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Chapter 2

HISTORICAL PATTERNS IN LICHEN COMMUNITIES OF MONTANE QUAKING ASPEN FORESTS

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ABSTRACT

Climate shifts and resource exploitation in Rocky Mountain forests have caused profound changes in quaking aspen (*Populus tremuloides* Michx.) structure and function since Euro-American settlement. It therefore seems likely that commensurate shifts in dependent epiphytes

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would follow major ecological transitions. In the current study, we merge several lines of inquiry to investigate historical changes using lichens as bioindicators of forest structure, air quality, and community composition. Though lichens are well known for their sensitivity to air borne pollutants, recent utilization in the monitoring realm has lead to novel uses as indicators of biodiversity and stand composition. A landscape-level investigation in northern Utah and southern Idaho, USA, was implemented to track contemporary and long-term impacts of humans on aspen forests and their dependent macrolichens. We use historical sources, climate data, fire records, and passive ammonia sensors alongside forest and lichen monitoring techniques to gain further insight into aspen and epiphytic lichen community change over the past 150 years. Our research shows that historic drought conditions correlated closely with pulses of aspen regeneration during this period. Aspen initiation was closely aligned with large-scale resource impacts of the late 19th century. During the 20th century a moist climate pattern generally favored shade-tolerant conifers. Additionally, results from nonmetric multidimensional scaling (NMS) ordination indicate a primary successional gradient in determining lichen communities, but also revealed a significant gradient of more recent impacts from nitrogen loading originating from local ammonia (NH₃) sources. While advancing succession generally favors lichen diversity, our findings suggest that medium-distance transport (10-50 km) of local air pollutants is already contributing to altered lichen communities. Overall, there are strong ties between landscape-level disturbance history and present aspen-dependent species assemblages. Effects on the epiphytic community are viewed as symptomatic of greater biodiversity and ecosystem impacts.

Keywords: Aspen, *Populus tremuloides*, lichens, climate, nonmetric multidimensional scaling, Rocky Mountains, monitoring, historical accounts, nitrogen loading, ammonia.

INTRODUCTION

How have forests changed over time in response to interactions of climate and human impacts? While this is a common question of ecological interest, the complexity of monitoring large landscapes for multiple influences over long time periods can be daunting. Nevertheless, numerous authors addressed these concerns in the context of quaking aspen (*Populus tremuloides* Michx.) forests of North America (Kulakowski *et al.*, 2004; Elliot and Baker, 2004;

Shepperd *et al.*, 2006; Brown *et al.*, 2006; Rogers *et al.*, 2007). While these studies place a premium on aspen dynamics through time and across landscapes, we wonder how aspen-dependent species will be affected by changes in dominant forest canopy. Further, we seek sensitive landscape indicators to help answer these multifaceted questions.

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 and Ryel, 2008; Rogers *et al.*, 2009). 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 and McCune, 1997; McCune, 2000; Pykälä, 2004). Lichen conservation efforts related to European aspen (*Populus tremula*) communities in Sweden has highlighted the importance of this tree in conservation of epiphytic diversity (Esseen *et al.*, 1996; Hedenås and Ericson, 2000). North American research highlighting aspen's epiphytic contributions to forest diversity have lagged behind European efforts (Rogers and Ryel 2008). We are unaware of work linking specific past landscape disturbance to present lichen species and community preferences.

While other fauna and flora may be somewhat dependent on aspen as a "keystone species" (Campbell and 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 (Barkman, 1958; Martin and Novak, 1999). For example, a common driver of stand-level lichen diversity is the number of tree species and general preferences for hardwoods and softwoods. In mid- to upper-elevation Rocky Mountain forests aspen is the primary, and often the only, hardwood present in landscapes dominated by softwood species.

Our objectives are, a) to build a historical and climatic chronology of aspen forests in the study area over the 150 years, b) to specifically relate successional and anthropogenic changes to aspen-dependent lichen communities, c) to advance strategies for management of aspen-dependent species under future climate scenarios. We will draw on a landscape survey of aspen forest structure and epiphytic lichens therein (Rogers and Ryel, 2008), an ammonia monitoring network for the adjacent valley (Rogers *et al.*, 2009), climate reconstructions, fire records, stand ages, and historical accounts since Euro-American settlement to address the stated goals. 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 should be informative to monitoring professionals, lichen specialists, aspen ecologists, conservationists, and land managers addressing future climate scenarios.

METHODS

Study Area

Our study area encompasses the Bear River Range in northern Utah and southern Idaho (Figure 1). These mountains are of block fault origin and trend in a north-south direction, approximately 120 by 30 km, with a total area of about 3,300 km². 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 northwestern portion of this ecoregion experiences summer drought without a seasonal southern moisture flow. Summer 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 consists 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).

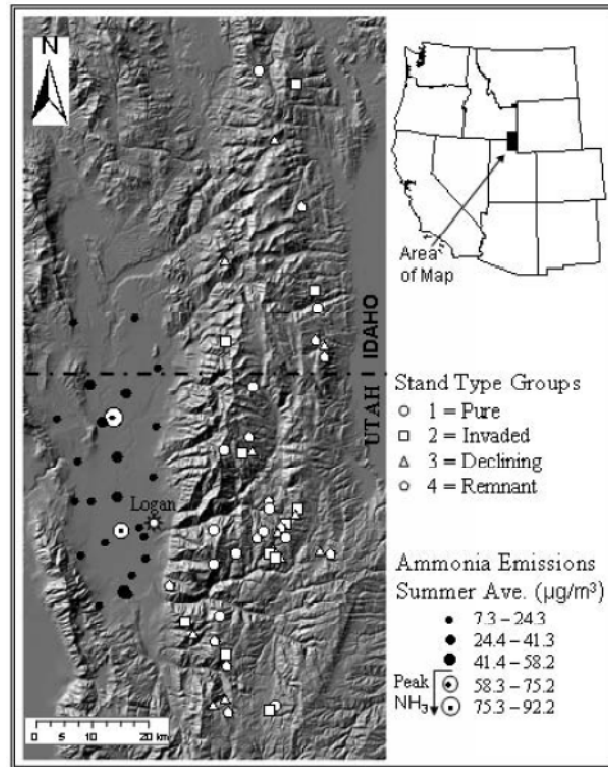


Figure 1. Study area that includes location of 47 lichen sampling plots, their stand type designations, ammonia (NH_3) monitoring stations, and the local urban center, Logan, Utah.

Landscape Aspen And Lichen Survey

We selected 47 field plots stratified by four successional groups (stand types) of aspen using Utah and Idaho vegetation cover maps (USGS, 2004; USGS, 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. Aspen grow above and below these elevations, but we wished to sample optimal growing conditions and avoid limitations on aspen-related lichens such as desiccation from lack of available moisture (low elevation) or exposure to wind (high elevation). Plots were stratified based on aerial photographic interpretation into four stand types based on aspen canopy cover:

1) pure, 2) invaded, 3) declining, and 4) remnant aspen (see Table 1 for group criteria; Figure 1). Further detail of the plot selection procedure may be found in Rogers and Ryel (2008).

Table 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

An independent set of ammonia (NH_3) monitoring sites were located throughout the adjacent Cache Valley, Utah and Idaho (Figure 1; Rogers *et al.*, 2009). During June and July of 2006, 25 gas-phase ammonia samplers were loaded with pads pre-coated with a citric acid solution and were deployed to yield a spatially resolved representation of ambient ammonia concentrations near potential sources. 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.

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 location 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. 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). Aspen tree rings are often difficult to accurately count owing to their faintness. Thus, potential sources of error (Campbell, 1981) in aging aspen were addressed in the field by a.) re-boring trees when the pith was not encountered; b.) moistening cores before counting; c.) viewing faint tree ring cores using direct sun as backlighting (this highlights translucent spring wood and increases contrast with the darker late-season wood); and d.) examining cores with a hand lens to discern narrow rings. We added five years to the mean cored age of all aspen

trees on plot to account for a reasonable estimate of time needed to reach breast height (Rogers *et al.*, 2010).

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 and 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). The entire plot area was systematically examined for presence of epiphytic macrolichens 0.5 m above the forest floor for up to two hours. The 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. Lichen sampling may not exceed two hours. We found an average of 60 – 75 minutes were required for the survey in our relatively dry 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 and Lesica, 1992). 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.

The advantage of a macrolichen survey approach is ease of training general field personnel, continental-scale standardization, and ability for results comparison (McCune 2000; Will-Wolf 2002), while a potential disadvantage is missing other functional lichen groups, such as microlichens (Ellis and Coppins, 2006). While there is certainly potential for distinction in microlichens for habitat and pollution sensitivity, there is currently little available data in our area asserting their ecological function. In contrast, numerous studies have addressed functional differences within macrolichen communities (Hedenås and Ericson, 2000; Jovan and McCune, 2006; Neitlich and McCune, 1997; Pykälä, 2004; Rogers *et al.*, 2009; van Herk, 1999).

Several derived variables related to the lichen survey were determined following data collection. We measured the distance from each plot to peak NH₃ 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 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 and McCune, 2006).

Table 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 and Jovan, 2005) (A) denotes aspen indicator species (Rogers *et al.* 2007b; Rogers and Ryel, 2007)

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

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 large 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 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, 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/stand type combination is greater than that found by chance. Output includes the stand type 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 and Ryel 2008; Rogers *et al.* 2009), 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 and 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 related to the areas of concern above. 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 of 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 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 *et al.*, 2002).

HISTORIC AND DATA OUTCOMES

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 influence on vegetation—correlating loosely with Native American density and distance from settlements—at higher elevations in the Rocky Mountains (Baker, 2002). Euro-American fur trappers, although mostly transitory in nature, nearly extirpated native beaver (*Castor canadensis* Kuhl) populations (Hovey, 1956), which relieved many riparian aspen stands of a common herbivore for at least two decades (c. 1820 – 1840 AD). Effects of beaver forage appear to be limited beyond 100 m from their “central place” (i.e., water source/domicile; Johnston and Naiman, 1990); thus, it unknown what longer term and larger scale impacts temporary extirpation 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). For a brief period 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 easily accessible timber was depleted and lumber imports from the West Coast, accompanying rail access, became more economical (Peterson, 1997). Potter (1902, p.9) 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 both region-wide and locally (Potter, 1902; Hoxie, 1910; Bird, 1964; Cermak, 2005), which accounts for more frequent fire intervals in the Bear River Range of the late 19th century (Wadleigh and Jenkins, 1996). Historical sources also confirm the exacerbating effect of a late 19-century regional drought on an overly taxed mountain ecosystem (e.g., Johnson, 2006). Potter’s (1903) 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 even 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, unpubl. records).

Stand Structure and Climate Data

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, $F = 28.81$, $p < 0.0001$) and total basal area (ANOVA, $F = 5.80$, $p = 0.002$) increased with stand type progression. Mean canopy cover and basal area values by stand type depict successional trends in aspen (Figure 2). 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 had hypothesized.

In addition to testing overall stand age linkages to stand structure and lichen variables, we attempted 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 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 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 3c). This figure indicates the early 20th century is among the wettest periods of the last millennium.

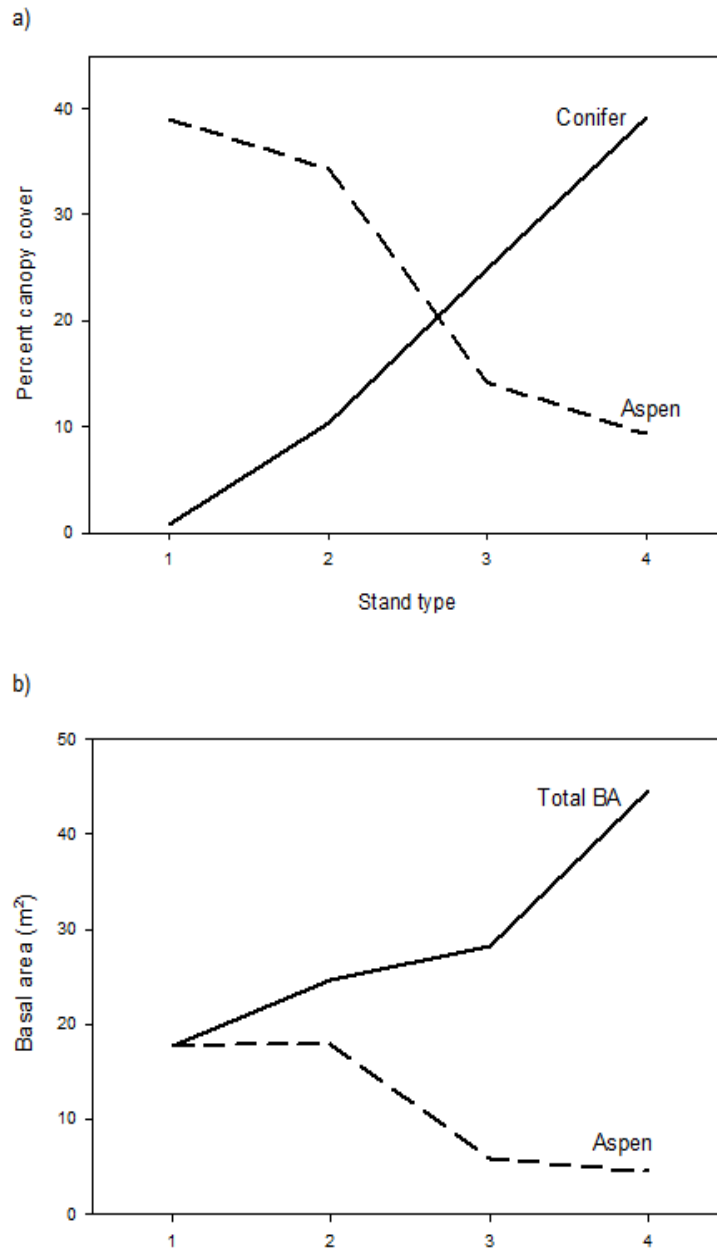


Figure 2. Stand structure trends using mean values over four aspen successional classes (stand types, see Table 1) for: a) percent canopy cover and b) basal area (m²).

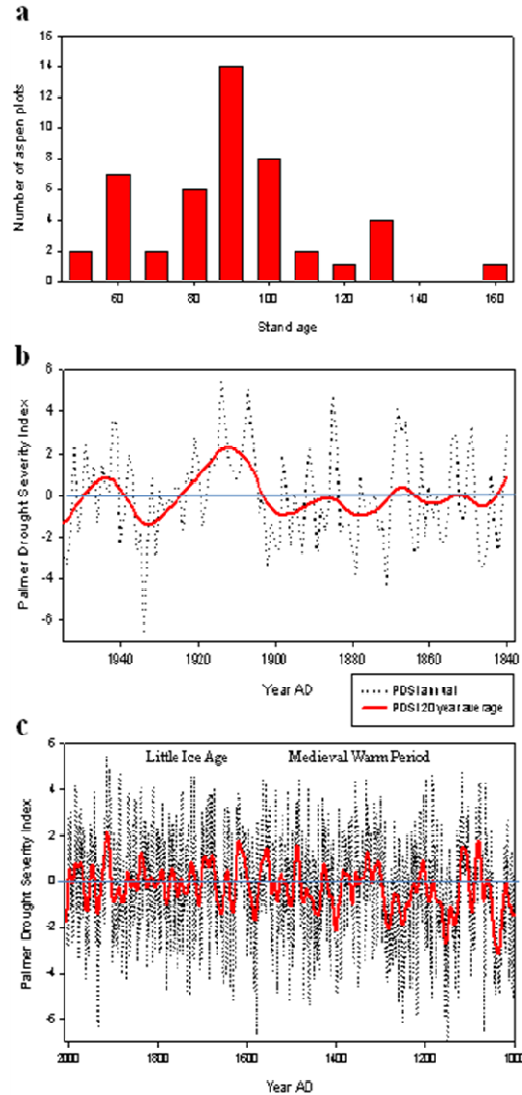


Figure 3. Aspen stand ages and climate patterns for the study area in northern Utah and southern Idaho, USA: a) shows all aspen stand ages for 47 stands in the study area; b) a composite 120-year Palmer Drought Severity Index (PDSI) reconstruction from four continental grid points surrounding the study area (Cook *et al.*, 2004); c) composite 1000-year PDSI reconstruction using the same geographic grid points as 3b above. The horizontal axis for each graph reads (left to right) from most recent to oldest in years. Figs. 3a and 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.

Lichen Community Analysis

Indicator Species Analysis results suggest significant preferences by lichen species for specific levels of aspen coverage (Rogers and Ryel, 2008). Table 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 (i.e., conifer forest types). 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 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 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 (PC-ORD, v.5, McCune and 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. The two primary axes explain the majority of variability in our lichen community data, thus we will focus our discussion there. Greater detail of these test results are found in Rogers *et al.* (2009).

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

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).

The centroid of the graph is determined by the tally of all lichens in the primary matrix and their abundances in relation to all other species (i.e., “species space”).

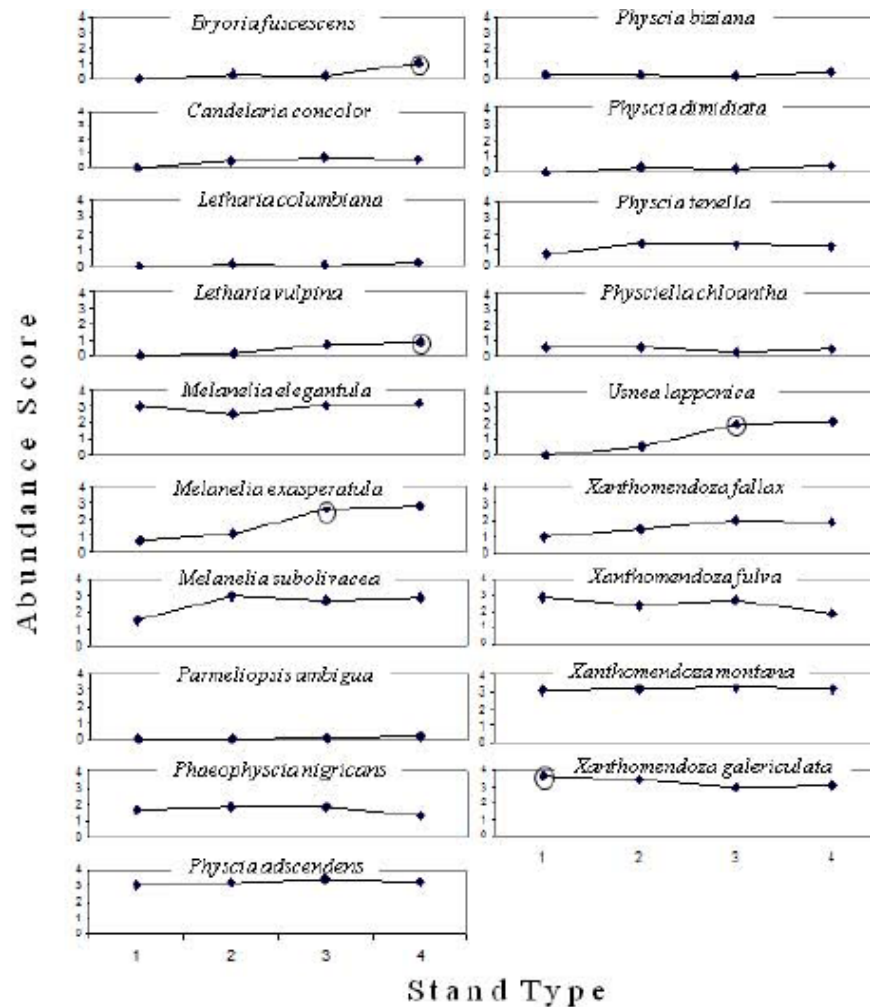


Figure 4. Line charts of lichen species occurring multiple times in the study area. Nodes are average abundance scores for species by stand type. Circles around individual nodes denote significant ($p < 0.05$) preference for specific stand types in Indicator Species Analysis (see Table 3). Stand types are defined in Table 1 above.

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 4. Labeled vectors shown in Figure 5 are those with $r = < -0.5$ or > 0.5 in Table 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). 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, Table 4).

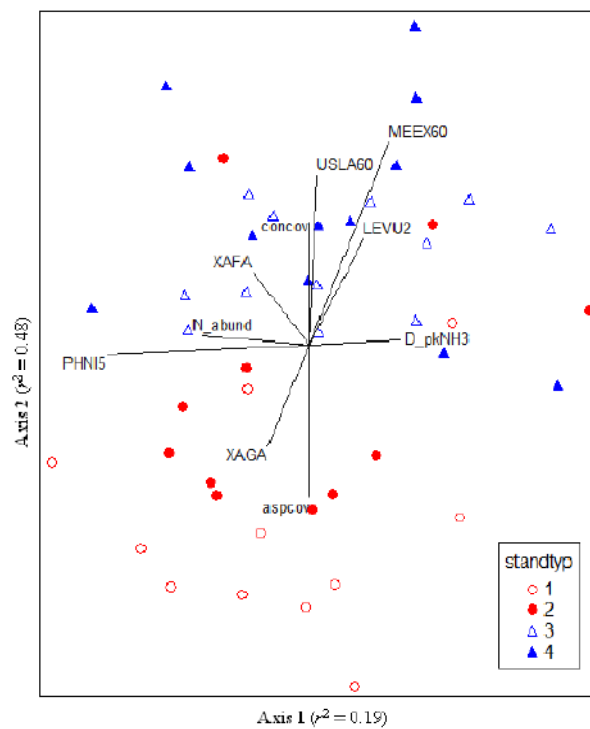


Figure 5. Ordination joint plot with significant lichen species ($r < -0.5$ or > 0.5) plotted as vectors. Vector directions and lengths designate correlation and strength, respectively, with the ordination in species space. Select significant environmental variables (concov, aspcov, N_abund, D_phNH3 – see Table 4 for abbreviations) are

included to enhance discussion. Stand types correspond to stratification by successional groups (Table 1).

Table 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

Variables	Abbreviation	<i>r</i> value	
		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			
<i>Bryoria fuscescens</i>	BRFU60	0.007	0.561
<i>Candelaria concolor</i>	CACO64	0.066	0.373
<i>Letharia columbiana</i>	LECO26	0.101	0.197
<i>Letharia vulpina</i>	LEVU2	0.476	0.634
<i>Melanelia elegantula</i>	MEEL5	-0.208	0.330
<i>Melanelia exasperatula</i>	MEEX60	0.488	0.734
<i>Melanelia subolivacea</i>	MESU61	-0.002	0.135
<i>Parmeliopsis ambigua</i>	PAAM60	0.031	0.345
<i>Phaeophyscia nigricans</i>	PHNI5	-0.771	-0.145
<i>Physcia adscendens</i>	PHAD60	0.129	0.164
<i>Physcia biziana</i>	PHBI6	-0.246	-0.057
<i>Physcia dimidiata</i>	PHDI12	-0.082	0.179
<i>Physcia tenella</i>	PHTE60	-0.239	-0.006
<i>Physciella chloantha</i>	PHCH4	-0.292	-0.113
<i>Usnea lapponica</i>	USLA60	0.270	0.830
<i>Xanthomendoza fallax</i>	XAFA	-0.385	0.490
<i>Xanthomendoza fulva</i>	XAFU	0.236	-0.302
<i>Xanthomendoza galericulata</i>	XAGA	-0.409	-0.599
<i>Xanthomendoza montana</i>	XAMO60	-0.007	0.047

Axis 1 describes a significant gradient of nitrophilous lichen abundance and distance from both urban and peak NH_3 centers (Figure 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). *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). Axis 1, a gradient of nitrogen loading related to distance from sources, revealed a strong link between abundance of nitrophilous species (Table 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), 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 particular aspen communities. While local impacts to the forest resource began slowly after 1856, by the 1870s timber extraction increased. Peterson (1997) and Arrington (1956) both show describe 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, p.57). 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 3a, b)(Wadleigh and 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 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 was 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 and Baker, 2004). Based on PDSI reconstructions used here (Figure 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 and Turner, 2004). More recently, land clearing from logging in Alberta evidently exposed enough mineral soil to facilitate successful seedling establishment where aspen was not previously present (Landhäuser *et al.*, 2010). Though empirical evidence for seedling establishment is not presented 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 most of our aspen stands, there was a climate shift toward higher moisture for most of the 20th century regionally (Millar *et al.*, 2004; Gray *et al.*, 2004) and locally (Figure 3). We note corresponding lapses in aspen establishment during this century; most prominently during the infamous 1930s drought (Figure 3a, b). As moisture returned in the 1940s this figure shows a parallel rise in aspen establishment. Dry climates generally favor frequent fires and vegetative reproduction, leading to aspen stand expansion, as opposed to new genotype initiation from seed (Elliot and Baker, 2004). In this way, prominent past climate epochs, such as the Warm Medieval Period (Figure 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 some mosaic of the four broad successional stages examined here are each important to community preservation across large landscapes. We acknowledge that there are many more states, or in reality a continuum, of aspen types in our study area. However, by combining lichen preferences for discrete aspen states with knowledge of historical environmental change in the area, we may begin to reconstruct past conditions and communities. A generalized timeline of environmental and human impacts on aspen forests and aspen-dependent lichens is presented in Figure 6. Certainly spatial and temporal variance within these broad groupings took place. Our objective in presenting this conceptual 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 habitats these forests provide.

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 often results 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 and 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, 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.

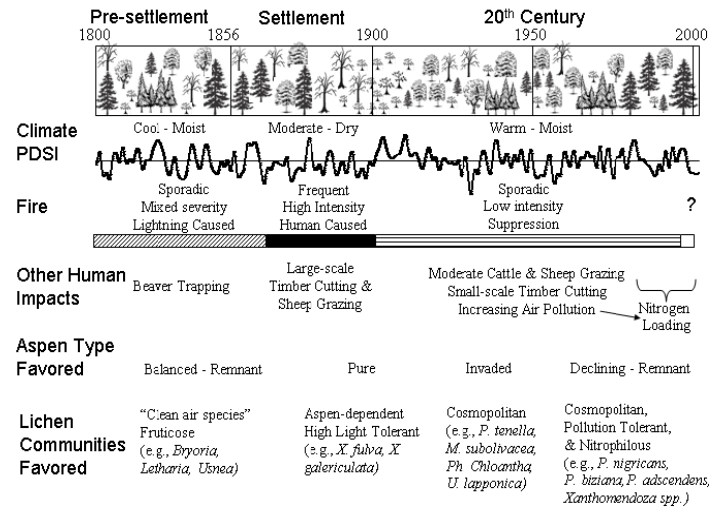


Figure 6. A generalized timeline of prominent forest, climate, disturbance (e.g., fire and human impacts), succession, and lichen community conditions over the last 200 years in the study area. Palmer Drought Severity Index (PDSI) is calibrated to this time period and follows the same index displayed in Figure 3B and 3C (Cook et al., 2004).

Because of dry conditions and greatly increased human ignitions—often intentional—fires were numerous, widespread, and intense, resulting in ample aspen regeneration (Figures 3 and 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 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, unpublished 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 and Baker, 2004; Baker *et al.*, 2007). We do know that pure aspen stands may act as fire breaks due to their decreased flammability (Fechner and Barrows, 1976), except where advancing succession by conifers may reverse this effect. The most recent regional drought (c.1995-2004) 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 and 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 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 (Johnston and Naiman, 1990). In contrast, resource extraction and fire ignition after settlement clearly shaped aspen successional patterns for the following century (Figure 3a). In our landscape-level analysis all aspen stands were initiated within the past 150 years. Our estimate of conditions prior to that time are based primarily on previous dendrochronology work (Wadleigh and Jenkins, 1996) and climate reconstructions (Gray *et al.*, 2004, local data from Cook *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, more intense logging and related ignitions lasted approximately two decades (c. 1860-1880), effectively obscuring clues of aspen coverage prior to that time in all but a few stands (Figure 3a). Severe range-wide sheep grazing during the late 19th century—in addition to initial removal of competing vegetation and stimulation of stand origin aspen suckers via burning (Schier and Campbell, 1978)—would subsequently limit new aspen suckers until cessation of the practice (DeByle, 1985). Moderate sheep and cattle grazing in the 20th century, combined with a moist climate and fire suppression, appears to have created 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 and Ryel, 2008), a condition that would preclude some stands from short-term conifer encroachment, although it is important to

recall that our study design excluded south facing slopes which locally tend toward stable aspen cover.

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 and Wilson (2001) found an increase in aspen stands themselves associated with elevated nitrogen in Canadian parklands. 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, Rogers *et al.*, 2009). Further research (e.g., Fenn *et al.*, 2003) is clearly needed relating to large recent increases in nitrogen deposition on natural systems, including aspen ecosystems, in alpine settings.

Our study contained equal samples of each succession-based aspen stand type (Table 1). The bottom of Figure 6 recreates predominant aspen conditions based on multiple lines of historic disturbance evidence. Given landscape-level preference for stand types (Figure 4) and results indicating macrolichen affinities for succession and air quality gradients (Figure 5), 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 or remnant aspen stands with moderate-to-high nitrogen loading. We acknowledge, however, the strong possibility of lichens being absent from the present community, or those that have invaded based on advantageous situations, that may skew our estimate of past assemblages. 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.

Management for Aspen-Dependent Species 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 and responsibility. Holling and Gunderson (2002), in outlining four stages of system development and renewal, describe disruption (release) and reorganization as positive elements as long as they have been planned for in some way. The four phases forming a comprehensive

cycle include: exploitation, conservation, release, and reorganization. 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 and 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. We now possess a broad ability to plan for expected disturbance patterns given future climate scenarios. In contrast to the settlement period, we have further ecological knowledge that allows for ecosystem altering behaviors that have deleterious effects.

Our current understanding enables us to project aspen response to general climate patterns (Elliot and Baker, 2004; Rogers *et al.*, 2007a; Rehfeldt *et al.*, 2009). We caution, however, against the limited application of “climate envelope” approaches which isolate temperature increases without consideration of considerable impacts on vegetation cover linked to disturbance patterns (e.g., Rehfeldt *et al.*, 2009). Overt human manipulations, such as timber cutting, livestock grazing, or intentional burning, may exacerbate climatic influences or operate independent of natural processes. 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 (Romme *et al.*, 2004). Conversely, extended warm and dry periods are characterized by frequent lower intensity fires and vegetative aspen reproduction (Elliot and 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 relatively frequent fire scenarios (Figure 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.*, 2009). We have shown that NH_3 is an important source of nitrogen affecting lichens in aspen (Rogers *et al.*, 2009), 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). Moreover, recent work modeling the invasive gypsy moth (*Lymantria dispar* L.) in Utah, projects significant mortality in montane aspen as gypsy moth increases its elevation

range with human-induced climate warming (Logan *et al.*, 2007). Climate warming may also enhance establishment at higher elevations where aspen establishment previously did not exist (Landhäuser *et al.*, 2010). In sum, each of these modern airborne 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, bearing in mind that aspen and dependent epiphytes may be regarded not only as important biodiversity elements on their own, but as broader early indicators of forest impacts that will eventually directly affect human well being. Unlike historic resource users, we have greater knowledge of natural systems and the ability to change course where human intrusions overreach environmental resilience.

CONCLUSION

Results of this work suggest strong ties between historical landscape-level disturbance and present aspen-dependent species assemblages. Lichens comprise valuable indicators of community diversity and change. 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 multivariate analysis and visually examining individual species trends (Figure 4) we found lichen preferences for particular successional stages were evident, stressing the importance of preserving a mosaic of successional diversity in aspen. Ordinations confirmed the strong influence of a successional gradient in determining lichen communities, but also revealed a significant gradient of recent nitrogen loading. Nitrophilous species collectively, and *Phaeophyscia nigricans* in particular, may act as key indicators of ammonia/ammonium deposition in the secondary gradient. We noted that certain “clean air species” indicators were found most often in declining and remnant aspen stands where they were furthest from pollution sources.

Climate reconstructions for our area mirror basic trends found in other western North American studies (Buechling and Baker, 2004; Gray *et al.*, 2004; Millar *et al.*, 2004). Prominent moist conditions correlated closely with pulses of aspen regeneration during the previous century and a half (Figure 3). Severe drought conditions and large-scale resource impacts of the late 19th century “set the stage” for the foremost period of aspen initiation (c. 1900 –

1920). 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 fire suppression to an unknown degree, promoted shade-tolerant conifers. While generally advancing succession favors increased 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 this lichen community study 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 stressed natural systems.

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