moist and warm-moist, resulting in increasing temperatures, but most notably marked by late century drought. Because of dry conditions and greatly increased human ignitions, often intentional, fires were numerous, widespread, and intense, resulting in ample aspen regeneration (Figure 5.6). Potter (1902, p. 4) describes the situation from a prominent ridge thus:

> "On top of the ridge north of Blind Hollow there has been a serious fire many years ago which entirely destroyed the conifer forest. There is no reproduction and the area is being covered with aspens [sic.]. All of the ridges on this side of the Logan River have aspen thickets covering most of their area."

The 20th century witnessed further changes in climate and land management. In addition to the PDSI record (Figure 5.3), other authors characterize this century as being moist and warm overall for the western region (Gray *et al.*, 2004; Millar *et al.*, 2004). Prominent drought periods (1930s, 1950s, 1970s) spawned minor fires in the Bear River Range (Wasatch-Cache National Forest, unpubl. records; Peterson, 1997), but none on a scale described by earlier accounts for the settlement period (Potter, 1902; Johnson, 2006). According to recent work, fire suppression probably had less of an effect at keeping fires from spreading than did a moist climate (Buechling & Baker, 2004; Baker *et al.*, 2007). We do know that pure aspen stands may act as fire breaks due to their decreased flammability (Fechner & Barrows, 1976), except where advancing succession by conifers may reverse this effect. The most recent regional drought (c.1995-present) does not present a long enough period to assess, though continuance of this warm and dry trend would facilitate wildfires in conifer encroached stands, further stimulating vegetative regeneration in aspen (Elliot & Baker, 2004; Rogers *et al.*, 2007a).

Though fire and climate patterns have probably affected aspen stands to the greatest degree, other human impacts of the past two centuries cannot be discounted (Figure 5.6). Depletion of beaver by fur trappers during the first half of the 19th century probably impacted riparian cottonwood (*Populus angustifolia* James) most and upland aspen to a lesser extent. In contrast, resource extraction and fire ignition after settlement clearly shaped aspen successional patterns for the following century (Figure5.3a). In our landscape-level analysis all aspen stands were initiated within the past 150 years. Our estimate of conditions prior to that time is based primarily on previous dendrochronology work (Wadleigh & Jenkins 1996) and climate reconstructions (local data from Cook *et al.*, 2004; Gray *et al.*, 2004). Another attempt in the Rocky Mountains to similarly estimate pre-pioneer-burning forest cover relied on a historic vegetation map (Kulakowski *et al.*, 2004). While Kulakowski *et al.* (2004) successfully document change between two point-in-time maps (1898, 1998), they are less convincing in their characterization of conditions prior to settler burning. In our area, the time and intensity of resource extraction and ignition lasted approximately two decades, effectively obliterating clues of aspen coverage prior to that time in all but a few stands (Figure 5.3a). Intense range-wide sheep grazing during the late 19th century, in addition to removing understory and stimulating aspen suckering via burning (Schier & Campbell, 1978), would effectively keep new aspen suckers at bay until cessation of the practice (DeByle, 1985). Moderate sheep and cattle grazing in the 20th century, combined with a moist climate and fire suppression, created nearly ideal conditions for advancing succession in seral aspen stands. We found previously that only 6 % of aspen stands in our study showed signs of long-term persistence (Rogers & Ryel, 2007); a condition that would preclude some stands from short-term conifer encroachment.

Aspen may be affected directly by some air-borne pollutants (Karnosky *et al.*, 2005); however, greater sensitivity of lichens because of their dependence on atmospheric nutrients provides a harbinger of adverse effects of air quality on higher plant forms (Richardson, 1992). Köchy & Wilson (2001) found an increase in aspen stands associated with elevated nitrogen in Canadian prairie aspens stands. It is unclear what effect modern nitrogen loading will have directly on montane aspen trees, although we found significant community impact from nitrogen in the form of local NH_3 sources on dependent lichen species (Figure 5.5; Rogers *et al.*, 2007c). Further research is clearly needed in the area of large influxes of nitrogen to natural systems in the past two decades (Fenn *et al.*, 2003), including aspen ecosystems.

Our study contained equal samples of each succession-based aspen stand type (Table 5.1). The bottom portion of Figure 5.6 recreates predominant aspen conditions based on multiple lines of historic disturbance evidence. Given landscape-level preference for stand types and previous work indicating lichen affinities for succession and air quality gradients (Rogers & Ryel, 2007; Rogers *et al.*, 2007c), we give examples of those species most likely to excel under various historical scenarios. Our results based on current lichen composition indicates, for example, that very different lichen communities prefer pure aspen stands or remnant aspen stands with moderate-to-high nitrogen loading. We acknowledge, however, the real possibility of lichens being absent from the present community or those that have invaded based on advantageous situations, that may skew our estimation of past assemblage. Nonetheless, the landscape condition approach taken here gives us a starting point for reconstructing aspen-dependent communities, and perhaps a toehold for forecasting future forest cover and epiphyte composition.

Strategies for management under future climate scenarios

The ability of humans to modify their behavior based on historical missteps and scientific evidence sets them apart from other species. This feature carries great privilege, as well as great responsibility. Holling & Gunderson (2002), in outlining four stages of system development and renewal, describe disruption and reorganization as positive elements as long as they have been planned for in some way. In their scheme, forest succession is used as a prime example of the "conservation" phase – used in both natural and social systems – characterized by a long build-up of resources prior to a "release" phase (Holling & Gunderson, 2002). Widespread human impacts in our study area during the settlement era constitute an unplanned release (a.k.a., disturbance) of aspen and epiphyte communities. Generally, we now have some ability to plan for expected disturbance patterns given broad future climate scenarios. In contrast to the settlement period, we have further ecological knowledge that allows for altering behaviors that have deleterious effects.

Our current understanding enables us to project aspen response to broad climate patterns (Elliot & Baker, 2004; Rogers *et al.*, 2007a). Of course, overt human manipulations, such as timber cutting, livestock grazing, or intentional burning, may exacerbate climatic influences or operate independent of natural systems. In general, however, wet and cool climatic epochs favor extended resource build-up, followed by high intensity forest fires, potentially producing a flush of aspen regeneration. These conditions may also facilitate genetic expansion through seedling germination, although unrestrained browsing can severely limit fecundity. Conversely, warm and dry periods are characterized by frequent lower intensity fires and vegetative aspen reproduction (Elliot & Baker, 2004; Rogers *et al.*, 2007a). We have yet to explore the genetic ramifications of these two scenarios on associated lichen populations, but we can expect to see populations of *Xanthomendoza spp.* increase where pure aspen stands predominate under frequent fire scenarios (Figure 5.6).

Atmospheric pollutants from industrial and agricultural emissions have both local and global ramifications (Tillman *et al.*, 2001; Fenn *et al.*, 2003; Rogers *et al.*, 2007c). We have shown that NH_3 is an important source of nitrogen affecting lichens in aspen (Rogers *et al.*, 2007c), but other work points to the detrimental side effects of CO_2 and ozone directly on aspen (Karnosky *et al.*, 2005). While CO_2 and ozone offset each other somewhat, elevated ozone levels may further weaken aspen stands, predisposing them to infection from other pathogens (Karnosky *et al.*, 2002). Finally, recent work modeling the invasive gypsy moth (*Lymantria dispar* L.) in Utah projects significant impacts on montane aspen over the coming century with human-induced climate warming (Logan *et al.*, 2007). In sum, each of these modern pollution-based disturbances will likely have direct or cascading effects on aspen and associated lichens if they proceed unchecked. However, managers, scientists, and to a certain extent humanity at-large, can take determined steps to stave off these intrusions. Unlike past resource users, we have greater knowledge of natural systems and the ability to change course where human intrusions overreach environmental resilience.

Conclusions

Results of this work suggest strong ties between historical landscape-level disturbances and present aspen-dependent species assemblages. Lichens provided a valuable monitoring tool for community diversity and change toward establishing this relationship. As expected, canopy cover and basal area of aspen decreased with stand types over a successional continuum. As overall lichen species diversity increased with advancing succession stages, lichens favoring aspen decreased. Using ISA and visually examining individual species trends (Figure 5.4) we found lichen preferences for particular successional stages were evident, suggesting the importance of preserving successional diversity in aspen. NMS ordination confirmed the primacy of the successional gradient in determining lichen communities, but also revealed a significant gradient of nitrogen loading originating from local ammonia sources. Nitrophilous species, particularly *Phaeophyscia nigricans*, were implicated in this secondary gradient. We noted that certain "clean air species" indicators were found most often in declining and remnant aspen stands where they were usually furthest from pollution sources.

Climate reconstructions for our area mirror basic trends found in other western North American studies (Buechling & Baker, 2004; Gray *et al.*, 2004; Millar *et al.*, 2004). Prominent drought conditions that favor wildfire correlated closely with pulses of aspen regeneration during a 120 year period spanning minimum and maximum stand ages of our 47 study plots. Aspen initiation was also closely aligned with large-scale resource impacts of the late 19th century (Figure 5.3). Sheep grazing and intentional fire ignitions resulted in a prominent aspen legacy evident on the Bear River Range landscape today. During the 20th century an overall moist climate pattern, and to a lesser degree fire suppression, promoted shade-tolerant conifers. While generally advancing succession should favor lichen diversity, our data suggest that medium-distance transport (10-50 km) of local pollutants is already altering, and potentially limiting, lichen communities. Understanding the combined effects of long-term human intrusions, climate fluctuations, and advancing succession on aspen systems has allowed us to place the findings of lichen community studies in a historical context. With this knowledge we believe we are better equipped to plan for future climate and disturbance scenarios, as well as change course (e.g., allow wildfire or mitigate pollution) where our collective impacts have overtaxed local natural systems.

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Table 5.1 Sample plots are stratified by aspen succession groups and cover requirements

	Succession groups			
	Pure	Invaded	Declining	Remnant
Group code	1	2	3	4
Percent aspen tree cover	> 90	50-90	49-10	< 10
Field plots sampled	12	11	12	12

Table 5.2 Summation of epiphytic macrolichens recorded on aspen plots (*n* = 47) in the Bear River Range, Utah and Idaho. (N) designates a nitrophilous species (van Herk 1999; McCune & Jovan, 2005). (A) denotes aspen indicator species (Rogers *et al.* 2007b; Rogers & Ryel, 2007).

Species*	Freq.	% Freq.
Bryoria fuscescens	13	28
Candelaria concolor (N)	12	26
Imshaugia aleurites	1	2
Letharia columbiana	4	9
Letharia vulpina	14	30
Melanelia elegantula	45	96
Melanelia exasperatula	33	70
Melanelia subolivacea	39	83
Parmelia sulcata	1	2
Parmeliopsis ambigua	3	6
Phaeophyscia nigricans (N)(A)	38	81
Phaeophyscia orbicularis (N)	1	2
Physcia adscendens (N)	47	100
Physcia biziana	10	21
Physcia dimidiata (N)	8	17
Physcia tenella (N)(A)	24	51
Physciella chloantha	13	28
Physconia isidiigera	1	2
Usnea hirta	1	2
Usnea lapponica	24	51
Usnea spp.	1	2
Xanthomendoza fallax (N)	32	68
Xanthomendoza fulva (N)(A)	42	89
Xanthomendoza galericulata (N)(A)	47	100

Xanthomendoza montana (N)	47	100

* Nomenclature follows Brodo et al. (2001), except for recent revisions of *Xanthomendoza* (formerly *Xanthoria*) online by McCune (unpubl. key at: http://oregonstate.edu/~mccuneb/Xanthoria.PDF), who is following Lindblom (2004, 2006).

Table 5.3 Indicator Species Analysis values for species tallied by maximum score group (1 = pure aspen, 2 = invaded, 3= declining, 4 =remnant). Asterisks (*) denote significant p-values (< 0.05) by maximum score groups. Single-occurrence species have no value as indicators therefore they are not shown here.

Species	Maximum score group	Indicator value	Mean
Bryoria fuscescens	*4	46.3	16.5
Candelaria concolor	3	17.5	15.8
Letharia columbiana	4	9.8	10.1
Letharia vulpina	*4	30.6	16.9
Melanelia elegantula	4	27.4	27.0
Melanelia exasperatula	*3	33.9	25.5
Melanelia subolivacea	2	30.3	26.8
Parmeliopsis ambigua	4	11.1	8.7
Phaeophyscia nigricans	3	22.7	27.1
Physcia adscendens	3	26.4	26.0
Physcia biziana	4	12.6	14.5
Physcia dimidiata	4	11.1	13.2
Physcia tenella	2	19.2	22.1
Physciella chloantha	2	11.6	16.4
Usnea lapponica	*3	38.7	21.9
Xanthomendoza fallax	4	24.6	25.1
Xanthomendoza fulva	1	28.5	27.2
Xanthomendoza montana	3	26.0	26.2
Xanthomendoza galericulata	*1	27.8	26.2

Table 5.4 Coefficients of determination (r-values) for correlations between environmental variables, lichen species, and primary ordination axes. Variables in boldface have r-values > 0.5 or < -0.5, indicating significant influence to lichen community makeup.

		r value	
Variables	Abbreviation	Axis 1	Axis 2
Aspect		-0.006	0.074
Aspen basal area per hectare	aspBA h	-0.454	-0.427
Aspen cover	**aspcov**	**-0.121**	**-0.752**
Aspen index score	**aspscore**	**-0.471**	**-0.865**
Basal area per hectare	BA h	-0.277	0.392
Conifer cover	**concov**	**0.031**	**0.684**
Dead basal area per hectare	deadBA h	-0.107	0.377
Distance to urban (Logan)	**D_logan**	**0.509**	**0.139**
Distance to peak NH3	**D_pkNH3**	**0.523**	**0.113**
Distance to valley (Cache)	D_cache	0.237	0.111
Lichen species richness	**sprich**	**-0.062**	**0.783**
Nitrogen abundance	**N_abund**	**-0.586**	**0.140**
Nitrogen richness	N_rich	-0.366	0.376
Percent aspen damage	paspdam	0.136	0.092
Percent aspen scars colonized	pscarcol	-0.102	0.135
Percent aspen bole scarring	pbolescar	0.065	0.074
Percent nitrogen abundance	**P_Nabund**	**-0.444**	**-0.781**
Slope		0.106	0.054
Stand age	stdage	-0.402	-0.033
Total lichen abundance	**totabund**	**-0.134**	**0.746**
Lichen species			
Bryoria fuscescens	**BRFU60**	**0.007**	**0.561**
Candelaria concolor	CACO64	0.066	0.373
Letharia columbiana	LECO26	0.101	0.197
Letharia vulpina	**LEVU2**	**0.476**	**0.634**
Melanelia elegantula	MEEL5	-0.208	0.330
Melanelia exasperatula	**MEEX60**	**0.488**	**0.734**
Melanelia subolivacea	MESU61	-0.002	0.135
Parmeliopsis ambigua	PAAM60	0.031	0.345
Phaeophyscia nigricans	**PHNI5**	**-0.771**	**-0.145**
Physcia adscendens	PHAD60	0.129	0.164
Physcia biziana	PHBI6	-0.246	-0.057
Physcia dimidiata	PHDI12	-0.082	0.179
Physcia tenella	PHTE60	-0.239	-0.006
Physciella chloantha	PHCH4	-0.292	-0.113

Usnea lapponica	USLA60	0.270	0.830
Xanthomendoza fallax	XAFA	-0.385	0.490
Xanthomendoza fulva	XAFU	0.236	-0.302
Xanthomendoza galericulata	**XAGA**	**-0.409**	**-0.599**
Xanthomendoza montana	XAMO60	-0.007	0.047

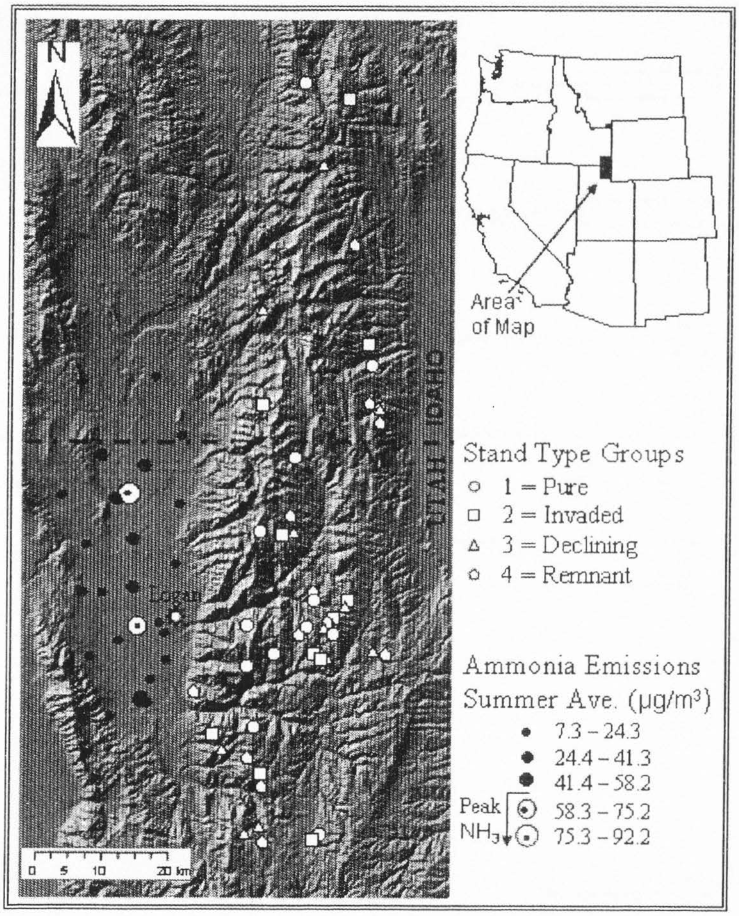

Figure 5.1 Study area that includes location of 47 lichen sampling plots, their stand type designations, ammonia (NH_3) monitoring stations, and the local urban center, Logan, Utah.

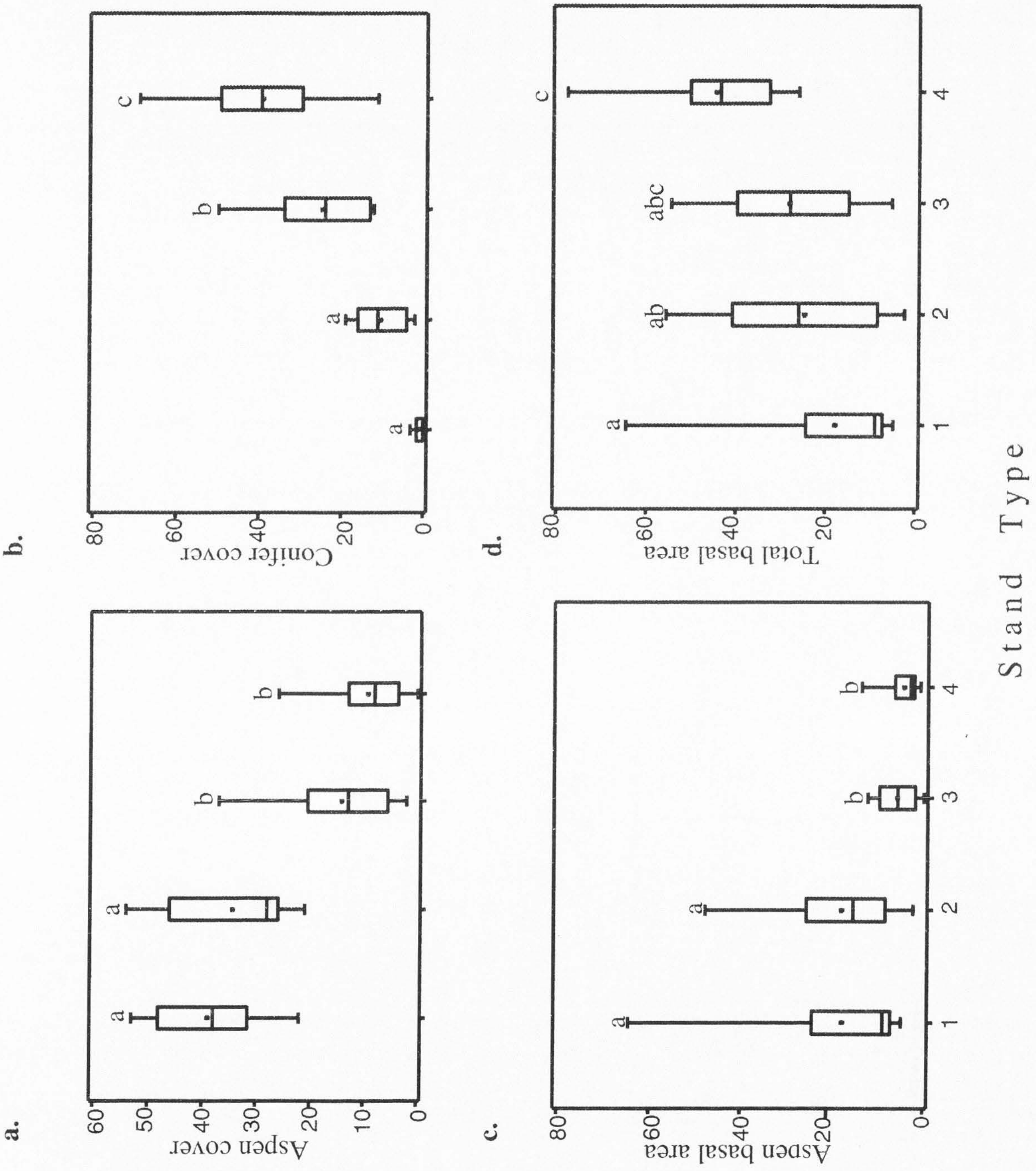
a.
Aspen cover
0
10
20
30
40
50
60
a
a
b
b
b.
Conifer cover
0
20
40
60
80
a
a
b
c
c.
Aspen basal area
0
20
40
60
80
a
a
b
b
1
2
3
4
d.
Total basal area
0
20
40
60
80
a
ab
abc
c
1
2
3
4
Stand Type

Figure 5.2 Stand structure trends over four aspen successional classes (stand types, see Table 5.1) for: (a) aspen cover, (b) conifer cover, (c) aspen basal area (m^2), and (d) total basal area (m^2). The dot inside the box symbolizes the mean by stand type, while the bottom and top of the box represents the 25th and 75th percentiles, respectively. The horizontal line inside each box is the median value. Whiskers represent extreme observations (variance). Bars with the same letter represent quantities that are not significantly different (Tukey-Kramer, $p<0.05$).

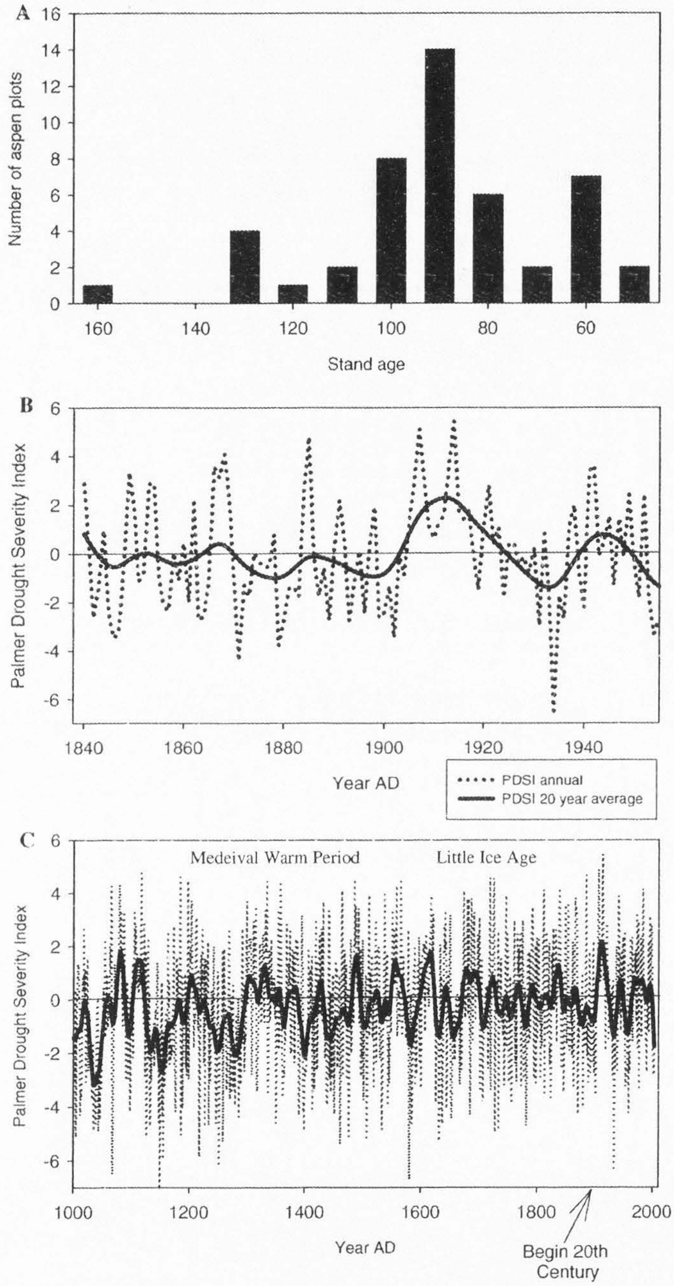

Figure 5.3 Aspen stand ages and climate pattern for the study area in northern Utah and southern Idaho, USA: a) shows all aspen stand ages for 47 stands in the study area; b) a composite120-year Palmer Drought Severity Index (PDSI) reconstruction from four continental grid points surrounding the study area (Cook *et al.*, 2004); c) composite 1000-year PDSI reconstruction using the same geographic grid points as 3b above. Figure 5.3a and 5.3b are aligned by

year for comparison of aspen establishment and climate trends. The 1000-year reconstruction (3c) gives approximate temporal locations for the Little Ice Age and the Medieval Warm Period for reference.

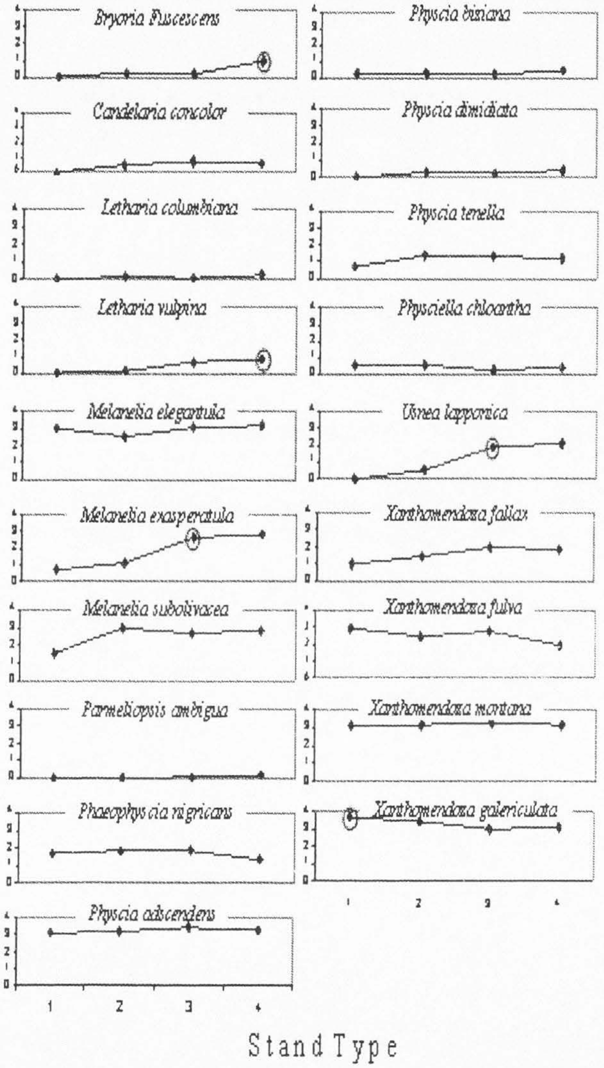

Figure 5.4 Line charts of lichen species occurring multiple times in the study area. Nodes are average abundance scores for species by stand type. Circles around individual nodes denote significant ($p < 0.05$) preference for specific stand

types in Indicator Species Analysis (see Table 5.3). Stand types are defined in Table 5.1 above.

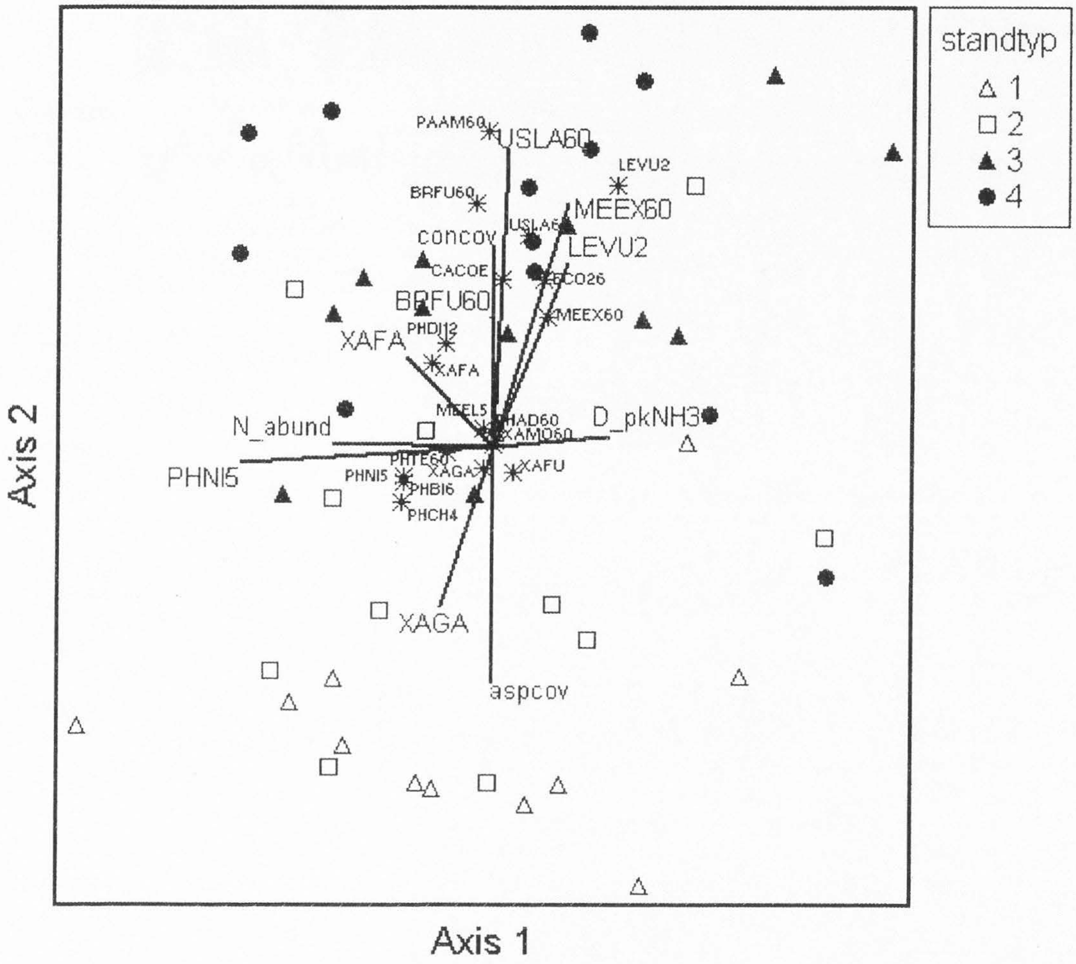

Figure 5.5 Ordination joint plot with significant lichen species (r < -0.5 or > 0.5) plotted as vectors and all species locations in the ordination shown as asterisks (*). Vector directions and lengths designate correlations with the ordination in species space. Select significant environmental variables (concov, aspcov, N_abund, D_pkNH3 – see Table 5.4 for abbreviations) are included to enhance discussion. Stand types correspond to stratification by successional groups (Table 5.1).

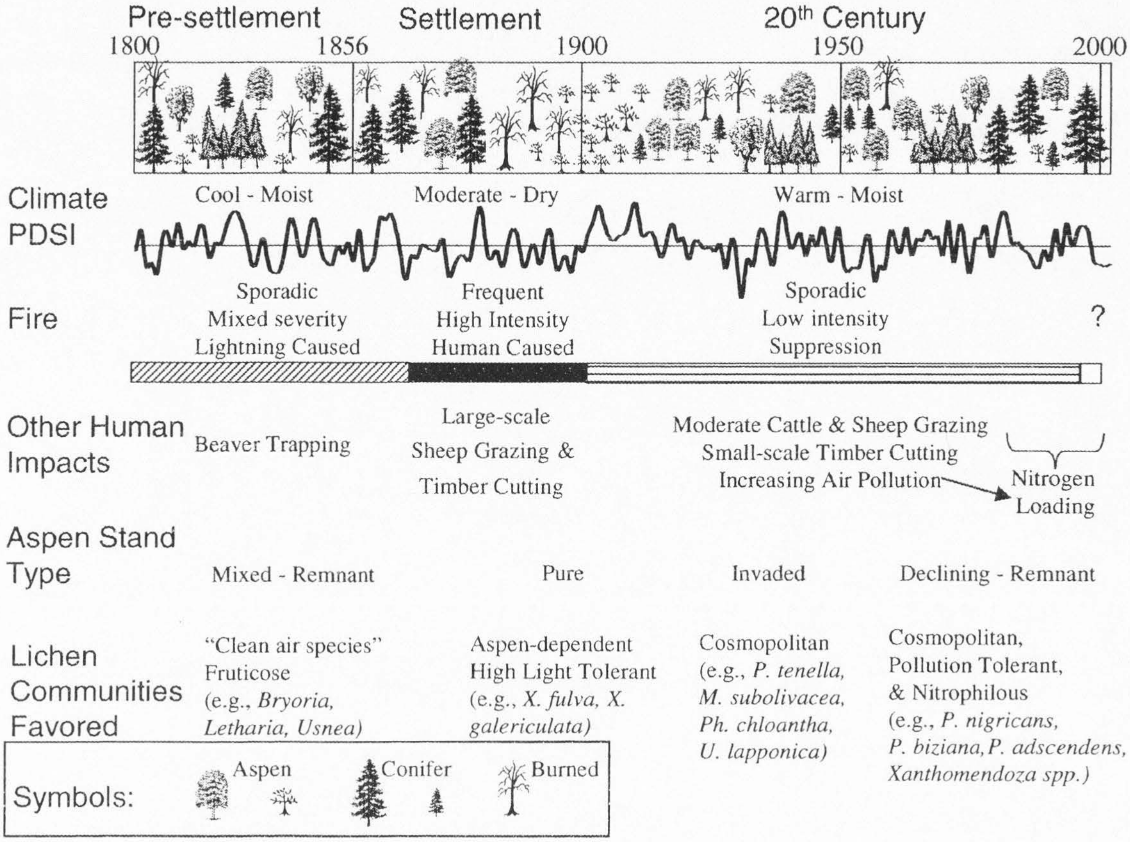

Figure 5.6 A generalized timeline of prominent forest, climate, disturbance (e.g., fire & human impacts), succession, and lichen community conditions over the last 200 years in the study area. Palmer Drought Severity Index (PDSI) is calibrated to this time period and follows the same index displayed in Figure 5.3b, c (Cook *et al.*, 2004).

CHAPTER 6

SUMMARY AND FUTURE RESEARCH

This dissertation has taken a logical course from simple to complex, from narrow to broad in scope. We started by examining lichen affinities for particular tree types and concluded with past and future projections of aspen and lichen communities. Though significant headway was achieved, naturally there is considerable work to be done in this field. The following paragraphs will touch on the high points of previous chapters. The second portion of this summary will explore future research topics related to the work conducted here.

Chapter summaries

The main objective of Chapter 2 was to distinguish between lichen communities on aspen and conifer substrates. A secondary goal was to obtain preliminary knowledge of lichen communities across the study area. Results of Multi-response Permutation Procedures (MRPP) showed no real differences between broad geographic zones from north to south in the Bear River Range. We did, however, establish statistically different communities between the two principal tree types, aspen and conifers, using a blocked MRPP (MRBP). In terms of lichen species, results of Indicator Species Analysis (ISA) found that three species, *Phaeophyscia nigricans*, *Xanthomendoza galericulata,* and *X. fulva*, were most faithful to aspen ramets. Three other species, *Melanelia exasperatula, M. subolivacea*, *Xanthomendoza montana*, showed statistical preference for conifer stems. About half of the lichen species in the study area with sufficient sample populations showed no preference for either conifers or aspen. Narrower sampling protocols (i.e., tree-level and transect sampling) used here produced fewer species than the landscape survey (Chapter 3) with sufficient sample sizes for statistical significance in ISA (i.e., stand-level sample used in subsequent chapters enables greater species capture). This tree-level experiment provided basic information on lichen species preferences for substrates that was valuable to the more extensive stand-level survey that followed.

Chapter 3 was designed to evaluate the effects of succession in aspen on epiphytic lichen communities. There are several related issues that accompany the broader theme of succession, such as stand age, tree canopy cover, regeneration/conifer invasion, and the onset of disease and bole scarring. We boiled these issues down to three basic objectives: study-wide lichen diversity, assessing effects of succession, and determining successional stage importance to overall lichen community diversity. First, we found 24 epiphytic macrolichens on mid-elevation plots with aspen present in the study area. Compared with other regions of the U.S. (Conkling et al., 2005) this is a relatively low diversity number for forested environments. Second, our focus on general successional trends yielded a clear picture of lichen diversity increasing and aspen-dependent lichens decreasing with advancing succession. An aspen index score proved valuable as a means of summarizing several lichen species reactions to successional trends and may be useful for future monitoring in Rocky Mountain aspen. Strong linkages were not found between lichen community trends and stand ages. Contrary to expectations, we found causality and levels of aspen bole scarring and levels of scar colonization were unrelated to lichen community composition. Third, definite preferences were revealed among lichen species, using ISA and trend visualizations, for each of the four succession classes used in our study design. Pure aspen stands favored *Xanthomendoza galericulata* and *X. fulva*, invaded *Melanelia subolivacea* and *Physcia tenella*, declining *M. exasperatula* and *Usnea lapponica*, and remnant *Bryoria fuscescens* and *Letharia vulpina*. This final conclusion argues for the importance of preserving a mosaic of successional classes on future landscapes to maintain species diversity.

In Chapter 4 we conduct a deeper investigation using multivariate analysis of factors explaining lichen diversity in aspen forests undergoing encroachment from conifers. We found that analysis of covariance was limited in its ability to uncover causality, but that results from this initial analysis confirmed the primacy of succession and pointed to air quality as being an important contributing factor. Nonmetric multidimensional scaling (NMS) ordination, however, allowed us to make a thorough analysis not only of numerous environmental factors, but also of lichen species relationships to these same factors and other species. Once again, forest succession seemed to be the strongest factor in explaining lichen community variation. Results of NMS suggested both a general pollution gradient and an ammonia/nitrogen (NH_3/N) gradient in relation to adjacent valley sources. NMS results and ordination joint plots illustrated several trends: 1) lichen species richness and total abundance were positively associative with conifer cover and negatively correlated to an aspen index score (see Chapter 3) and aspen canopy cover; 2) total abundance of nitrophilous lichens was strongly negatively correlated to distance from a local urban center and peak sources of

NH_3; 3) the lichen most strongly associated with increasing conifer cover was *Usnea lapponica* (all fruticose lichens showed this trend), and *Xanthomendoza galericulata* was mostly closely aligned with aspen cover; 4) *Phaeophyscia nigricans* proved to be a strong indicator of N-loading in montane forests at 10-60 km from peak local sources; 5) depletion of acid-loving lichen species (e.g., *Letharia spp.*) in the study area may already be well underway as a result of NH_3-related nitrogen deposition.

Chapter 5 places the focused experiments of previous chapters into a broader context of aspen change since Euro-American settlement. We investigated human impacts on Bear River Range forests and incorporated climate reconstructions into our analysis of landscape-level disturbance on aspen and associated lichen communities. Early settlers had little large-scale influence on forests, but by the late part of the 19th century widespread human impacts associated with grazing and intentional burning, coupled with a 20-year drought, resulted in ample opportunities for aspen stand initiation. The 20th century was characterized by shifts in climate and forest policy. Increased moisture in the region supplemented fire suppression efforts resulting in conditions favoring shade-tolerant conifers. Based on work from Chapters 3 and 4 and historical sources used here, we constructed a generalized chronology of aspen and lichen trends for the study area and speculated on future climate scenarios favoring specific aspen and lichen communities. Though forests have been generally moving toward conifer dominance (i.e., declining and remnant types) locally degraded air quality may confound trends toward increased lichen diversity. If the most recent drought persists, we may see increased wildfire leading toward creation of more pure aspen stands and increasing aspen-dependent lichens. However, warming climate trends may favor further exotic invasions and atmospheric pollutants directly threatening aspen and dependent species at a regional level. Consideration of past climate-disturbance-vegetation interactions, such as those raised here, will help scientists and policy-makers prepare for these and other future management scenarios.

Future research

My work has touched off a number of opportunities for future inquiry. For example, effects of N-loading on montane ecosystems in our region has been little investigated with the advent of new and large sources (Fenn et al., 2003b). Germane to this dissertation, can we distinguish between these regional sources of N (i.e., NH_3/ammonium NH_4) and local connections documented herein? An experiment establishing regional and local N transects using lichens present on a single tree substrate (aspen) may address this question. Use of a single tree species eliminates a host of confounding factors such as more variable bark pH, texture, and moisture (van Herk, 1999). Bark sampling of aspen along transects for chemical and pH fluctuations may further crystallize our understanding of N-loading on these systems.

Our use of lichens in the present study is as a monitoring tool to elucidate broader impacts on aspen systems. In the case of N-loading, there is the strong possibility that relatively recent increases in nitrogen are affecting other plant communities at a variety of scales (Tilman et al., 2001; Fenn et al., 2003a). In fact, research in Alberta's parklands has suggested direct impacts in the form of aspen expansion near sources of elevated nitrogen (Köchy and Wilson, 2001). We do not know how increased nitrogen influences montane aspen or the many floral and faunal species found in this environment. A multifaceted approach involving chemical testing of soils, aspen and conifer bark and foliage, ubiquitous vascular plants and lichens, and spatial analysis documenting areas of recent aspen expansion (or not) and distances to local and regional sources will provide a starting point for this work.

Air pollutants related to acid deposition have proven deleterious to lichen communities, but may be declining in influence as NH_3/NH_4 impacts are on the rise (van Herk et al., 2003; Jovan and McCune, 2005). As communities consider building new coal-fired power plants and cleaning up older industrial sources (including power plants) of nitrogen dioxide (NO_2) and sulfur dioxide (SO_2) it may be beneficial to remeasure lichen monitoring points near industrial sources (Peterson and Neitlich, 2001), many of them in montane aspen-conifer forests, to document recovery (or not) of these systems.

In our study area we are plagued with climatic inversions that trap small particulates (PM 2.5) in the air in the low-lying Cache Valley during winter months. Some lichen species, such as *Xanthomendoza spp.*, are known to bloom on multiple substrates as a result of excess dust and other air-borne particles (Rosentreter, 1990). Affects on human health have focused much of the attention of PM 2.5 impacts on valley residents. While casual observation of urban lichens shows high and nearly exclusive *Xanthomendoza spp.* communities, there is a dearth of information on particulate impacts in adjacent wildlands.

Another area of possible lichen-aspen exploration is the genetic perspective. Researchers at Utah State University (Karen Mock, genetic researcher, personal communication.) have established an intensive landscape grid to determine size of local aspen clones. Genetic differences in bark chemistry, bark smoothness and scarring, palatability of stems to wildlife (resulting in scars), or other genotypic-related factors may influence lichen species colonization. Ordination analysis conducted on stand-level lichen inventories of aspen may reveal important genetic traits favoring epiphytic assemblages or species. I am unaware of investigations to date of this nature on aspen in western North America.

Finally, in terms of lichen-associated work related to the present study, a range wide inventory of epiphytic lichens is desirable. Work conducted for this study was limited to a 350 m elevation zone to limit large-scale effects of moisture associated with altitude (Chapter 3 methods). Also, no plots sampled riparian habitat where greater moisture and additional tree substrates would likely increase lichen diversity. Expanded field sampling at all elevations and moisture regimes would provide a better backdrop for more focused lichen-based research in the study area. Additionally, the Utah State University herbarium wishes to enhance their currently deficient lichen collection (Mary Barkworth, herbarium director, personal communication).

Questions related to aspen ecology more generally abound. Briefly, a current Rocky Mountain region-wide episode of sudden aspen mortality is fueling considerable speculation of causality and methods needed for documentation of this alleged phenomenon. Once again, climate induced drought is at the forefront of prospective culprits, but there are likely connections to historical disturbance and recent management that may be further explored. Another avenue of aspen research related to air pollution issues is ozone (O_3) damage to foliage. A national forest monitoring system uses aspen as an ozone bioindicator (Coulston et al., 2003), but there is little evidence to support leaf injury from O_3 in dryer western forests. In eastern forests, intensive field-based O_3 fumigations have yielded detailed knowledge of effects from O_3 and elevated carbon on aspen physiology (Karnosky et al., 2005). A western extension of this work is needed, as there are likely differences associated not only with regional climate, but with possible genotypic differences in widely disparate aspen populations. Follow-up in any of these potential research areas will be beneficial to the management, monitoring, and academic arenas.

Ecological analyses found within this dissertation have revealed novel connections between dominant forest cover and dependent species. As earlier noted, direct impacts on aspen have cascading effects on associated lichen species, but lichens are also affected directly by anthropogenic intrusions, such as air pollution. As climatic and human influences have changed in our recent history the interactions between aspen, conifers, and substrate-dependent lichens have shifted concurrently. While these lines of inquiry are in their infancy, further investigation into the multiple factors affecting aspen systems are needed to facilitate greater scientific understanding and more informed land management.

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APPENDIX

July 2, 2007

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Dear Kori D. Moore:

I am in the process of preparing my dissertation at Utah State University. I hope to complete in the summer of 2007.

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9 May 2007

To Whom It May Concern:

This letter is to confirm that Paul Rogers has permission to reprint, as a part of his Ph.D dissertation, a manuscript that has been accepted for publication in Evansia. Evansia is a peer-reviewed, quarterly journal published by the American Bryological and Lichenological Society (ABLS). The manuscript is currently scheduled for publication in the 24(2) issue of Evanisa to be distributed at the end of June this year. If you have further questions or concerns please feel free to contact me directly.

Best wishes,

Larry L. St. Clair
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CURRICULUM VITAE

Paul C. Rogers
(July 2007)

CAREER OBJECTIVE:

To attain a professional position in the study of human impacts on vegetation at landscape and regional scales.

EDUCATION:

BS in Geography, minor in History at Utah State University (1983)
Emphasis in Physical Geography, courses in geomorphology, meteorology, geology.
Specialties; Western U.S. and cartography.

MS in Geography, minor in Cartography at University of Wisconsin – Madison (1986)
Specialties; Physical Geography, geomorphology, alpine environments, wildland management, and remote sensing

PhD in Forest Ecology at Utah State University (2007)
Specialties; Aspen ecology, lichen monitoring, biogeography, disturbance ecology, and international large-scale forest monitoring.

EXPERIENCE:

Technical Writer/Editor Management and Engineering Technologies International (2004-2006).
* Conduct library searches and maintain bibliographic database on all aspects of aspen ecology for project reference.
* Authored major sections in a comprehensive synthesis of aspen ecology (see Shepperdet al. 2006 below).
* Project editor, including assembly/organization of all text, photos, figures, tables, and appendices.
* Manage project communications and maintain electronic manuscript files and backup systems.
Ecologist U.S. Forest Service, Rocky Mountain Research Station
(June 1992-2004)
* Forest Inventory and Analysis analyst: analyze data, compile reports, review forest health indicators and issues.

* Forest Health Monitoring Regional Analyst: analyze and publish data on issues in the Interior West.
* Train and supervise interdisciplinary research crews (6-20 people) for field work in AZ, UT, NV, CO, ID, WY.
* Plan, budget, and manage field work and personnel to collect ecological field data for a multi-state program.

Forestry Technician U.S. Forest Service, Rocky Mountain Research Station
(June 1988-May 1992)
* Conduct forest inventory, including plant I.D., mensuration, and multiple resource evaluations (MT,ID,UT).
* Supervise field and aerial photo interpretation crews.

Naturalist/Instructor Max McGraw Wildlife Foundation, Dundee, Illinois
(February-May 1989)
* Design and conduct natural history learning sessions for all ages.
* Assisted in wildlife research projects and prescribed burning.

Biological Technician U.S. Forest Service, Bridger-Teton National Forest
(June-Nov. 1987)
* Mapped grizzly bear habitat by field I.D. of plant species.
* Digitized all road and timber sale maps for forest.

Cartographic Aid U.S. Forest Service, Payette National Forest
(August-October 1986)
* Compiled watershed maps of select forest watersheds.
* Digitize land-type and road maps for forest plan.

Project Assistant Environmental Remote Sensing Ctr., Univ. of Wisc.-Madison
(September 1985-July 1986)
* Ordered aerial photos of hazardous waste sites
* Searched and updated computer base project bibliography.
* Digitized aerial photos for color sequencing, enhancement, and analysis.

SKILLS:

Computers:
* Knowledge of Pascal, Basic, Fortran.
* Word processing and bibliographic databases.
* Use of SAS, SPSSx, PC-ORD, Access.
* ArcMap GIS for publication and analysis.

Communication:
* Public speaking and instruction of technical information.
* Employee relations and supervision.
* Professional publication of scientific material.
* Large-scale program planning and organization.

TRAINING, SEMINARS, MEETINGS

* 6th North American Forest Ecology Workshop, Vancouver, BC. Presenter: “Change in aspen dependent species with succession: the case for epiphytic macrolichens as indicator species,” June 18-22, 2007.
* PC-ORD (software for ordination of ecological community data) training seminar, Portland, OR, May 2006.
* Managing Aspen in Western Landscapes Conference, Cedar City, Utah, Presenter: “Using forest inventory data to assess aspen health in Utah,” Sept. 22, 2004.
* 89th Ecological Society of America Meeting, Portland, Oregon, Presenter: “Monitoring statewide aspen community health with extensive inventory data in Utah,” August 1–6, 2004.
* 4th North American Forest Ecology Workshop, Corvallis, Oregon. Session Chair: “Inventory, Monitoring, and ChangeDetection,” June 16-20, 2003.
* 3rd North American Forest Ecology Workshop, Duluth, Minnesota. Session Chair: “Using inventory and monitoring data toevaluate forest change,” June 30-July 1, 2001.
* International trainer, Forest Health Monitoring field methods and analysis: Belarus (1995), Kenya and Tanzania (2001, 2002, 2006)
* 2nd North American Forest Ecology Workshop, Orono, Maine. Presenter: “Forest health and aspen decline in the Southern Rockies ecoregion,” June 27-30, 1999.
* National Forest Health Monitoring Workshops 1996-2000, 2002, 2004. Reporting and analysis focus group chairman (‘96-98) and paper presentation (‘98,’99,’02).
* Disturbance Ecology Center Detail (2 months), USDA Forest Service, Rocky Mountain Research Station, Logan, Utah and Utah State University. January-February 1995.
* Pollution Bioindicators Workshop, Research Triangle Park, NC, Dec.1994.
* Fire Danger and Forest Health Conference, Spokane, WA, Sept. 1994.
* Lichen Indicator National Trainers Training (Forest Health Monitoring), Portland, OR, May, 1994; Tucson, AZ, (’02-’04).
* Quality Assurance, Quality Control Meeting (Forest Health Monitoring), Las Vegas, NV, April, 1994.
* Statistical Applications Training (Office of Personnel Management), Seattle, WA, Jan. 1994.
* Landscape Ecology Graduate Seminar (Dr. John Bissonette), Utah State University, Fall 1992.

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