

AN ABSTRACT OF THE DISSERTATION OF

Sarah Jovan for the degree of Doctor of Philosophy in Botany and Plant Pathology
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Title: Bioindication of Air Quality in Forests of Northern and Central California Using
Epiphytic Macrolichen Communities

Abstract approved:

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Bruce McCune

The unifying purpose of this dissertation was to describe, model, and map relationships between epiphytic macrolichen communities and air quality in forests of northern and central California. First, multivariate analyses were used to subdivide the large study area into three model areas with similar climate, topography, and lichen communities: the NW Coast, the greater Central Valley, and the greater Sierra Nevada. Dividing the study area helped to reduce within model-area environmental variability, which may otherwise overpower lichen community responses to more localized pollutant gradients.

We then developed a gradient model for the greater Central Valley using lichen community surveys from 98 forested sites. Non-metric multidimensional scaling related community composition to climate, geography, stand characteristics, and common anthropogenic pollutants including ammonia, nitrogen dioxide, ozone, and sulfur dioxide. One prominent lichen community gradient was related to ammonia deposition as evidenced by an index of known indicator species, the proportion of nitrophile abundance. We used the model to estimate relative ammonia deposition to

each sampled forest. A second community gradient correlated with ozone, nitrogen dioxide, and a coast-to-inland humidity gradient. Because little is known about lichen community responses to ozone and nitrogen dioxide, we could not clearly differentiate pollution vs. climate effects along that gradient.

Lastly, we derived a gradient model for ammonia bioindication in the greater Sierra Nevada. We used nonlinear regression to correct the model for elevation effects, which appeared to confound the lichen community response to ammonia. We used the adjusted model to estimate relative ammonia deposition to 115 forested sites and geographic patterns were descriptively compared to preexisting direct monitoring data. Sources of noise and the underlying mechanism of the ammonia-nitrophile relationship are discussed. Ammonia bioindication is particularly important in California due to high emissions from automobile exhaust and agriculture. Furthermore, ammonia deposition is not measured directly by state or federal agencies. Other pollutants, like ozone and nitric acid, are also believed to be negatively affecting forest health in the region. More basic research is needed, however, to determine whether lichens are viable indicator species for these pollutants.

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Bioindication of Air Quality in Forests of Northern and Central California Using
Epiphytic Macrolichen Communities

by
Sarah Jovan

A DISSERTATION

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Sarah Jovan, Author

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DEDICATION

This dissertation is dedicated to George and Pamela Jovan, my parents, who have provided boundless encouragement and support throughout the years.

Without them I'd be lost

Bioindication of Air Quality in Forests of Northern and Central California Using Epiphytic Macrolichen Communities

Chapter 1. Introduction

When used for air quality bioindication, lichens are analogous to canaries in a coal mine. Lichen studies are commonly used for early detection of air quality issues and evaluation of potential impacts to natural resources. For physiological reasons not always understood, some pollutants have deleterious effects while others positively impact sensitive lichen species. Modern bioindication techniques have evolved to harness the insight provided by gradient analysis, which allows simultaneous consideration of many species sensitivities (e.g. McCune 1988, McCune et al. 1997a, van Dobben and ter Braak 1998, van Haluwyn and van Herk 2002, van Herk 1999 and 2001). The resulting models, in many cases, can be used to detect deposition gradients of particular pollutants.

Our overall goal was to develop models for indicating air quality in northern and central California. Analyses were largely based on epiphytic macrolichen community data collected by the Forest Inventory and Analysis Program (FIA; United States Department of Agriculture) for monitoring the health of United States forests. We tested for correlations between community composition and specific pollutants, which involved integration of direct pollutant measurements, estimated concentrations, and prior investigations on lichen indicator species.

Chapter 2 is devoted to characterizing the diverse epiphytic macrolichen flora and forest habitats of northern and central California. The primary objective was to divide 211 FIA plots into model areas encompassing relatively homogeneous climate, topography, and lichen communities. At such broad spatial extents, steep environmental gradients can overwhelm lichen responses to air quality. This was, in essence, our initial attempt to control for confounding environmental factors, an issue we revisit at a smaller spatial scale in Chapter 4. We used multivariate methods to

define three model areas: the NW Coast, the greater Central Valley, and the greater Sierra Nevada. Major lichen community gradients are discussed.

Chapter 3 presents the air quality bioindication model for greater Central Valley forests. We used non-metric multidimensional scaling (Kruskal 1964) to determine the strongest gradients in lichen community composition from 98 forested sites. We attempted to calibrate the model with direct pollutant measurements for ozone (O_3), nitrogen dioxide (NO_2), sulfur dioxide (SO_2), and estimated concentrations of O_3 and ammonia (NH_3). Lichen communities were strongly patterned along an NH_3 gradient, as evidenced by a simple index of indicator species known as "nitrophiles." We used the model to estimate relative NH_3 deposition to all study plots and to examine geographic patterns. Community gradients in relation to O_3 and NO_2 were confounded with a coast-to-mountain macroclimatic gradient. Lichen community responses to photochemicals are understudied, leaving us with little basis to differentiate climatic vs. pollutant effects.

Chapter 4 summarizes a similar bioindication model developed for the greater Sierra Nevada. Located just downwind of the Central Valley, forest degradation from air pollution is a critical management issue in this mountainous region where many National Parks and popular recreation areas are located. We focused our efforts on characterizing NH_3 patterns, known to be the predominant source of N deposition to the Sierra Range (Bytnerowicz and Fenn 1996; Bytnerowicz and Riechers 1995, Bytnerowicz et al. 2002, Fenn et al. 2003a). The lichen community response to NH_3 was confounded by elevation, which led us to compare the efficacy of three regression methods for extricating NH_3 effects from elevation effects. We used the final bioindication model, adjusted for elevation, to score all forested plots for relative NH_3 deposition. Potentially important sources of noise in the nitrophile- NH_3 relationship are acidic deposition and bark pH.

Air quality biomonitoring with lichens can be a cost-effective alternative or supplement to direct pollutant monitoring. Being relatively inexpensive to implement, the lichen biomonitoring approach allows a much higher sampling intensity. One can easily monitor forests in remote areas that lack power for running active deposition

samplers. A means to evaluate potential risks to forests is of major importance considering their ecological, economic, and recreational value.

Chapter 2

Regional Variation in Epiphytic Macrolichen Communities in Northern and Central California Forests

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ABSTRACT

We studied epiphytic macrolichen communities in northern and central California to 1) describe how gradients in community composition relate to climate, topography, and stand structure and 2) define subregions of relatively homogeneous lichen communities and environmental conditions. Non-metric multidimensional scaling was used to characterize landscape-level trends in lichen community composition from 211 plots. We found two gradients in lichen community composition that corresponded with macroclimatic gradients: one correlated with temperature variables and elevation, the second with moisture variables. Moist, warm plots supported more cyanolichen species while warm but dry plots supported a diverse nitrophilous flora. Ammonia pollution, which was not accounted for in the analysis, may also explain spatial patterns in nitrophilous species and deserves further study. Cluster analysis and indicator species analysis were used to divide lichen communities into more homogeneous groups and identify group indicator species. Three groups of plots differing in topography, macroclimate, and community composition were defined: the Greater Central Valley group; the Sierra, Southern Cascades, and Modoc group; and the NW Coast group. Communities in the Greater Central Valley group were typically diverse and dominated by nitrophilous species, averaging 14 species and 40% nitrophiles. Cyanolichens common to this group were mainly diminutive species from the genera *Leptogium* and *Collema*. Indicator species strongly associated with the Greater Central Valley included *Melanelia glabra*, *Candelaria concolor*, and *Parmelina quercina*. Communities from the Sierra, Southern Cascades, and Modoc group had the lowest species richness and total lichen abundance. Cyanolichens were absent while nitrophiles such as *Candelaria concolor* and *Xanthoria fulva* were frequent. Indicator species included *Letharia vulpina*, *L. columbiana*, and *Nodobryoria abbreviata*. The NW Coast group had the highest species richness, cyanolichen diversity, and cyanolichen abundance while nitrophiles were rare. Indicator species included *Platismatia glauca*, *Esslingeriana idahoensis*, and *Cetraria orbata*.

INTRODUCTION

This study is part of the development of a comprehensive air quality biomonitoring framework for California under the Forest Inventory and Analysis Program (FIA) of the USDA. The FIA program monitors regional forest health with biological indicators such as epiphytic lichens. The utility of lichens as indicators of air quality is well documented, especially with regard to acidifying and fertilizing pollution (de Bakker 1989; Gilbert 1970; Hawksworth and Rose 1970; McCune 1988; McCune et al. 1997a; Muir and McCune 1988; van Dobben and de Bakker, 1996; van Herk 1999, 2001).

Epiphytic macrolichen communities in northern and central California are diverse, owing greatly to the topographical and climatic complexity of this region. North of Santa Barbara, the California landscape is comprised of several large mountain ranges, valleys, and volcanic tablelands. The desert scrublands and *Juniperus occidentalis*-dominated stands of the Modoc Plateau in the northeast, for instance, host very distinct lichen assemblages compared to the *Abies*-dominated high Sierra, the hardwood savanna of the Central Valley, or the chaparral and temperate mixed conifer stands of the Coast Ranges. The complex lichen flora and steepness of environmental gradients in California pose a common difficulty for modeling air quality with community data. When applying air quality models at large spatial scales, the response of lichen communities to steep gradients (climate and topography, in this case) often overwhelms the influence of more localized gradients (air pollution).

Our objectives were to 1) describe gradients in epiphytic lichen communities across the landscape 2) determine how these gradients relate to climate, topography, and stand structure and 3) synthesize this information to define subregions differing in lichen communities and environmental conditions. This analysis serves a dual purpose. We will ultimately utilize the delineated subregions as model areas in a second FIA study of how lichen communities respond to air quality in northern and central California. Basing models on subregions that are relatively homogeneous in

terms of community composition, climate, and topography, will improve our ability to detect air pollution effects.

Additionally, we aim to fill some critical gaps in our knowledge of lichen biogeography in the region. Numerous researchers have explored the lichen flora of particular wilderness areas (Ryan 1990*a*, 1990*b*), national or state parks (Baltzo 1989; Smith 1980; Smith 1990; Wetmore 1985), watersheds (Ryan and Nash 1991) and broader geographic regions (Herbert and Meyer 1984). Conspicuously lacking, however, are landscape-level floristic studies and analyses of how community composition varies according to environmental variables such as climate, topography, and stand structure. The only such study (Jovan 2002) was limited to patterns in species richness in northern and central California.

Our examination of lichen communities includes describing the distributions of lichens from the cyanolichen and nitrophile functional groups because of their known value as indicator species. Cyanolichens fix atmospheric nitrogen through a cyanobacterial partner and can serve as important source of nitrogen for forest ecosystems (Antoine 2001). Some cyanolichens are indicators of acidic deposition (Denison et al. 1977; Gauslaa 1995; James et al. 1977) and ecological continuity (Goward 1994; Rose 1976, 1988). Nitrophilous ("nitrogen-loving") lichens are frequently associated with agricultural areas where deposition of reduced nitrogen pollutants is high (de Bakker 1989; van Dobben and de Bakker 1996; van Herk 1999, 2001). Indicator species in this group are used extensively in the Netherlands to detect ammonia pollution from agriculture.

METHODS

Field procedure

Field crews collected lichen community data from 211 permanent plots on a 27 km hexagonal grid run by the FIA program. Plots span all land ownerships. Plot density was lower in some areas where plots fell on land with restricted access or that were not forested. Due to extremely low plot density in southern California, we

analyzed only plots north of Santa Barbara. The climatically different Great Basin of the Sierra Nevada was also excluded.

Collection of the lichen community data followed a standardized FIA protocol (McCune et al. 1997b, detailed methodology and raw lichen data are available at <http://fia.fs.fed.us/lichen/>). Field crews visited each 0.38 hectare circular plot once over a four-year time span (1998-2001) and collected specimens of all epiphytic macrolichens occurring above 0.5 m on woody species or in the litter. Each species was assigned an abundance class: 1 = rare (< 3 thalli), 2 = uncommon (4-10 thalli), 3 = common (> 10 thalli present but species occurs on less than 50% of all boles and branches), and 4 = abundant (> 10 thalli present and species occurs on more than 50% of all boles and branches). Field workers surveyed for lichens for at least thirty minutes and up to two hours or until ten minutes elapsed without encountering additional species. Specimens were sent to professional lichenologists for identification. Additional data on stand structure were collected at each plot: total basal area, total overstory tree diversity, percent hardwood (broad-leaved) basal area, overstory diversity of hardwoods, percent softwood (conifer) basal area, and overstory diversity of softwoods.

Quality Assurance

Field workers were typically non-specialists but underwent three days of intensive training and passed a certification exam before conducting surveys. To be certified, field workers had to capture 65% of the species found by a professional lichenologist in a practice plot. Field workers were not required to accurately assign names to lichen species in the field but were trained to carefully distinguish between species based upon morphology. Professional lichenologists periodically audited field crews throughout the field season during "hot checks" (both specialists and field crew surveyed a plot simultaneously) and "blind checks" (specialists re-measured a plot within two months of the crew survey). Crews were audited fifteen times over four years of data collection and field workers always captured at least 65% of the species

found by specialists. During 80% of audits, field workers captured at least 80% of the species. McCune et al. (1997b) tested the efficacy of the 65% capture criterion using FIA lichen community data and non-metric multidimensional scaling (NMS; Kruskal 1964), the same ordination analysis used in this study. They found that plot scores on ordination axes were highly repeatable as long as the 65% criterion was met. Non-specialist scores will typically deviate about 2% to 10% from specialist scores along an environmental gradient.

Specimen identification and location

Voucher specimens reside at the Oregon State University herbarium (OSC). Most identifications followed the nomenclature of McCune and Geiser (1997). *Physconia* identifications follow the taxonomy of Esslinger (2000) and *Xanthoria* identifications followed the taxonomy of Lindblom (1997). Nomenclature for species in the *Pannariaceae* followed the work of (Jørgenson 2000, 2002). *Usnea* taxonomy followed the keys of Tavares (1997). Thin-layer chromatography was not used to aid identifications because all species in our dataset could be reliably identified by morphology and chemical tests.

Analysis

Plots without lichens and duplicate surveys from quality assurance (QA) plots were excluded from the dataset. One survey was retained for each QA plot: the survey done by a non-specialist with the highest species richness. To reduce noise in the data, infrequent lichen species, defined as species occurring within <2% of the plots, were excluded from the analysis. After removing 71 infrequent species, the analysis was based upon a total of 96 species. Deletion of infrequent species typically improves correlations between ordination axes and environmental variables (McCune and Grace 2002), which was appropriate for our goal of resolving the most prominent gradients in epiphytic lichen community composition.

Climate data, averaged over 1961 to 1990, were extracted from the Precipitation-Elevation Regressions on Independent Slopes Model (PRISM; Daly et

al. 1994, 2001, 2002): mean annual dew temperature, mean annual temperature, mean annual maximum temperature, mean annual minimum temperature, mean annual precipitation, mean number of wetdays per year, and mean annual relative humidity. Additionally, elevation, latitude, longitude, total basal area, total tree species richness, and percent basal area and diversity of hardwoods and softwoods were included in the analysis.

We characterized community composition in terms of nitrophile and cyanolichen species diversity in the plots. Four indices were calculated before we removed infrequent species from the dataset: cyanolichen species richness (raw number of species), % cyanolichen richness (% of all species present that were cyanolichens), nitrophile species richness, and % nitrophile richness. Species considered nitrophilous in this study are indicated in Table 2.1. Most nitrophile designations were based upon the determinations of Hawksworth and Rose (1970), McCune and Geiser (1997), and van Herk (1999, 2001). Diminutive species were excluded from the cyanolichen indices as they are frequently overlooked, making their distributions unreliable. All species were excluded from the following genera: *Collema*, “*Dendriscoaulon*”, *Fuscopannaria*, *Leptochidium*, *Leptogium*, *Pannaria*, and *Polychidium*. Total species richness was examined for each subregion defined by the gradient analysis although a more in-depth examination of species richness in the study area can be found in Jovan (2002).

All statistical analyses were conducted using PC-ORD software (McCune and Mefford 1999). To delineate distinctive model areas, plots were separated into preliminary groups using hierarchical, agglomerative cluster analysis with relative Sorensen distance measure and Ward’s linkage method. This analysis puts plots into relatively homogenous groups based upon differences in their species composition. An indicator species analysis (ISA; Dufrêne and Legendre 1997) described differences in species composition among groups and determined how strongly each lichen species was associated with a particular group.

Non-metric multidimensional scaling ordination was conducted on a matrix of sample units by species abundances to detect prominent gradients in species

composition. Using the relative Sørensen distance measure, the data underwent 500 iterations per run and we chose the best (lowest stress) solution from 500 runs with real data, each run beginning with a random configuration. PC-ORD follows Mather (1976) in handling tied distances. A Monte Carlo test evaluated the strength of patterns relative to 500 runs with randomized data. We calculated coefficients of determination between original plot distances and distances in the final ordination solution to assess how much variability in lichen community composition was represented by the NMS axes (McCune and Grace 2002). We maximized correlations between environmental variables and the ordination solution using orthogonal rotation. Environmental variables were related to the strongest gradients (axes) in species composition using overlays and correlation coefficients (McCune and Grace 2002). Differences in environmental conditions and lichen community composition among the groups defined by cluster analysis were visualized as ordination overlays. Boxplots showed univariate relationships among groups.

RESULTS AND DISCUSSION

Defining groups

The cluster analysis dendrogram was cut at 25% of the information remaining, wherein plots were apportioned into three groups. The groups, which differed in topography and macroclimate, will provide the basis for the future development of three air quality bioindication models: the Greater Central Valley model; the Sierra, Southern Cascades, and Modoc model¹; and the Northwest Coast model (Figure 2.1). The ISA identified ten or more lichens as statistically significant indicator species for each model area (Table 2.1). Stronger indicators have higher indicator values, which quantify the faithfulness and exclusivity of a species to a particular group (McCune and Grace 2002).

Table 2.1. Summary of macrolichen species found in California FIA plots. % Freq is the percentage of plots where the species occurred. Species in boldface were statistically significant indicators of one of the model areas ($p < 0.05$). Associated indicator values (IV) are reported for each group. (N) = species considered nitrophilous in this study. SCM = Sierra Nevada, Southern Cascades, and Modoc model area.

Species	Total (n=211)		Central Valley (n=67)		SCM (n=85)		NW Coast (n=59)	
	%Freq	IV	%Freq	IV	%Freq	IV	%Freq	
<i>Ahtiana sphaerosporella</i>	13.27	-	1.49	24.3	28.24	-	5.08	
<i>Alectoria imshaugii</i>	0.95	-	0.00	-	1.18	-	1.69	
<i>Alectoria sarmentosa</i>	13.27	-	0.00	-	2.35	43.2	44.07	
<i>Alectoria vancouverensis</i>	0.95	-	0.00	-	0.00	-	3.39	
<i>Bryoria capillaris</i>	7.11	-	0.00	-	1.18	22.5	23.73	
<i>Bryoria fremontii</i>	12.32	-	0.00	12.4	21.18	-	13.56	
<i>Bryoria friabilis</i>	0.95	-	0.00	-	1.18	-	1.69	
<i>Bryoria fuscescens</i>	1.90	-	0.00	-	2.35	-	3.39	
<i>Bryoria pseudofuscescens</i>	1.42	-	0.00	-	1.18	-	3.39	
<i>Bryoria simplicior</i>	1.90	-	0.00	-	2.35	-	3.39	
<i>Bryoria tortuosa</i>	1.42	-	0.00	-	0.00	5.1	5.08	
<i>Bryoria trichodes</i>	0.95	-	0.00	-	1.18	-	1.69	
<i>Candelaria concolor</i> (N)	43.60	51.2	79.10	-	41.18	-	6.78	
<i>Cetraria chlorophylla</i>	11.37	-	1.49	-	8.24	23.1	27.12	
<i>Cetraria merrillii</i>	28.91	-	14.93	20.8	42.35	-	25.42	
<i>Cetraria orbata</i>	24.17	-	10.45	-	15.29	44.5	52.54	
<i>Cetraria pallidula</i>	2.37	-	0.00	-	3.53	-	3.39	
<i>Cetraria platyphylla</i>	25.59	-	2.99	-	29.41	27.7	45.76	

Table 2.1 (Continued)

<i>Cetrelia cetrarioides</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Cladonia chlorophaea</i>	0.95	-	0.00	-	1.18	-	1.69
<i>Cladonia coniocraea</i>	1.42	-	1.49	-	0.00	-	3.39
<i>Cladonia fimbriata</i>	3.32	-	1.49	-	0.00	8.5	10.17
<i>Cladonia furcata</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Cladonia ochrochlora</i>	2.84	-	2.99	-	0.00	-	6.78
<i>C. squamosa v. subsquam.</i>	1.42	-	0.00	-	0.00	5.1	5.08
<i>Cladonia transcendens</i>	5.21	-	0.00	-	0.00	18.6	18.64
<i>Cladonia verruculosa</i>	1.42	-	0.00	-	0.00	5.1	5.08
<i>Collema furfuraceum</i>	10.43	24.7	28.36	-	0.00	-	5.08
<i>Collema nigrescens</i>	8.06	-	10.45	-	0.00	9.8	16.95
<i>Collema subflaccidum</i>	0.47	-	1.49	-	0.00	-	0.00
<i>"Dendriscoaulon" sp.</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Esslingeriana idahoensis</i>	18.96	-	4.48	-	4.71	48.7	55.93
<i>Evernia prunastri</i>	32.23	31.9	53.73	-	8.24	-	42.37
<i>Flavoparmelia caperata</i> (N)	0.95	-	2.99	-	0.00	-	0.00
<i>Flavopunctelia flaventior</i> (N)	14.22	41.5	43.28	-	0.00	-	1.69
<i>Flavopunctelia soledica</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Fuscopannaria leucostictoides</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Fuscopannaria mediterranea</i>	1.42	-	1.49	-	0.00	-	3.39
<i>Fuscopannaria pacifica</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Fuscopannaria pulveracea</i>	0.47	-	0.00	-	0.00	-	1.59

Table 2.1 (Continued)

<i>Heterodermia leucomelos</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Hypogymnia apinnata</i>	2.37	-	0.00	-	0.00	8.5	8.47
<i>Hypogymnia enteromorpha</i>	7.58	-	0.00	-	1.18	24.2	25.42
<i>Hypogymnia imshaugii</i>	58.77	-	29.85	-	68.24	36.4	77.97
<i>Hypogymnia inactiva</i>	8.06	-	2.99	-	0.00	23.0	25.42
<i>Hypogymnia metaphysodes</i>	1.42	-	0.00	-	0.00	5.1	5.08
<i>Hypogymnia occidentalis</i>	6.16	-	4.48	-	1.18	12.6	15.25
<i>Hypogymnia physodes</i>	1.90	-	4.48	-	0.00	-	1.69
<i>Hypogymnia tubulosa</i>	4.27	-	5.97	-	0.00	-	8.47
<i>Leptochidium albociliatum</i>	1.90	-	2.99	-	0.00	-	3.39
<i>Leptogium brebissonii</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Leptogium cellulosum</i>	1.42	-	0.00	-	0.00	5.1	5.08
<i>Leptogium corniculatum</i>	0.95	-	2.99	-	0.00	-	0.00
<i>Leptogium gelatinosum</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Leptogium lichenoides</i>	12.80	19.0	28.36	-	0.00	-	13.56
<i>Leptogium polycarpum</i>	0.95	-	1.49	-	0.00	-	1.69
<i>Leptogium pseudofurfuraceum</i>	6.64	17.6	19.40	-	0.00	-	1.69
<i>Leptogium saturninum</i>	1.42	-	2.99	-	0.00	-	1.69
<i>Leptogium tenuissimum</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Leptogium teretiusculum</i>	1.42	-	0.00	-	0.00	5.1	5.08
<i>Letharia columbiana</i>	38.39	-	8.96	56.0	74.12	-	20.34
<i>Letharia vulpina</i>	56.87	-	17.91	47.9	85.88	-	59.32

Table 2.1 (Continued)

<i>Lobaria hallii</i>	2.37	-	1.49	-	0.00	6.2	6.78
<i>Lobaria oregana</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Lobaria pulmonaria</i>	6.64	-	0.00	-	0.00	23.7	23.73
<i>Melanelia elegantula</i>	17.54	-	5.97	27.2	35.29	-	5.08
<i>Melanelia exasperatula</i>	13.27	-	5.97	11.3	21.18	-	10.17
<i>Melanelia fuliginosa</i>	2.84	5.7	7.46	-	0.00	-	1.69
<i>Melanelia glabra</i>	27.01	67.2	74.63	-	5.88	-	3.39
<i>Melanelia subargentifera</i>	2.37	7.5	7.46	-	0.00	-	0.00
<i>Melanelia subaurifera</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Melanelia subelegantula</i>	6.16	-	0.00	-	10.59	-	6.78
<i>Melanelia subolivacea</i>	41.23	-	43.28	-	48.24	-	28.81
<i>Nephroma bellum</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Nephroma helveticum</i>	8.53	-	1.49	-	0.00	27.2	28.81
<i>Nephroma resupinatum</i>	4.74	-	1.49	-	0.00	14.7	15.25
<i>Niebla cephalota</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Nodobryoria abbreviata</i>	30.81	-	2.99	25.9	49.41	-	35.59
<i>Nodobryoria oregana</i>	20.85	-	0.00	15.9	31.76	-	28.81
<i>Parmelia hygrophila</i> (N)	11.85	-	5.97	-	3.53	22.9	30.51
<i>Parmelia pseudosulcata</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Parmelia saxatilis</i>	1.42	-	1.49	-	0.00	-	3.39
<i>Parmelia sulcata</i>	27.01	-	22.39	-	15.29	29.2	49.15
<i>Parmeliella triptophylla</i>	1.42	-	2.99	-	0.00	-	1.69

Table 2.1 (Continued)

<i>Parmelina quercina</i>	20.85	52.1	58.21	-	1.18	-	6.78
<i>Parmeliopsis ambigua</i>	3.79	-	0.00	-	4.71	-	6.78
<i>Parmeliopsis hyperopta</i>	3.79	-	0.00	-	1.18	11.4	11.86
<i>Parmotrema arnoldii</i>	2.37	-	2.99	-	0.00	-	5.08
<i>Parmotrema austrosinense</i>	0.95	-	2.99	-	0.00	-	0.00
<i>Parmotrema chinense</i>	1.90	6.0	5.97	-	0.00	-	0.00
<i>Peltigera collina</i>	9.00	-	13.43	-	0.00	-	16.95
<i>Peltigera membranacea</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Peltigera praetextata</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Phaeophyscia ciliata</i>	2.37	-	5.97	-	0.00	-	1.69
<i>Phaeophyscia hirsuta</i> (N)	0.47	-	1.49	-	0.00	-	0.00
<i>Phaeophyscia orbicularis</i> (N)	9.00	21.8	23.88	-	2.35	-	1.69
<i>Physcia adscendens</i> (N)	22.75	39.8	52.24	-	9.41	-	8.47
<i>Physcia aipolia</i> (N)	17.06	20.4	32.84	-	2.35	-	20.34
<i>Physcia americana</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Physcia biziana</i>	15.64	39.0	43.28	-	1.18	-	5.08
<i>Physcia caesia</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Physcia dimidiata</i> (N)	5.21	-	8.96	-	5.88	-	0.00
<i>Physcia dubia</i> (N)	2.37	-	4.48	-	2.35	-	0.00
<i>Physcia stellaris</i> (N)	9.48	17.7	22.39	-	4.71	-	1.69
<i>Physcia tenella</i> (N)	10.43	-	13.43	-	10.59	-	6.78
<i>Physciella chloantha</i>	0.95	-	2.99	-	0.00	-	0.00

Table 2.1 (Continued)

<i>Physciella melanchra</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Physconia americana</i>	28.44	31.6	53.73	-	5.88	-	32.20
<i>Physconia enteroxantha</i> (N)	19.43	21.1	34.33	-	9.41	-	16.95
<i>Physconia fallax</i>	5.69	7.2	10.45	-	4.71	-	1.69
<i>Physconia isidiigera</i>	26.07	49.1	62.69	-	4.71	-	15.25
<i>Physconia leucoleiptes</i>	1.90	-	1.49	-	1.18	-	3.39
<i>Physconia perisidiosa</i> (N)	29.86	38.7	59.70	-	5.88	-	30.51
<i>Platismatia glauca</i>	22.75	-	5.97	-	7.06	55.4	64.41
<i>Platismatia herrei</i>	7.11	-	0.00	-	0.00	25.4	25.42
<i>Platismatia stenophylla</i>	7.11	-	0.00	-	0.00	25.4	25.42
<i>Polychidium muscicola</i>	0.95	-	0.00	-	0.00	-	3.39
<i>Pseudocyphellaria anomala</i>	9.48	-	4.48	-	0.00	25.3	28.81
<i>Pseudocyphellaria anthraspis</i>	14.69	-	14.93	-	0.00	25.0	35.59
<i>Pseudocyphellaria crocata</i>	0.00	-	0.00	-	0.00	-	0.00
<i>Punctelia subrudecta</i>	6.16	19.4	19.40	-	0.00	-	0.00
<i>Ramalina dilacerata</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Ramalina farinacea</i>	11.37	-	17.91	-	0.00	-	20.34
<i>Ramalina leptocarpha</i>	1.42	-	2.99	-	0.00	-	1.69
<i>Ramalina menziesii</i>	3.32	8.4	8.96	-	0.00	-	1.69
<i>Ramalina pollinaria</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Ramalina roesleri</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Ramalina sinensis</i>	0.47	-	1.49	-	0.00	-	0.00

Table 2.1 (Continued)

<i>Ramalina subleptocarpha</i> (N)	4.74	10.1	11.94	-	2.35	-	0.00
<i>Ramalina thrausta</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Sphaerophorus globosus</i>	5.69	-	1.49	-	0.00	17.5	18.64
<i>Sticta fuliginosa</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Sticta limbata</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Teloschistes chrysophthalmus</i>	0.00	-	0.00	-	0.00	-	0.00
<i>Teloschistes flavicans</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Tholurna dissimilis</i>	0.47	-	0.00	-	1.18	-	0.00
<i>Usnea arizonica</i>	2.84	-	5.97	-	0.00	-	3.39
<i>Usnea cavernosa</i>	2.37	-	0.00	-	0.00	8.5	8.47
<i>Usnea ceratina</i>	1.42	-	0.00	-	0.00	-	5.08
<i>Usnea chaetophora</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea cornuta</i>	1.42	-	1.49	-	0.00	-	3.39
<i>Usnea diplotypus</i>	3.32	-	0.00	-	1.18	9.1	10.17
<i>Usnea esperantiana</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea filipendula</i>	16.59	-	0.00	-	9.41	39.5	45.76
<i>Usnea fragilescens</i>	0.47	-	1.49	-	0.00	-	0.00
<i>Usnea glabrata</i>	1.90	-	1.49	-	0.00	-	5.08
<i>Usnea glabrescens</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea hirta</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea lapponica</i>	1.42	-	1.49	-	1.18	-	1.69
<i>Usnea pacificana</i>	5.69	-	1.49	-	1.18	16.0	16.95

Table 2.1 (Continued)

<i>Usnea rubicunda</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea scabrata</i>	7.11	-	1.49	-	2.35	18.2	20.34
<i>Usnea subfloridana</i>	6.16	-	1.49	-	1.18	16.7	18.64
<i>Usnea substerilis</i>	3.79	-	5.97	-	1.18	-	5.08
<i>Usnea wasmuthii</i>	0.47	-	0.00	-	0.00	-	1.69
<i>Usnea wirthii</i>	3.32	-	0.00	-	0.00	11.9	11.86
<i>Vulpicida canadensis</i>	6.16	-	2.99	-	3.53	9.3	13.56
<i>Xanthoria candelaria</i> (N)	12.80	-	13.43	-	18.82	-	3.39
<i>Xanthoria fallax</i> (N)	10.43	12.6	19.40	-	10.59	-	0.00
<i>Xanthoria fulva</i> (N)	9.95	-	8.96	11.6	17.65	-	0.00
<i>Xanthoria hasseana</i> (N)	18.48	16.0	31.34	-	8.24	-	18.64
<i>Xanthoria oregana</i> (N)	18.01	17.2	29.85	-	18.82	-	3.39
<i>Xanthoria parietina</i> (N)	1.90	6.0	5.97	-	0.00	-	0.00
<i>Xanthoria polycarpa</i> (N)	17.54	33.4	41.79	-	7.06	-	5.08
<i>Xanthoria tenax</i> (N)	2.37	-	5.97	-	1.18	-	0.00

Gradient analysis

Climatic and geographic differentiation of the groups is apparent in the NMS ordination joint plot, where environmental variables were overlaid on the solution as vectors (Figure 2.2). The ordination had two axes because the addition of a third axis afforded only a slight improvement in fit (minimum stress). A Monte Carlo test of 500 runs with randomized data indicated the minimum stress of the 2-d solution was lower than would be expected by chance ($p = 0.009$). The final stress and instability of the 2-d solution were 23.52 and 0.003, respectively. The first ordination axis captured

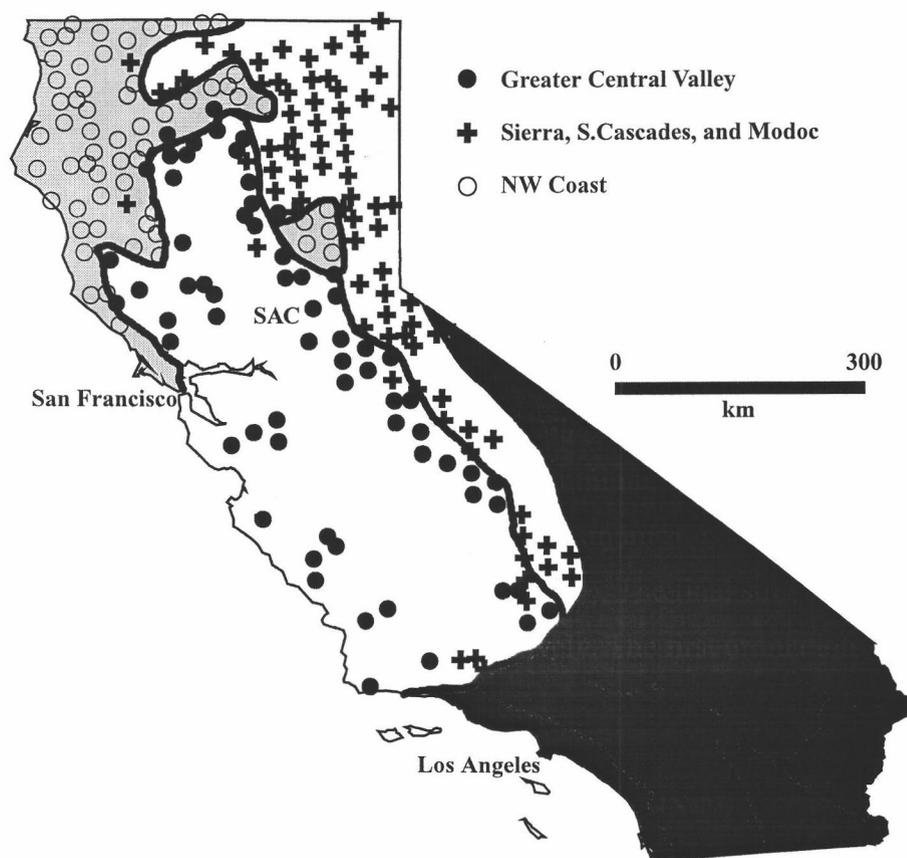


Figure 2.1. Approximate boundaries of model areas. The NW Coast model area is shaded in gray and the blackened area was excluded from the analysis. Plots were grouped according to an agglomerative, hierarchical cluster analysis with relative Sørensen distance measure and Ward's linkage method. SAC = approximate location of Sacramento.

36.3% of the variability in the dataset and the second captured 34.8% (cumulative $r^2 = 0.711$).

Gradients in lichen community composition reflected two major macroclimatic gradients: the first axis described a temperature-elevation gradient and the second, a moisture gradient (Figure 2.2). Elevation ($r = 0.79$), mean temperature (-0.78), dew temperature (-0.74), minimum temperature (-0.74), and maximum temperature (-0.76) were all highly correlated with axis 1 (Table 2.2). As expected, diversity of hardwood species and % basal area in hardwoods both correlated negatively with axis 1 ($r = -0.61$ and -0.70 , respectively), showing the typical trend of more hardwoods at low elevations. Wetdays, precipitation, and longitude, all variables related to moisture, were strongly correlated with axis 2 ($r = -0.71$, -0.66 , and 0.61 , respectively; Table 2.2).

Cyanolichen and nitrophile indices

Each functional group index was correlated with both macroclimatic gradients (Table 2.2, Figure 2.2). Cyanolichen richness and proportion of total species richness were higher in moister, warmer habitats. Contrastingly, nitrophile richness and % nitrophile richness were higher in warmer, drier plots. The moderate to high correlations of the nitrophile and cyanolichen indices with the ordination axes portrays the benefit of using a community approach to indicate environmental conditions. These indices are more likely to be linearly related to environmental variables than distributions of individual species.

Model areas

Greater Central Valley

The geographic extent of the Greater Central Valley group includes the San Francisco Bay area, the central coast, and parts of the Sierra Nevada foothills (Figure 2.1). Lichen community composition indicates regionally high temperatures and low

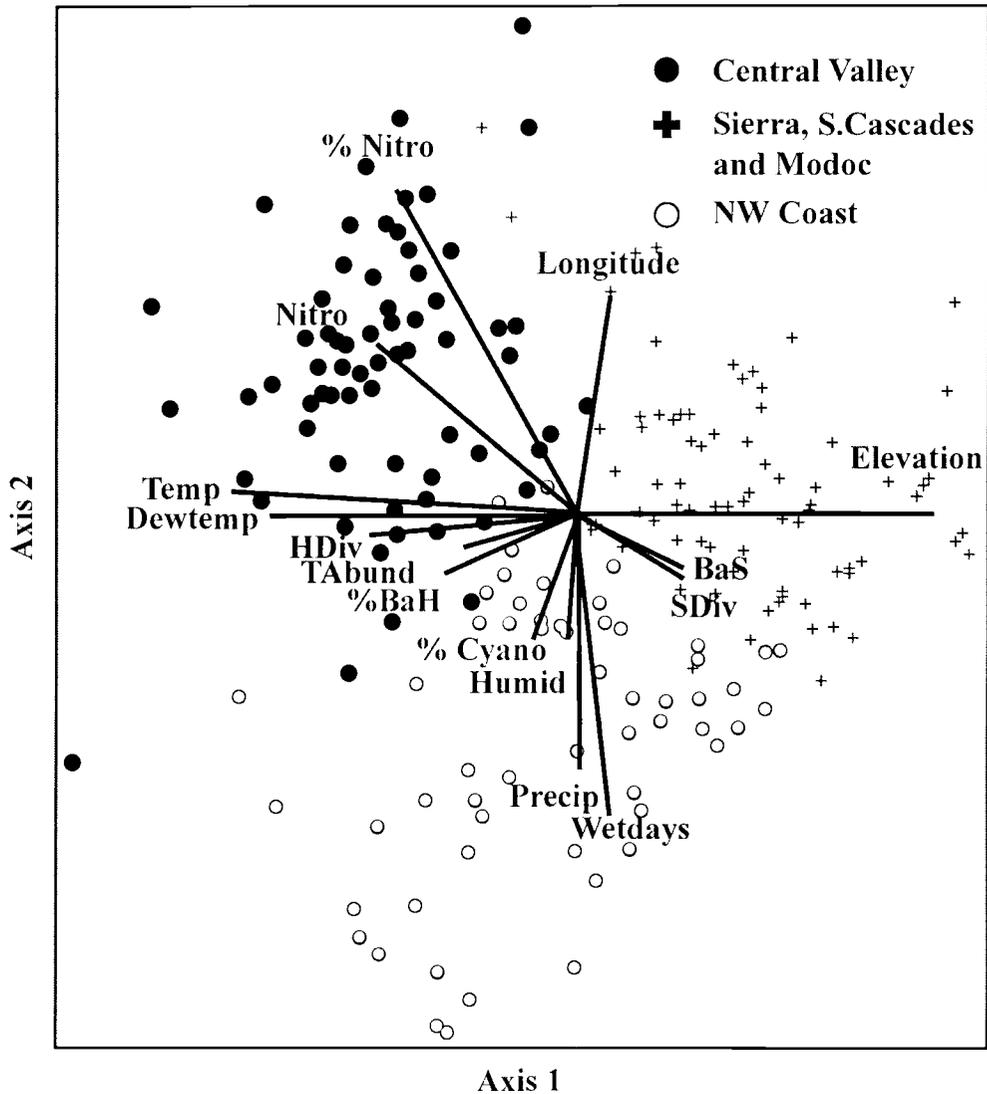


Figure 2.2. Ordination plotted to scale in a joint plot with environmental variables overlaid. Symbols indicate field plots. Vector length and direction indicates correlations of the variable with ordination axes. Only vectors with an $-0.42 < r > 0.42$ for one axis are shown to prevent crowding. Related variables with overlapping vectors of similar strength are designated by a single label: "Temp" (temperature) includes mean temperature, minimum temperature, and maximum temperature. Nitro = nitrophile diversity, % Nitro = percent nitrophile diversity. BaS = basal area in softwoods. SDiv = softwood diversity, Precip = precipitation, Humid = humidity, %Cyano = percent cyanolichens, %BaH = percent basal area in hardwoods, TABund = total lichen abundance, HDiv = hardwood diversity, Dewtemp = dew temperature.

moisture relative to the other regions in the study area, which is consistent with the PRISM climatic data (Figures 2.2 and 2.3). According to the ISA, the five strongest indicators of the Greater Central Valley group were *Melanelia glabra*, *Candelaria concolor*, *Parmelina quercina*, *Physcia adscendens*, and *Physconia isidiigera* (Table 2.1). Overall, a high proportion of indicator species for this group were nitrophilous species, including many species from the genera *Physcia*, *Physconia*, and *Xanthoria*.

Table 2.2. Correlations between environmental variables and ordination axes and between community summary variables and ordination axes.

Variable	Axis	
	1	2
	r	r
Longitude	0.23	0.61
Latitude	0.16	-0.50
Elevation	0.79	0.00
Dew temperature	-0.74	-0.02
Maximum temperature	-0.76	0.20
Mean temperature	-0.78	0.21
Wetdays	0.23	-0.71
Minimum temperature	-0.74	0.20
Precipitation	-0.01	-0.66
Humidity	-0.14	-0.45
Total basal area	0.23	-0.43
Overstory tree diversity	-0.04	-0.44
% Basal area in hardwoods	-0.70	0.19
Hardwood basal area	-0.49	-0.32
Hardwood diversity	-0.61	-0.18
Softwood basal area	0.42	-0.30
Softwood diversity	0.43	-0.33
Lichen species richness	-0.40	-0.27
Total lichen abundance	-0.44	-0.23
Cyanolichen diversity	-0.24	-0.41
% Cyanolichens	-0.29	-0.47
Nitrophile diversity	-0.59	0.53
% Nitrophiles	-0.57	0.75

Most cyanolichen species were uncommon, excepting diminutive species from the genera *Leptogium* and *Collema* (Table 2.1). Species richness for the area was high because plots tended to have a high diversity and abundance of nitrophiles (Figures 2.2 and 2.3). Over 50% of the lichen abundance was from nitrophiles in over 60% of plots from this group.

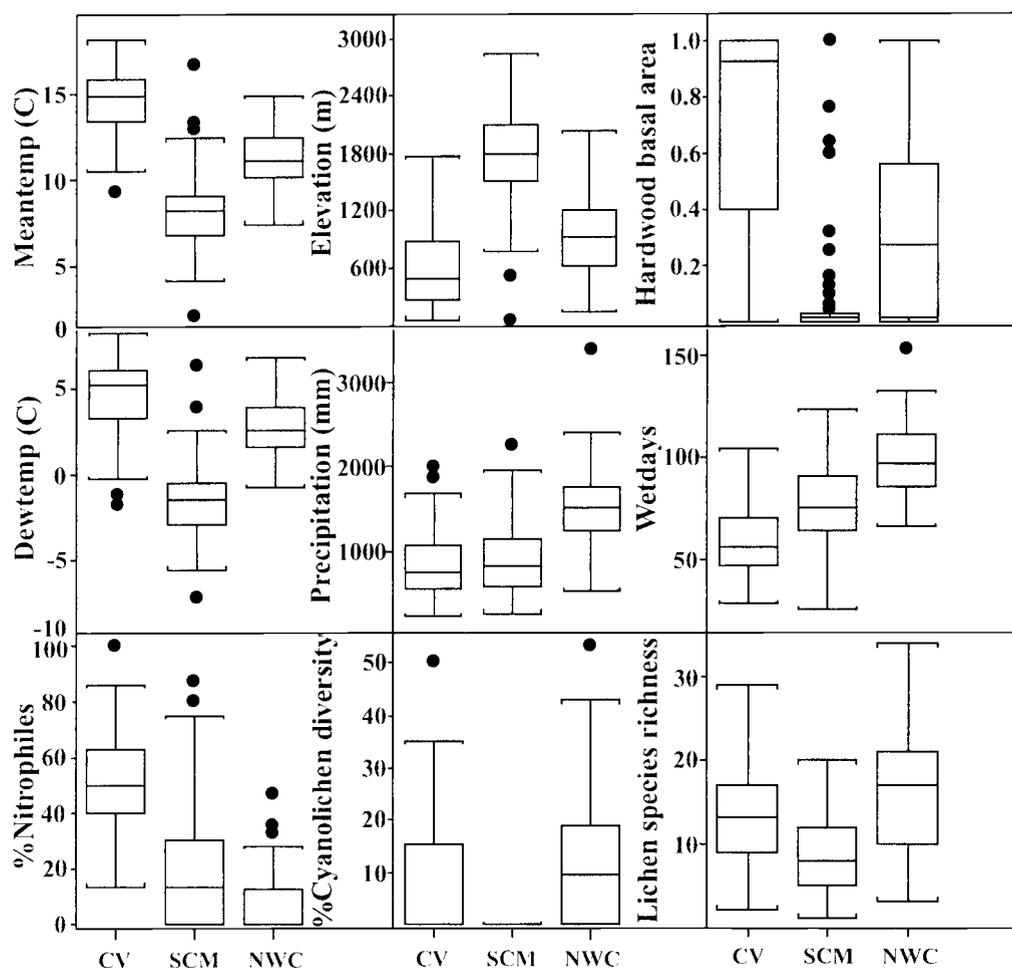


Figure 2.3. Boxplots of selected environmental variables, functional group indices, and species richness. The horizontal lines divide the data into quartiles. The center lines indicate medians and points represent outliers. CV = Greater Central Valley; SCM = Sierra, Southern Cascades, and Modoc; NWC = Northwest Coast.

Considering the strong association between nitrophile abundance, diversity, and ammonia demonstrated elsewhere (e.g. van Herk 1999, 2001), nitrophile dominance in the lichen communities is probably promoted, at least in part, by ammonia deposition. The greater Central Valley is one of the most agriculturally intensive areas in the United States and ammonia emissions from fertilizers and animal wastes are regionally high (California Air Resources Board 1999; Potter et al. 2001). Because the greater Central Valley climate is hot and dry, the apparent correlation of nitrophile richness with climate may actually reflect an underlying ammonia gradient (Figure 2.2). The lack of ammonia monitoring in California impedes our ability to differentiate between effects of climate vs. ammonia. However, the relationship may become clearer when an air quality model is derived for the Greater Central Valley. Ecological impacts of ammonia and the relationship between nitrophiles and dry habitats are discussed further in the following section.

Sierra, Southern Cascades, and Modoc

The Sierra, Southern Cascades, and Modoc group (hereafter referred to as "Sierra group") forms a continuous band along the eastern boundary of the study area (Figure 2.1). The western boundary includes an extension into the Klamath and Cascade Ranges, which are otherwise encompassed within the NW Coast group. At this intersection of model areas, the higher elevation plots (> 1830 m) tended to be classified within the Sierra group.

As indicated by both the lichen communities and climate data for the region, plots are relatively dry and cool (Figures 2.2 and 2.3). This region had the lowest species richness, with a total of 70 species among all plots. No cyanolichen species were found (Figure 2.3). Indicator species strongly associated with this group, such as the top two, *Letharia columbiana* and *L. vulpina*, are characteristic of dry habitats at high elevations (Table 2.1). No nitrophilous species were indicators for this region although *Candelaria concolor* was present in about 40% of the plots, about half the frequency of the Central Valley (Table 2.1). Other nitrophiles like *Xanthoria*

candelaria, *X. fulva*, and *X. oregana* were occasional. In most plots, however, fewer than 30% of the species were nitrophiles.

The Modoc Plateau region in northeastern California, encompassing Modoc and Lassen counties, was the driest and coldest part of the model area. Plots there had the lowest species richness in the dataset, most with less than 10 species. Most lichen communities sampled on the Modoc Plateau were 30% to 55% nitrophiles. Greater percentages of nitrophiles tended to occur in low diversity plots, which generally coincided with the driest areas. *Candelaria concolor*, *Xanthoria candelaria*, *X. fallax*, and *X. fulva* were the dominant nitrophiles, often co-occurring with *Letharia* sp., *Melanelia elegantula*, and *Nodobryoria abbreviata* in low diversity plots.

There are several possible explanations for the abundance of nitrophilous species. First, cattle grazing is a major land use throughout the model area. The percentage of land used for grazing is approximately 40% for some counties (Lassen and Modoc) and is greater than 30% for several others (Momsen 2001). Thus, ammonia enrichment by manure potentially fosters the nitrophile-dominated communities in the region. An association between nitrophilous species and semi-desert regions was also observed in southern Idaho (Neitlich et al. 2003), where *X. fallax* and *X. polycarpa* were identified as indicator species. Neitlich et al. (2003) suggested that dust from nitrogen-rich soils could stimulate colonization by nitrophilous species, which may result from natural as well as anthropogenic sources. A third possible contribution could be calcareous dust, which van Herk (1999) hypothesized as promoting nitrophile establishment in dry climates.

The significance of a large nitrophile presence in the Modoc region is unclear as is the apparent association between low overall species richness and high nitrophile richness. Are certain nitrophiles exceptionally drought tolerant or simply better able to cope with harsh climatic conditions? Does nitrogen or calcium-rich dust promote nitrophile establishment? Developing a means to monitor ammonia in California is critical because eutrophication by chronic nitrogen deposition is implicated in a variety of detrimental ecological impacts to Western forests, including alteration of

species composition of lichen, fungi, and plant communities (Fenn et al. 2003b). Perhaps the greatest barrier to harnessing the utility of these indicator species, particularly in drier climates, is the lack of information on how climate, dry-deposited gaseous ammonia, and dust interact to promote nitrophile establishment.

NW Coast

The NW Coast model area encompasses the coast, Klamath Mountain range, and part of the southern Cascade Range. This group includes a small group of plots disjunct from the NW Coast area, occurring in the Sierra foothills just east of Oroville (Figure 2.1; henceforth referred to as the "Oroville anomaly"). Lichen community composition and climate data show that the model area experiences relatively high precipitation and mild temperatures (Figure 2.2 and 2.3). The NW Coast area had the highest species richness of 137 species (Figure 2.3). Both cyanolichen indices showed the highest richness and abundance in this model area while nitrophilous species were relatively low (Figures 2.2 and 2.3). Indicator species identified by the ISA were varied, including a high proportion of large cyanolichens (i.e. *Nephroma helveticum*, *Pseudocyphellaria anthraspis*), species with oceanic affinities (i.e. *Sphaerophorus globosus*, *Usnea wirthii*), and species known to inhabit moist, montane habitats (*Bryoria capillaris*, *Alectoria sarmentosa*; Table 2.1). The three indicator species with the highest indicator values for the model area were *Platismatia glauca*, *Esslingeriana idahoensis*, and *Cetraria orbata*.

The three strongest NW Coast indicators were abundant in the Oroville anomaly but were infrequent or absent elsewhere in the Greater Central Valley and Sierra model areas (Table 2.1). Other NW Coast indicator species with high frequencies in the Klamath Mountains or Coast Ranges occurred in the disjunct plots, including *Hypogymnia occidentalis*, *Parmeliopsis hyperopta*, *Parmelia hygrophila*, *Pelitigera collina*, *Platismatia herrei*, and *Usnea filipendula*. These are primarily montane species, infrequent to common at elevations between 600 to 1500 m and their known distributions in California include the western slope of the Sierra Nevada (Hale and Cole 1988). Thus, their occurrence in plots of the Oroville anomaly, which range

in elevation from 530 to 1550 m, is not unusual. What is noteworthy, however, is the co-occurrence of these species with a mix of the strongest indicators for the Sierra model area (e.g. *Letharia columbiana*, *L. vulpina*, and *Nodobryoria abbreviata*) and half the strongest indicators for the Greater Central Valley group (e.g., *Melanelia glabra*, *Physcia adscendens*, and *Physconia isidiigera*, Table 2.1), which altogether make an unusual community.

Additional epiphytic lichen communities were surveyed throughout the Sierra model area (based upon the Sierra group defined here) in 2003 (Jovan and McCune, unpublished data). Three plots located in the vicinity of the Oroville anomaly, in Grass Valley, Nevada City, and Quincy, had communities like the disjunct plots with the same mix of indicator species as well as additional species typical of the Klamath and Coast Ranges, such as *Alectoria imshaugii*, *A. sarmentosa*, and "*Dendriscoaulon*". Otherwise, plots outside the anomaly were more characteristic of lichen communities classified within the Sierra group.

While we have not found written records of unusual vascular plant distributions in the Oroville area, the late botanist Dr. Daniel Axelrod, observed uncharacteristically moist areas of forest occurring between Oroville and Sonora (M. Barbour, pers. comm.) where unusual plant species occurred. One example he noted was the sporadic presence of *Cytisus scoparius* in moist stands, an invasive species otherwise restricted to coastal habitats. He proposed that gaps in the Coast Range to the southwest allow the oceanic climate to erratically penetrate the Sierra Nevada foothills in the described region. Plots in the anomaly did have exceptional climatic conditions for both the Sierra and Greater Central Valley model areas. Precipitation (1340-2130 mm/yr) and mean temperature (9.3-12.2°C) were comparable to averages for the humid, temperate montane habitats of the western NW Coast model area (Figure 2.3). These unique lichen communities in the Sierra foothills may correspond to a climatic anomaly, with atypically mesic forests. Considering the proximity of the northern Sierra foothills to all three model areas, however, the anomaly may simply be an intersection point where species with distributions typical of humid, montane

habitats intermingle with species more characteristic of the high Sierras and Central Valley.

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ENDNOTES

1. The Sierra, Southern Cascades, and Modoc model area was later shortened to the "greater Sierra Nevada," as it is referred to throughout Chapter 4.

Chapter 3

Bioindication of Air Pollution in the Greater Central Valley of California, U.S.A. with
Epiphytic Macrolichen Communities

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ABSTRACT

Air quality monitoring in the United States is typically focused on urban areas even though the detrimental effects of pollution often extend into surrounding ecosystems. The purpose of this study was to construct a model, based upon epiphytic macrolichen community data, to indicate air quality and climate in forested areas throughout the greater Central Valley of California. The structure of epiphytic lichen communities is widely recognized as an effective biological indicator of air quality as sensitivities to common anthropogenic pollutants vary by species. We used non-metric multidimensional scaling ordination to analyze lichen community data from 98 plots. To calibrate the model, a subset of plots was co-located with air quality monitors that measured ambient levels of ozone, sulfur dioxide, and nitrogen dioxide. Two estimates of ammonia deposition, which is not regularly monitored by any state or federal agency in California, were approximated for all plots using land-use maps and emissions estimates derived from the California Gridded Ammonia Inventory Modeling System. Two prominent gradients in community composition were found. One ordination axis corresponded with an air quality gradient relating to ammonia deposition. Ammonia deposition estimates ($r = -0.63$ and -0.51), percent nitrophilous lichen richness ($r = -0.76$), and percent nitrophile abundance ($r = -0.78$) were correlated with the air quality axis. Plots from large cities and small, highly agricultural towns had relatively poor air quality scores, indicating similar levels of ammonia deposition between urban and agrarian land-uses. The second axis was correlated with humidity ($r = -0.58$), distance from the coast ($r = 0.62$), kriged estimates of cumulative ozone exposure ($r = 0.57$), maximum one hour measurements of ozone ($r = 0.58$), and annual means of nitrogen dioxide ($r = 0.63$). Compared to ammonia, ozone and nitrogen dioxide impacts on lichen communities are poorly known, making it difficult to determine whether the second axis represents a response to climate, pollution, or both. Additionally, nitric acid may be influencing lichen communities although the lack of deposition

data and research describing indicator species prevented us from evaluating potential impacts.

INTRODUCTION

It is well known that air pollution can compromise the productivity and biodiversity of natural ecosystems (e.g. Hutchinson and Meema 1987, Olson et al. 1992) yet disproportionate amounts of air quality monitoring resources are often allocated to urban areas. In California, for example, the California Air Resources Board (CARB) and National Atmospheric Deposition Program (NADP) provide the most comprehensive air quality monitoring data. So few monitoring stations are located in rural areas, however, that regional studies of air quality impacts on forest health must be largely based upon excessive extrapolation and guesswork. Likewise, some prevalent pollutants such as ammonia (NH_3) are not typically measured by state and federal agencies in the United States.

Analysis of biological indicators can be an efficient, inexpensive alternative to air quality monitoring with permanent instrumentation (Nimis and Purvis 2002). Epiphytic macrolichens are used in the USDA Forest Inventory and Analysis (FIA) research program to describe both spatial and temporal trends in air quality and assess potential impacts to forest health. Lichen bioindication models are a widely accepted tool and are used to investigate air pollution extent and severity over a broad range of spatial scales, from localized effluents at point sources to studies of regional trends over time (e.g. de Bakker 1989, Kubin 1990, McCune 1988, McCune et al. 1997a, Muir and McCune 1988, Pilegaard 1978, van Herk 1999). Certain air pollutants cause mortality or extensive physiological injury to many lichen species. Other species are tolerant or even positively associated with some pollutants. Because sensitivities to different pollutants vary by lichen species, the mixture of species in a community, their physical appearance, and their relative abundances can be correlated with local air quality (reviewed by van Haluwyn and van Herk 2002).

Many studies have documented how certain species respond negatively to sulfur dioxide (SO_2) and the acidic deposition resulting from common anthropogenic

effluents such as SO₂ and nitrogen oxides (NO_x; Gauslaa 1995, Gilbert 1970, Gilbert 1986, Hawksworth and Rose 1970, McCune 1988, van Haluwyn and van Herk 2002). Also, several Dutch researchers have demonstrated a close relationship between the diversity and abundance of nitrophilous ("nitrogen-loving") lichen species and deposition of NH₃ (de Bakker 1989, van Dobben and de Bakker 1996, van Herk 1999, 2001). In contrast, research on community effects of photochemical pollutants such as nitrogen dioxide (NO₂) and ozone (O₃) is sparse. Two studies in the Netherlands suggested that NO₂ affects community composition although the data were confounded by SO₂ concentrations (van Dobben and de Bakker 1996, van Dobben and ter Braak 1998). It is also unclear whether lichen communities exhibit a clear response to O₃ as field studies have yielded conflicting results (McCune 1988, Ruoss and Vonarburg 1995, Sigal and Nash 1983).

Our primary objective was to develop a gradient model that relates epiphytic lichen community composition to air quality and climatic patterns throughout the greater Central Valley region in California, U.S.A. We explore the contribution of some of the most common pollutants in the study area, SO₂, NO₂, NH₃, and O₃, by integrating several sources of deposition data. The model will be applicable in both rural and urban forests throughout the Sacramento Valley, San Joaquin Valley, San Francisco Bay area, the central coast, and parts of the Sierra Nevada foothills (Figure 3.1). The model may also be used to monitor temporal trends when additional lichen community data are collected in the future. Although the model is site specific, the basic methodology is applicable in most forest landscapes where epiphytic lichens are present.

STUDY AREA

The extent of the greater Central Valley model area (Figure 3.1) was based upon a gradient analysis of epiphytic lichen community data from FIA plots spanning northern and central California (Jovan and McCune 2004¹). Our analysis identified regions with lichen communities and climate that were relatively homogeneous, at

least in comparison to variability present in the entire FIA dataset. These were: the greater Central Valley, the greater Sierra Nevada, and the Northwest Coast. Carving up California reduced the influence of climate on community composition within subregions, thereby enhancing our ability to detect and isolate the effects of air quality. Remaining climatic variability in the greater Central Valley model area primarily relates to

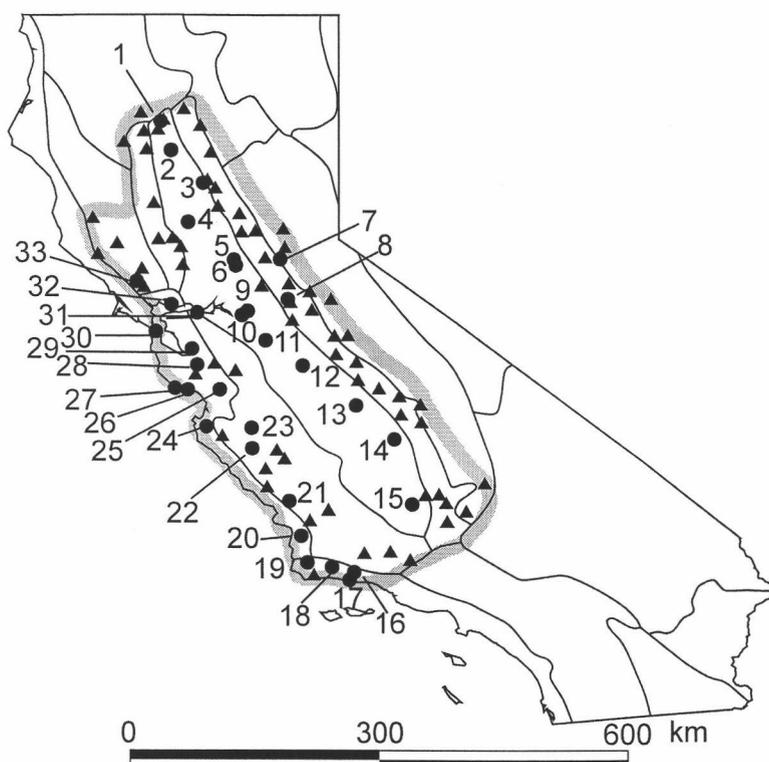


Figure 3.1. Map of greater Central Valley model area. Model boundary is delineated by thick gray line. Thinner black lines indicate Bailey's ecoregions (Bailey 1983). Triangles indicate on-frame plots while circles indicate off-frame plots. Off-frame plots are numbered as follows: 1 = Redding, 2 = Red Bluff, 3 = Chico, 4 = Colusa, 5 = North Highland, 6 = Sacramento, 7 = Placerville, 8 = San Andreas, 9 = Stockton, 10 = Pittsburg, 11 = Modesto, 12 = Merced, 13 = Fresno, 14 = Visalia, 15 = Bakersfield, 16 = Los Padres National Forest, 17 = Goleta, 18 = Santa Ynez, 19 = Lompoc, 20 = Nipomo, 21 = Atascadero, 22 = King City, 23 = Pinnacles National Monument, 24 = Carmel Valley, 25 = Gilroy, 26 = Santa Cruz, 27 = Davenport, 28 = San Jose, 29 = Fremont, 30 = San Francisco, 31 = Crockett, 32 = Vallejo, 33 = Santa Rosa.

temperature, oceanic salt-loading, and moisture differences between the Central Valley, the Sierra Nevada foothills, and the coastal regions. According to the Precipitation-Elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994, 2001, 2002), the Central Valley generally experiences relatively low mean annual precipitation (range approximately 150-850 mm/yr) and high mean annual temperatures (16-19°C). Precipitation is higher in the Sierra Nevada foothills (450-1100 mm/yr), central coast and Bay areas (500-1300 mm). The latter two, having more oceanic climates, experience milder mean annual temperatures (13-15°C) and higher salt-loading.

Most stands were dominated by hardwood tree species, including many oaks (*Quercus agrifolia*, *Q. chrysolepis*, *Q. douglasii*, *Q. garryana*, *Q. kelloggii*, *Q. lobata*, *Q. wislizenii*) and others (*Acer negundo*, *A. macrophyllum*, *Aesculus californica*, *Fraxinus latifolia*, *Juglans nigra*, *Populus fremontii*). Conifers such as *Pinus sabiniana* and *Pseudotsuga menziesii* were occasional. Some plots in the central coast region included chaparral communities, dominated by species from the genera *Arctostaphylos*, *Ceanothus*, *Rhamnus*, as well as *Adenostoma fasciculatum* and *Heteromeles arbutifolia*.

The boundaries of the model area coincide well with the California ecoregions as defined by Bailey (1983; Figure 3.1). From the coast, the southernmost boundary coincides with the Santa Clara River and proceeds eastward along the southernmost boundaries of the California Coastal Ranges, Sierra Nevada Foothills, and Sierra Nevada ecoregions. The eastern boundary is approximated by the Sierra Nevada foothill ecoregion but includes areas up to 25 km east of the ecoregion boundary at elevations of 1800 m or less. The northern boundary of the model area is formed by the northern boundaries of the Northern California Interior Coast Ranges, Sierra Nevada Foothills, and Great Valley ecoregions. From the south, the Pacific coast is the western boundary up to and including San Francisco County. Cities surrounding San Pablo Bay are included but the eastern boundary of the Northern California Coast ecoregion otherwise forms the western boundary. Within the adjacent Northern

California Interior Coast Ranges ecoregion, only land south of Willits is considered part of the model area.

Major industries in the model area include crop farming, orchards, livestock operations, food processing, petroleum refining, and various types of manufacturing and processing facilities. The Central Valley and adjacent areas are among the most agriculturally intensive regions of the United States. Fertilized crops and concentrated animal waste from livestock enclosures are major point sources of NH_3 in rural areas while automobile exhaust is an important NH_3 source in larger cities. Ammonia is a major pollutant of concern in California where deposition rates have been chronically high, contributing to nitrogen saturation in some forest ecosystems (reviewed by Bytnerowicz and Fenn 1996).

Combustion of fossil fuels from automobiles, manufacturing facilities, and petroleum refining plants releases SO_2 and NO_x , which contribute to acidic deposition. Acidic deposition and SO_2 levels have remained relatively low throughout most of northern and central California for over two decades while NO_x emissions have declined by almost 30% since 1990 (California Air Resources Board 2002, Takemoto et al. 1995). Ambient concentrations of NO_x compounds remain problematic, however, as evidenced by the infamous smog problems in central and southern California. Ozone (O_3), which results from the photochemical transformation of NO_x and volatile organic hydrocarbons in the atmosphere, is particularly abundant throughout the inland regions of the study area. In 2002, the CARB designated nearly all counties included in the study area as O_3 non-attainment areas because hourly measurements of O_3 levels consistently exceeded the state standard of 0.09 ppm.

METHODS

Field data

FIA field crews collected lichen community data from 66 permanent 0.38 hectare circular plots on FIA's hexagonal sampling grid (Messer et al. 1991; Figure 3.1), hereafter referred to as on-frame plots. On-frame plots occurred on both public

and private land and were visited once in the summer over a four-year period (1998-2001). Most plots were approximately 27 km away from their nearest neighbor although sampling density was lower where forested land was lacking or plot access was restricted by the landowner.

Lichen community inventories followed a standardized FIA protocol (see McCune et al. 1997b). Field crews collected a specimen of each epiphytic macrolichen species occurring above 0.5 m on woody plants or in the litter and assigned an abundance class: 1 = rare (< 3 thalli), 2 = uncommon (4-10 thalli), 3 = common (> 10 thalli present but species occurs on less than 50% of all boles and branches), and 4 = abundant (> 10 thalli present and species occurs on more than 50% of all boles and branches). Surveys lasted a minimum of 30 minutes and a maximum of two hours or until ten minutes passed before encountering a different species. Field workers were typically non-specialists but were trained to differentiate between species in the field. Professional lichenologists identified all specimens and conducted periodic audits of field crew performance (Jovan and McCune 2004).

An additional 33 "off-frame" plots were surveyed outside the sampling grid and spanned six CARB air quality basins: the San Francisco Bay Area, Sacramento, San Joaquin, North Central Coast, South Central Coast, and part of the Mountain Counties air basin (Figure 3.1). Most off-frame plots were located in urban areas and all plots coincided with a CARB air quality monitor to calibrate lichen data with direct pollutant measurements. Most monitors measured ambient concentrations of only 2-3 pollutants, with few measuring sulfur dioxide (SO₂) and none regularly measuring ammonia (NH₃). Monitors measuring SO₂ or multiple pollutants were given the highest priority in site selection. Off-frame plots were located in public parks, usually < 0.4 km downwind of the monitor and where possible, plots were installed directly adjacent to the monitor. Plot locations in the parks were selected to minimize distance from the monitor and encompass a non-landscaped area with native tree species. Field methods followed the same protocol as used for on-frame plots.

Voucher specimens reside at the Oregon State University herbarium. The nomenclature of McCune and Geiser (1997) was used for most identifications.

Physconia identifications follow the taxonomy of Esslinger (2000), *Heterodermia* identification was based upon Esslinger and Bratt (1998), *Xanthoria* identifications followed the taxonomy of Lindblom (1997), and *Usnea* taxonomy followed the keys of Tavares (1997). Thin-layer chromatography was not used to aid identifications.

Analysis

Rare species in less than 4 % of the plots were excluded from the analysis to reduce noise in the data. The inconspicuous species *Hyperphyscia adglutinata* and *Leptogium cellulorum* were also excluded because they could easily be overlooked by field crews. No lichens occurred in an off-frame plot in downtown Bakersfield, forcing us to exclude it from the statistical analyses, which cannot utilize data consisting entirely of zeros. The analysis was conducted on a final matrix of 98 plots by 64 species (Table 3.1).

Table 3.1. Summary of species found in FIA plots. Species considered nitrophilous are designated by (N), % Freq = percentage of plots where the species occurred, and Ave = average abundance class per plot.

Species	Off-frame (n=33)		On-frame (n=65)	
	%Freq	Ave	%Freq	Ave
<i>Ahtiana sphaerosporella</i>	0.00	0.00	1.43	0.01
<i>Candelaria concolor</i> (N)	96.87	3.22	80.00	2.27
<i>Cetraria chlorophylla</i>	3.12	0.03	1.43	0.03
<i>Cetraria merrillii</i>	6.25	0.09	12.86	0.34
<i>Cetraria orbata</i>	0.00	0.00	8.57	0.17
<i>Cetraria platyphylla</i>	0.00	0.00	2.86	0.07
<i>Cladonia coniocraea</i>	0.00	0.00	1.43	0.04
<i>Cladonia fimbriata</i>	0.00	0.00	1.43	0.04
<i>Cladonia ochrochlora</i>	0.00	0.00	2.86	0.06
<i>Cladonia transcendens</i>	3.12	0.06	0.00	0.00
<i>Collema furfuraceum</i>	15.62	0.38	24.29	0.67
<i>Collema nigrescens</i>	25.00	0.53	10.00	0.29
<i>Collema subflaccidum</i>	0.00	0.00	1.43	0.03
<i>Esslingeriana idahoensis</i>	0.00	0.00	4.29	0.11

Table 3.1 (Continued)

<i>Evernia prunastri</i>	59.37	1.28	51.43	1.46
<i>Flavoparmelia caperata</i> (N)	21.87	0.69	2.86	0.10
<i>Flavopunctelia flaventior</i> (N)	65.62	1.97	41.43	1.16
<i>Flavopunctelia soledica</i>	0.00	0.00	1.43	0.04
<i>Fuscopannaria mediterranea</i>	0.00	0.00	1.43	0.04
<i>Heterodermia leucomelos</i>	12.50	0.28	1.43	0.04
<i>Hypogymnia imshaugii</i>	6.25	0.13	27.14	0.71
<i>Hypogymnia inactiva</i>	0.00	0.00	2.86	0.07
<i>Hypogymnia occidentalis</i>	0.00	0.00	4.29	0.06
<i>Hypogymnia physodes</i>	0.00	0.00	4.29	0.10
<i>Hypogymnia tubulosa</i>	0.00	0.00	5.71	0.10
<i>Leptochidium albociliatum</i>	0.00	0.00	2.86	0.04
<i>Leptogium brebissonii</i>	0.00	0.00	1.43	0.01
<i>Leptogium cellulosum</i>	9.38	0.13	0.00	0.00
<i>Leptogium corniculatum</i>	0.00	0.00	2.86	0.07
<i>Leptogium lichenoides</i>	0.00	0.00	24.29	0.54
<i>Leptogium polycarpum</i>	0.00	0.00	1.43	0.04
<i>Leptogium pseudofurfuraceum</i>	3.12	0.03	18.57	0.47
<i>Leptogium saturninum</i>	0.00	0.00	2.86	0.07
<i>Leptogium teretiusculum</i>	3.12	0.06	0.00	0.00
<i>Letharia columbiana</i>	0.00	0.00	11.43	0.33
<i>Letharia vulpina</i>	3.12	0.06	17.14	0.40
<i>Melanelia elegantula</i>	0.00	0.00	7.14	0.16
<i>Melanelia exasperatula</i>	3.12	0.09	4.29	0.13
<i>Melanelia fuliginosa</i>	6.25	0.09	5.71	0.11
<i>Melanelia glabra</i>	34.37	0.72	70.00	2.10
<i>Melanelia subargentifera</i>	18.75	0.53	7.14	0.19
<i>Melanelia subaurifera</i>	6.25	0.06	1.43	0.03
<i>Melanelia subolivacea</i>	0.00	0.00	47.14	1.31
<i>Nephroma helveticum</i>	0.00	0.00	1.43	0.04
<i>Nephroma resupinatum</i>	0.00	0.00	1.43	0.01
<i>Niebla cephalota</i>	15.62	0.38	1.43	0.03
<i>Nodobryoria abbreviata</i>	0.00	0.00	2.86	0.07
<i>Parmelia hygrophila</i> (N)	6.25	0.13	2.86	0.09
<i>Parmelia sulcata</i>	9.38	0.09	18.57	0.49
<i>Parmeliella triptophylla</i>	0.00	0.00	2.86	0.09

Table 3.1 (Continued)

<i>Parmelina quercina</i>	12.50	0.25	54.29	1.50
<i>Parmotrema arnoldii</i>	3.12	0.09	2.86	0.07
<i>Parmotrema austrosinense</i>	6.25	0.06	2.86	0.07
<i>Parmotrema chinense</i>	21.87	0.47	5.71	0.14
<i>Peltigera collina</i>	3.12	0.03	10.00	0.24
<i>Phaeophyscia ciliata</i>	0.00	0.00	5.71	0.14
<i>Phaeophyscia hirsuta</i> (N)	28.12	0.78	1.43	0.03
<i>Phaeophyscia orbicularis</i> (N)	75.00	1.97	24.29	0.67
<i>Physcia adscendens</i> (N)	90.62	2.75	52.86	1.41
<i>Physcia aipolia</i> (N)	25.00	0.69	34.29	1.00
<i>Physcia americana</i>	3.12	0.09	1.43	0.04
<i>Physcia biziana</i>	9.38	0.16	41.43	1.20
<i>Physcia caesia</i>	3.12	0.03	1.43	0.04
<i>Physcia dimidiata</i> (N)	25.00	0.53	10.00	0.29
<i>Physcia dubia</i> (N)	3.12	0.03	5.71	0.16
<i>Physcia stellaris</i> (N)	18.75	0.44	21.43	0.61
<i>Physcia tenella</i> (N)	81.25	2.13	14.29	0.40
<i>Physciella chloantha</i>	0.00	0.00	2.86	0.09
<i>Physciella melanchra</i>	0.00	0.00	1.43	0.04
<i>Physconia americana</i>	25.00	0.66	51.43	1.43
<i>Physconia enteroxantha</i> (N)	37.50	0.91	32.86	0.93
<i>Physconia fallax</i>	12.50	0.28	11.43	0.30
<i>Physconia isidiigera</i>	65.62	1.88	60.00	1.74
<i>Physconia leucoleiptes</i>	3.12	0.03	2.86	0.06
<i>Physconia perisidiosa</i> (N)	50.00	1.31	57.14	1.61
<i>Platismatia glauca</i>	3.12	0.06	4.29	0.07
<i>Pseudocyphellaria anomala</i>	3.12	0.03	2.86	0.07
<i>Pseudocyphellaria anthraspis</i>	0.00	0.00	11.43	0.29
<i>Punctelia subrudecta</i> (N)	34.37	0.88	18.57	0.49
<i>Ramalina farinacea</i>	40.62	1.13	17.14	0.47
<i>Ramalina leptocarpha</i>	50.00	1.13	2.86	0.10
<i>Ramalina menziesii</i>	25.00	0.47	8.57	0.24
<i>Ramalina pollinaria</i>	12.50	0.28	1.43	0.03
<i>Ramalina sinensis</i>	0.00	0.00	1.43	0.06
<i>Ramalina subleptocarpha</i> (N)	37.50	0.97	12.86	0.34
<i>Sphaerophorus globosus</i>	0.00	0.00	1.43	0.03

Table 3.1 (Continued)

<i>Teloschistes chrysophthalmus</i>	21.87	0.38	0.00	0.00
<i>Teloschistes flavicans</i>	0.00	0.00	1.43	0.01
<i>Usnea arizonica</i>	0.00	0.00	5.71	0.11
<i>Usnea cornuta</i>	15.62	0.34	1.43	0.04
<i>Usnea diplotypus</i>	9.38	0.16	0.00	0.00
<i>Usnea fragilesceus</i>	0.00	0.00	1.43	0.01
<i>Usnea glabrata</i>	12.50	0.25	1.43	0.03
<i>Usnea hirta</i>	6.25	0.16	0.00	0.00
<i>Usnea lapponica</i>	15.62	0.25	1.43	0.04
<i>Usnea pacificana</i>	0.00	0.00	1.43	0.01
<i>Usnea scabrata</i>	0.00	0.00	1.43	0.04
<i>Usnea subfloridana</i>	3.12	0.06	1.43	0.04
<i>Usnea substerilis</i>	6.25	0.09	5.71	0.14
<i>Vulpicida canadensis</i>	0.00	0.00	2.86	0.07
<i>Xanthoria candelaria</i> (N)	0.00	0.00	12.86	0.31
<i>Xanthoria fallax</i> (N)	28.12	0.88	21.43	0.59
<i>Xanthoria fulva</i> (N)	6.25	0.09	12.86	0.36
<i>Xanthoria hasseana</i> (N)	40.62	1.03	34.29	0.83
<i>Xanthoria oregana</i> (N)	68.75	1.94	31.43	0.87
<i>Xanthoria parietina</i> (N)	12.50	0.25	5.71	0.13
<i>Xanthoria polycarpa</i> (N)	65.62	1.84	40.00	1.13
<i>Xanthoria tenax</i> (N)	50.00	1.53	7.14	0.21

Environmental variables

Climate variables were extracted from the PRISM model (Daly et al. 1994, 2001, 2002), which included annual means of: dew temperature, maximum temperature, minimum temperature, mean temperature, precipitation, number of wetdays, and relative humidity. Climate estimates were averaged over 1961 to 1990. As lichens are poikilohydric, fog and even moisture from non-saturated air (Matthes-Sears and Nash 1985) are also important water sources for some species. Unfortunately, no such climate data were available for the study area. Geographic and stand structure variables included elevation, latitude, longitude, total live basal area,

total tree species richness, species richness and % basal area in live hardwoods, and species richness and % basal area in live softwoods.

Biological variables

Biological variables were constructed to aid in description of lichen communities: overall species richness, total lichen abundance (sum of all abundance classes per plot), cyanolichen richness, nitrophile richness, nitrophile abundance, and % richness and abundance in nitrophiles. Cyanolichens were defined by the ability to fix nitrogen and included tripartite lichens with cyanobacteria in cephalodia. We included cyanolichen richness since this group contains many species that are characteristically sensitive to acidic deposition (Denison et al. 1977, Gauslaa 1995, James et al. 1977). The other indices were omitted for cyanolichens, however, because they were very infrequent throughout the study area. Nitrophilous species are indicated in Table 3.1. Designations of nitrophily were guided by the observations of Hawksworth and Rose (1970), McCune and Geiser (1997), and van Herk (1999, 2001).

Air quality variables

Air quality information was integrated from several sources. Direct air quality measurements from CARB monitors were available for the 33 urban plots. Most monitors measured ambient levels of O₃ (n = 30, maximum 1-hr value; range 68 to 139 ppb), and NO₂ (n = 22, annual arithmetic mean; range 3 to 25 ppb), while few measured SO₂ (n = 14, annual arithmetic mean; range 1 to 5 ppb). All CARB measurements were averaged from 1999 to 2002. We also used kriged data, based upon CARB measurements from all monitors in California, to estimate O₃ levels at all FIA plots (T. Pritchard, unpublished data). Kriged data were "SUM60" values, which are sums of all hourly O₃ concentrations at or above 60 ppb from June 1 to August 31, 2002 (range 21 to 7.81x10⁴ ppb-hrs).

It is important to note that kriged data are interpolations and thus, may deviate somewhat from actual deposition. The ambient O₃ measurements are certainly more accurate although 139 ppb, the highest maximum 1-hr value recorded from within the model boundaries, is probably considerably lower than concentrations experienced at eastern FIA plots in the Sierra foothills. California Air Resources Board monitors were mostly located in large urban areas yet O₃ concentrations are expected to peak downwind to the east, where the prevailing winds transport its photochemical precursors. We know ambient O₃ may reach at least 155 ppb in our southeastern plots, as suggested by measurements at CARB monitors downwind of the San Joaquin valley, just beyond the eastern model area boundary. It is still possible we are understating maximum O₃ concentration, however, since CARB monitors were sparse in the Sierra Nevada foothills.

As no direct NH₃ measurements were available, we approximated deposition for all lichen community plots in two ways, using 1) high-resolution land use maps and 2) modeled NH₃ emissions estimates. Emissions should be a reasonable approximation of deposition since NH₃ has a high dry deposition velocity, meaning that a high proportion of deposition occurs near the emission source (Asman and van Jaarsveld 1992). The land use maps were developed for the California Gap Analysis Project (Davis et al 1998), which identified agricultural and urban land within the model area. The minimum mapping unit was not consistent across the map coverage and small parcels (<100 ha) of agricultural land were not represented in all cases.

The modeled NH₃ emissions data consisted of 1 km by 1 km gridded estimates for seven source categories: mobile sources, area sources (includes livestock and confined feeding operations), domestic sources, soils, residential wood burning, stationary point sources, and fertilizers. The grids were developed by ENVIRON International Corporation (2002), using a GIS-based emissions modeling technique, the California Gridded Ammonia Inventory Modeling System (CalGAIMS). Emissions estimates were derived from the integration of high-resolution land use spatial data and NH₃ emission factors from the literature. We centered circular areas

with 5 km radii on each FIA plot. Areas of agriculture and urban development were extracted from the GAP dataset as sums and percentages of the total land area. Ammonia emissions from the CalGAIMS data were summed within each circular area.

Statistical analysis

We used the PC-ORD software package version 4.20 (McCune and Mefford 1999) for analysis of community gradients. Non-metric multidimensional scaling ordination (NMS; Kruskal 1964) was used to extract gradients in community composition from a matrix of species abundance codes by sample units. The data underwent 500 iterations per run using the relative Sørensen distance measure. The solution with the lowest stress was selected from 500 runs with real data. "Stress" measures departure of fit between the ordination and the data. Stress is calculated as a departure from monotonicity between the two series of distances (McCune and Grace 2002). A Monte Carlo test of 500 runs with randomized data was used to evaluate the strength of patterns in the NMS solution.

We used orthogonal rotation of the NMS solution to maximize correlations of axes to environmental and lichen community variables. Gradient scores were calculated for all plots. We used overlays and coefficients of determination to relate the strongest gradients (axes) in species composition to environmental variables (McCune and Grace 2002). Linear regression was used to relate the partial datasets of NO₂, O₃, and SO₂ from the CARB monitors to the NMS axis scores.

We used nonparametric multiplicative regression (NPMR; McCune et al. 2003) to determine how individual species distributions related to the two strongest NMS community gradients. Model building is iterative and exploratory as NPMR assumes no particular relationship between response and predictor variables (McCune et al. 2003). Ordination axis scores were used as possible predictors. We used a local mean estimator and Gaussian kernel function (Bowman and Azzalini 1997). Models were based on a minimum average neighborhood size of 3. The standard deviation

(tolerance) of the kernel function was optimized by maximizing cross validated coefficients of determination ($\times R^2$).

We visualized response curves for a subset of lichen species that were abundant (most occurred in $> 20\%$ of plots) and were either described by a strong model or were indicator species of particular interest. A preliminary analysis showed that most species distributions had nonlinear relationships to both ordination axes. Thus, to accurately depict a species response along axis 1, we needed to control for interactions with axis 2 and the converse. To model species' responses to axis 1, for example, we first determined each species' optimum on axis 2. We then sliced the 3-dimensional responses of each species to both axes at the optimum along axis 2. Abundance estimates were based on a minimum average neighborhood size of five. This procedure was then repeated, fitting response curves for axis 2 at each species' optimum for axis 1. All NPMR analyses were conducted with HyperNiche (Version 1.00.60 beta, McCune and Mefford 2004).

RESULTS

The NMS ordination suggested a final solution with three axes; the addition of a fourth axis afforded only a slight reduction in minimum stress. The Monte Carlo test indicated that the minimum stress of the 3-dimensional solution with real data was lower than would be expected by chance ($p < 0.01$). The final stress and instability of the 3-dimensional solution were 20.74 and 0.06, respectively. Considered together, the three axes explained most of the variability in lichen community structure (Total $r^2 = 0.78$; $r^2 = 0.29$ for axis 1, 0.35 for axis 2, and 0.14 for axis 3). Because the third axis was relatively weak and had only low correlations with environmental variables, it will not be discussed further in this paper.

According to the NPMR models, most species distributions were only weakly to moderately related to the two ordination axes (Table 3.2 and Figure 3.2), which is unsurprising since the axes represent complex community gradients. Cross-validated R^2 ranged from -0.02 to 0.81. The shapes of species response curves varied widely and were typically nonlinear (Figures 3.3 and 3.4).

Table 3.2. Summary of NPMR models for each lichen species in the analytical dataset. xR^2 = cross-validated coefficient of determination, Ave. Neigh. = average neighborhood size. Possible predictor variables (Var.) are designated by either 1 (axis 1 scores) or 2 (axis 2 scores). Tolerance (Tol.) is the standard deviation of the preceding variable.

Species	xR^2	Ave. Neigh.	Var.	Tol.	Var.	Tol.
<i>Candelaria concolor</i>	0.30	13.61	1	0.26	2	0.37
<i>Cetraria merrillii</i>	0.20	9.49	1	0.26	2	0.25
<i>Cetraria orbata</i>	0.43	8.88	1	0.13	2	0.49
<i>Collema furfuraceum</i>	0.13	13.61	1	0.26	2	0.37
<i>Collema nigrescens</i>	0.00	47.54	1	1.96	2	0.49
<i>Evernia prunastri</i>	0.45	8.37	1	0.52	2	0.12
<i>Flavoparmelia caperata</i>	0.46	8.37	1	0.52	2	0.12
<i>Flavopunctelia flaventior</i>	0.59	4.77	1	0.26	2	0.12
<i>Heterodermia leucomelos</i>	0.37	19.10	1	0.39	2	0.37
<i>Hypogymnia imshaugii</i>	0.66	4.89	1	0.13	2	0.25
<i>Hypogymnia tubulosa</i>	0.11	17.07	1	0.26	2	0.49
<i>Leptogium lichenoides</i>	0.16	4.77	1	0.26	2	0.12
<i>Leptogium pseudofurfuraceum</i>	0.20	13.61	1	0.26	2	0.37
<i>Letharia columbiana</i>	0.13	4.89	1	0.13	2	0.25
<i>Letharia vulpina</i>	0.15	4.77	1	0.26	2	0.12
<i>Melanelia elegantula</i>	0.13	7.06	1	0.13	2	0.37
<i>Melanelia exasperatula</i>	0.08	9.49	1	0.26	2	0.25
<i>Melanelia fuliginosa</i>	0.05	8.88	1	0.13	2	0.49
<i>Melanelia glabra</i>	0.71	9.49	1	0.26	2	0.25
<i>Melanelia subargentifera</i>	0.05	13.61	1	0.26	2	0.37
<i>Melanelia subolivacea</i>	0.07	13.35	1	0.39	2	0.25
<i>Niebla cephalota</i>	0.34	19.10	1	0.39	2	0.37
<i>Parmelia hygrophila</i>	0.01	18.84	1	0.65	2	0.25
<i>Parmelia sulcata</i>	0.30	17.07	1	0.26	2	0.49
<i>Parmelina quercina</i>	0.60	4.89	1	0.13	2	0.25
<i>Parmotrema austrosinense</i>	0.13	40.38	2	0.37	—	—
<i>Parmotrema chinense</i>	0.81	4.77	1	0.26	2	0.12
<i>Peltigera collina</i>	0.30	8.88	1	0.13	2	0.49
<i>Phaeophyscia ciliata</i>	0.00	32.38	1	0.26	—	—
<i>Phaeophyscia hirsuta</i>	0.26	4.89	1	0.13	2	0.25

Table 3.2 (Continued)

<i>Phaeophyscia orbicularis</i>	0.17	19.10	1	0.39	2	0.37
<i>Physcia adscendens</i>	0.53	16.44	1	0.52	2	0.25
<i>Physcia aipolia</i>	0.06	45.44	1	0.39	—	—
<i>Physcia biziana</i>	0.31	7.06	1	0.13	2	0.37
<i>Physcia dimidiata</i>	0.10	17.07	1	0.26	2	0.49
<i>Physcia dubia</i>	0.06	7.06	1	0.13	2	0.37
<i>Physcia stellaris</i>	0.04	8.88	1	0.13	2	0.49
<i>Physcia tenella</i>	0.22	9.49	1	0.26	2	0.25
<i>Physconia americana</i>	0.28	13.61	1	0.26	2	0.37
<i>Physconia enteroxantha</i>	-0.02	82.20	1	1.18	—	—
<i>Physconia isidiigera</i>	0.11	14.26	2	0.12	—	—
<i>Physconia perisidiosa</i>	0.24	13.35	1	0.39	2	0.25
<i>Platismatia glauca</i>	0.14	4.77	1	0.26	2	0.12
<i>Pseudocyphellaria anthraspis</i>	0.27	8.88	1	0.13	2	0.49
<i>Punctelia subrudecta</i>	0.36	4.89	1	0.13	2	0.25
<i>Ramalina farinacea</i>	0.54	28.13	2	0.25	—	—
<i>Ramalina leptocarpha</i>	0.43	13.61	1	0.26	2	0.37
<i>Ramalina menziesii</i>	0.22	7.06	1	0.13	2	0.37
<i>Ramalina pollinaria</i>	0.32	19.10	1	0.39	2	0.37
<i>Ramalina subleptocarpha</i>	0.16	23.51	1	0.52	2	0.37
<i>Teloschistes chrysophthalmus</i>	0.15	4.89	1	0.13	2	0.25
<i>Usnea arizonica</i>	0.17	23.51	1	0.52	2	0.37
<i>Usnea cornuta</i>	0.48	9.49	1	0.26	2	0.25
<i>Usnea glabrata</i>	0.27	4.89	1	0.13	2	0.25
<i>Usnea lapponica</i>	0.14	8.37	1	0.52	2	0.12
<i>Usnea substerilis</i>	0.06	4.89	1	0.13	2	0.25
<i>Xanthoria candelaria</i>	0.00	45.44	1	0.39	—	—
<i>Xanthoria fallax</i>	0.25	6.77	1	0.39	2	0.12
<i>Xanthoria fulva</i>	-0.02	90.82	1	1.96	—	—
<i>Xanthoria hasseana</i>	0.00	16.44	1	0.52	2	0.25
<i>Xanthoria oregana</i>	0.28	15.55	1	0.13	2	1.84
<i>Xanthoria parietina</i>	-0.02	79.27	1	1.05	—	—
<i>Xanthoria polycarpa</i>	0.09	16.44	1	0.52	2	0.25
<i>Xanthoria tenax</i>	0.39	4.89	1	0.13	2	0.25

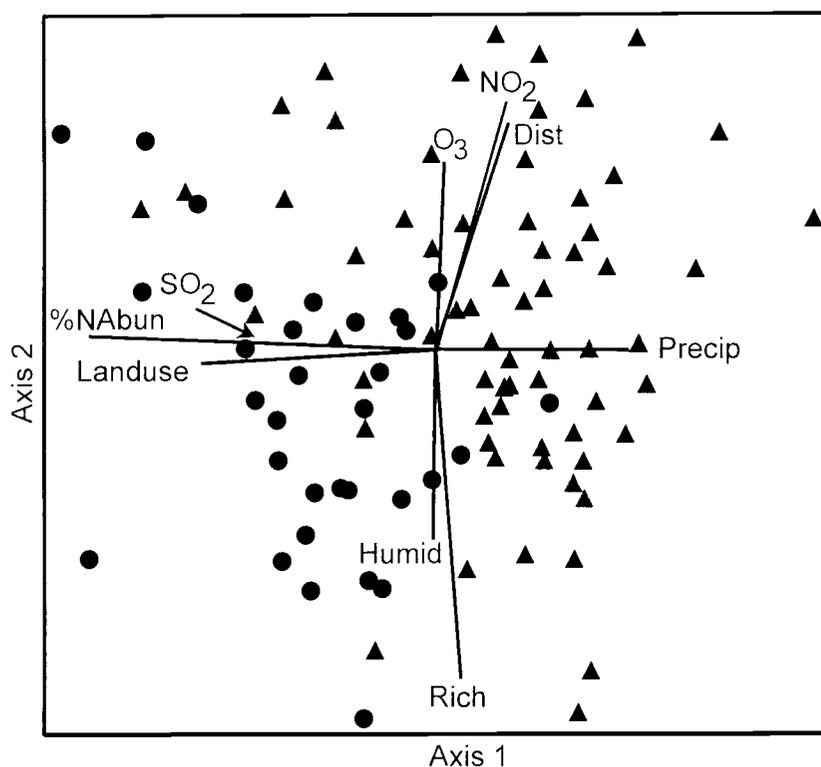


Figure 3.2. Ordination joint plot with environmental variables overlaid. Triangles indicate on-frame plots while circles indicate off-frame plots. Vector lengths and directions indicate correlations with the ordination. Most vectors with $r > 0.55$ are shown. Abbreviations for environmental vectors are: Dist = distance from the coast, Precip = mean annual precipitation, Rich = total lichen species richness, Humid = relative humidity, Landuse = % urban and agricultural land, %Nabun = percent nitrophile abundance, SO_2 = sulfur dioxide, O_3 = ozone, NO_2 = nitrogen dioxide. The end of the SO_2 vector is indicated by an arrow. Percent nitrophile richness and sum of agricultural land are not pictured due to crowding. Both vectors align closely with axis 1. The O_3 vector represents the correlation of both sum60 kriged estimates and CARB measurements with axis 2.

Relationship of axis 1 to NH_3 and nitrophile indices

The first axis in community composition was negatively correlated with all variables indicating NH_3 deposition (Figure 3.2 and Table 3.3). Percent agricultural and urban land ($r = -0.63$) and total NH_3 emissions from the CalGAIMS data ($r = -0.51$) were both negatively correlated with axis 1. Several subcategories from the GAP land-use and CalGAIMS datasets had similar relationships with the axis, such as sum

of urban land ($r = -0.48$), sum of agricultural land ($r = -0.56$) and estimated NH_3 emissions from mobile ($r = -0.51$) and domestic sources ($r = -0.43$).

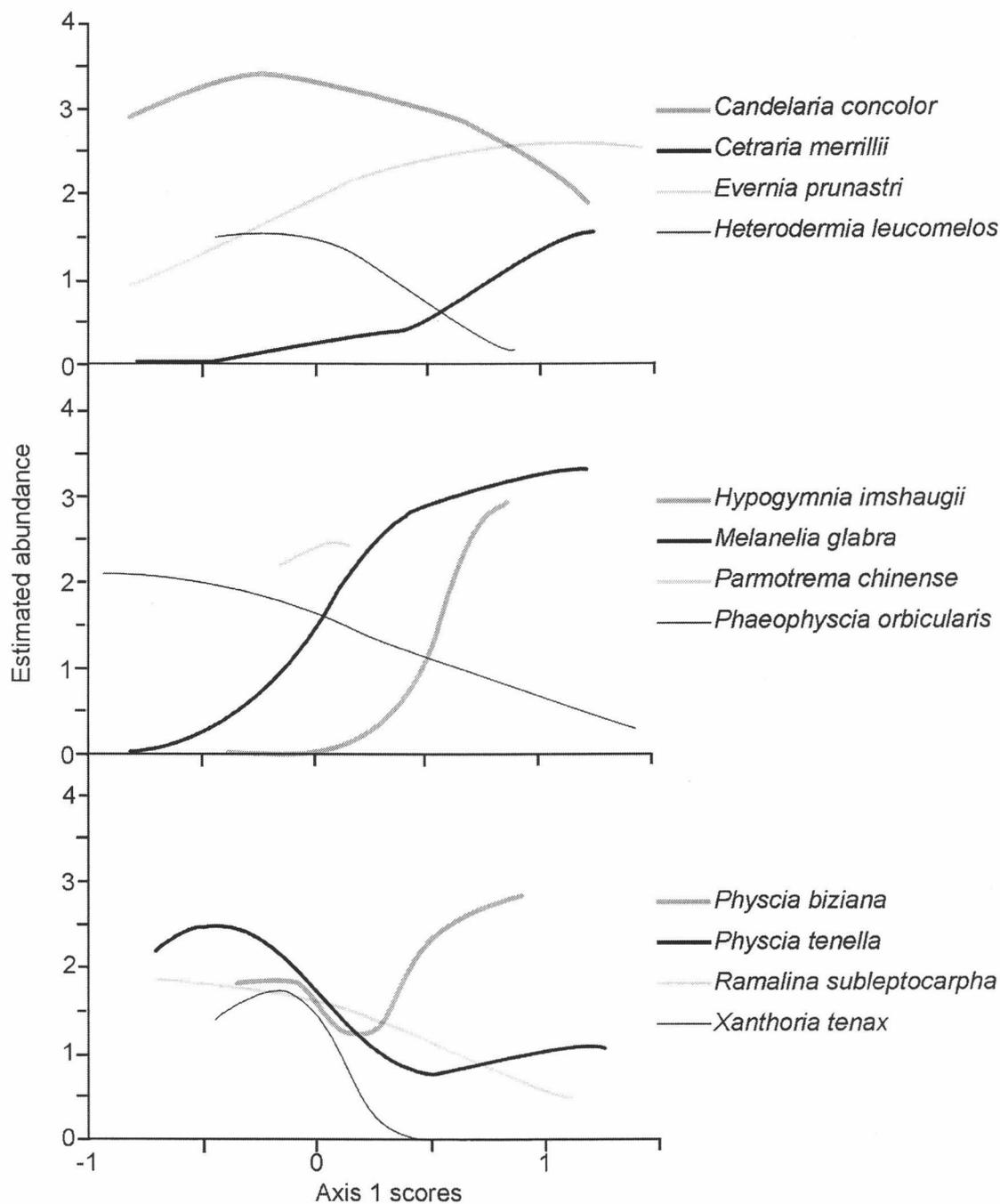


Figure 3.3. Nonparametric multiplicative regression response curves for selected species along axis 1.

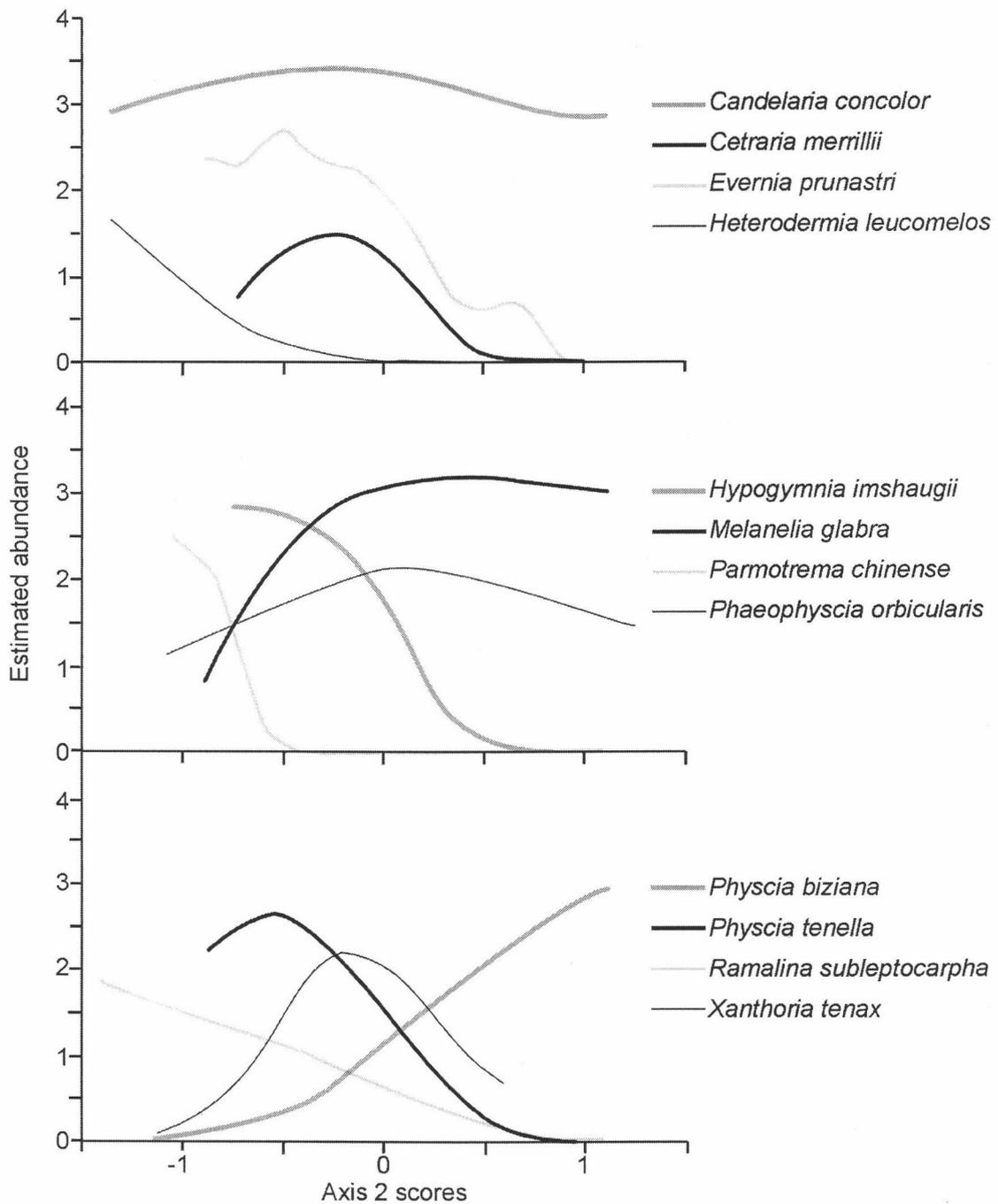


Figure 3.4. Nonparametric multiplicative regression response curves for selected species along axis 2.

Most urban, off-frame plots had low axis scores, especially plots from large, populous cities such as Fresno, San Francisco, San Jose, and Stockton, which occurred

at the extreme end of the gradient (Figures 3.2 and 3.5). Off-frame plots located in small urban areas with agriculture-based economies such as King City, Merced, Santa Ynez, and Visalia, had similarly low axis scores. Plots with higher scores tended to occur in more remote forested areas.

The relativized nitrophile indices, % nitrophile abundance and % nitrophile richness, were also negatively linearly correlated with axis 1 ($r = -0.78$ and -0.76 , respectively). Their corresponding vectors aligned closely with the NH_3 deposition variables in the NMS solution (Figure 3.2). The unrelativized indices, nitrophile diversity and abundance, were more strongly correlated with axis 2 (Table 3.3). Species distributions had a wide variety of relationships to axis 1 (Figure 3.3). Nearly all nitrophile distributions had maxima at low axis scores (Figure 3.3; e.g. *Candelaria concolor*, *Phaeophyscia orbicularis*, *Physcia tenella*, *Ramalina subleptocarpha*, and *Xanthoria tenax*), including species with relatively weak models (Table 3.2). Contrastingly, the abundances of species in genera considered NH_3 -sensitive by van Herk ("acidophytes"; 1999, 2001), such as *Cetraria*, *Evernia*, and *Hypogymnia*, tended to increase at higher axis scores (Figure 3.3).

Relationship of axis 1 to other variables

Two moisture variables, mean annual precipitation ($r = 0.58$) and number of wetdays ($r = 0.51$) were also correlated with axis 1, roughly opposite of NH_3 deposition variables and the relativized nitrophile indices (Figure 3.2 and Table 3.3). Pollutant data for NO_2 and O_3 show a lack of alignment although the partial SO_2 data was negatively correlated with axis 1 ($r = 0.59$; Figure 3.2 and Table 3.3).

Relationship of axis 2 to humidity, O_3 , and NO_2

Axis 2 correlated with climatic and geographic variables such as humidity ($r = -0.58$), distance from the coast ($r = 0.62$), and longitude ($r = 0.43$), suggesting a coast to inland humidity gradient. The humidity gradient is generally evident in the geographic distribution of plot scores for axis 2 (Figure 3.6), and is consistent with the

Table 3.3. Coefficients of determination for correlations between environmental variables and ordination axes. Variables with $r > 0.55$ or < -0.55 are in boldface.

Variable	r	
	Axis 1	Axis 2
Longitude	-0.19	0.43
Latitude	0.46	0.05
Elevation	0.30	0.35
Distance from the coast	0.34	0.62
Dew temperature	-0.12	-0.34
Minimum temperature	-0.14	0.12
Maximum temperature	-0.13	-0.03
Mean temperature	-0.16	0.04
Wetdays	0.51	-0.18
Precipitation	0.58	-0.09
Humidity	-0.11	-0.58
Total live basal area	0.32	-0.06
Overstory diversity	-0.19	-0.11
% Hardwood basal area	-0.13	-0.12
Hardwood richness	-0.32	-0.09
% Softwood basal area	0.13	0.12
Softwood richness	0.18	-0.04
Lichen species richness	0.19	-0.76
Total lichen abundance	0.22	-0.71
Cyanolichen richness	0.36	-0.31
Nitrophile richness	-0.28	-0.53
% Nitrophile richness	-0.76	0.22
Nitrophile abundance	-0.26	-0.48
% Nitrophile abundance	-0.78	0.12
Landuse	-0.63	-0.19
Sum of agricultural land	-0.56	-0.17
Sum of urban land	-0.48	-0.05
Total NH ₃	-0.51	-0.01
NH ₃ -Area sources	-0.36	0.09
NH ₃ -Domestic sources	-0.43	-0.11
NH ₃ -Fertilizer	-0.26	-0.16

Table 3.3 (Continued)

NH ₃ -Mobile Sources	-0.51	-0.01
NH ₃ -Soil	-0.30	-0.02
NH ₃ -Stationary sources	-0.17	0.05
NH ₃ -Wood burning	-0.24	-0.21
Ozone (Sum60)	0.06	0.57
Ozone (Max. 1hr value)	0.14	0.58
NO₂ (annual mean)	-0.33	0.63
SO₂ (annual mean)	0.59	0.10

PRISM data. The NMS solution also suggested a possible correlation between axis 2, kriged O₃ estimates ($r = 0.57$), CARB O₃ measurements ($r = 0.58$) and CARB NO₂ measurements ($r = 0.63$). The pollutant and humidity gradients opposed one another, indicating increasing O₃ and NO₂ concentrations with decreasing humidity as one proceeds eastward across the study area (Figures 3.2, 3.6 and Table 3.3). The lowest plot scores for axis 2 occurred in the greater San Francisco Bay area and near the coastline of Santa Barbara and San Luis Obispo counties. High plot scores tended to occur in the San Joaquin Valley, the Sierra Nevada foothills, and near Red Bluff and Chico in the northern Sacramento Valley.

Relationship of axis 2 to species richness and total lichen abundance

Species richness and total abundance of lichens were negatively associated with axis 2 (Figure 3.2: $r = -0.76$ and -0.71 , respectively). Diversity and abundance were highest in coastal plots where 21 to 29 species were typically found, especially in plots on the immediate coast. Several species-rich plots did occur in the central Sierra Nevada foothills around Placerville and San Andreas although most foothill plots had 3 to 17 species. Communities in the southern foothills were especially species poor, most with 10 species or less. The most depauperate communities were found in public

parks of the larger cities of the San Joaquin, such as Fresno (4 species) and Bakersfield (0 species).

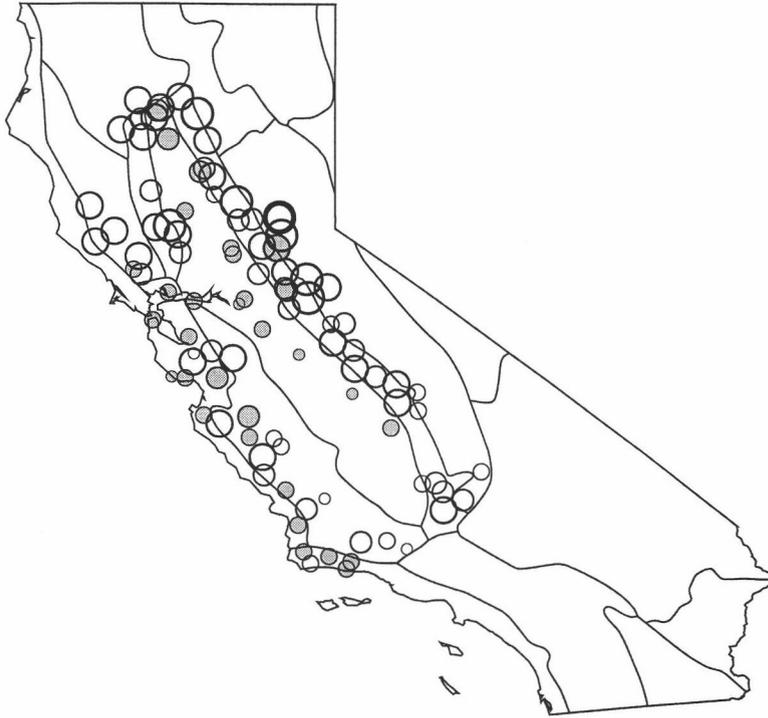


Figure 3.5. Map of air quality scores from axis 1 of the ordination. Symbol sizes are proportional to scores on axis 1. Off-frame plots are shaded in gray.

Several species with known oceanic affinities had maxima at low axis scores, steeply declining at higher scores (e.g. *Heterodermia leucomelos* and *Parmotrema chinense*; Figure 3.4). Species characteristic of more continental but moist, lowland habitats, such as *Evernia prunastri* (Figure 3.4) and *Ramalina farinacea* (not shown), declined more gradually along axis 2. Overall, only a few species had clearly positive associations to axis 2 scores (e.g. *Melanelia glabra* and *Physcia biziana*). Nitrophile responses to the axis were varied: several species had barely discernable (e.g. *Candelaria concolor* and *Phaeophyscia orbicularis*) to prominent maxima (e.g. *Xanthoria tenax*) near the center of the axis. Distributions of most other nitrophiles

had broad maxima at the low end of the axis (e.g. *Physcia tenella*) or nearly linear, negative associations with axis scores (e.g. *Ramalina subleptocarpha*).

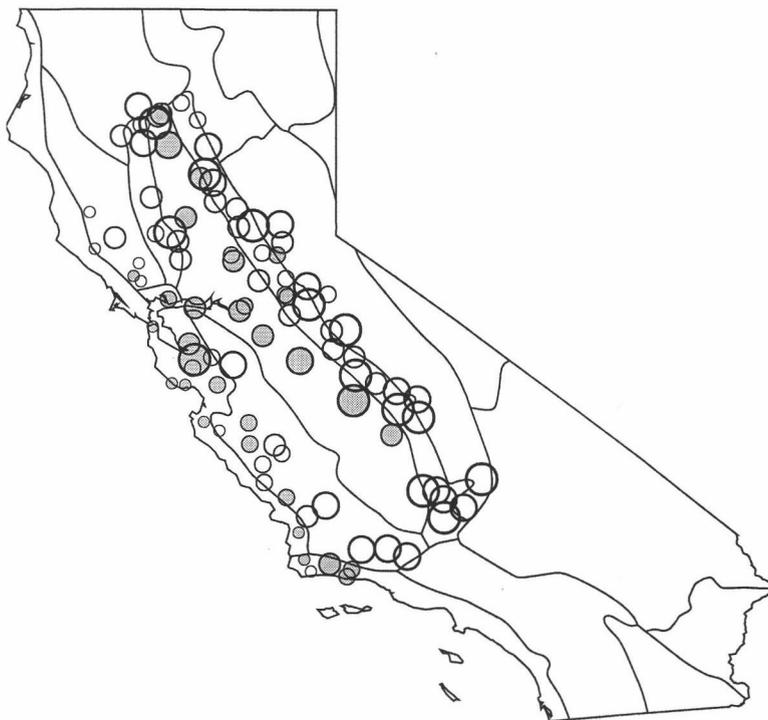


Figure 3.6. Map of scores from axis 2 of the ordination. Symbol sizes are proportional to scores on axis 2. Off-frame plots are shaded in gray.

DISCUSSION

Ammonia deposition in the greater Central Valley

The strong relationship between axis 1, NH_3 deposition data, and the relativized nitrophile indices (Figure 3.2 and Table 3.3) suggests that plots receiving low axis scores: 1) correspond with areas of higher estimated NH_3 deposition, 2) are either more urbanized, more agricultural, or a combination of these two land uses, and 3) have a higher relative abundance and diversity of nitrophilous lichens. In agriculturally intensive areas we would expect high NH_3 volatilization from both fertilized fields and concentrated animal wastes at livestock enclosures such as dairies and pastures. Ammonia impacting forests in or near major cities such as Fresno and

San Francisco is more likely derived from automobile exhaust and industrial emissions.

Unsurprisingly, greater SO₂ levels coincided with plots in more highly developed areas, as suggested by the similar position of the SO₂ and land use vectors in the ordination biplot (Figure 3.2). However, SO₂ was probably not a major factor driving axis 1 despite the correlation (Table 3.3). The CARB data show extremely low SO₂ levels throughout the study area with annual arithmetic means rarely surpassing 3 ppb in major urban centers. The most SO₂ sensitive lichen species are thought to be tolerant to up to 5 to 15 ppb in the Pacific Northwest (Peterson et al. 1992), which should be similar in our study area.

Accordingly, many species that dominated plots with the highest SO₂ levels are considered SO₂ sensitive species, such as *Candelaria concolor*, *Ramalina farinacea*, *Xanthoria fallax*, and *X. polycarpa* (Peterson et al. 1992). Nor did we observe the typical community response to SO₂ along axis 1, depression of species richness (van Haluwyn and van Herk 2002; Figure 3.2). Wet deposition of related pollutants, like sulfate, is comparably low. National Atmospheric Deposition Program monitoring sites in Davis and Pinnacles National Monument recorded winter means (December to February) from 1999 to 2000 ranging from 0.16 to 0.47 mg/L. Emissions of sulfur-based pollutants are much less in the western U.S. than in the east (Takemoto et al. 1995).

Our results were broadly consistent with the work of van Herk (1999, 2001), who correlated mean number of nitrophilous species per tree at plots of 10 clustered trees (Nitrofile Indicatie Waarde, NIW) with NH₃ deposition and presence of nearby livestock enclosures. Our relativized nitrophile indices conveyed a much clearer representation of the lichen community gradient along axis 1 than the distributions of individual nitrophiles and the un-relativized nitrophile indices (Figures 3.2 and 3.3). We speculate that the strong correlation between the relativized indices and the NH₃ calibration data is due to two factors, 1) the positive association of nitrophiles with NH₃ and 2) NH₃ intolerance by certain non-nitrophilous species, acidophytes (Figure 3.3).

Van Herk (2001) found that an index based upon acidophytes, the AIW (Acidofiele Indicatie Waarde), related to NH_3 concentrations in a nearly equal but opposite fashion to the NIW. North American workers have yet to investigate the usefulness of acidophytes for bioindication of NH_3 so we lack research indicating what species fit into this group. According to the AIW, candidates from our dataset include *Cetraria* spp., *Evernia prunastri*, *Hypogymnia* spp., *Platismatia glauca* (not pictured), and some *Usnea* spp (not pictured; Figure 3.3).

Relationship of land use to precipitation

When dealing with such a large model area, correlations between climate and air quality are usually unavoidable. In our case, precipitation patterns were generally related to land use patterns. The San Joaquin and southern Sacramento Valleys encompass the majority of large urban centers and major highways in the study area and are among the most agriculturally intensive regions of the U.S. Likewise, the San Joaquin Valley produces over half the estimated NH_3 emissions from fertilizers and confined cattle operations in California (California Air Resources Board 1999, Potter et al. 2001). These regions received a high proportion of the poorest air quality scores and also happen to receive the least precipitation. However, the poor air quality scores and dominance of nitrophilous species in relatively moist, coastal urban areas such as San Francisco, Davenport, Santa Cruz, and Goleta suggest that axis 1 is primarily related to NH_3 , not moisture patterns (Figures 3.2 and 3.5).

Correlation between humidity, NO_2 , and O_3

There are amazingly few field studies that investigate effects of photochemical pollutants on lichen communities. Without any clear information describing lichen responses to NO_2 and O_3 under natural conditions, our interpretation of the second model axis necessarily remains exploratory. Generally, the inverse correlation of humidity with NO_2 and O_3 is unsurprising. The geographic distribution of O_3 is often intimately confounded by climate (Bloomfield et al. 1996, Cox and Chu 1996, Flaum et al. 1996). Hot, clear weather favors the formation of O_3 , explaining the observed

close relationship of decreasing O₃ with increasing humidity. Likewise, NO₂ is a chemical precursor to O₃, hence the similar geographic distribution. As O₃ is a secondary pollutant, concentrations tend to peak downwind to the east of major urban areas where the majority of O₃ precursor pollutants are emitted.

NO₂

Nitrogen dioxide was negatively related to species richness in the Netherlands (van Dobben and de Bakker 1996, van Dobben and ter Braak 1998) although NO₂ measurements in their study were confounded by correlations with SO₂. The results are thus ambiguous since SO₂ is often associated with a depression of lichen biodiversity (van Haluwyn and van Herk 2002). The west to east decrease in species richness and abundance in our model did coincide with increased NO₂ along axis 2 although the pattern could be easily attributed to humidity, to be discussed more in the "Humidity" section.

Research shows nitrogen dioxide does affect lichen physiology but exactly how is still unclear. Short-term fumigations with extraordinarily high levels of NO₂ caused decreased chlorophyll concentrations in four lichen species (Nash 1976). Contrastingly, Von Arb et al. (1990) found higher chlorophyll concentrations in *Parmelia sulcata* thalli collected from areas in Switzerland exposed to much lower NO₂ levels but again, NO₂ was confounded by SO₂. Regardless, non-lethal effects on lichen physiology and morphology would not be detected with the given study protocol. Clearly, there is a great need for investigations of NO₂ toxicity to lichens in their natural habitats and most importantly, we need unambiguous evidence that NO₂ affects lichen communities via the differential mortality or promotion of species.

Nitric acid vapor (HNO₃) may actually be more ecologically important than NO₂ in greater Central Valley forests due to its higher deposition rate to plant surfaces (Munger et al. 1996). Fumigation experiments have shown that realistically high HNO₃ concentrations can cause foliar lesions on common California tree species such as *Quercus kelloggii* and *Pinus ponderosa* (Bytnerowicz et al 1999). In contrast, NO₂ is known to be phytotoxic only at exceptionally high concentrations (Bytnerowicz et

al. 1998). Nitric acid, like NH_3 , has a high deposition velocity and readily absorbs into many plant surfaces (reviewed by Hanson and Lindberg 1991).

Acid deposition is known to favor certain epiphytic lichen species over others, which may mean one could detect HNO_3 deposition with a lichen gradient model. However, supporting studies typically document impacts of bark acidification via SO_2 , acid precipitation of unknown chemical composition, or acidic deposition wherein sulfuric acid (H_2SO_4) is likely the predominant constituent (e.g. Gauslaa 1995, Gilbert 1986, O'Hare 1974, Robitaille et al. 1977, Skye and Hallberg 1969). Even though both are strong acids, we can not confidently assume H_2SO_4 and HNO_3 effects on lichens are analogous (Scott et al. 1989), a subject that has barely been broached in the literature. Thus, we were forced to exclude HNO_3 from our analysis due to the lack of direct monitoring data and the absence of research specifically documenting HNO_3 effects on lichen communities. Considering its toxicity and potentially great contribution to total dry N in parts of California (Takemoto et al. 1995), future lichen biomonitoring work will ideally include short-term passive monitoring of HNO_3 and an attempt to identify unequivocal indicator species.

O_3

It remains debatable whether and under what circumstances lichen communities respond to O_3 . The few existing field studies present different results: Sigal and Nash (1983) potentially found a relationship between O_3 levels and community composition although McCune (1988) and Ruoss and Vonarburg (1995) did not. Ozone levels were highest in the study area of Sigal and Nash (1983). Thus, concentrations in the latter studies may have been beneath the critical load for epiphytic lichens. Ambient O_3 does reach at least 155 ppb (maximum 1-hr value) in our southeastern plots, as suggested by measurements at CARB monitors downwind of the San Joaquin valley. Unfortunately, our O_3 data are not directly comparable with Sigal and Nash (1983) as we used different O_3 measurements.

Fumigation studies have documented various forms of physiological impairment from O_3 , such as reduced chlorophyll fluorescence and depressed

photosynthesis (Nash and Sigal 1979, Ross and Nash, 1983, Scheidegger and Schroeter 1995) although there is no clear, direct evidence that these effects lead to lichen mortality under natural conditions. The lichen communities studied by Sigal and Nash (1983), for instance, could have been responding to other pollutants not examined in their study, as suggested by Nash and Sigal (1999).

A further complication is the poorly understood role of climate in lichen susceptibility to O₃ damage. Ruoss and Vonarburg (1995) argued that lichens are insensitive to O₃ under natural conditions because physiological activity ceases during daily O₃ peaks when humidity levels are typically low. If severity of O₃ damage is indeed dependent upon thallus hydration, then local pollution levels and climate patterns would interact to determine lichen responses. Summer fog is common in the mountains near the Los Angeles Basin, making it possible that lichens were hydrated during the high O₃ episodes studied by Sigal and Nash (1983). As summer fog is relatively rare in our study area, particularly at inland eastern areas where O₃ levels are high, lichens could be better protected from O₃ damage. In any case, the current state of lichen-O₃ research leaves us with little basis to differentiate between O₃, NO₂, and moisture effects along axis 2 (see below).

Humidity

Atmospheric moisture is indisputably an important factor influencing lichen distributions as lichens are poikilohydric, deriving most moisture and nutrients directly from the atmosphere. Considering the large spatial scale of this project, community composition would be expected to show a pronounced coast to inland humidity gradient. Several species with strong negative relationships with axis 2 are characteristic of moist habitats, suggesting that humidity contributes, at least partly, to the community gradient (Figures 3.4 and Table 3.2). The west to east decrease in lichen biodiversity and abundance could be easily attributed to a decrease in atmospheric moisture.

CONCLUSIONS

Considering the prevalence of O_3 and NO_2 pollution in California, a tidy method for bioindication would be an invaluable contribution to lichenology and air quality research. Unfortunately, the suitability of our model for this purpose remains dubious and we recommend that the model not be used to indicate either pollutant. Nitric acid might be influencing community composition although we could not investigate relationships because deposition data are lacking for the study area. Neither could we describe HNO_3 patterns with community indices, much like the nitrophile indices we used for NH_3 , since there is no research describing lichen indicator species. Progress towards the development of lichen community-based methods for monitoring photochemicals will be hampered until several basic questions are answered, most importantly: 1) how do local climate and thallus hydration affect severity of damage? 2) does damage result in lichen mortality or only physiological impairment? 3) what concentrations are required to elicit a response?

Due in part to a strong research foundation, we were much more successful at modeling the lichen community response to NH_3 . Development of NH_3 monitoring programs are particularly important for the U.S. since deposition is not typically monitored by state or federal agencies. Ecological effects of NH_3 and excess nitrogen deposition are a growing concern for the western United States where emissions are high and continue to rise (Fenn et al. 2003b and 2003c). Besides altering the species composition of epiphytic lichen communities, prolonged exposure is implicated in a myriad of negative impacts to forest and shrub-dominated ecosystems, such as inhibition of mycorrhizal symbioses (Menge and Grand 1978, Termorshuizen and Shaffers 1993, van der Eerden et al. 1992), alteration of ectomycorrhizal community structure (Lilleskov et al. 2001, 2002), inducement of conifer needle injury or loss (van der Eerden et al. 1992), and reduction of frost hardiness in trees (Pietilä et al. 1991).

The rapid dry deposition of NH_3 makes concentrations highly variable over the landscape, which would necessitate maintenance of a dense monitoring network to accurately capture geographic deposition patterns (Asman and van Jaarsveld 1992).

Bioindication with lichen communities allows flexible, intensive sampling across a landscape without the costs of installing and maintaining permanent instrumentation, a more feasible option for NH₃.

We have presented here the first lichen-based model for indication of NH₃ patterns in the U.S. Additional lichen communities may be sampled within the defined study area, incorporated into the model, and assigned air quality scores with NMS to indicate relative, local NH₃ deposition. In the absence of a multivariate lichen community model, % nitrophile richness or abundance may be used as a rough but nonetheless, useful estimate of NH₃ deposition. Most species that we designated as nitrophiles are widely accepted among lichenologists, such as *Candelaria concolor*, and species from *Phaeophyscia*, *Physcia*, and *Xanthoria*. The next advancement in NH₃ biomonitoring research will ideally involve close calibration of lichen community data with direct NH₃ measurements.

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ENDNOTES

1. This article is synonymous with Chapter 2.

Chapter 4

Using Epiphytic Macrolichen Communities for Biomonitoring Ammonia in Forests of
the Greater Sierra Nevada, California

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ABSTRACT

Chronic, excessive nitrogen deposition is potentially an important ecological threat to forests of the greater Sierra Nevada in California. We developed a model for ammonia bioindication, a major nitrogen pollutant in the region, using epiphytic macrolichens. We used non-metric multidimensional scaling to extract gradients in lichen community composition from surveys at 115 forested sites. A strong ammonia deposition gradient was detected, as evidenced by a high linear correlation with an index of ammonia indicator species conventionally known as "nitrophiles" ($r = 0.93$). This gradient, however, was confounded by elevation ($r = -0.54$). We evaluated three statistical techniques for controlling the influence of elevation on nitrophiles: simple linear regression, nonlinear regression, and nonparametric regression. We used the unstandardized residuals from nonlinear regression to estimate relative ammonia deposition at each plot, primarily because this model had the best fit ($r^2 = 0.33$), desirable asymptotic properties, and it is easy to apply to new data. Other possible sources of noise in the nitrophile-ammonia relationship, such as substrate pH and acidic deposition, are discussed. Lichen communities indicated relatively high deposition to forests of the southern Sierra Nevada, the Modoc Plateau, as well as in stands near urban areas. Evidence of elevated ammonia was also detected for popular recreation areas such as Sequoia and Yosemite National Parks. Lichen communities from forests in the Tahoe basin, northern Sierra Nevada, southern Cascades, and eastern Klamath Range appeared considerably less impacted. This model will be used for continual assessment of eutrophication risks to forest health in the region.

INTRODUCTION

As most forest ecosystems in the northern hemisphere are nitrogen (N) limited, short term atmospheric deposition of anthropogenic N tends to enhance plant productivity (Aber et al. 1989). Chronic exposure to elevated levels, however, can culminate in a syndrome of ecosystem effects known as N saturation, which may include reduced soil fertility, enhanced volatilization of greenhouse gases from the soil, and in extreme cases, forest decline (Aber et al. 1989). Especially within or

downwind of agricultural areas, ammonia (NH_3) is typically the dominant component of N deposition. Excess NH_3 has been implicated in various impacts to terrestrial ecosystems, such as accelerated needle senescence in conifers, greater susceptibility of trees to frost damage and disease, reduced drought tolerance, reductions in diversity and abundance of ectomycorrhizal symbioses, shifts in herb community composition, and alteration of epiphytic lichen communities (reviewed by Krupa 2003).

The affinity of certain epiphytic lichen species for NH_3 is well documented in the lichenological literature (e.g. de Bakker 1989; Jovan and McCune 2005¹; van Dobben and de Bakker 1996; van Herk 1999, 2001). These indicator species, known as "nitrophiles," are common, conspicuous components of the lichen flora in urban and agricultural landscapes. Van Herk (1999, 2001) found that an index of epiphytic nitrophile abundance, the Nitrofiële Indicatie Waarde (NIW) could be positively, linearly related to NH_3 deposition in the Netherlands. A similar index developed by Jovan and McCune (2005), is currently used for NH_3 biomonitoring in forests of the greater Central Valley of California. The continual refinement and use of such models is particularly important in the United States where NH_3 is not regularly measured by state and federal air programs.

Epiphytic macrolichen communities are monitored by the Forest Inventory and Analysis Program (FIA) of the United States Department of Agriculture (USDA) to evaluate air quality impacts on forest health. Our main objective was to derive a gradient model, based upon FIA lichen data, to indicate NH_3 deposition in the greater Sierra Nevada (Figure 4.1). We adapted the methodology of Jovan and McCune (2005) to circumvent a common difficulty with large-scale biomonitoring across mountainous terrain: the tendency for elevation to confound the relationship between indicator species and the environmental factor of interest. In our case, NH_3 varied according to elevation, as did other physiologically important climatic gradients like moisture and temperature. To extract the influence of elevation from the lichen community response to NH_3 , we evaluated the pros and cons of using simple linear

regression (SLR), nonlinear regression (NLR), and nonparametric regression (NPR; Bowman and Azzalini 1997).

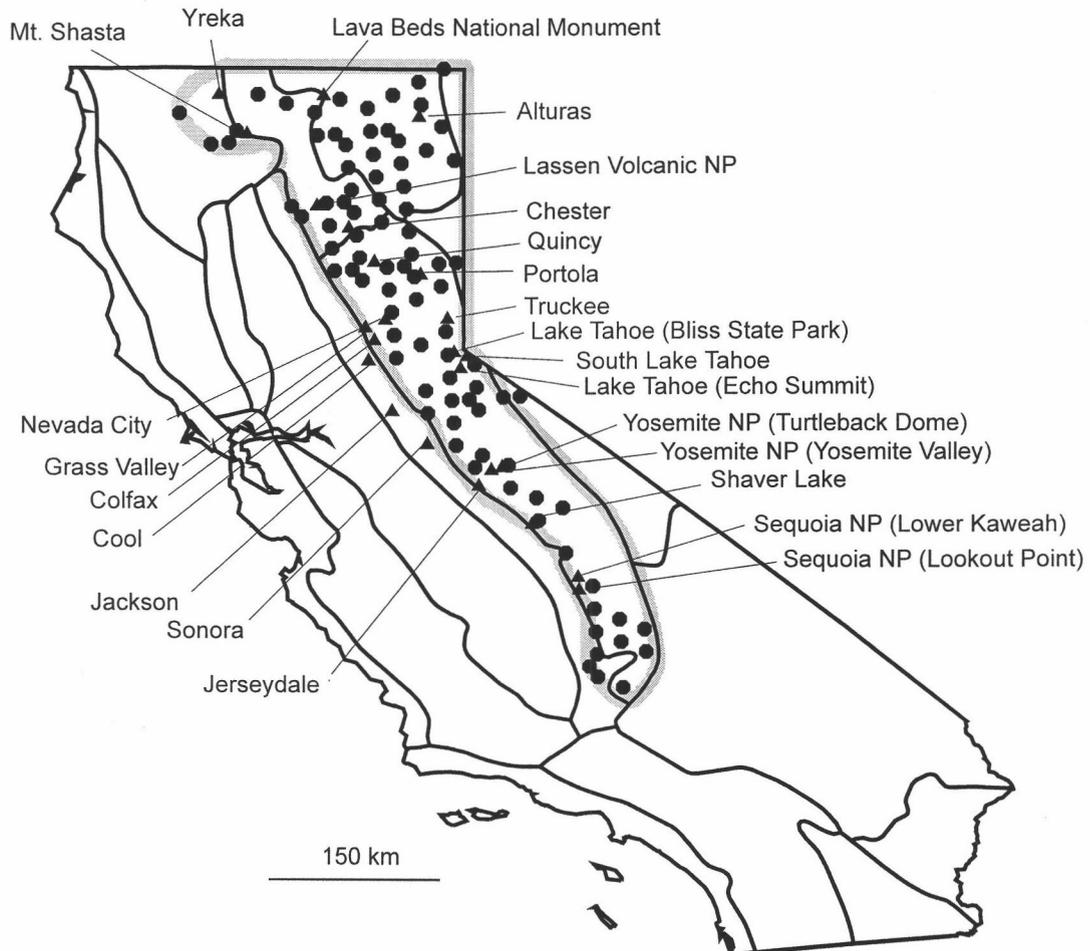


Figure 4.1. Map of greater Sierra Nevada model area. Model boundary is delineated by thick gray line. Thinner black lines indicate Bailey's ecoregions (Bailey 1983). Triangles indicate off-frame plots while circles indicate on-frame plots. NP = National Park.

We used the 'best' approach to adjust the bioindication model and estimate relative NH_3 deposition at 115 FIA forest health monitoring plots. Sites included popular recreation areas in Yosemite and Sequoia National Parks. While we focus on lichens and NH_3 , our general methodology could be used for a wide variety of monitoring objectives and indicator organisms.

Degradation of air quality in greater Sierra Nevada forests has become a critical management issue, attributed mainly to the burgeoning tourism industry, forest fires, local agriculture, and long distance transport of pollutants from the highly agricultural and industrialized Central Valley (Figure 4.1; Cahill et al. 1996, Fenn et al. 2003a, National Park Service 2000). After ozone (O_3), experts consider chronic, excessive N the greatest potential threat to forest health in the region (Fenn et al. 2003a). Recent studies suggest NH_3 is the primary constituent of total N deposition (Bytnerowicz and Fenn 1996, Bytnerowicz and Riechers 1995; Bytnerowicz et al. 2002, Fenn et al. 2003a). Some California forests adjacent to the Los Angeles Basin are already considered N saturated (reviewed in Takemoto et al. 2001) although deposition to the Sierra Range is more moderate, suggesting stands are still in the accumulation phase of the N saturation trajectory (Fenn et al. 2003a).

STUDY AREA

The boundaries of the greater Sierra Nevada model area are based on a previous analysis of epiphytic macrolichen community data from FIA plots in northern and central California forests (Jovan and McCune 2004). Jovan and McCune (2004) used multivariate analysis to group plots into three model areas with relatively similar lichen communities, climate, and topography. The strategy was to reduce environmental variability within the model areas, which may otherwise confound lichen responses to air quality. The Sierra Nevada model area encompasses four ecoregions as defined by Bailey (1983): the Southern Cascades, Modoc Plateau, Northwestern Basin and Range, and Sierra Nevada sections (Figure 4.1). The northwestern boundary follows the Southern Cascades Section but technically includes high elevation sites in the eastern Klamath Range (>1500 m) that are north of Castle Crags Wilderness and east of Scott Valley. A few plots from small cities in the Sierra Foothills section were also included.

Because the greater Sierra Nevada is mountainous and has a large geographic scope (Figure 4.1), climate and forest composition were still considerably heterogeneous. Plot elevations ranged from 379 to 2895 m with more than 85% of

plots over 1000 m. According to the Precipitation-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994, 2001, 2002), average annual precipitation tends to increase with elevation (range: ~ 256 to 2261 mm) with a greater proportion of precipitation falling as snow. Mean annual temperature generally decreases with elevation (range: ~2 to 15.7 C). A notable exception is the cool, high elevation desert of the Modoc Plateau, which lies in the rain shadow of the Klamath Range and southern Cascades.

Most plots occurred in mixed conifer stands dominated by species such as *Abies concolor*, *A. magnifica*, *Calocedrus decurrens*, *Pinus contorta*, *P. jeffreyii*, *P. ponderosa*, and *Pseudotsuga menziesii*. Riparian and low elevation stands often had a hardwood component (e.g. *Alnus rubra*, *Quercus chrysolepis*, *Q. douglasii*, and *Q. wislizenii*). *Ceanothus* spp. and *Arctostaphylos* spp. provided important lichen substrate in the forest understory and in chaparral communities. Vegetation in the Modoc Plateau was more characteristic of the Great Basin, with open stands of *Juniperus occidentalis* and abundant *Artemisia* spp.-steppe.

METHODS

Sampling and survey protocol

Epiphytic macrolichen communities were surveyed at 115 FIA circular 0.38-ha plots (Figure 4.1). Ninety-one were permanent “on-frame” plots, located on a 27 km by 27 km FIA hexagonal sampling grid (Messer et al. 1991). On-frame plots occurred on both public and private land, each surveyed once in the summer between 1998 - 2001. Plots falling on non-forested land or where the landowner restricted access were excluded from the sample, leading to a variable density of plots across the landscape (Figure 4.1). We surveyed an additional 24 “off-frame” plots in July 2003 (Figure 4.1), which occurred in residential, urban, and highly recreated areas like National Parks and National Monuments.

Surveys followed the standardized FIA protocol (McCune et al. 1997b) employed by Jovan and McCune (2005). Field crews collected specimens of each epiphytic macrolichen occurring above 0.5 m on woody substrates or in the litter. Each

species was assigned an abundance class: 1 = rare (< 3 thalli), 2 = uncommon (4-10 thalli), 3 = common (> 10 thalli present but species occurs on less than 50% of all boles and branches), and 4 = abundant (> 10 thalli present and species occurs on more than 50% of all boles and branches). Surveys lasted a minimum of 30 minutes and a maximum of two hours or until ten minutes passed before encountering a different species. Lichen collections were identified by professional lichenologists. The nomenclature of McCune and Geiser (1997) was used for identification of all genera except *Physcia* (Moberg 2002), *Physconia* (Esslinger 2000), and *Xanthoria* (Lindblom 1997). Voucher specimens from off-frame plots reside at the Oregon State University Herbarium (OSC).

Field workers were not required to accurately assign names to lichen species in the field but were trained to differentiate between species based upon morphology during a three day intensive training session. All workers were required to pass a certification exam, for which they had to capture $\geq 65\%$ of the species found by a professional lichenologist in a practice plot. Crew performance was periodically audited a total of nine times, by "hot checks" (both specialists and field crew surveyed a plot simultaneously) and "blind checks" (specialists re-measured a plot within two months of the crew survey). Field workers always captured at least 65% of the species found by specialists. McCune et al. (1997b) determined that plot scores on ordination axes were highly repeatable as long as the 65% criterion was met.

Analysis

Plots without lichens and duplicate surveys from audited plots were excluded from the dataset. For duplicates, we retained the survey conducted by the non-specialist who found the highest species richness. Infrequent species occurring in less than 5% of the plots were excluded from the dataset, which typically improves correlations between ordination axes and environmental variables (McCune and Grace 2002). After removal of 39 infrequent species, the analysis was based on a total of 52 species in 115 plots (Table 4.1).

Table 4.1. Summary of species found in lichen community plots. (N) designates species considered nitrophilous. % Freq = percentage of plots where the species occurred.

Species	% Frequency	
	On-frame (n = 91)	Off-frame (n = 24)
<i>Ahtiana sphaerosporella</i>	27.5	16.7
<i>Alectoria imshaugii</i>	1.1	4.2
<i>Alectoria sarmentosa</i>	2.2	4.2
<i>Bryoria capillaris</i>	1.1	0.0
<i>Bryoria fremontii</i>	18.7	8.3
<i>Bryoria friabilis</i>	1.1	0.0
<i>Bryoria fuscescens</i>	2.2	0.0
<i>Bryoria pseudofuscescens</i>	1.1	0.0
<i>Bryoria simplicior</i>	2.2	0.0
<i>Bryoria trichodes</i>	1.1	0.0
<i>Candelaria concolor</i> (N)	41.8	83.3
<i>Cetraria canadensis</i>	1.1	0.0
<i>Cetraria chlorophylla</i>	9.9	8.3
<i>Cetraria merrillii</i>	44.0	62.5
<i>Cetraria orbata</i>	19.8	4.2
<i>Cetraria pallidula</i>	4.4	4.2
<i>Cetraria platyphylla</i>	30.8	20.8
<i>Cladonia chlorophaea</i>	1.1	0.0
<i>Collema furfuraceum</i>	5.5	20.8
<i>Collema nigrescens</i>	0.0	4.2
" <i>Dendriscocaulon</i> " sp.	0.0	4.2
<i>Esslingeriana idahoensis</i>	8.8	12.5
<i>Evernia prunastri</i>	15.4	54.2
<i>Flavopunctelia flaventior</i> (N)	1.1	16.7
<i>Hypogymnia enteromorpha</i>	1.1	0.0
<i>Hypogymnia imshaugii</i>	70.3	79.2
<i>Hypogymnia occidentalis</i>	1.1	4.2
<i>Hypogymnia tubulosa</i>	1.1	8.3
<i>Koerberia biformis</i>	0.0	4.2
<i>Leptochidium albociliatum</i>	1.1	0.0
<i>Leptogium celluloseum</i>	0.0	4.2
<i>Leptogium furfuraceum</i>	2.2	0.0
<i>Leptogium lichenoides</i>	6.6	0.0
<i>Letharia columbiana</i>	65.9	58.3
<i>Letharia vulpina</i>	84.6	62.5
<i>Lobaria hallii</i>	1.1	0.0
<i>Melanelia elegantula</i>	34.1	50.0

Table 4.1 (Continued)

<i>Melanelia exasperatula</i>	20.9	16.7
<i>Melanelia glabra</i>	16.5	29.2
<i>Melanelia subargentifera</i>	0.0	20.8
<i>Melanelia subelegatula</i>	12.1	12.5
<i>Melanelia subolivacea</i>	49.5	79.2
<i>Nodobryoria</i>	0.0	37.5
<i>Nodobryoria abbreviata</i>	50.6	16.7
<i>Nodobryoria oregana</i>	31.9	0.0
<i>Parmelia hygrophila</i> (N)	9.9	12.5
<i>Parmelia pseudosulcata</i>	1.1	0.0
<i>Parmelia saxatilis</i>	1.1	0.0
<i>Parmelia sulcata</i>	23.1	58.3
<i>Parmelina quercina</i>	6.6	20.8
<i>Parmeliopsis ambigua</i>	4.4	4.2
<i>Parmeliopsis hyperopta</i>	3.3	0.0
<i>Peltigera collina</i>	5.5	0.0
<i>Phaeophyscia ciliata</i>	2.2	4.2
<i>Phaeophyscia orbicularis</i> (N)	3.3	29.2
<i>Physcia adscendens</i> (N)	12.1	54.2
<i>Physcia aipolia</i> (N)	8.8	29.2
<i>Physcia biziana</i>	5.5	8.3
<i>Physcia dimidiata</i> (N)	6.6	0.0
<i>Physcia stellaris</i> (N)	5.5	54.2
<i>Physcia tenella</i> (N)	14.3	66.7
<i>Physcia tribacia</i> (N)	0.0	4.2
<i>Physconia americana</i> (N)	13.2	45.8
<i>Physconia enteroxantha</i> (N)	13.2	58.3
<i>Physconia fallax</i> (N)	5.5	29.2
<i>Physconia isidiigera</i> (N)	12.1	45.8
<i>Physconia perisidiosa</i> (N)	16.5	66.7
<i>Platismatia glauca</i>	14.3	25.0
<i>Platismatia herrei</i>	0.0	0.0
<i>Pseudocyphellaria anomala</i>	2.2	0.0
<i>Pseudocyphellaria anthraspis</i>	3.3	0.0
<i>Punctelia perreticulata</i> (N)	0.0	8.3
<i>Ramalina farinacea</i>	0.0	4.2
<i>Ramalina subleptocarpha</i> (N)	2.2	25.0
<i>Tholurna dissimilis</i>	1.1	0.0
<i>Usnea diplotypus</i>	1.1	0.0
<i>Usnea filipendula</i>	9.9	8.3
<i>Usnea lapponica</i>	1.1	0.0

Table 4.1 (Continued)

<i>Usnea nidulans</i>	1.1	0.0
<i>Usnea pacificana</i>	2.2	0.0
<i>Usnea scabrata</i>	2.2	0.0
<i>Usnea subfloridana</i>	1.1	0.0
<i>Usnea substerilis</i>	1.1	8.3
<i>Vulpicida canadensis</i>	3.3	12.5
<i>Xanthoria candelaria</i> (N)	18.7	12.5
<i>Xanthoria fallax</i> (N)	8.8	25.0
<i>Xanthoria fulva</i> (N)	16.5	37.5
<i>Xanthoria hasseana</i> (N)	12.1	45.8
<i>Xanthoria oregana</i> (N)	19.8	45.8
<i>Xanthoria parietina</i> (N)	2.2	0.0
<i>Xanthoria polycarpa</i> (N)	11.0	62.5

Climate data were extracted from the PRISM data (Daly et al. 1994, 2001, 2002) and averaged over 1961 to 1990. Climate variables (annual means) included: precipitation, number of wetdays, relative humidity, dew temperature, mean temperature, maximum temperature, and minimum temperature. Geographic and stand structure variables collected for each plot included elevation, latitude, longitude, total live basal area, basal area of live hardwoods, and basal area of live softwoods.

We derived several variables to describe lichen community gradients: overall lichen species richness, total lichen abundance (sum of all abundance classes per plot), nitrophile richness, nitrophile abundance, proportion of nitrophiles (proportion of species richness in nitrophiles), and proportion of nitrophile abundance (PNA; proportion of total abundance in nitrophiles). The nitrophile indices were based on Jovan and McCune (2004, 2005) and were comprised of species designated in Table 4.1.

Ordination

We used PC-ORD software (version 4.20; McCune and Mefford 1999) to extract the strongest gradients in lichen community composition following the methodology of Jovan and McCune (2005). Non-metric multidimensional scaling

(NMS; Kruskal 1964) ordination with Sorensen distance measure was conducted on a matrix of sample units by species abundance. The data underwent 999 runs, each consisting of a maximum of 500 iterations. We selected the ordination solutions with the lowest stress for a given dimensionality. Among those, we chose the final solution using a stress improvement criterion of five. In other words, a solution with n dimensions was favored over a solution with $n-1$ dimensions only if the additional axis reduced stress by five or more.

The final solution was evaluated against a Monte Carlo test of 500 runs with randomized data to determine whether patterns were stronger than would be expected by chance. We calculated coefficients of determination between original plot distances and distances in the final ordination solution to determine how much variability in lichen community composition was represented by the NMS axes (McCune and Grace 2002). We used orthogonal rotation to maximize correlations of NMS axes to environmental and lichen community variables.

Elevation models and air quality score adjustment

To extract elevation effects, we adjusted the lichen community response to NH_3 with a strategy similar to McCune et al. (1998). They used the standardized residuals from a SLR of elevation on an index of pollution indicator species as "adjusted air scores". We modeled the relationship between PNA and elevation using three methods: SLR, NPR with a local mean model, and NLR with the following 3-parameter generalized sigmoid curve:

$$Y = \frac{a}{1 + (\text{Elevation}/c)^b}$$

where Y is the fitted value, a is the upper asymptote, b is a coefficient, and c is the elevation at the inflection point. We compared the applicability, ease of communication and use, performance, and inherent bias along the response curve of each statistical approach. The unstandardized residuals from the "best" approach served as estimates of relative NH_3 deposition at each plot, hereafter referred to as "air scores." We used SPSS (2001) to conduct the NLR and HyperNiche (McCune and

Mefford 2004) for the SLR and NPR.

We included NPR as it can resolve complex response curves. Unlike traditional regression, NPR does not calculate coefficients for a mathematical function relating the response variable to predictors. Instead model building iteratively optimizes model fit without reference to a specific global model form. The investigator specifies a local model or kernel function (Bowman and Azzalini 1997). The local model defines how plots are weighted for a prediction at a given point in the habitat space and specifies the shape of the function used to fit points. We used a local mean estimator and Gaussian kernel function to relate proportion of nitrophiles to elevation. We selected a minimum average neighborhood size of 3 plots. The standard deviation (tolerance) of the kernel function was optimized by cross-validated coefficients of determination (xr^2), the statistic we used to evaluate model fit.

RESULTS AND DISCUSSION

Ordination results

The NMS ordination had two axes with a final stress and instability of 20.05 and 0.03, respectively. Minimum stress of the ordination was lower than would be expected by chance ($p < 0.005$). Axis 1 explained most of the variability in lichen community structure ($r^2 = 0.57$) while axis 2 was relatively weak ($r^2 = 0.24$). As axis 2 appeared primarily driven by climatic gradients, it will not be fully discussed in this paper (Figure 4.2 and Table 4.2).

The high linear correlations of nitrophile abundance ($r = 0.84$) and PNA ($r = 0.93$) with axis 1 suggest NH_3 is a major factor driving this lichen community gradient (Figure 4.2 and Table 4.2). Indices of nitrophile richness were similarly correlated (Table 4.2). Although NH_3 deposition data were not available for model calibration, our interpretation is strongly supported by the lichenological literature (Benfield 1994; de Bakker 1989; Jovan and McCune 2005; van Dobben and de Bakker 1996; van Herk 1999, 2001). The PNA index was strongly, positively related to estimated NH_3 deposition in the greater Central Valley (Jovan and McCune 2005). Likewise, van Herk (1999, 2001) found a comparable relationship between atmospheric NH_3 and

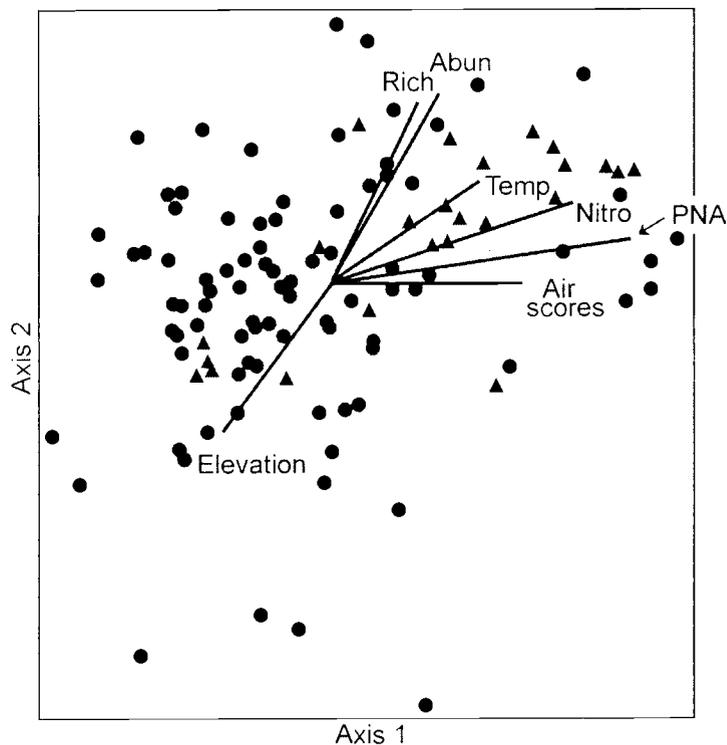


Figure 4.2. Ordination joint plot with environmental and lichen community variables overlaid. Triangles indicate off-frame plots while circles indicate on-frame plots. Vector lengths and directions indicate correlations with the ordination. Most vectors with $r^2 > 0.25$ are shown. To prevent crowding, related variables with overlapping vectors of similar strength are designated by a single label: Temp (temperature) represents dew temperature, mean temperature, minimum temperature, and maximum temperature; Nitro includes nitrophile diversity and abundance; and PNA includes proportion of species richness and lichen abundance at a plot in nitrophiles. Abbreviations for other environmental vectors are: Rich = total lichen species richness, Abun = total lichen abundance (sum of abundance codes), and Air scores = air quality scores adjusted for elevation.

NIW scores in the Netherlands, calculated as the mean abundance of nitrophiles over ten *Quercus robur* trees.

We must consider, however, that nitrophiles were probably also responding to climatic variability (Figure 4.3). As anticipated, elevation also had an appreciable correlation with axis 1 ($r = -0.54$; Figure 4.2) as did climatic variables normally patterned on elevation, like temperature and precipitation (Table 4.2). We are

Table 4.2. Summary of correlation coefficients for correlations between ordination axes and topographic, environmental, and lichen community variables.

Variable	<i>r</i>	
	Axis 1	Axis 2
Longitude	0.21	-0.39
Latitude	-0.32	0.17
Elevation	-0.54	-0.63
Dew temperature	0.63	0.55
Maximum temperature	0.60	0.60
Mean temperature	0.67	0.55
Minimum temperature	0.67	0.45
Humidity	-0.06	0.13
Wetdays	-0.46	0.10
Precipitation	-0.19	0.31
Total live basal area	-0.28	0.07
Hardwood basal area	0.47	0.21
Softwood basal area	-0.35	0.52
Lichen species richness	0.52	0.72
Total lichen abundance	0.57	0.73
Proportion of nitrophile abundance	0.93	0.37
Proportion of nitrophile richness	0.91	0.36
Nitrophile abundance	0.84	0.49
Nitrophile richness	0.83	0.50
Adjusted air scores	0.75	0.02

unaware of a documented “upper elevation limit” for nitrophiles. Nonetheless, epiphytic lichen diversity and abundance generally tend to decrease with increasing elevation in the study area, as clearly illustrated by the almost diametrically opposed richness, abundance, and elevation vectors in the ordination (Figure 4.2).

A small contingent of non-nitrophilous species, such as *Ahtiana sphaerosporella*, *Letharia vulpina*, *L. columbiana*, and *Cetraria merrillii*, usually dominate high-elevation forests throughout the Cascades and Sierra Nevada ranges. These high-elevation habitats are arguably harsher from a lichen’s perspective, due to factors like lower temperatures (Figure 4.2) and higher proportions of precipitation falling as snow (not measured; Figure 4.3). Nitrophile distributions in particular may

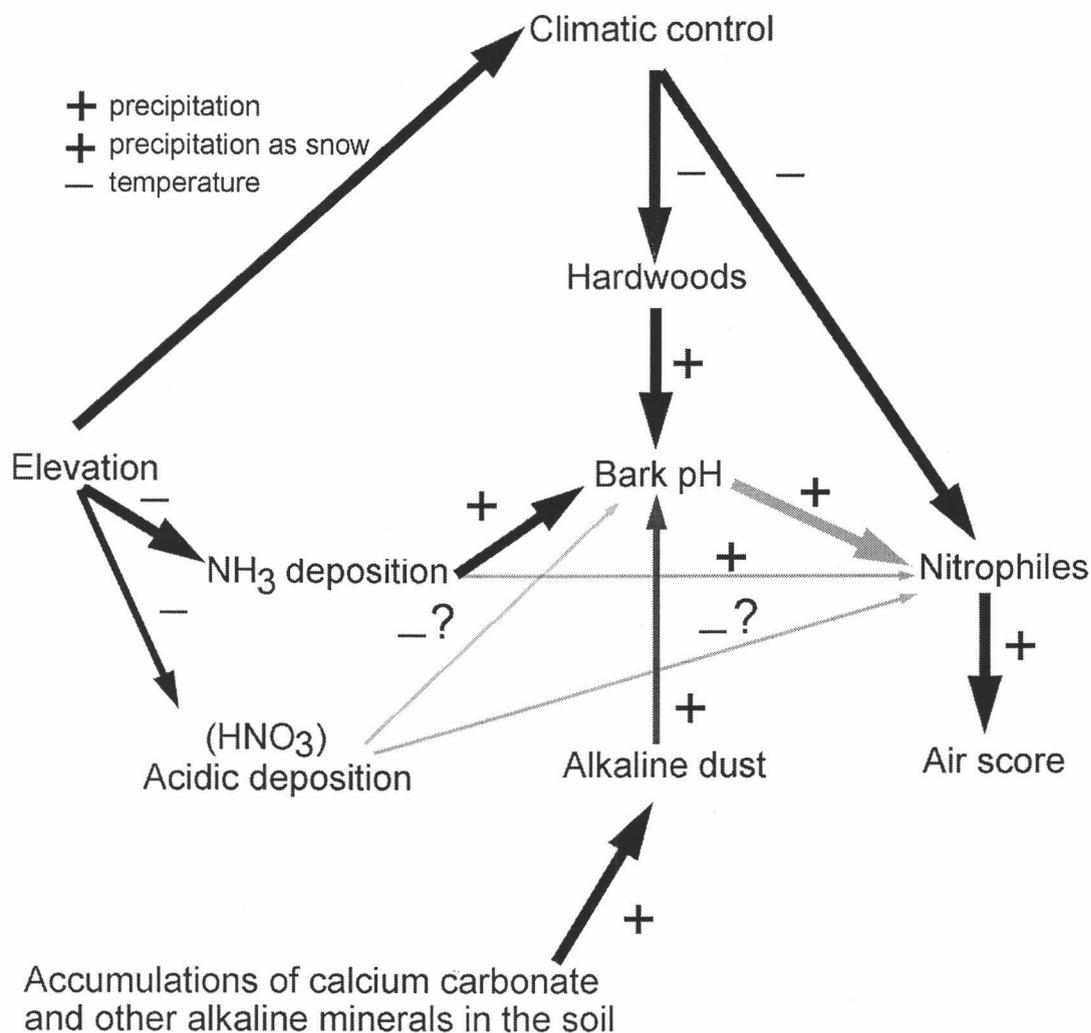


Figure 4.3. Hypothesized environmental effects on nitrophiles in the greater Sierra Nevada model area. Anticipated positive (+) and negative (-) correlations are noted above each arrow. Arrow thickness indicates expected effect size. We emphasize the hypothesis that the nitrophile-NH₃ relationship is mediated by bark pH although the other predominant mechanism (NH₃ affects nitrophiles directly) is also included in the diagram. Gray arrows indicate understudied phenomena or effects for which there are competing hypotheses. Alkaline dust is typically associated with the soil taxonomic order Aridisols. It is diagrammed independently of climatic variables because the formation of Aridisols is associated with both climatic (aridic soil moisture regime and a thermic to cryic soil temperature regime) and non-climatic factors (e.g. composition of soil parent material, site geologic history).

also be affected by the scarcity of hardwood substrates at mid to high elevations (Figure 4.3). Nitrophiles are not exclusively associated with hardwoods but there is evidence that richness and abundance within a community are positively affected by the chemical properties of hardwood bark, to be discussed further in the “Effect of natural bark pH” subsection.

Confounding thus occurs as NH_3 varies with elevation (Figure 4.3). Ammonia emissions sources are more concentrated in the low elevation foothills. This geographic belt, especially in the south, has a greater density of cities, larger cities, more farms, and more ranching (Momsen 2001; Figure 4.3). Additionally, foothill forests are nearest to the highly agricultural Central Valley where NH_3 emissions are high and lichen communities characteristically dominated by nitrophiles (Jovan and McCune 2004, 2005). Ammonia has a high deposition velocity so a high proportion is deposited locally, just downwind of the emissions source (Asman and van Jaarsveld 1992). Direct monitoring data do show higher bulk N deposition at lower elevation forests of the western Sierra Nevada (Bytnerowicz et al. 2002; reviewed in Fenn et al. 2003a) although few comparable data are available for NH_3 specifically.

Model adjustment

A scatterplot between elevation and PNA showed a relationship resembling either a straight line or sigmoid curve (Figure 4.4). According to SLR, elevation represented 31% of the variance in the PNA ($p < 0.001$; Figure 4.4). A one hundred-meter increase in elevation is associated with an average decrease of 2.7% in PNA (95% confidence interval: 1.9% to 3.5%). NLR explained slightly more variability in the data ($r^2 = 0.33$; Table 4.3) but yielded a more complex sigmoid model (Figure 4.4). Hyperniche fit an approximately sigmoid curve to the NPR model with a cross-validated r^2 of 0.26 (Figure 4.4). The NPR response curve was based upon an average neighborhood size of 36 and an optimized tolerance (standard deviation) of 252 m for elevation. This tolerance means that points within ± 252 m elevation of a target point are given the most weight in the local mean.

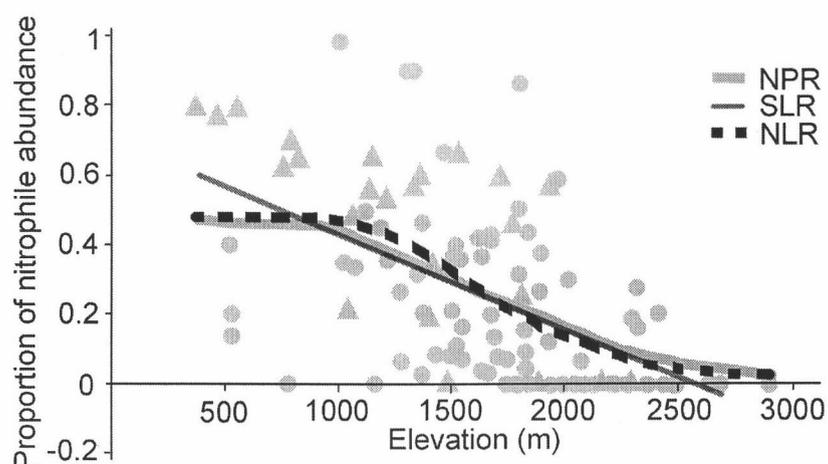


Figure 4.4. Regressions of proportion of nitrophile abundance on elevation with three methods: nonparametric regression (NPR), simple linear regression (SLR), and nonlinear regression (NLR). Gray triangles indicate off-frame plots and gray circles indicate on-frame plots.

Simple linear regression appeals in its ease of application, ease of communication, and generally good fit to the data (Table 4.4). Yet the model is fatally flawed since the regression line crosses the x-axis (Figure 4.4). Thus, a plot higher than 2600 m would need to have an impossible negative abundance of nitrophiles to be assigned a low air score, a low air score being roughly equivalent to low NH_3 deposition for a given elevation. The remaining two models yielded similar response curves but we favored NLR because it had the better fit to the data and additional plots could be easily fit with the regression equation (Table 4.4).

Table 4.3. Best fit values for parameters of generalized sigmoid model found by nonlinear regression of proportion of nitrophile abundance on elevation. SE = standard error.

Parameter	Estimate	SE	95% Confidence Interval
Asymptote	0.48	0.06	0.37 to 0.60
Inflection point	1690	108	1476 to 1904
Slope	5.91	1.89	2.17 to 9.66

Table 4.4. Comparison of pros and cons for three different modeling approaches.

Criteria	Simple linear regression	NPR local mean	Nonlinear regression
Ease of application	New response values can easily be predicted using the regression equation	NPR does not generate an equation so the investigator must use statistical software to estimate new values.	New response values can easily be predicted using the regression equation
Ease of communication	This technique is the easiest to communicate, being mechanistically simple and commonly used	NPR is the most difficult to communicate, being a statistical approach that is unfamiliar to many.	Nonlinear regression is a more common analysis technique than NPMR in biological studies. However, the investigator must determine which mathematical function is most appropriate for modeling and justify that choice.
Fit (r^2 or xr^2)	$r^2 = 0.31$	$xr^2 = 0.26$	$r^2 = 0.33$
Fit (areas of bias)	The regression line crosses the x-axis, meaning plots at elevations above 2600 m will always be scored as having poor air quality.	More low elevation plots (~250 to 1000 m) would be classified as having poor air quality scores relative to the linear model. Please see description of bias for nonlinear regression.	Scoring by the nonlinear model is less conservative than the linear and NPR models at mid elevations (1000 to 1570 m): proportionally fewer plots would be classified as having better air quality than expected for a given elevation. The opposite is true for plots between 1700 and 2270 m. However, these differences are slight.

To score plots, one first calculates the PNA from the lichen community data using the nitrophile designations in Table 4.1:

$$\text{PNA}_i = \frac{\sum_{j=1}^S x_{ij} w_j}{\sum_{j=1}^S x_{ij}}$$

where S = number of species, x_{ij} = the abundance of species j in plot i , and w_j = a vector of binary values indicating whether each species is a nitrophile ($w_j = 1$) or not ($w_j = 0$). Plot elevation in meters is plugged into the following NLR equation to find the expected proportion of nitrophiles, the fitted value (Y):

$$Y = \frac{0.48}{1 + (\text{Elevation}/1689)^{5.91}}$$

The final air score is the unstandardized residual from the NLR model multiplied by 100:

$$\text{Air quality score} = 100 (\text{PNA} - Y)$$

Air scores are interpreted as the percentage of nitrophiles above or below what is expected for a given elevation, so higher scores indicate relatively higher NH_3 deposition.

Interpretation of air scores and sources of variability

The vector for air scores was strongly correlated with NMS axis 1 ($r = 0.75$) and aligned closely with the nitrophile indices (Figure 4.2). Most plots scoring on the extreme high end of axis 1 were off-frame, and thus were located in urban, residential and heavy recreation areas (Figure 4.2). We would logically expect higher NH_3 deposition in areas with higher human activity due to: 1) emissions from motor vehicle catalytic converters, which constitute a major NH_3 source in California (Committee on the Environment and Natural Resources Air Quality Research Subcommittee 2000); 2)

point source emissions from industry; 3) biomass burning (i.e. emissions from wood stoves, campfires, forest fires); and 4) the presence of farms and livestock.

The cumulative frequency of air scores shows that considerably more off-frame plots had poor (high) air scores than on-frame plots (Figure 4.5). The 25th, 50th, 75th, and 90th percentiles were based on scores for on-frame plots only (Figures 4.5 and 4.6) since the FIA program will not re-sample and track lichen communities at off-frame plots. The median air score for on-frame plots was -0.06, and 50% scored between -0.13 to 0.06 (Figure 4.5). The median for off-frame plots was much higher at 0.15, with 50% of plots scoring between -0.07 and 0.24.

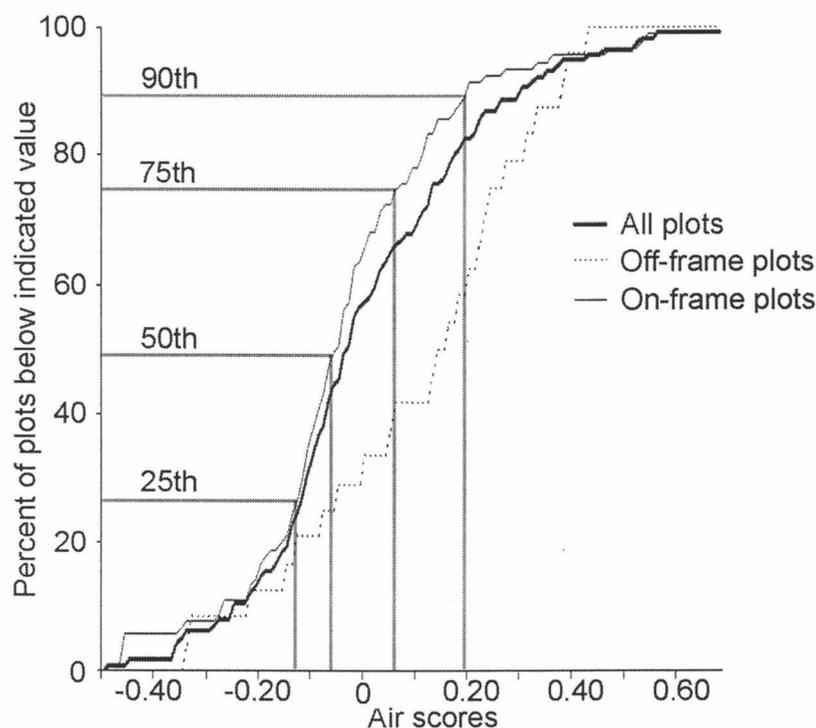


Figure 4.5. Cumulative frequency distribution of air scores. Data are divided into the 25th, 50th, 75th, and 90th percentiles for on-frame plots. Higher scores indicate worse air quality.

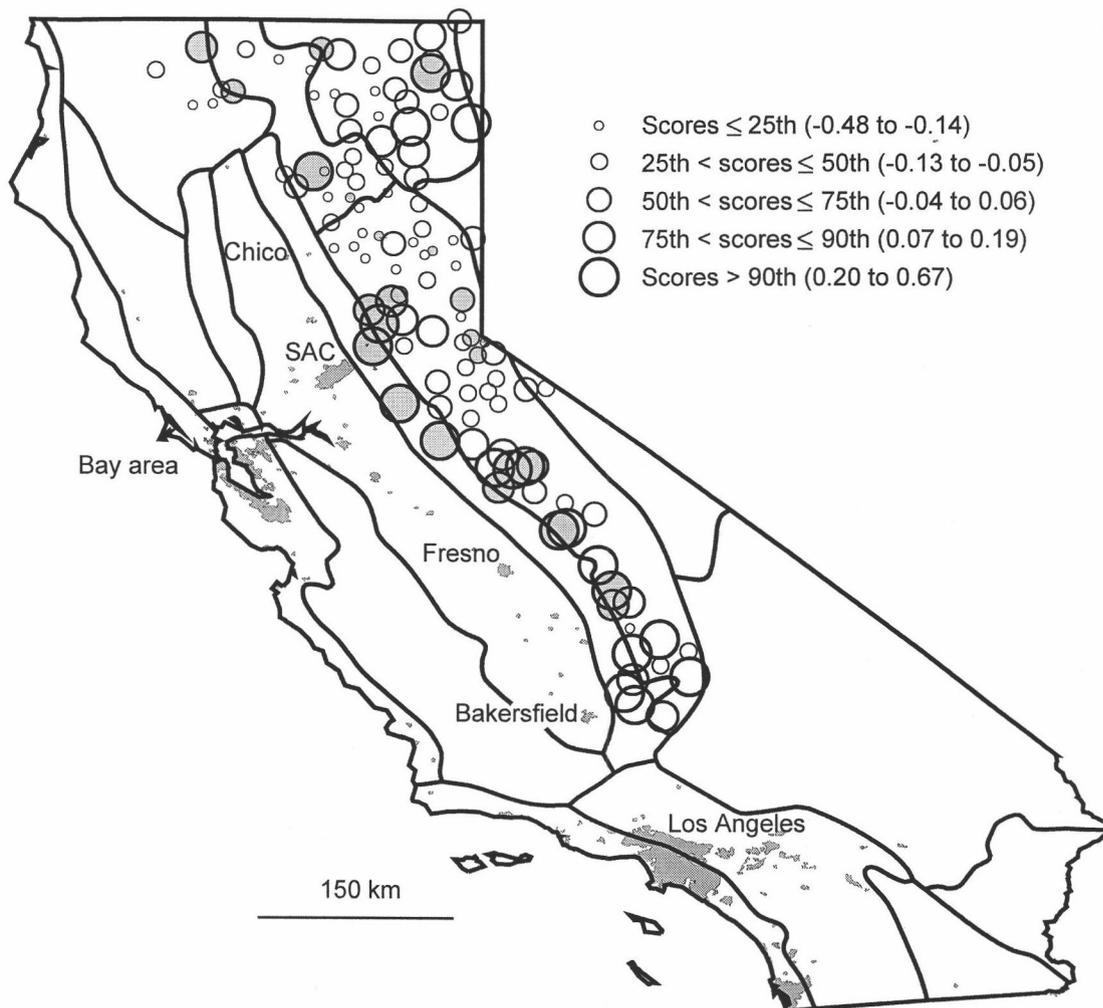


Figure 4.6. Map of air scores. Circles represent lichen community plots. Classes are based upon the 25th, 50th, 75th, and 90th percentiles of air scores at on-frame plots. Off-frame plots and urban areas are shaded gray. SAC = Sacramento.

Air scores may have a linear relationship to NH_3 deposition as the PNA had a linear relationship to estimated NH_3 in the adjacent greater Central Valley (Jovan and McCune 2005). The related NIW index was also linearly related to NH_3 deposition in the Netherlands (van Herk 1999, 2001). By controlling for confounding factors associated with elevation (Figure 4.3), we have indeed improved our chances of capturing this simple linear relationship. However, there remain two potentially

important sources of noise in our data, both relating closely to the alleged mechanism of the nitrophile-NH₃ association.

As the name “nitrophile” implies, lichenologists have long held the notion that these species require abundant N. Yet there is considerable evidence for an alternative mechanism: that nitrophiles are primarily promoted by substrates with high pH rather than high N content (van Dobben and de Bakker 1996; van Dobben and ter Braak 1998; van Herk 1999, 2001). Being the only alkaline gas in the atmosphere, nitrophile abundances are often easily tied to NH₃ concentrations (e.g. van Herk 1999, 2001; Jovan and McCune 2005) presumably via raising bark pH (Figure 4.3). This appears to be the favored mechanism, suggested by its prominence in the lichenological literature over the last decade. Yet there certainly is no consensus (van Haluwyn and van Herk 2002).

Effect of natural bark pH

“Natural” variability in bark pH (i.e. unaffected by pollutant deposition), thus, probably adds noise to the nitrophile-NH₃ relationship. This effect can be tempered by sampling lichen communities from a single tree species like van Herk (1999, 2001). Yet such restriction is often impossible, as in our case, when modeling a sizeable, topographically heterogeneous area. At such large spatial scales, the predominance of hardwoods at sampled plots is important to consider (Figure 4.3) as hardwood bark, in general, is naturally more alkaline than conifer bark (e.g. Barkman 1958). Conceivably, conifers must intercept more NH₃ deposition to achieve the same nitrophile loading, all else being equal. Natural pH effects on our air scores should have been considerably subdued by adjusting the model for elevation, since hardwood basal area decreases with elevation (Table 4.2 and Figure 4.3). Accordingly, a post hoc SLR of hardwood basal area on air scores showed only a weak correlation ($r^2 = 0.09$; $p < 0.01$). Regardless, natural variability in bark pH may be an important source of noise in large-scale models.

Acidic deposition effect?

Ammonia and acidic deposition may have antagonistic effects on nitrophile abundance (van Dobben 1983, van Dobben and ter Braak 1998; Figure 4.3). This hypothesis has not been rigorously tested although it seems worthy of consideration, given the evidence that substrate pH plays an intermediary role in the lichen-NH₃ association. Of particular import in the greater Sierra Nevada is nitric acid (HNO₃), a major component of acidic deposition in California (California Environmental Protection Agency 2000, Takemoto et al. 1995). As discussed by Jovan and McCune (2005), the relationship between lichens and HNO₃ is virtually unknown. The lack of comprehensive HNO₃ monitoring data for northern and central California has so far precluded any informative investigation.

We expect NH₃ is the primary factor controlling nitrophile abundance in our study area. Nitrogen-apportionment data for the southwestern Sierra Nevada show NH₃ makes a far greater contribution to total N deposition than HNO₃ (Bytnerowicz and Riechers 1995, Bytnerowicz et al. 2002). We also know that reduced N compounds (NH_x) dominate N deposition where measured in the western Sierra Nevada (Fenn et al. 2003a). Additionally, the geographic distribution of air scores coincides well with known NH₃ deposition and land use patterns as described below in the "Distribution of air scores" section. Even so, without additional pollutant data, we cannot conclude with certainty that HNO₃ has no effect.

Effects of other major pollutants

Other major anthropogenic pollutants probably have little, if any, influence on air scores. Jovan and McCune (2005) found that the PNA was independent of O₃ and NO₂ concentrations, which are both high in parts of the greater Sierra Nevada. Sulfur dioxide effects are also unlikely as ambient levels in California are beneath the threshold at which research suggests even the most sensitive lichen species respond (Peterson et al. 1992). Direct measurements from the California Air Resources Board monitoring network show annual means that are usually below 3 ppb in northern and

central California. Nitrophile sensitivities to various common air pollutants are reviewed more elaborately by Jovan and McCune (2005).

Distribution of air scores

More than half of the plots scoring above the 90th percentile were concentrated in the southern Sierra Nevada adjacent to the San Joaquin Valley (Figure 4.6). Accordingly, a high proportion of both on and off-frame plots in this region scored above the 75th percentile (Figure 4.6), which is consistent with preexisting data regarding NH₃ deposition and emission patterns. Over 50% of estimated NH₃ emissions from fertilizers and confined cattle operations in California originate in the San Joaquin Valley (California Air Resources Board 1999, Potter et al. 2001). Reduced N pollutant deposition along a north-south transect in the Sierra Nevada is highest in the southwestern part of the range (reviewed in Fenn et al. 2003a). Some low-elevation chaparral watersheds in the region are showing early signs of N saturation (Fenn et al. 2003a). These results complement Jovan and McCune (2005), who suggested that epiphytic lichen communities in the San Joaquin Valley were, overall, the most severely impacted by NH₃ in the greater Central Valley.

Other plots scoring above the 75th percentile include off-frame plots downwind of the Sacramento metropolitan area, Alturas in the Modoc Plateau, and Yreka near the Interstate-5 corridor (Figure 4.6). Several plots in the Modoc plateau also had PNA greater than 10% of the expected value. Even though this area is relatively remote and sparsely populated (approximately 43,300 in total), agriculture is a major land use. Modoc and Lassen host the highest acreage in farms relative to all other counties in the study area (Momsen 2001). Because this region is relatively arid, however, calcareous or alkaline dust may also promote nitrophiles (Figure 4.3), a phenomenon inferred by Gilbert (1976), Neitlich et al. (2003) and van Herk (1999).

Otherwise, lichen community data suggest that NH₃ deposition is comparatively low at most on-frame plots in the northern third of the study area (Figure 4.6). The same general pattern was found for total N deposition, which is low in northern forests (2-4 kg N/ha/year; Blanchard and Michaels 1994) relative to sites

in the southwestern Sierra Nevada (2-17 kg N/ha/year; reviewed in Fenn et al. 2003a). All but one plot scoring below -0.20 occur in this region. Lichen communities at many of these plots were diverse, resembling what we'd expect for mixed conifer stands with low NH₃ deposition. At plots scoring below the 25th percentile especially, communities were typified by high abundances and diversity of *Hypogymnia*, *Cetraria*, *Melanelia*, *Nodobryoria*, *Letharia* and common instances of *Bryoria fremontii*, *Evernia prunastri*, *Parmelia sulcata*, and *Usnea filipendula*. Most of these genera contain species van Herk identifies as sensitive to NH₃ deposition (1999, 2001).

Tahoe Basin

High elevation plots near the Tahoe Basin also had low air scores (-0.15 to -0.03; Figure 4.6) even though local N deposition is implicated, at least partly, in the decrease in lake clarity observed over the last five decades (Cahill et al. 1996, Jassby et al. 1994). Our inability to detect analogous evidence of eutrophication with nitrophiles is probably because high-elevation oligotrophic lakes like Lake Tahoe have extremely low N critical loads. Nitrogen deposition (4-5 kg N/ha/year; Fenn et al. 2003a) is actually low relative to the southwestern Sierras. Likewise, phosphorous is also believed to be an important fertilizing agent in the lake (reviewed in Fenn et al. 2003a) but would not be likely to affect nitrophile abundance. A third consideration is that NO_x compounds, also not believed to affect nitrophile abundance, make up a large proportion of total local N deposition (Fenn et al. 2003a).

Sequoia and Yosemite National Parks

The model indicated elevated NH₃ deposition in the southern National Parks, Sequoia and Yosemite, where plots received a mixture of high air scores. The plot along the Lower Kaweah river in Sequoia had the highest score (0.39) while the plot at Turtleback Dome in Yosemite, located above the parking lot of a popular viewpoint, also scored well above the 90th percentile (0.35). The plots at Yosemite Village (0.21), the hub of commerce and heavy traffic congestion in the park, and at Lookout Point in

Sequoia National Park (0.11) were somewhat lower (Figure 4.6). These results are congruent with previous air quality work conducted in Sequoia National Park. Bytnerowicz et al. (2002) found elevated NH_3 at the Lower Kaweah site (seasonal mean = $2.6 \mu\text{g}/\text{m}^3$) although deposition at a lower elevation site not sampled in our study, Ash Mountain, was even higher ($4.5 \mu\text{g}/\text{m}^3$). Other studies have documented relatively high N deposition in canopy throughfall in Sequoia National Park (6-15 kg N/ha/yr; reviewed in Fenn et al. 2003a). Nitrogen deposition patterns in Yosemite National Park are less well known.

Some air pollution in these forests probably originates from the San Joaquin Valley. However, tourism is likely an additional major source of NH_3 emissions and other air pollutants. According to the National Park Service (NPS), 1.4×10^6 people visited Sequoia and 3.3×10^6 people visited Yosemite in 2002 alone. In addition to area sources of pollution (e.g. hotels, campsites, housing developments, sewage treatment facilities), motor vehicle exhaust is recognized as a major ecological threat in both parks, but especially in the Yosemite Valley (National Park Service 2000). Plans to restrict use of private vehicles in Yosemite have been the recent focus of a heated debate among visitors, lawmakers, and NPS managers. Baum et al. (2000) suggested that scientists have underestimated the contribution of motor vehicle exhaust to NH_3 deposition. They found that, on average, a car emits 94 mg/km traveled. Emissions have dramatically increased since the widespread adoption of 3-way catalytic converters for NO_x control. Back in 1981, for instance, Pierson and Brachaczek (1983) calculated an NH_3 emission rate of $1.3 \pm 3.5 \text{ mg}/\text{km}^{-1}$.

CONCLUSIONS

Forest Inventory and Analysis plots adjacent to the San Joaquin Valley as well as plots near some urban areas indicate relatively high NH_3 deposition. Epiphytic lichen communities near Yosemite and Sequoia National Parks also show strong evidence of NH_3 enrichment. Overall, NH_3 deposition appears to be low in most rural plots in our study area, outside the southwestern Sierra Nevada. The severity of NH_3 impacts to lichen communities on the Modoc Plateau remains unclear until we better

understand the contributions of alkaline dust versus NH_3 to nitrophile abundance. We anticipate that air scores are affected minimally by HNO_3 deposition. Nevertheless, future biomonitoring work in the greater Sierra Nevada should include concurrent lichen community surveys and short-term passive monitoring of NH_3 and HNO_3 to clarify this assumption.

Ammonia bioindication is very important for the greater Sierra Nevada where nascent signs of N saturation have been detected in some southern chaparral communities (Fenn et al. 2003a). Comprehensive direct NH_3 monitoring is lacking even though much of the study area regularly intercepts polluted air masses from the highly agricultural and industrialized Central Valley (Cahill et al. 1996). Local emissions are expected to increase as the human population in the Sierra Nevada alone are forecasted to increase by 1.5 to 2.4 million people by 2040 (University of California SNEP Science Team and Special Consultants 1996).

Lichens provide an excellent, inexpensive alternative for estimating fine-scale distributions of NH_3 . Because of its high deposition velocity (Asman and van Jaarsveld 1992), NH_3 is difficult to accurately map without a high density of monitoring locations. Tracking epiphytic lichen communities with the presented FIA bioindication model is an important first step towards determining eutrophication risks to forest health in the region. Ultimately we envision this modeling approach as a stepping stone to more sophisticated bioindication, namely towards models that yield more quantitative NH_3 estimates. Such an accomplishment, however, greatly hinges upon our progress identifying and controlling for major sources of noise in the nitrophile- NH_3 relationship.

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ENDNOTES

1. This article is synonymous with Chapter 3.

Chapter 5. Conclusions

There are several approaches one can take to capitalize upon the sensitivities of epiphytic lichens to common air pollutants. With the community approach one can often relate lichen abundances to deposition gradients of specific pollutants, given a prerequisite understanding of relevant indicator species and their autecologies. Using indices of nitrophile abundance, a relatively well-studied group of indicator species, we were able to derive ammonia bioindication models for forests of the greater Central Valley and the greater Sierra Nevada. Ammonia is not regularly monitored in these regions where it is widely considered a major pollutant of concern.

Our attempt to relate lichen community gradients in the greater Central Valley to ozone and nitrogen dioxide deposition was less fruitful in large part because their impacts on lichens are understudied. We do not yet know whether indicator species exist for these pollutants. A second difficulty was the close correlation between these pollutants and a steep coast to inland moisture gradient. In short, the scarcity of information on indicator species precluded differentiation between pollutant and macroclimatic effects. Similarly, lichen community responses to nitric acid remain a mystery. For these reasons we did not embark on a similar pursuit to model photochemical gradients with the greater Sierra Nevada model. These datasets may be revisited in the future when photochemical pollution effects on lichens are better understood.

The ammonia bioindication models were used to estimate relative deposition at all forested plots. Under the FIA program, these lichen communities will be tracked over time to evaluate potential impacts to forest health. The greater Central Valley model suggested, in general, relatively high ammonia deposition to forests in large urban areas and agriculturally intensive regions. Lichen communities in the Sacramento and San Joaquin valleys appeared especially impacted, consisting almost exclusively of nitrophilous species. A typical lichen community, using the survey from Stockton as an example, had seven lichen species and a total lichen abundance of 20 that was 95% nitrophilous. A comparatively "clean" remote site, just west of Stockton

in the low elevation Sierra Nevada foothills, had 22 species and a total lichen abundance of 46 that was 19% nitrophilous.

Accordingly, the greater Sierra Nevada model suggested relatively high ammonia deposition to forests in the foothills bordering the Central Valley and particularly to the south along the San Joaquin valley. These geographic patterns are consistent with preexisting estimates and measurements of ammonia deposition. A high proportion of lichen communities sampled in the Modoc Plateau also appeared impacted although the relative importance of ammonia versus calcareous dust for enhancing nitrophile abundance is unclear.

Indeed, our current understanding of the nitrophile-ammonia relationship is less than perfect. Perhaps most importantly, there remains uncertainty regarding the exact underlying mechanism of the association: are nitrophiles positively associated with high substrate pH or actual ammonia deposition? If the former is true, then natural variability in bark pH, acidic deposition, and the presence of alkaline dust are probable sources of noise into the relationship. The more quantitative and accurate we intend to be with future models, the more imperative it is that we address these potentially confounding influences.

LITERATURE CITED

- Aber, J. D., K. J. Nadelhoffer, P. Steudler and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. *BioScience* 39:378-386.
- Antoine, M. E. 2001. Ecophysiology of the lichen *Lobaria oregana*. Masters Thesis. Oregon State University: Corvallis, OR, USA.
- Asman, W. A. H., and J. A. van Jaarsveld. 1992. A variable-resolution transport model applied for NH_x for Europe. *Atmospheric Environment* 26:445-464.
- Bailey, R. G. 1983. Delineation of ecosystem regions. *Environmental Management* 7:365-373.
- Baltzo, D. E. 1989. Lichens of Mount Diablo State Park, Contra Costa County, California. *Mycotaxon* 34:37-46.
- Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum: Assen, Germany.
- Baum, M. M., E. S. Kiyomiya, S. Kumar, A. Lappas, and H. Lord, III. 2000. Multicomponent remote sensing of vehicle exhaust by dispersive absorption spectroscopy. 1. Effect of fuel type and catalyst performance. *Environmental Science & Technology* 34:2851-2858.
- Benfield, B. 1994. Impact of agriculture on epiphytic lichens at Plymtree, east Devon. *Lichenologist* 26:91-94.
- Blanchard, C. L. and H. Michaels. 1994. Regional estimates of acid deposition fluxes in California. Final Report No. A132-149. Air Resources Board: Sacramento, CA, USA.
- Bloomfield, P. J., J. A. Royle, L. J. Steinber, and Q. Yang. 1996. Accounting for meteorological effects in measuring urban ozone levels and trends. *Atmospheric Environment* 30:3067-3077.
- Bowman, A. W., and A. Azzalini. 1997. Applied smoothing techniques for data analysis. Clarendon Press: Oxford, U.K.
- Bytnerowicz, A., and M. Fenn. 1996. Nitrogen deposition in California forests: a review. *Environmental Pollution* 92:127-146.
- Bytnerowicz, A. and G. Riechers. 1995. Nitrogenous air pollutants in a mixed conifer stand of the western Sierra Nevada, California. *Atmospheric Environment* 29:1369-1377.

- Bytnerowicz, A., T. Dueck, and S. Godzik. 1998. Nitric oxide, nitrogen dioxide, nitric acid vapor and ammonia. Sections 5-1 to 5-17 *in* R. Flagler, editor. Recognition of Air Pollution Injury to Vegetation: a Pictorial Atlas. Air and Waste Management Association: Pittsburg, PA, USA.
- Bytnerowicz, A., P. Padgett, K. Percy, M. Krywult, G. Riechers, and J. Horn. 1999. Direct Effects of Nitric Acid on Forest Trees. Pages 270-287 *in* P. R. Miller and J. R. McBride, editors. Oxidant Air Pollution Impacts in the Montane Forests of Southern California. Ecological Studies 134. Springer-Verlag: New York, NY, USA.
- Bytnerowicz, A., M. Tausz, R. Alonso, D. Jones, R. Johnson, and N. Grulke. 2002. Summer-time distribution of air pollutants in Sequoia National Park, California. Environmental Pollution 118:187-203.
- Cahill, T. A., J. J. Carroll, D. Campbell, and T. E. Gill. 1996. Chapter 48: Air Quality. Pages 1227-1261 *in* Status of the Sierra Nevada. U.S. Geological Survey Digital Data Series Publication DDS-043. Sierra Nevada Ecosystem Project. Final Report to Congress, vol. II. University of California Centers for Water and Wildland Resources: Davis, CA, USA.
http://ceres.ca.gov/snep/pubs/web/PDF/VII_C48.PDF
- California Air Resources Board. 1999. Estimates of ammonia emissions from beef and dairy cattle in California (review draft). Planning and Technical Support Division: Sacramento, CA, USA.
- California Air Resources Board. 2002. The 2002 California almanac of emissions and air quality. Planning and Technical Support Division, Sacramento, California, USA.
- California Environmental Protection Agency. 2000. Atmospheric Acidity Protection Program: Final assessment. California Air Resources Board: Sacramento, CA, USA. <http://www.arb.ca.gov/research/acid-dep/AAPrpt.pdf>
- Committee on the Environment and Natural Resources Air Quality Research Subcommittee. 2000. Atmospheric ammonia: sources and fate; a review of ongoing federal research and future needs. Air Quality Research Subcommittee Meeting Report. NOAA Aeronomy Laboratory: Boulder, CO, USA.
<http://www.al.noaa.gov/AQRS/reports/Ammonia.pdf>
- Cox, W., and S. Chu. 1996. Assessment of interannual ozone variation in urban areas from a climatological perspective. Atmospheric Environment 30:2615-2625.

- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33:140-158.
- Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. *Climate Research* 22:99-113.
- Daly, C., G.H. Taylor W. P. Gibson, T. W. Parzybok, G. L. Johnson, and P. Pasteris. 2001. High-quality spatial climate data sets for the United States and beyond. *Transactions of the American Society of Agricultural Engineers* 43:1957-1962.
- Davis, F. W., D. M. Stoms, A. D. Hollander, K. A. Thomas, P. A. Stine, D. Odion, M. I. Borchert, J. H. Thorne, M. V. Gray, R. E. Walker, K. Warner, and J. Graae. 1998. The California Gap Analysis Project (final report). University of California: Santa Barbara, CA, USA.
- De Bakker, A. J. 1989. Effects of ammonia emission on epiphytic lichen vegetation. *Acta Botanica Neerlandica* 38:337-342.
- Denison, R., B. Caldwell, B. Bormann, L. Eldred, C. Swanberg, and S. Anderson. 1977. The effects of acid rain on nitrogen fixation in western Washington coniferous forests. *Water, Air, and Soil Pollution* 8:21-34.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- ENVIRON International Corporation. 2002. Ammonia Emissions Improvement Projects in Support of CRPAQS Aerosol Modeling and Data Analyses: Draft Ammonia Inventory Development.
- Esslinger, T. L. 2000. A key for the lichen genus *Physconia* in California, with descriptions for three new species occurring within the state. *Bulletin of the California Lichen Society* 7:1-6.
- Esslinger, T. L., and C. Bratt. 1998. The *Heterodermia erinacea* group in North America and a remarkable new disjunct distribution. Pages 25-36 *In* M. G. Glenn, R. C. Harris, R. Dirig, and M. S. Cole, editors. *Lichenographia Thomsoniana: North American Lichenology in Honor of John W. Thomson*. Mycotaxon Ltd., Ithaca, New York, U.S.A.
- Fenn, M. E., M. A. Poth, A. Bytnerowicz, J. O. Sickman, and B. K. Takemoto. 2003a.

- Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. Pages 111-155 in A. Bytnerowicz, M. J. Arbaugh, and R. Alonso, editors. *Ozone Air Pollution in the Sierra Nevada--Distribution and Effects on Forests*. Elsevier Science Ltd.: Oxford UK.
- Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johnson, and P. Neitlich. 2003b. Ecological effects of nitrogen deposition in the western United States. *BioScience* 53:404-420.
- Fenn, M. E., R. Haeuber, G. S. Tonnesen, J. S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, H. M. Rueth, and J. O. Sickman. 2003c. Nitrogen emissions, deposition, and monitoring in the Western United States. *BioScience* 53:391-403.
- Flaum, J., S. T. Rao, and I. Zurbenko. 1996. Moderating the influence of meteorological conditions on ambient ozone concentrations. *Journal of Air and Waste Management Association* 46:35-46.
- Gauslaa, Y. 1995. Lobarion, an epiphytic community of ancient forests, threatened by acid rain. *Lichenologist* 27:59-76.
- Gilbert, O. L. 1970. A biological scale for the estimation of sulfur dioxide air pollution. *New Phytologist* 69:629-634.
- Gilbert, O. L. 1976. An alkaline dust effect on epiphytic lichens. *Lichenologist* 8:173-178.
- Gilbert, O. L. 1986. Field evidence for an acid rain effect on lichens. *Environmental Pollution* 40:227-231.
- Goward, T. 1994. Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada. *Acta Botanica Fennica* 150:31-38.
- Hale, M. E., and M. Cole. 1988. *Lichens of California*. University of California Press: Berkeley, CA, USA.
- Hanson, P., and S. E. Lindberg. 1991. Dry deposition of reactive nitrogen compounds: a review of leaf, canopy, and non-foliar measurements. *Atmospheric Environment* 25A:1615-1634.
- Hawksworth, D. L., and F. Rose. 1970. Qualitative scale for estimating sulfur dioxide air pollution in England and Wales using epiphytic lichens. *Nature (London)* 227:145-148.

- Herbert, J. R., and R. W. Meyer. 1984. Lichens of the San Joaquin Experimental Range, California. *The Bryologist* 87:251-254.
- Hutchinson, T. C., and K. Meema. 1987. The Effects of Acidic Deposition on Forests, Wetlands and Agricultural Ecosystems. Series G: Ecological Sciences, Vol. 16. Springer-Verlag: Heidelberg, Germany.
- James, P. W., D. L. Hawksworth, and F. Rose. 1977. Lichen communities in the British Isles: a preliminary conspectus. Pages 295-413 in M.R.D. Seaward, editor. *Lichen ecology*. Academic Press: London, UK.
- Jassby, A. D., J. E. Reuter, R. P. Axler, C. R. Goldman, and S. H. Hackley. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada). *Water Resources Research* 30:2207-2216.
- Jørgenson, P. M. 2000. Survey of the lichen family Pannariaceae on the American continent, north of Mexico. *The Bryologist* 103: 670-704.
- Jørgenson, P. M. 2002. *Pannaria*. Pages 304-307 in T. H. Nash III, B. D. Ryan, C. Gries, and F. Bungartz, editors. *Lichen Flora of the Greater Sonoran Desert Region I*. Lichens Unlimited, Arizona State University: Tempe, AZ, USA.
- Jovan, S. 2002. A landscape-level analysis of epiphytic lichen diversity in northern and central California: environmental predictors of species richness and potential observer effects. *Bulletin of the California Lichen Society* 9:1-7.
- Jovan, S., and B. McCune. 2004. Regional variation in epiphytic macrolichen communities in northern and central California forests. *The Bryologist* 107: 328-339.
- Jovan, S. and B. McCune. 2005. Bioindication of Air Pollution in the Greater Central Valley of California, U.S.A. with Epiphytic Macrolichen Communities. *Ecological Applications*: in press.
- Krupa, S.V. 2003. Effects of atmospheric ammonia (NH₃) on terrestrial vegetation: a review. *Environmental Pollution* 124:179-221.
- Kruskal, J. B. 1964. Non-metric multidimensional scaling: a numerical method. *Psychometrika* 29:115-129.
- Kubin, E. 1990. A survey of element concentrations in the epiphytic lichen *Hypogymnia physodes* in Finland in 1985-86. Pages 421-446 in P. Kauppi, P. Anttila, and K. Kenttämies, editors. *Acidification in Finland*. Springer-Verlag: Berlin, Germany.

- Lilleskov, E. A., T. J. Fahey, and G. M. Lovett. 2001. Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient. *Ecological Applications* 11:397-410.
- Lilleskov, E. A., T. J. Fahey, T. R. Horton, and G. M. Lovett. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology* 83:104-115.
- Lindblom, L. 1997. The genus *Xanthoria* (Fr.) Th.Fr. in North America. *Journal of the Hattori Botanical Laboratory*. 83:75-172.
- Mather, P. M. 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. J. Wiley & Sons: London, UK.
- Matthes-Sears, U., T. H. Nash, III, and D. W. Larson. 1986. The ecology of *Ramalina menziesii*. IV. Estimation of gross carbon gain and thallus hydration source from diurnal measurements and climatic data. *Canadian Journal of Botany* 64:1698-1702.
- McCune, B. 1988. Lichen communities along O₃ and SO₂ gradients in Indianapolis. *The Bryologist* 9:223-228.
- McCune, B. and L. Geiser. 1997. *Macrolichens of the Pacific Northwest*. Oregon State University Press and U.S.D.A. Forest Service: Corvallis, OR, USA.
- McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software: Gleneden Beach, OR, USA.
- McCune, B. and M. J. Mefford. 1999. *Multivariate analysis on the PC-ORD system. Version 4*. MjM Software: Gleneden Beach, OR, USA.
- McCune, B. and M. J. Mefford. 2004. *Nonparametric Multiplicative Habitat Modeling. Version 1.00.60 beta*. MjM Software: Gleneden Beach, OR, USA.
- McCune, B., Rogers, P., Ruchty, A., and B. Ryan. 1998. *Lichen communities for Forest Health Monitoring in Colorado, USA. A report to the USDA/Forest Service*. Oregon State University, Department of Botany and Plant Pathology: Corvallis, OR, USA.
- McCune, B., S. D. Berryman, J. H. Cissel, and A. I. Gitelman. 2003. Use of a smoother to forecast occurrence of epiphytic lichens under alternative forest management plans. *Ecological Applications* 13:1110-1123.

- McCune, B., J. Dey, J. Peck, K. Heiman, and S. Will-Wolf. 1997a. Regional gradients in lichen communities of the Southeast United States. *The Bryologist* 100:145-158.
- McCune, B., J. P. Dey, J. E. Peck, D. Cassell, K. Heiman, S. Will-Wolf, and P. N. Neitlich. 1997b. Repeatability of community data: species richness versus gradient scores in large-scale lichen studies. *The Bryologist* 100:40-46.
- Menge, J. A., and L. F. Grand. 1978. Effect of fertilization on production of epigeous basidiocarps by mycorrhizal fungi in loblolly pine plantations. *Canadian Journal of Botany* 56:2357-2362.
- Messer, J. J., R. A. Linthurst, and W. S. Overton. 1991. An EPA program for monitoring ecological status and trends. *Environmental Monitoring and Assessment* 17:67-78.
- Moberg, R. 2002. *Physcia*. Pages 358-373 in T. H. Nash III, B. D. Ryan, C. Gries, and F. Bungartz, editors. *Lichen Flora of the Greater Sonoran Desert Region I*. Lichens Unlimited. Arizona State University: Tempe, AZ, USA.
- Momsen, J. H. 2001. Agriculture in the Sierra. Pages 497-528 in *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol II, Assessments and scientific basis for management options*. University of California: Davis, CA, USA. http://ceres.ca.gov/snep/pubs/web/PDF/VII_C17.PDF
- Muir, P. S. and B. McCune. 1988. Lichens, tree growth, and foliar symptoms of air pollution: are the stories consistent? *Journal of Environmental Quality* 17:361-370.
- Munger, J. W., S. C. Wofsy, P. S. Bakwin, S. M. Fan, M. L. Goulden, B. C. Daube, A. H. Goldstein, K. E. Moore, and D. R. Fitzjarrald. 1996. Atmospheric deposition of reactive nitrogen oxides and ozone in a temperate deciduous forest and a sub-arctic taiga woodland. I. Measurements and mechanisms. *Journal of Geophysical Research* 101:12.639-12.657.
- Nash, T. H., III. 1976. Sensitivity of lichens to nitrogen dioxide fumigations. *The Bryologist* 79:103-106.
- Nash, T. H., III. and L. L. Sigal. 1979. Gross photosynthetic response of lichens to short-term ozone fumigations. *The Bryologist* 82:280-285.
- Nash, T. H., III. and L. L. Sigal. 1999. Epiphytic lichens in the San Bernardino mountains in relation to oxidant gradients. Pages 223-234 in P. R. Miller, J. R. McBride, editors. *Oxidant Air Pollutant Impacts on the Montane Forests of*

Southern California: A Case Study of the San Bernardino Mountains.
Ecological Studies 134. Springer-Verlag: New York, NY, USA.

- National Park Service. 2000. Final Yosemite Valley Plan/Supplemental Environmental Impact Statement, Vol. 1a. National Park Service: Yosemite National Park, CA, USA.
http://www.nps.gov/yose/planning/yvp/seis/pdf/Volume_1A.pdf
- Neitlich, P., P. Rogers, and R. Rosentreter. 2003. Lichen communities indicator results from Idaho: baseline sampling. USDA Forest Service General Technical Report RMRS-GTR-103. Rocky Mountain Research Station: Fort Collins, CO, USA
- Nimis, P. L., and O. W. Purvis. 2002. Monitoring lichens as indicators of pollution. Pages 7-10 in P. L. Nimis, C. Scheidegger, and P. A. Wolseley, editors. Monitoring with Lichens-monitoring lichens. IV. Earth and Environmental Sciences vol. 7. Kluwer Academic Publishers: Dordrecht, the Netherlands.
- O'Hare, G. P. 1974. Lichens and bark acidification as indicators of air pollution in west central Scotland. *Journal of Biogeography* 1:135-146.
- Olson, R. K., D. Binkley, and M. Böhm. 1992. Response of Western Forests to Air Pollution. Ecological Studies vol. 97. Springer-Verlag: New York, NY, USA.
- Peterson, J., D. Schmoltdt, D. Peterson, J. Eilers, R. Fisher, and R. Bachman. 1992. Guidelines for evaluating air pollution impacts on Class I Wilderness Areas in the Pacific Northwest. USDA Forest Service General Technical Report PNW-299. Pacific Northwest Research Station: Portland, OR, USA.
- Pierson, W. R. and W. W. Brachaczek. 1983. Particulate Matter Associated with Vehicles on the Road. II. *Aerosol Science and Technology* 2:1-40.
- Pietilä, M., P. Lahdesmaki, P. Pietilainen, A. Ferm, J. Hytonen, and A. Patila. 1991. High nitrogen deposition causes changes in amino acid concentrations and protein spectra in needles of the Scots pine (*Pinus sylvestris*). *Environmental pollution* 72:103-115.
- Pilegaard, K. 1978. Airborn metals and SO₂ monitored by epiphytic lichens in an industrial area. *Environmental Pollution* 17:81-92.
- Potter, C., C., Krauter, and S. Klooster. 2001. Statewide Inventory Estimates of Ammonia Emissions from Native Soils and Chemical Fertilizers in California. Final report. Contract # ID: 98-716. California Air Resources Board Emissions

Inventory Branch: Sacramento, CA, USA. <ftp://ftp.arb.ca.gov/carbis/reports/1522.pdf>

- Robitaille, G., F. LeBlanc, and D. N. Rao. 1977. Acid rain: a factor contributing to the paucity of epiphytic cryptogams in the vicinity of a copper smelter. *Revue Bryologique et Lichénologique* 43:53-66.
- Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. Pages 279-307 in D. H. Brown, D. L. Hawksworth, and R. H. Bailey, editors. *Lichenology: Progress and Problems*. Academic Press: London, UK.
- Rose, F. 1988. Phytogeographical and ecological aspects of *Lobarion* communities in Europe. *Botanical Journal of the Linnean Society* 96:69-79.
- Ross, L. J., and T. H. Nash, III. 1983. Effect of ozone on gross photosynthesis of lichens. *Environmental and Experimental Botany* 23:71-77.
- Ruoss, E., and C. Vonarburg. 1995. Lichen diversity and ozone impact in rural areas of Central Switzerland. *Cryptogamic Botany* 5:252-263.
- Ryan, B. 1990*a*. *Lichens and Air Quality in the Emigrant Wilderness, California: a Baseline Study*. Arizona State University: Tempe, AZ, USA.
- Ryan, B. 1990*b*. *Lichens and Air Quality in Wilderness Areas of California: a Series of Baseline Studies*. Arizona State University: Tempe, AZ, USA.
- Ryan, B., and T. H. Nash, III. 1991. Lichen Flora of the eastern Brook Lakes Watershed, Sierra Nevada Mountains, California. *The Bryologist* 94:181-195.
- Scheidegger, C., and B. Schroeter. 1995. Effects of ozone fumigation on epiphytic macrolichens: ultrastructure, CO₂ gas exchange and chlorophyll fluorescence. *Environmental Pollution* 88:345-354.
- Scott, M. G., T. C. Hutchinson, and M. J. Feth. 1989. A comparison of the effects on Canadian boreal forest lichens of nitric and sulphuric acids as sources of rain acidity. *New Phytologist* 111:663-671.
- Sigal, L. L., and T. H. Nash, III. 1983. Lichen communities on conifers in southern California: an ecological survey relative to oxidant air pollution. *Ecology* 64:1343-1354.
- Skye, E., and I. Hallberg. 1969. Changes in the lichen flora following air pollution. *Oikos* 20:547-552.

- Smith, C. W. 1990. Toward an inventory of lichens of Pinnacles National Monument. Pages 159-168 in C. Van Riper III, T. J. Stohlgren, S. D. Veirs Jr., and S. C. Hillyer, editors. Examples of Resource Inventory and Monitoring in National Parks of California. Proceedings of 3rd Biennial Conference on Research in California's National Parks, September 13-15 1998 at University of California, Davis. Trans. and Proceedings Series No.8. U.S. Department of the Interior: Washington DC, USA.
- Smith, D. W. 1980. A taxonomic survey of the macrolichens of Sequoia and Kings Canyon National Parks. Masters thesis. San Francisco State University: San Francisco, CA, USA
- SPSS for Windows. 2001. Rel. 11.0.1. SPSS Inc.: Chicago, IL, USA.
- Takemoto, B. K., A. Bytnerowicz, and M. E. Fenn. 2001. Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests. *Forest Ecology and Management* 144:159-173.
- Takemoto, B. K., B. E. Croes, S. M. Brown, N. Motallebi, F. D. Westerdahl, H. G. Margolis, B. T. Cahill, M. D. Mueller, and J. R. Holmes. 1995. Acidic deposition in California: findings from a program of monitoring and effects research. *Water, Air, and Soil Pollution* 85:261-272.
- Tavares, I. I. 1997. A preliminary key to *Usnea* in California. *Bulletin of the California Lichen Society* 4:19-23.
- Termorshuizen, A. J., and A. Schaffers. 1991. The decline of carpophores of ectomycorrhizal fungi in stands of *Pinus sylvestris* L. in the Netherlands: possible causes. *Nova Hedwigia* 53:267-289.
- University of California SNEP Science Team and Special Consultants. 1996. Chapter 2: People and Resource Use. Pages 17-45 in Status of the Sierra Nevada. U.S. Geological Survey Digital Data Series Publication DDS-043. Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II. University of California Centers for Water and Wildland Resources: Davis, CA, USA.
http://ceres.ca.gov/snep/pubs/web/PDF/v1_ch02.pdf
- Van der Eerden, L. J. M., L. J. A. Lekkerkerk, S. M. Smeulders, and A. E. Jansen. 1992. Effects of atmospheric ammonia and ammonium sulfate on Douglas fir (*Pseudotsuga menziesii*). *Environmental Pollution* 76:1-9.
- Van Dobben, H.F. 1983. Changes in the epiphytic lichen flora and vegetation in the surroundings of 's-Hertogenbosch (The Netherlands) since 1900. *Nova Hedwigia* 37:691-719.

- Van Dobben, H. F. and A. J. de Bakker. 1996. Re-mapping epiphytic lichen biodiversity in The Netherlands: effects of decreasing SO₂ and increasing NH₃. *Acta Botanica Neerlandica* 45:55-71.
- Van Dobben, H. F., and C. J. F. ter Braak. 1998. Effects of atmospheric NH₃ on epiphytic lichens in the Netherlands: The pitfalls of biological monitoring. *Atmospheric Environment* 32:551-557.
- Van Haluwyn, C. and C. M. van Herk. 2002. Bioindication: the community approach. Pages 39-64 in P. L. Nimis, C. Scheidegger, and P. A. Wolseley, editors. *Monitoring with Lichens-monitoring lichens. IV. Earth and Environmental Sciences vol. 7.* Kluwer Academic Publishers: Dordrecht, the Netherlands.
- Van Herk, C. M. 1999. Mapping of ammonia pollution with epiphytic lichens in the Netherlands. *Lichenologist* 31:9-20.
- Van Herk, C. M. 2001. Bark pH and susceptibility to toxic air pollutants as independent causes of changes in epiphytic lichen composition in space and time. *Lichenologist* 33:419-441.
- Von Arb, C., C. Mueller, K. Ammann, and C. Brunold. 1990. Lichen physiology and air pollution II: statistical analysis of the correlation between SO₂, NO₂, NO, and O₃, and chlorophyll content, net photosynthesis, sulphate uptake and protein synthesis of *Parmelia sulcata* Taylor. *New Phytologist* 115:431-437.
- Wetmore, C. M. 1985. Lichens and Air Quality in Sequoia National Park. Final Report. National Park Service Contract CX 0001-2-0034.