Lichen Communities for Forest Health Monitoring in Colorado, USA

A Report to the USDA Forest Service

by

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29 June 1998

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CONTENTS

Abstract

Lichen communities were included in the Forest Health Monitoring program because they help to answer several key assessment questions. These questions concern the contamination of natural resources, biodiversity, forest health, and sustainability of timber production. Field crews collected data on epiphytic macrolichens from throughout forested areas of Colorado from 1992-1996. Repeated sampling of these permanent plots will allow us to document changes in the condition of lichen communities over time. Additional plots were taken in urban and industrial areas, for a total of 185 plots reported on here.

This work establishes a baseline from which we can measure impacts of future changes in climate and air quality in Colorado. We provide the quantitative tools for doing so and document the repeatability of the method.

We constructed a gradient model of lichen communities in Colorado, isolating and describing climatic and air quality gradients. The climatic gradient was based on non-metric multidimensional scaling (NMS). Our air quality index was based on the ratio of the number of pollution-tolerant indicator species to the total number of species. We adjusted the raw scores to reduce the influence of elevation by calculating residuals from the regression of raw scores on elevation. The adjusted score expresses the air quality as a number of standard deviations away from expectation for a given elevation. Low air quality scores were found on the east side of the Front Range near Denver and Boulder, the Steamboat Springs area, and the Grand Junction area.

The first two axes of the NMS ordination explained 74% of the variation in the data. The site factor most strongly related to the lichen communities was elevation, which had $r^2 = 0.56$ with the first axis, which in turn explained about 37% of the variation in lichen communities. We interpret this as a gradient in available moisture, given the well known relationships between elevation, precipitation, and temperature. Axis 2 was most strongly correlated with the binary variable contrasting the urban/industrial sites with the remote sites.

Repeat measurement error was assessed by analysis of variance of data from "reference plots." Three plots were repeatedly visited by multiple observers. Observers differed in their ability to detect species in the reference plots, as shown by the significant differences among observers with respect to species richness and total lichen abundance (the sum of the abundance codes for all species in a plot). Fortunately observers did not differ significantly in their gradient scores (moisture and adjusted air quality). Ideally the observer error (sampling noise) should be small compared to the range of observed values. We evaluated this by calculating a signal-to-noise ratio, the signal being the range in values observed from throughout Colorado, the noise being the observer error. The signal is strong relative to the noise for the moisture score and the adjusted air quality score. Species richness and total abundance are both relatively noisy.

To better understand gradients in lichen communities (and other indicators) in Colorado, we need better information on local climates. The most cost-effective first step would be to modify the PRISM model to produce precipitation estimates for exact locations of all FHM plots in Colorado.

More intensive sampling is needed in the Park Range and the Front Range, to better monitor future changes in lichen communities and forest health resulting from air pollution. We recommend intensifying the sampling grid by 3X in those areas. To strengthen the link to direct air quality monitoring data we recommend sampling a special set of plots adjacent to NADP wet/dry deposition monitoring stations throughout Colorado.

Introduction

Lichens in the Forest Health Monitoring Program

The Forest Health Monitoring (FHM) program seeks to assess the condition and trend of the forests of the United States (Riiters et al. 1992; NAPAP 1993). The goals and progress of the FHM program in Colorado were described by Rogers et al. (1997). FHM is linked with the national sampling grid established by the Environmental Monitoring and Assessment Program (EMAP) of the Environmental Protection Agency. Epiphytic lichen communities were included in FHM because they help to answer several key assessment questions. These questions concern the contamination of natural resources, biodiversity, forest health, and sustainability of timber production. See http://willow.ncfes.umn.edu/fhm_fact/list.htm for more information on the FHM program and http://willow.ncfes.umn.edu/fhm_fact/lichen.htm for more information on the lichen community indicator within FHM.

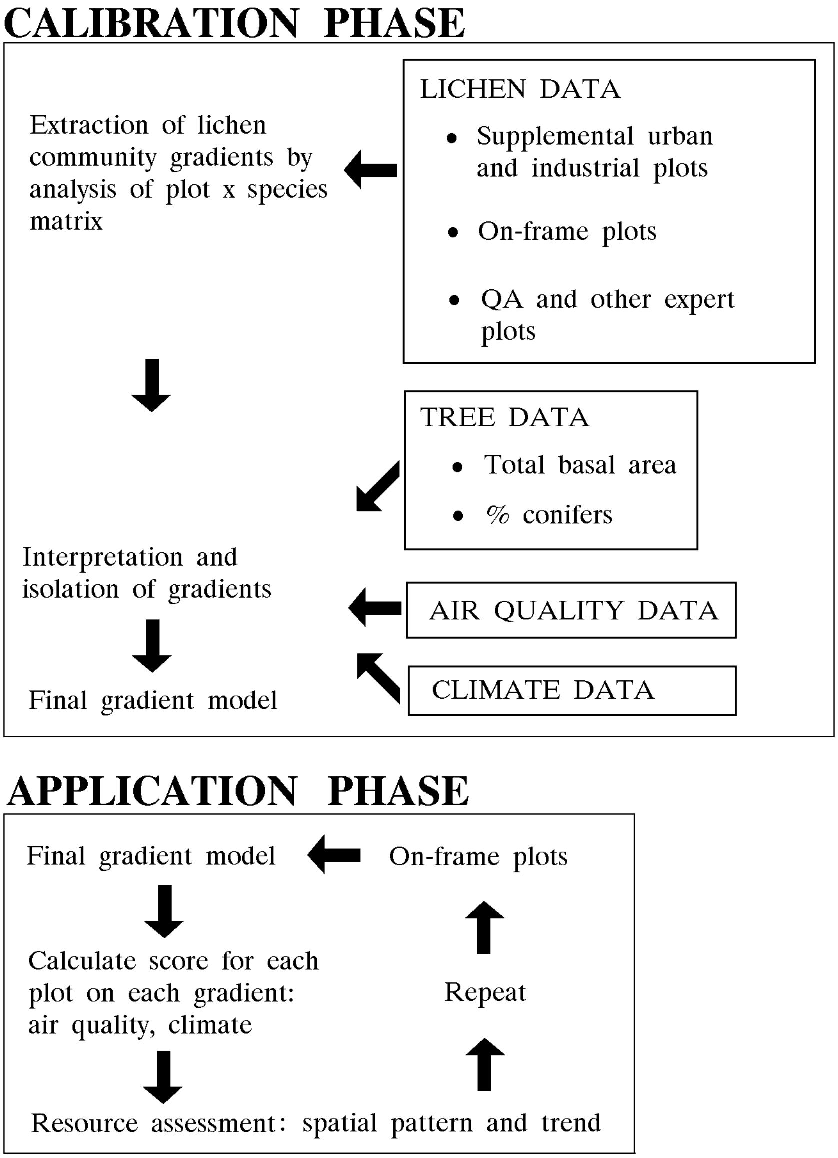
Hundreds of papers worldwide (chronicled in the series "Literature on air pollution and lichens" in the *Lichenologist*) and dozens of review papers and books (e.g., Nash & Wirth 1988; Richardson 1992; Seaward 1993; Smith et al. 1993; van Dobben 1993) published during the last century, have documented the close relationship between lichen communities and air pollution, especially SO_2 and acidifying or fertilizing nitrogen and sulfur-based pollutants. A quantitative relationship between lichen communities and air pollutants can be established when sufficient direct air quality data are available (McCune 1988; de Wit 1976, 1983; van Dobben 1993). In a comparison of biological responses between nearby and remote areas surrounding a coal-fired power plant, lichens gave a much clearer response (in terms of diversity, total abundance, and community composition) than either foliar symptoms or tree growth (Muir & McCune 1988). Lichens were one of the few components of terrestrial ecosystems to show a clear relationship to gradients of acidic deposition in the eastern United States (Showman 1992; NAPAP 1991). Much of the sensitivity of epiphytic lichens to air quality apparently results from their lack of a cuticle and their reliance on atmospheric sources of nutrition. Although trees may respond to moderate, chronic levels of air pollution deposition, all of the other influences on tree growth, such as variation in soils, make the responses of trees to pollutants difficult to measure in the field. Lichen communities provide, therefore, not only a measure of air pollution impacts upon lichens, but also suggest air pollution impacts on aspects of forest health that are difficult to measure directly.

In addition to their utility as indicators of air quality, epiphytic lichens are an important component of many forests. Lichens often comprise a large portion of the diversity of macrophytic species in a forest. Lichens have numerous functional roles in temperate forests, including nutrient cycling (especially nitrogen fixation in moist forests; Pike 1978) and as components of food webs (Dawson et al. 1987; Maser et al. 1986; Maser et al. 1985; Rominger & Oldemeyer 1989; Servheen & Lyon 1989).

The Lichen Community Indicator

The lichen community indicator is implemented in two phases (Figure 1): (1) construct a gradient model of lichen communities to isolate and describe climatic and air quality gradients and (2) apply the model to calculate gradient scores for additional plots. Scores for these plots are then used to describe the regional condition and geographic variation in lichen communities. Repeated sampling of these permanent plots will allow us to document changes in the condition of lichen communities over time. All lichen data are archived with the Information Management group for Forest Health Monitoring, Environmental Protection Agency, Las Vegas, Nevada, and at Oregon State University.

Figure 1. Implementation of the lichen communities as an indicator in the Forest Health Monitoring Program.



Previous Work on Lichen Communities in Colorado

Although Colorado has one of the best known lichen floras of any state (see list and references in Weber & Wittman 1992), the ecology of lichens in Colorado has not received much formal study. Gough (1973, 1975) studied lichens on conifers at five sites in Boulder County, Colorado. Carmer (1975) compared lichen communities on different species of hardwoods in the Front Range. She included both crustose lichens and macrolichens and provided detailed notes on taxonomic characters. Jackson et al. (1996) studied elemental content of lichens in Routt National Forest, but did not include lichen community data. Preliminary lichen results from the FHM Program were summarized in Rogers et al. (1997).

Methods

Field Methods

We designed the field method for use by non-lichenologists for practical reasons of staffing field crews. Field crews received four days of intensive training in the lichen community method. The method has been closely scrutinized and documented for repeatability (McCune et al. 1997a).

The FHM lichen community method determines the presence and abundance of macrolichen species on all standing woody plants in each FHM plot. This "whole-plot ocular" method emphasizes species capture at the expense of accurate estimates of abundance (McCune & Lesica 1992). The coarse abundance scale is rapid and repeatable The field crew collects samples for mailing to lichen specialists. The field methods are described in detail in Tallent-Halsell (1994) and McCune et al. (1997b). Quality assurance (QA) procedures and results are described in Cline (1995) and McCune et al. (1997a). Vouchers are stored at Oregon State University.

The method has two parts that are performed simultaneously. (1) In each plot the field crew collects specimens for identification by a specialist, the collection representing the species diversity of macrolichens in the plot as fully as possible. The population being sampled consists of all macrolichens occurring on woody plants, excluding the 0.5 m basal portions of trees and shrubs. Lichens on fallen branches and other lichen litter are included. Given the large plot area, fallen branches always provide a sample of the canopy lichens (2) The field crew estimates the abundance of each species using a four-step scale: 1 = rare (1-3 individuals in plot); 2 = uncommon (4-10 individuals in plot); 3 = common (> 10 individuals in plot but less than half of the boles and branches have that species present); and 4 = abundant (more than half of boles and branches in the plot have the subject species present). Note that the field crew need not accurately assign species names to the lichens (that is done later by a specialist), but must be able to distinguish among species.

Data on other variables were included to facilitate the interpretation of the lichen community data. These additional variables were latitude, longitude, state, county, elevation, aspect, slope, topographic position, stand basal area, and percent of stand basal area in conifers.

Data Sources

This report summarizes results from 185 plots, as described below.

On-frame data. "On frame" refers to plots selected on a formal sampling framework, according to standard sampling protocols for the EMAP hexagonal grid (Messer et al. 1991). The strict sampling criteria applied to the on-frame data allow regional estimates of lichen community parameters. On-frame data can be used for assessment of regional status and trends because it consists of an unbiased sample (Messer et al. 1991). In contrast, off-frame data, while useful in building a gradient model, cannot be used to answer such questions as, "Is lichen diversity in Colorado decreasing through time?"

We analyzed lichen community data collected by summer field crews in 112 on-frame permanent plots in 1992, 1994, 1995, and 1996. Some of these represent repeated visits, but most plots were visited in only one year. Half of the plots collected in 1992 never made it to the analysis stage, as they were lost during storage in Las Vegas sometime during the period 1992-1997. No lichen data were collected in 1993. Lichen community plots were also collected in 1997, but those specimens have not been identified and were not included in this round of analysis. Specimens collected in 1994 were identified primarily by Bruce Ryan; those from other years primarily by Andrea Ruchty.

Training plots. Two training plots near Boulder were sampled by trainees and McCune in 1994 and identified by McCune. One set was a practice plot, in an open *Pinus ponderosa* - shrub - *Pseudotsuga* woodland. The other set was a test plot (the basis for certifying crew members) in a *Pseudotsuga* - *Populus tremuloides* forest at a somewhat higher elevation than the practice plot.

Audit plots. Two audit plots were conducted in 1994 by a lichen specialist (P. Neitlich). The purpose of audit plots is mid-season evaluation and corrections of performance of field crews.

Reference plots. Reference plots were visited repeatedly by different crews to measure repeatability of the method. The reference plots were northeast of Boulder in Boulder County. Plot 1 was in *Pinus ponderosa*, plot 2 in riparian *Populus tremuloides* with a few *Pinus contorta*, and plot 3 in *Abies* - *Picea* with abundant *Usnea* and *Bryoria*. In 1994 the three plots were each sampled twice by each of four crews, plus one of the plots by an additional crew member, for a total of 25 plots. In 1995 reference plots 1 and 2 were each sampled twice by each of two crews, for a total of 8 plots and a grand total of 33 reference plots.

Supplemental urban/industrial plots. Data for 23 off-frame plots, 20 of these near urban and industrial settings or in fringe areas, were collected in June 1995 by McCune, R. Rosentreter, and A. DeBolt. The purpose of the supplemental plots was to improve the basis for recognizing lichen indications of either deterioration or improvement in air quality. Most of these plots were in or near Denver, Boulder, and Steamboat Springs. Of the 20 plots, several were near the mountain front, but in sheltered sites that probably do not experience pollutant levels as high as the remaining urban/industrial plots.

Air quality data. Ideally we would like to calibrate lichen community data against specific pollutants. The Colorado Department of Public Health and Environment monitors air quality in the state (CDPHE 1996, 1997). These publications identify air quality problems in Colorado and describe the local direct monitoring of air pollutants through instrumentation. Unfortunately, no extensive statewide monitoring network exists for air pollutants. The limited funds for monitoring are focused on a small number of sites insufficient to map air pollution levels over the state. (Herein lies the utility of biomonitoring!) Lacking useful fine-grained regional direct air monitoring data derived from atmospheric sampling, we resorted to simply creating a binary variable indicating plots in urban and industrial areas (polluted=1) vs. those in remote areas (polluted=0). This categorization was the basis for detecting lichen indicators of air quality (see "Data Analysis" below). It does not, however, provide a basis for calibrating our air quality index against specific pollutants.

Climatic data. Sparse climatic data in Colorado make it very difficult to relate our lichen data to climate. Long-term averages in broad climatic divisions (Fovell & Fovell 1993), as used in McCune et al. (1997b) were far too coarse spatially to be useful in this mountainous state. More promising was interpolating precipitation data using the PRISM model (Daly et al. 1994; http://www.ocs.orst.edu/prism/prism_new.html). Long-term means are available for the whole state with a cell size of 0.04167 degrees on each side. However, we could only approximately match our sample locations with the interpolated values. Incorporating elevations of our plots into the interpolations of PRISM would be necessary for more accurate estimates of long-term precipitation averages.

Ecoregions. Bailey's Ecoregions (Bailey 1995) provide a classification of the United States into ecological regions. These regions are defined by combinations of physiography, soils, potential vegetation, and climate. Of the seven ecoregions present in Colorado (see map in Rogers et al. 1997), four were represented by four or more lichen plots. Of the analytical data set (see below), 106 plots fell in the Southern Rocky Mountain Region, 10 in the Great Plains, and 4 in each of the Desert-Semidesert and Nevada-Utah Mountains.

Data Analysis

Our data analyses included:

- Summaries of epiphytic lichen diversity and total abundance in each plot.
- Evaluation of repeatability of various lichen community parameters using analysis of variance of the reference plots.
- Comparison of lichen communities between urban/industrial plots and on-frame plots using MRPP (Mielke 1984; Zimmerman et al. 1985) and Indicator Species Analysis (Dufrêne & Legendre 1997). MRPP is a nonparametric multivariate methods for testing for differences between two or more groups. The p-statistic, derived by permuting the data, measures the probability of obtaining a test statistic as extreme or more extreme than that actually obtained. The R statistic measures the strength of the difference from random expectation ($R = 0$).
- Multivariate analysis (gradient modeling) of lichen community structure and its relationship to environmental variables (McCune and Mefford 1997).

The Analytical Data Set

From the 185 total plots we extracted a subset of the data for gradient analysis, omitting the repeatedly sampled plots (reference and training plots). We then removed an additional 11 plots that lacked tree basal area or other important site data, leaving 127 plots. Species occurring in fewer than 5% of the plots were then eliminated to reduce noise from the analysis. Outlier analysis (McCune & Mefford 1997) showed only one serious outlier. Plot 3710647 had an average distance from other plots of 4.7 standard deviations higher than the average distance among other plots. This plot was exceptionally diverse, containing 32 species, well above the next contender. It was mostly conifers with some hardwoods, on a gentle south slope at 2650 m in Mineral County in southern Colorado, and sampled by Susan Geer in 1994. To avoid undue influence of this single plot on the analysis it was removed from the analytical data set. The resulting analytical data set contained 126 plots *x* 35 species.

Gradient Modeling

The dominant gradients in lichen communities were determined using the analytical data set (described above). The gradients were extracted with nonmetric multidimensional scaling (NMS; Kruskal 1964; Mather 1976; McCune & Mefford 1997). NMS has proved one of the most robust and effective methods for multivariate data reduction, especially with species x sample data and city-block distance measures (Beals 1984; Faith et al. 1987). NMS is well-suited to data that are non-normal or are on arbitrary or discontinuous scales (Mather 1976).

Gradient scores were calculated for each sample unit in the analytical data set. The scores represent positions of each sample unit on each gradient as defined by community composition. These scores were then analyzed for their relationships to other variables (forest structure, air quality, and climate).

The gradient model can then be used to score additional plots not included in the analytical data set. This model can be applied to future plots in the same region (explained below).

We used NMS with the quantitative version of the Sørensen distance measure. The dimensionality of the data set was first determined by plotting a measure of fit ("stress") to the number of dimensions. Two- through four-dimensional solutions revealed stronger structure in the data than expected by chance (Figure 2). A two-dimensional solution was selected because additional dimensions provided only a slight improvement in fit (Figure 2). Five hundred iterations were used for each NMS run, using random starting coordinates. Several NMS runs were used for each analysis to ensure that the solution was stable and represented a configuration with the best possible fit. Varimax rotation was used to maximize the loadings of the species on the resulting axes.

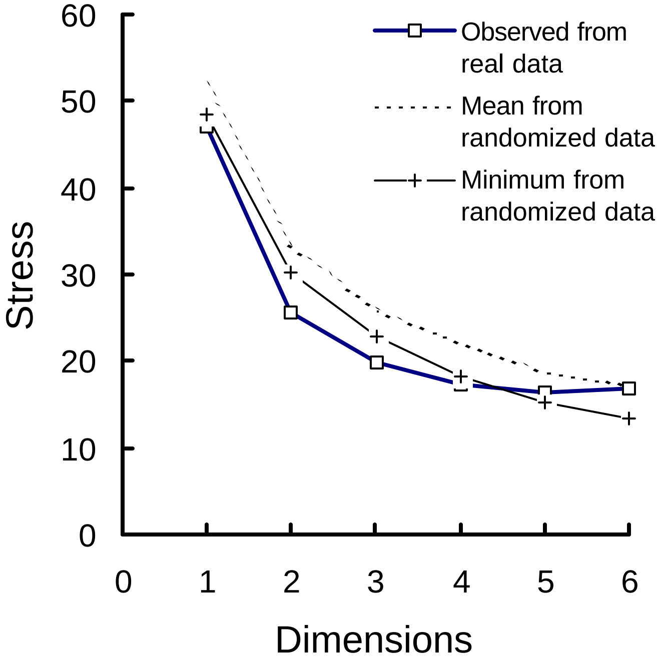


Figure 2. Stress in NMS ordination for 1- through 6-dimensional solutions, compared with 99 runs based on randomized data. Stress is an inverse measure of fit between distances in the ordination space and differences in species composition. The "observed" line is the best of eight runs with different starting configurations using the non-randomized data.

Lichen Indicators of Air Quality

Characteristics of the data forced us to derive a new method for describing an air quality gradient. In contrast to the lichen - air quality model used for the southeastern United States (McCune et al. 1997b), air quality was intimately confounded with climate (in particular elevation; discussed further under "Results").

To separate an air quality gradient we first eliminated plots higher than the maximum elevation of plots in the urban-industrial data set (2805 m), leaving 87 plots. We then sought species indicating the urban/industrial group of plots using Indicator Species Analysis (Dufrêne & Legendre 1997; McCune & Mefford 1997). A randomization (Monte Carlo) test measures statistical significance for the maximum indicator value (IV) obtained for each species. Plots were randomly reassigned to groups (urban/industrial vs. not) 5000 times, providing an measure of the likelihood of obtaining the observed IV by chance.

We then calculated the abundance of indicator species relative to other species, providing our "raw" score for each plot as an index of air quality:

$$Raw\ air\ score = 100\left(1 - \frac{S_{poll}}{S}\right)$$

where S_{poll} is the sum of the abundance classes of lichen species indicating air pollution and S is the sum of the abundance classes of all species recorded for the plot. The raw score has a minimum of zero when all species are pollution-tolerant indicators. The maximum possible value is 100, when none of the species present are pollution indicators. Very diverse plots will have a high score regardless of the presence of pollution indicators, since S_{poll} will be small relative to S.

We adjusted the raw scores to reduce the influence of elevation by calculating residuals from the regression of raw scores on elevation:

$$Adjusted\ air\ score = \frac{Raw\ score - (a \bullet Elevation + b)}{SD}$$

where a is the slope of the regression equation, b is the intercept, and SD is the standard deviation of the residuals. The adjusted score expresses the air quality as a number of standard deviations away from expectation for a given elevation.

Note that this adjustment does not entirely eliminate climatic factors related to elevation, because in complex topography slope, aspect, and topographic position strongly modify local climate, often shifting species composition in ways similar to elevation.

Assigning Scores to New Plots with NMS

Only a subset of the available plots, the "analytical data set" was used in multivariate analysis. Therefore, we had scores on the major gradients in lichen communities for only these plots. The remaining plots were assigned positions on the lichen gradients using predictive-mode NMS. The same procedure can be used to assign scores on the same gradients to plots collected in the future.

Before predictive-mode NMS the analytical data set and the resulting NMS scores are saved. Combined, these represent the gradient model, rather than a model of the usual form of a linear combination of the original variables. Subsequent plots are fit to the gradient, one plot at a time, finding the position of best fit without shifting the positions of the original set of points (using module NMS Scores in PC-ORD v. 4.0 beta). A hierarchical fitting procedure is used to home in on the position of best fit for each new plot.

Reference Plot Study

Lichen community parameters from the 33 reference plots (repeated visits of three plots by different observers) were analyzed with a blocked analysis of variance. Plots were considered blocks and observers were considered treatments. We thus tested for a block (plot) effect and an observer effect, but did not include an interaction term. The mean-squared error for observers measures the variability among observers. We used ratio of the range of the community response variable across plots in the analytical data set to the observer error as our estimate of the signal-to-noise ratio.

Data Archive

The data archive consists of three parts: paper files, lichen specimens, and computer files. Each of these is described below.

Paper files from this project are in two places, the USDA Forest Service Intermountain Research Station (Ogden, Utah) and McCune's laboratory (Corvallis, Oregon). Files in Ogden include exact plot locations, directions to the plots, aerial photography. Paper files in Corvallis include data sheets prepared by the lichen specialists, plot packing slips (1994-1996), and specimen mailing forms (1994-1996).

Lichen specimens fall into three categories: voucher specimens, labeled and sorted specimens from 1994, and bagged specimens from other years. The voucher specimens were deposited in the Oregon State University herbarium (OSC). These include vouchers from 1992-1996 selected by Bruce Ryan and Andrea Ruchty, as well as specimens collected in the urban-industrial plots from 1995 by Bruce McCune, Roger Rosentreter, and Ann DeBolt. Specimens from 1994 were labeled and alphabetized by species by Jeri Peck in 1995. These are stored in boxes in McCune's lab and will be kept for 10 years, then their status re-evaluated. Other specimens (from 1992, 1995, and 1996), not including the vouchers described above, are in the original collecting bags in boxes in McCune's lab. These will be stored for 10 years, then their status re-evaluated.

Computer files from this project were archived in two ways: files deposited with the FHM data managers in Las Vegas, Nevada (contacts: Brian Cordova and Chuck Liff) and as two 1.44 MB archive diskettes stored at the Intermountain Research Station and McCune's lab. Copies were also deposited with the FHM National Office in Research Triangle Park (contact: Ken Stolte). The contents of the archive disks are summarized in Table 1. All files were prepared on desktop computers with the Windows-95 operating system.

Table 1. Computer files on the archive disks.

File Name	Readable by	Contents
Colorado.mdb	Microsoft Access 7.0	Database containing all plot-level data except data on individual species. The main table is "Colorado". Fields are explained under design view. Queries for creating subsets of plots and integrating data from other sources are included. A "Form" is provided for viewing individual plots. Herbarium labels for individual plots can be produced under "Reports."
ColoSite.xls	Microsoft Excel 7.0	Selected plot-level environmental data used to produce the analytical data set. Derived from Colorado.mdb.
ColoSit4.wk1	PC-ORD 3.0, Excel 7.0, and Lotus 2.0 and higher	Plot-level environmental data to match the analytical data set, ColoSp4.wk1; a subset of ColoSite.xls
ColoSp4.wk1	PC-ORD 3.0 and spreadsheet programs.	Plot-level lichen species data: the "analytical data set" used for most of the multivariate analyses. Use this file as the "calibration data set" for predictive-mode NMS for calculating scores for new plots with PC-ORD.
NMSVarMx.gph	PC-ORD 3.0 and text editors (ascii file)	Ordination scores on two NMS axes for the analytical data set, after varimax rotation. Use this file as the "calibration scores" for predictive-mode NMS for calculating scores for new plots with PC-ORD.
Epiphyte.spp	PC-ORD 3.0 and text editors (ascii file)	Dictionary for lichen species codes for all North American epiphytic macrolichens. Used by PC-ORD with compact format file (ColoAll.raw) to produce full plot *x* species matrix.
ColoAll.raw	PC-ORD 3.0 and text editors (ascii file)	Species abundance data, in PC-ORD compact format, containing lists of data pairs of species codes and abundances, convertible to full plot *x* species matrix with PC-ORD. Sections of data are separated by the key word "break". A separate break group is used for each combination of plot type and year (e.g. on-frame plots from 1994 constitute a break group).
ColoSpp.txt	Ascii text editor or import to database or spreadsheet	List of Year, Plot, Sequence number, Species code, Species abundance, each record being a single occurrence of a species in a given plot. Fixed-width fields.
ColoAll.Sav	SPSS for Windows, Release 8.0.1	Plot-level variables from ColoSite.wk1, ColoSp4.wk1, ordination scores, and other calculated variables.
RefOnly.Sav	SPSS for Windows, Release 8.0.1	Community parameters from reference plots in 1994 and 1995. Used for analysis of variance.
ColoRept.Doc	Microsoft Word 7.0	This document, formatted for HP Laserjet 5L.

Results and Discussion

Repeat Measurement Error

Observers differed in their ability to detect species in the reference plots (Table 2), as shown by the significant differences among observers with respect to species richness and total lichen abundance (the sum of the abundance codes for all species in a plot). Fortunately observers did not differ significantly in their gradient scores (moisture, air quality, and adjusted air quality, $p > 0.3$). All community parameters differed among the reference plots (Table 2). Although all three plots were in the Boulder area, they included a low-elevation *Pinus ponderosa* stand, a riparian *Populus tremuloides* - *Pinus contorta* stand, and a *Picea* - *Abies* forest.

Table 2. Range, observer error, and signal-to-noise ratio for the lichen community parameters. F-ratios and p-values from the ANOVA of the reference plot experiment indicate differences among the three reference plots ("Plot") and differences among five observers ("Person"). The signal-to-noise ratio is the range in the analytical data set divided by the mean squared error due to different observers.

	Analytical Data Set			Reference Plots, F-ratio (p)		Signal:
Community parameter	Min.	Max.	Mean	Plot, d.f.=2	Person, d.f.=4	Noise
Species richness	1	96	24.8	6.6 (0.005)	6.6 (0.001)	0.8
Total abundance	1	32	9.3	11.2 (<0.001)	7.6 (<0.001)	0.3
Moisture score	-1.7	2.2	0.0	2.8 (0.08)	1.1 (0.38)	7.4
Air quality score	0	100.0	77.0	4.2 (0.03)	0.4 (0.81)	1.7
Adjusted air quality score	-3.9	2.7	0.0	11.4 (<0.001)	0.4 (0.81)	22.1

Ideally the observer error (sampling noise) should be small compared to the range of observed values. We evaluated this by calculating a signal-to-noise ratio (Table 2), the signal being the range in values observed from throughout Colorado, the noise being the observer error. The signal is strong relative to the noise for the moisture score and the adjusted air quality score. The raw air quality score has a low, barely acceptable signal-to-noise ratio. Species richness and total abundance are both relatively noisy.

These results are qualitatively identical to those observed from the southeast United States in the Forest Health Monitoring program (McCune et al. 1997a). Species richness was difficult to estimate accurately, being subject to considerable observer error. Gradient scores, on the other hand, were relatively reliable. Comparisons of the 1992-1996 results with future results should, therefore, rest more heavily on the gradient scores than on species richness.

Biodiversity

Colorado's lichen flora is most conspicuous on rocks. Compared to boreal, coastal, and eastern North America the epiphytic lichen flora of Colorado has relatively few species. Nevertheless, sufficient numbers of epiphytic macrolichens (averaging 9.2 species per plot; Table 3) were present to make lichen community sampling worthwhile. Eighty-eight taxa were found overall. Excluding ten taxa at the genus level (recorded when the species was not identifiable), leaves 78 species of macrolichens (see "The Species" below).

Lichens in Colorado represent several functional groups and provide various kinds of indicator values (Table 4). The most important of these, with respect to the goals of Forest Health Monitoring, is their value as indicators of air quality. Lichen communities provide an inexpensive, sensitive means of detecting effects of air pollutants on ecosystems. In most cases the responsible pollutants are inferred to be nitrogen and sulfur oxides and their acidic and fertilizing reaction products.

Table 3. Number of epiphytic macrolichen species observed from different data sources.

Data source	Plots	Total number of species	Average number of species per plot
On-frame, 1992, 4, 5, and 6	112	80	8.5
Quality assurance audits, 1994	2	17	11
Reference plots, 1994 + 1995	33	53	8.7
Training plots, 1994	15	28	12
Off-frame, 1995			
Denver, urban & suburban	4	7	3
Boulder, urban & suburban	2	14	8
Denver & Boulder, fringe	8	37	11
vic. Steamboat Springs	6	20	10
Remote	3	30	19
All of the above	185	88	9.2

Table 4. Characteristics of some common macrolichen genera growing on trees in Colorado.

Genus	Appearance	Indicator value and functional roles
Bryoria	Brown, hairlike	Pollution-sensitive; forage lichen; many uses by animals
Candelaria	Yellow, very small foliose	Pollution and dust tolerant, mainly on hardwoods
Collema and *Leptogium*	Grey or black, gelatinous, foliose	Pollution sensitive, nitrogen fixers
Flavoparmelia and *Flavopunctelia*	Greenish, broad-lobed foliose	Moderate pollution tolerance
Hypogymnia	Grey or brown, foliose, hollow lobes	Mainly on conifers, some species pollution tolerant
Imshaugia	Small white foliose, brown apothecia	Mostly restricted to conifers
Melanelia	Brown to olive, foliose, medium size	Nearly ubiquitous; some species pollution tolerant; on both hardwoods and conifers
Parmelia	Grey, foliose, medium size, black below	Widespread, pollution tolerant, on both hardwoods and conifers
Phaeophyscia	Small, cryptic, grey or brownish, foliose	Usually on hardwoods; most species pollution tolerant
Physcia	Small, white, foliose	Most species nitrogen-loving; some species almost restricted to hardwoods; some species in very dry habitats
Physciella	Small, cryptic, grey, foliose	Usually on hardwoods; pollution tolerant
Physconia	Small, frosty-coated, foliose, often forming neat rosettes; brown, grey or white	Usually on hardwoods; pollution tolerant, nitrogen-loving
Usnea	Greenish fruticose, tufted or hanging, branches have a central cord	Abundant in the mountains, somewhat pollution sensitive but persisting in polluted areas as dwarfed, compact forms
Xanthoria	Orange or yellow, foliose	Widespread but more abundant in areas of elevated nitrogen, somewhat pollution tolerant

Rock-dwelling lichen species are unusually frequent as epiphytes in Colorado, as compared with other regions with FHM lichen data. Most of these (Table 5) occurred on bare wood rather than bark. We presume that hard, bare, dust-impregnated wood in a strongly continental climate such as Colorado approaches rock in its physico-chemical characteristics as a substrate for lichens.

Table 5. Typically rock-dwelling species occasionally found on bark or wood in Colorado.

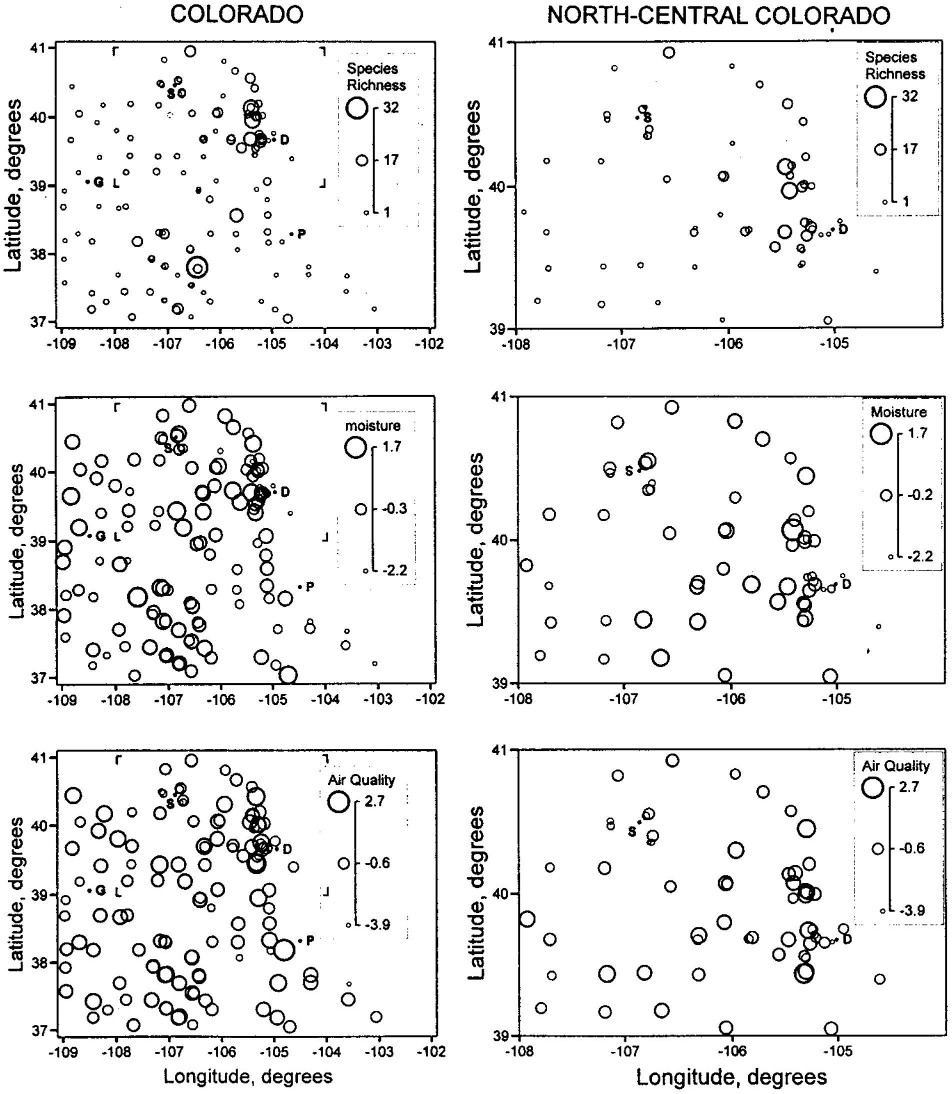
Melanelia disjuncta
Melanelia tominii
Physcia callosa
Physcia dubia
Rhizoplaca chrysoleuca
Rhizoplaca melanophthalma
Xanthoria elegans
Xanthoparmelia coloradoensis
Xanthoparmelia cumberlandia
Xanthoparmelia lavicola
Xanthoparmelia lineola
Xanthoparmelia plittii
Xanthoparmelia subdecipiens

Ecoregions (Rogers et al. 1997) differed in lichen species composition (MRPP: $p << 0.0001$; $R = 0.033$), but only a few indicator species were found. *Melanelia subolivacea* and *M. exasperatula* were associated with both the Southern Rocky Mountains and the Nevada-Utah Mountains. *Physcia dimidiata* was most abundant and consistent in the Nevada-Utah Mountains. *Usnea lapponica* was strongly associated with the Southern Rocky Mountain region, as compared with the other ecoregions in Colorado. *Phaeophyscia hirsuta* was the only species detected as indicative of forested areas in the Great Plains region. None of these species separates perfectly by ecoregion.

The small number of lichen indicators of ecoregions in Colorado suggests that a different system of defining ecological regions or physiographic regions might be fruitful. Some of the attempts to define life zones and physiographic regions in Colorado are summarized in Gregg (1963).

Lichen species richness does not show a clear geographic pattern (Figure 3). Instead we see a rather low number of species statewide with sporadic plots containing a large number of species. Only one plot lacked epiphytic macrolichens (4010882, sampled in 1995). This plot was half non-forested. The other half contained *Juniperus* with conspicuous crustose lichens.

Figure 3. Distribution of lichen species richness, moisture scores, and adjusted air quality scores in Colorado (left panels) and north-central Colorado (right panels). Right-angle brackets in the left panel show the north-central region that is expanded in the right panel. Each symbol represents a plot. Species richness is the number of epiphytic macrolichens recorded on the plot. Moisture scores are measured in standard deviations away from the mean position on the first NMS axis; larger symbols indicate more moisture availability. Air quality scores are measured in standard deviations away from expectation, given the elevation of the plot; larger symbols indicate better air quality. The size of the symbol is proportional to the size of the variable, as shown in the insets. Cities are indicated with a single letter: D = Denver, G = Grand Junction, P = Pueblo, and S = Steamboat Springs. The higher density of plots near Denver and Steamboat Springs resulted from the addition of urban/industrial off-frame plots.



The Species

The following list includes all epiphytic macrolichens collected in all 185 FHM plots, both on-frame and off-frame, from 1992 through 1996. Each taxon is followed by a number indicating the number of plots in which it was found, followed by taxonomic and ecological notes. Genera without specific epithets refer to specimens identifiable to genus, but not to species, usually because of small size.

Bryoria 11. Most of the unnamed *Bryoria* specimens are small and esorediate, but probably in the *B. fuscescens* group.

Bryoria chalybeiformis 2. This species typically occurs on the ground in alpine habitats. It is part of the *B. fuscescens* complex and seems to intergrade with that species. For the most part we did not attempt to separate species within this group. A few specimens, however, fit the morphology of *B. chalybeiformis*.

Bryoria fremontii 1. Routt County: Rabbit Ears Pass, *Abies - Pinus - Picea* forest, off-frame plot CO-17.

Bryoria fuscescens 47. This name was used in a broad sense; easily the most common *Bryoria* in Colorado.

Bryoria lanestris 2. Part of the *B. fuscescens* complex and seeming to intergrade with that species. For the most part we did not attempt to separate species within this group. A few specimens, however, clearly fit the morphology of *B. lanestris*.

Candelaria concolor 36.

Cetraria coralligera 1. This identification is tentative and may be just a warty extreme of *C. fendleri*.

Cetraria fendleri 10. This species is typically small and inconspicuous and is more common in Colorado than the small number of plots would indicate.

Cladonia 16. Poorly developed specimens and squamules without podetia were common in the plots.

Cladonia carneola 1. Jackson County: 2773 m, plot 4010558.

Cladonia chlorophaea 3.

Cladonia deformis 1.

Cladonia fimbriata 3.

Cladonia ochrochlora 3. Specimens from Colorado are typically short and poorly developed compared to more northern and coastal populations. We applied this name in the broad sense, including *C. coniocraea*.

Cladonia pyxidata 1.

Collema furfuraceum 1. Archuleta County: *Abies concolor - Pseudotsuga* forest on slope near creek, 2377 m, plot 3710627. This plot was rich in lichens, especially *Usnea*, and included a number of other uncommon species, such as *Ramalina sinensis*, *Leptogium teretiusculum*, *Hypogymnia bitteri*, and *Nephroma parile*. *C. furfuraceum* is fairly frequent in Colorado on mossy rock but is apparently rare as an epiphyte in that state. In less continental climates *C. furfuraceum* is commonly an epiphyte.

Collema nigrescens 1. Archuleta County: 2743 m, plot 3710724. This surprising record is probably part of the cyanolichen summer-wet floristic element found in the mountains of Arizona and New Mexico. It is unknown northward in the Rocky Mountains, being mainly restricted to the coastal states. Some *Sticta* species show a similar pattern. Other unusual species present were *Physconia elegantula* and *Leptogium furfuraceum*.

Evernia divaricata 3. Boulder, Jackson, and Routt Counties. Sporadic in moist mountain forests. Collected twice in Reference Plot 3.

Flavoparmelia caperata 1. Boulder County: Boulder Canyon, *Pseudotsuga - Picea - Populus tremuloides* forest, 2805 m, plot CO-16. More common than this single record would indicate. The superficial similarity of this species with the far more common *Flavopunctelia* species effectively hides *F. caperata* from the field crews in Colorado.

Flavopunctelia 7.

Flavopunctelia flaventior 8.

Flavopunctelia soredica 55.

Hypogymnia austerodes 16.

Hypogymnia bitteri 5. All occurrences were near the Continental Divide, and all but one in the southern third of the state: plots 3710627, 3710667, 3810666, 3710771, and 3910567.

Imshaugia 1.

Imshaugia aleurites 1.

Imshaugia placorodia 15.

Leptogium furfuraceum 1. Archuleta County: 2743 m, plot 3710724; see comments under *Collema nigrescens*.

Leptogium saturninum 1. Rio Grande County: 3200 m, plot 3710655.

Leptogium teretiusculum 1. Archuleta County: *Abies concolor - Pseudotsuga* forest on slope near creek, 2377 m, plot 3710627. Collected accidentally as part of another specimen, this extremely minute species has rarely been collected in North America. Although most collections farther north are from bark of deciduous hardwoods, this one was on *Pseudotsuga* bark. See additional notes on this site under *Collema furfuraceum*.

Letharia vulpina 3. Boulder, Clear Creek, and Grand Counties. Although this species is most frequent in dry habitats in the northern Rockies and Pacific Northwest, in Colorado it is was found in mesic mountain forests in the northern half of the state.

Melanelia 5.

Melanelia elegantula 71.

Melanelia disjuncta 1. Normally a rock-dwelling species.

Melanelia exasperatula 107.

Melanelia subaurifera 1. Grand County, 2743 m, plot 4010611Q.

Melanelia subolivacea 156.

Melanelia tominii 1. Normally a rock-dwelling species.

Nephroma parile 1. Archuleta County: *Abies concolor - Pseudotsuga* forest on slope near creek, 2377 m, plot 3710627. See additional notes on this plot under *Collema furfuraceum*. *N. parile* is fairly frequent in Colorado on mossy rock but is apparently rare as an epiphyte.

Parmelia sulcata 33.

Parmeliopsis ambigua 42.

Parmeliopsis hyperopta 14.

Phaeophyscia 5. Many of the *Phaeophyscia* specimens were small and fragmented, and often detected incidentally in a collection of another species.

Phaeophyscia cernohorskyi 3.

Phaeophyscia ciliata 14. Possibly some confusion with pre-sorediate juvenile *P. orbicularis*.

Phaeophyscia hirsuta 36. Quite common in Colorado, despite its sparse representation in herbaria. Often present in small amounts mixed with other genera and other species of *Phaeophyscia*.

Phaeophyscia nigricans 25. The species is relatively distinct and easily identified, despite its small size and the usually scrappy specimens.

Phaeophyscia orbicularis 12.

Physcia 9.

Physcia adscendens 112.

Physcia aipolia 22. *P. aipolia*, and *P. stellaris* were sometimes difficult to separate. We distinguished *P. aipolia* from *P. stellaris* solely on the K reaction of the medulla, the other characters seemingly uncorrelated with the K reaction.

Physcia biziana 83. There is a continuous gradation in pruinosity, lobe shapes, and thallus size between *P. biziana* and *P. stellaris*. Nevertheless, the extremes of these species are easily differentiated. Ruchty identified specimens that were only moderately pruinose, with short, rounded, and a bit scalloped lobes as *P. biziana*. On the other hand, if a specimen of moderate pruinosity had narrower lobes of the *aipolia* type, and the medulla was K-, the specimen was named *P. stellaris*. Specimens with little or no pruinosity and K- medulla were named *P. stellaris* regardless of lobe size. Physcia biziana tolerates drier conditions than *P. stellaris* and *P. aipolia*.

Physcia caesia 14.

Physcia callosa 1.

Physcia dimidiata 30.

Physcia dubia 2.

Physcia stellaris 63. See notes under *P. biziana* and *P. aipolia*.

Physcia tenella 14.

Physciella chloantha 21. Very common but small and often bark colored and easily overlooked by the field crews. In some urban, suburban, and riparian habitats this species is a dominant on tree trunks.

Physciella melanchra 6. In a range of habitats similar to *P. chloantha*, but always more sparse than that species.

Physciella nepalensis 5. On deciduous hardwoods at lower elevations. Boulder Co.: Legion Park, 1675 m, plot CO-11. Garfield Co., 2134 m, plot 3910847. Pitkin Co., 2682 m, plot 3910722. Routt Co.: open forest of *Populus tremuloides* and *Quercus* between Rabbit Ears Pass and Steamboat Springs, 2597 m, CO-18. Very similar in top view to *Phaeophyscia ciliata.* We confirmed these specimens by the paraplectenchymatous lower cortex visible in longitudinal sections under the compound microscope. One specimen was verified by T. L. Esslinger in 1995.

Physconia elegantula 1. Archuleta County: 2743 m, plot 3710724. See additional notes on this plot under *Collema nigrescens*.

Physconia enteroxantha 3.

Physconia perisidiosa 5.

Pseudevernia intensa 8. Found in mesic mountain forests in two areas: the Front Range north and east of Denver and southern Colorado.

Punctelia subrudecta 6.

Ramalina sinensis 8. This includes both broad-lobed and narrow-lobed forms.

Rhizoplaca chrysoleuca 5.

Rhizoplaca melanophthalma 2.

Usnea 43. Small, poorly developed *Usnea* specimens were common in the collections. Many of these had not developed reproductive structures and were not identifiable to species.

Usnea cavernosa 2.

Usnea hirta 90.

Usnea lapponica 85. This name is used in the broad sense, including all specimens that were papillate, tufted, and with soredia erupting through craters in the cortex with reflexed edges.

Usnea subfloridana 4. We used this name for tufted, papillate, isidiate *Usnea* species pending clarification of the taxonomy of this group.

Vulpicida pinastri 30.

Xanthoria 2.

Xanthoria candelaria 1. Although this name has been widely and indiscriminately used, in the restricted sense of Lindblom (1997) the species is relatively rare as an epiphyte in Colorado.

Xanthoria elegans 2.

Xanthoria fallax 71. This name was applied broadly prior to Lindblom (1997). Many of our specimens have been re-examined and a small fraction were found to be *X. fulva.* The similar *X. oregana* is also known from Colorado (Lindblom 1997).

Xanthoria fulva 5. Usually easy to separate from *X. fallax* by the narrow, often richly branched lobes.

Xanthoria montana 130. Previously reported as *X. polycarpa*, the recent revision of *Xanthoria* by Lindblom (1997) results in reassignment of the Colorado material to *X. montana*.

Xanthoparmelia 6. Specimens of *Xanthoparmelia* large enough to have distinguishing reproductive features were analyzed by thin-layer chromatography. The remaining specimens were not identified to species. All are typically rock-dwelling species with sporadic occurrences on hard bare wood, and even less often on bark.

Xanthoparmelia coloradoensis 5.

Xanthoparmelia cumberlandia 7.

Xanthoparmelia lavicola 1.

Xanthoparmelia lineola 4.

Xanthoparmelia plittii 6.

Xanthoparmelia subdecipiens 3.

Climatic Gradient

The first two axes of the NMS ordination (Figure 4) explained 74% of the variation in the analytical data set. The site factor most strongly related to the lichen communities was elevation, which had $r^2 = 0.56$ with the first axis, which in turn explained about 37% of the variation in lichen communities. We interpret this as a gradient in available moisture, given the well known relationships between elevation, precipitation, and temperature. Axis 2 was most strongly correlated with the binary variable contrasting the urban/industrial sites with the remote sites.

Precipitation variables were only weakly related to the ordination. Because elevation is a primary determinant of the precipitation estimates based on the PRISM model, we conclude that the link between the geographic coordinates of the PRISM estimates and our plot locations were too weak. This is no criticism of the PRISM model; on the contrary our detection of an elevation gradient suggests that we should try to improve the link between the grid used by the PRISM model and the FHM plot locations. Two steps should be taken: (1) use exact plot locations rather than EMAP grid centers for on-frame plots (FHM data managers would not allow us to use exact locations because of confidentiality requirements of private landowners), and (2) interpolate between PRISM points using elevation in addition to latitude and longitude.

Most of the lichen species in Colorado respond to this moisture gradient (Table 6). The richest sites for epiphytes tend to be in mesic sites, such as high elevation slopes and in sheltered canyons. There are relatively few species with peak abundance in the drier sites; epiphytic macrolichens are scarce in very dry habitats in Colorado.

Unlike many North American mountain ranges, such as the northern Rocky Mountains, Cascade Range, and Sierra Nevada, there was no consistent difference in the epiphytic lichens between the east slope of the Rockies and the west slope (Figure 3). According to Conrad's index (Trewartha 1961), western Colorado has a somewhat more continental climate than eastern Colorado. But from the perspective of the lichen communities, the opposing sides of the Continental Divide appear to be similarly continental in climate. While some species are more common on one side of the mountains than the other, the relationship is not strong enough to be expressed alongside the elevational, topographic, and air quality gradients. We hypothesize that most of the geographic variation in moisture score (Figure 3) derives from variation in local topography and elevation rather than regional synoptic gradients.

The proportion of basal area in conifers vs. hardwoods was unrelated to the major gradients in lichen communities. This surprised us because the lichens clearly discriminate between them on a tree-to-tree scale, hardwoods having a distinct lichen community from conifers. Occasionally this is expressed at the stand level (for example dry *Pinus contorta* stands having almost no epiphytic lichens). But the small number of plots containing pure hardwoods or conifers relegates this factor to a minor role in the regional picture. In other words, while the hardwood vs. conifer distinction is very important at the tree-to-tree scale, it is not an important factor at the regional scale. If, however, aspen is gradually lost from Colorado's forests, then the presence/absence of hardwoods may explain a larger proportion of the variation in Colorado's lichen communities than now.

Figure 4. Ordination of remote (+) and urban/industrial (•) plots on the basis of epiphytic lichens. Lines radiating from the centroid indicate the direction and strength of correlations between the two NMS axes and other parameters: Elev = elevation, Raw Air Score = the raw score for air quality (see methods), Adj. Air Score = score for air quality after adjusting for elevation, and S = number of species that are not indicators of air pollution.

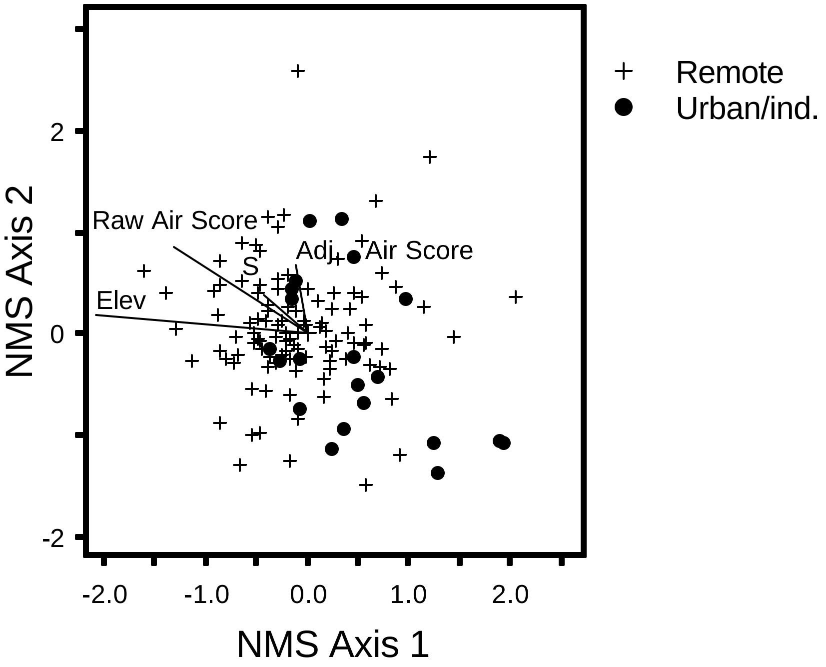


Table 6. Abundance and position of epiphytic lichens on the moisture gradient. Species are classed by the position of peak abundance on the first axis of the ordination. Scores on the moisture axis are expressed in standard deviations away from the average plot. Deviations are reversed from scores in Figure 4, so that negative deviations indicate drier than average conditions and positive deviations indicate wetter than average conditions.

Moisture optimum	Common species	Occasional species
-2 to -1 Dry	*Phaeophyscia hirsuta* *Xanthoria fallax*	
-1 to -0.3 Semi-dry	*Flavopunctelia soredica* *Phaeophyscia nigricans* *Physcia biziana* *Physciella chloantha*	*Cetraria fendleri* *Physciella melanchra* *Physconia perisidiosa*
-0.3 to 0.3 Modal	*Candelaria concolor* *Imshaugia placorodia* *Melanelia elegantula* *Melanelia subolivacea* *Parmelia sulcata* *Physcia adscendens* *Physcia aipolia* *Physcia dimidiata* *Usnea hirta* *Xanthoria montana*	*Flavopunctelia flaventior* *Imshaugia aleurites* *Phaeophyscia orbicularis* *Physcia caesia* *Physcia stellaris* *Physciella nepalensis* *Physconia enteroxantha* *Punctelia subrudecta*
0.3 to 1 Moist	*Bryoria fuscescens* *Hypogymnia austerodes* *Melanelia exasperatula* *Parmeliopsis ambigua* *Usnea hirta*	*Evernia divaricata* *Hypogymnia bitteri* *Letharia vulpina* *Parmeliopsis hyperopta* *Phaeophyscia ciliata* *Physcia tenella* *Pseudevernia intensa* *Ramalina sinensis* *Vulpicida pinastri*

Air Quality

We assessed the relationship between air quality and lichens in Colorado primarily by contrasting a set of 20 off-frame plots near industries and urban areas with the other plots in Colorado. Lichen communities differed between urban/industrial plots and other plots in the analytical data set (MRPP: $p << 0.001$, $R = 0.022$). Typical plots in Colorado had about 10-20 epiphytic macrolichen species on the trees. Species in our most urban and industrial plots included several recognized pollution tolerant species, such as *Candelaria concolor* and *Xanthoria fallax*. Furthermore, we found fewer species (Table 3) and lower total cover in these areas.

Indicator species analysis identified 10 indicators of low air quality, based on contrasting the urban/industrial plots to the remaining plots in the same elevation range as the urban/industrial plots (Table 7). No indicators of clean air were detected, owing to the heterogeneity of the clean-air plots. For a species to be detected as a clean air indicator by this analysis, it must be frequent across the range of remote plots, and largely absent from the urban/industrial plots.

The raw air quality index increased with elevation (Figure 5). A linear model is not entirely appropriate because of the constrained upper end of the air quality index. Having no better alternative measure of moisture, we adjusted the air quality index based on this relationship. The adjusted air quality index for a plot is simply its standardized residual from this relationship. In other words, the adjusted air quality index expressed air quality as a departure from expectation for a given elevation. This departure is expressed as a number of standard deviations above or below the regression line. This adjustment produced several plots with outlying low residuals (to -3.9 standard deviations below the mean; Table 2); otherwise, the residuals were normally distributed.

The site factor most strongly associated with the second NMS ordination axis was the adjusted air quality index. Adjusting the air quality index for elevation reduced the relationship between air quality and the moisture gradient (axis 1). This can be seen by noting the relatively broad angle between the adjusted air quality index ("Adj Air Score" in Figure 4) and elevation, as compared with the acute angle between the vectors representing elevation and the raw air quality index ("Raw Air Score" in Figure 4).

Species richness ("S" in Figure 4) had a loose positive relationship with both moisture and air quality. This is shown by the short vector pointing into the upper left quadrant of the ordination.

Table 7. Indicator species analysis, contrasting urban/industrial plots with other plots. Only plots with elevation < 2900 m are included. Only those species occurring in 6 or more of the 127 plots in the calibration data set are included. Indicators of urban/industrial plots are in **bold** face. Monte Carlo tests of significance (p) of observed maximum indicator value are based on 5000 randomizations of group assignments (urban/industrial vs. "other").

	Observed Indicator Values (IV)		Monte Carlo tests with randomized groups		
Species	Urban/ industrial	Other plots	Mean maximum IV	sd*	p**
Bryoria	0	5	4.3	2.15	0.565
Bryoria fuscescens	6	13	14.5	4.21	0.636
Candelaria concolor	**22**	2	11.8	3.81	0.019
Cetraria fendleri	0	6	5.0	2.53	0.565
Cladonia	0	5	4.4	2.01	0.575
Flavopunctelia flaventior	4	3	6.0	2.73	0.752
Flavopunctelia soredica	20	16	22.7	4.78	0.654
Hypogymnia austerodes	0	6	5.1	2.55	0.558
Imshaugia placorodia	0	8	6.0	2.71	0.326
Melanelia elegantula	**36**	17	27.9	4.72	0.073
Melanelia exasperatula	27	26	31.5	4.80	0.854
Melanelia subolivacea	28	47	43.6	3.64	0.161
Parmelia sulcata	17	3	11.1	3.79	0.108
Parmeliopsis ambigua	16	4	11.8	3.89	0.140
Parmeliopsis hyperopta	2	3	6.0	2.75	1.000
Phaeophyscia ciliata	1	6	7.0	3.01	0.573
Phaeophyscia hirsuta	**28**	8	18.9	4.32	0.050
Phaeophyscia nigricans	**34**	2	13.7	4.02	0.002
Phaeophyscia orbicularis	**21**	2	9.7	3.47	0.011
Physcia adscendens	21	32	33.1	4.64	0.531
Physcia aipolia	**24**	2	11.8	3.87	0.010
Physcia biziana	**13**	41	33.6	4.52	0.089
Physcia caesia	**17**	2	9.2	3.55	0.034
Physcia dimidiata	10	16	18.4	4.51	0.684
Physcia stellaris	8	23	20.8	4.53	0.283
Physcia tenella	0	11	7.7	3.07	0.195
Physciella chloantha	**31**	2	12.5	3.89	0.003
Pseudevernia intensa	6	1	6.0	2.80	0.579
Ramalina sinensis	0	6	5.2	2.59	0.533
Usnea	1	18	13.8	4.08	0.151
Usnea hirta	17	33	31.5	4.78	0.314
Usnea lapponica	12	23	23.9	4.70	0.467
Vulpicida pinastri	12	3	9.1	3.50	0.199
Xanthoria fallax	**52**	17	32.4	4.48	0.002
Xanthoria montana	33	44	43.0	3.68	0.351

* standard deviation of mean maximum IV from randomized trials.

** proportion of randomized trials with maximum IV equal to or exceeding the observed IV.

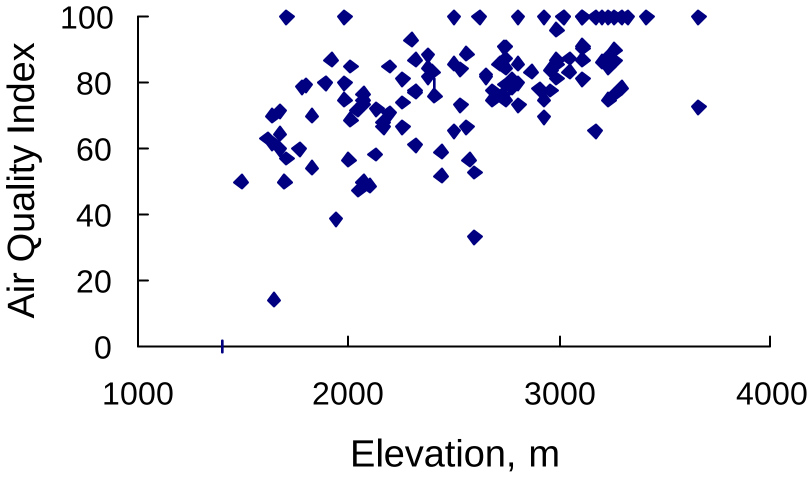


Figure 5. Relationship between the raw air quality index and elevation. Regression equation: *Index* = .0191(*Elevation*) + 28.776; $r^2 = 0.35$.

The urban/industrial plots were concentrated in two areas (Figure 3), the east side of the Front Range near Denver and Boulder, and the Steamboat Springs area. Each of these areas is described in more detail below. Low air quality scores were also seen an a few other scattered plots, but with no other concentrations in the state except for the Grand Junction area (Figure 3).

East Front: The Denver area has lower lichen diversity and abundance than areas deeper in the adjoining mountains. The presence of pollution-tolerant species and the absence of pollution-sensitive species suggests that air pollution is the cause of the altered lichen communities in the Denver area. Communities at low elevations in Boulder also had lower lichen abundance, lower diversity, and few pollution-sensitive species, although the pattern was not as strong as in the Denver area. This pattern appears to rapidly diminish west of the city and at higher elevations. Lichen communities in the mountains west of Denver and Boulder were relatively species rich and included pollution-sensitive species.

Steamboat Springs area: Steamboat Springs and the Park Range (Routt County) are downwind of several large coal-fired utilities (Jackson et al. 1996). Combined the power plants emit an estimated 22,000 short tons (1 short ton = 0.91 metric tons) of sulfur dioxide and 27,000 tons of nitrogen oxides. Snowpacks and precipitation in the Park Range have elevated sulfate and nitrate as compared with other high elevation sites in Colorado (Ely et al. 1993; Turk et al. 1992; Ingersoll 1996; CDPHE 1997). Data from NADP sites show low pH and high sulfate and nitrate deposition in Routt County (CDPHE 1997; http://nadp.sws.uiuc.edu/).

Jackson et al. (1996), studying biogeochemistry and lichen physiological processes in the Mount Zirkel Wilderness and surrounding areas, concluded:

> *Potential impacts on physiological functions of the lichens and moss from power station emissions are not obvious outside the Yampa River Valley in this study. The chemical data show clearly that the deposition is elevated and accumulation in the environment is highly possible. It is not clear yet, when these*

> *accumulations may reach a threshold level for the lichens to become damaged or for us to detect damage.*

Our off-frame sampling in the vicinity of Steamboat Springs and Hayden (6 plots) suggest that lichen communities have already been altered. On the lower to mid slopes near Steamboat Springs lichen diversity was lower than in many other areas that we sampled. The most abundant species (in the genera *Xanthoria*, *Physcia*, *Phaeophyscia*, and *Physciella*) are indicative of nutrient enrichment. Interestingly, *Xanthoria* was more prolific on conifers than usual, even on small needle-bearing twigs. This could be related to either higher calcium carbonate deposition or to deposition of nitrates, or both.

The situation on Rabbit Ears Pass east of Steamboat Springs seemed quite different. The lichens in an older conifer forest that we visited there appeared healthy and diverse, including a number of fruticose species thought to be pollution sensitive. On the other hand, this is one of the highest precipitation areas in Colorado, so a richer lichen flora would be expected.

Based on these preliminary observations, it appears that if there are effects of the power plants west of Steamboat Springs on the lichen communities in the Park Range, these effects would most likely be found at low to mid elevations. Although low pH and high sulfate in precipitation has been observed at high elevations in the Park Range, it is not yet clear whether this has had an effect on the lichen communities at high elevations.

More intensive sampling near Steamboat Springs and on the east slope of the Front Range are needed to better document the pattern. We recommend an intensified EMAP grid along the length of the Park Range, from Carbon County in southern Wyoming to the Colorado River in southwest Grand County. These data would allow a much more detailed analysis of gradients in climate and air quality in Colorado, as viewed by the lichens.

Aspen Decline

Epiphytic lichens communities differ dramatically between hardwoods and conifers. Because aspen (*Populus tremuloides*) is one of the primary hardwoods in Colorado, a decline in aspen would result in reductions in some lichen species. Mature to old aspen host a distinctive lichen community. Loss of aspen would affect all of the species dependent on it, including the characteristic lichen communities.

Research Needs

- To better understand gradients in lichen communities (and other indicators) in Colorado, we need better information on local climates. This is important to allow us to separate forest changes induced by climatic change from other kinds of temporal changes. The most cost-effective first step would be to modify the PRISM model to produce precipitation estimates for exact locations of all FHM plots in Colorado. Given latitude, longitude, and elevation of the plots, the interpolation procedure in PRISM can produce precipitation and temperature estimates far improved over the present approximation. A second goal is to calculate potential evapotranspiration (PET) based on slope, aspect, and temperature. Estimates of PET and precipitation will allow us to effectively document the relationship between Colorado's forests and climate. This information will be useful not only for interpreting lichen results, but also for interpreting most other indicators in the FHM program.
- More intensive sampling is needed in the Park Range and the Front Range, to better

monitor future changes in lichen communities and forest health resulting from air pollution. We recommend intensifying the EMAP sampling grid by 3X in those areas.

- To strengthen the link between the lichen indicator and direct air quality monitoring data we recommend sampling a special set of plots adjacent to NADP wet/dry deposition monitoring stations throughout Colorado.
- The items above should receive higher priority than continuous on-frame sampling in Colorado. We suggest not revisiting the on-frame plots for several years. Then revisit all plots in a single year or re-instate the quarter-interpenetrating sampling design, sampling a quarter of the plots per year for four years. Changes in lichen communities are likely to be slow and gradual. Efficiency of training, sampling, and data analysis can be improved by focusing the field work into fewer years.

Acknowledgments

We thank the FHM field crews, logistics coordinators, indicator development staff, program managers, and reviewers for their efforts. We appreciate the field assistance of Ann DeBolt, Peter Neitlich, Roger Rosentreter. Jeri Peck did much of the initial data management. Theodore Esslinger assisted with some difficult specimens of *Phaeophyscia* and *Physciella*. William Weber provided useful guidance and access to the lichen herbarium at the University of Colorado. We thank the cities of Denver and Boulder and Boulder County and Jefferson County Parks for permission to sample in city and county parks. Linda Geiser and USFS personnel in Colorado provided assistance and information on the Park Range and surrounding areas. Brian Cordova extracted data for us from the FHM databases in Las Vegas. Sharon LeDuc provided information on the Climatic Divisions used by the National Climatic Data Center. Chris Daly helped us obtain precipitation estimates with his PRISM model. Funding was provided by the Forest Health Monitoring Program, an interagency program including the USDA Forest Service, the U. S. Environmental Protection Agency, USDI Bureau of Land Management, USDA Natural Resource Conservation Service, and participating state agencies. The research described in this paper has not been subjected to reviews by any of those agencies. Therefore, it does not necessarily reflect the views of the agencies. No official endorsement should be inferred.

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