

## AIR-QUALITY BIOINDICATION IN THE GREATER CENTRAL VALLEY OF CALIFORNIA, 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 (USA). 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 nonmetric 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  $-0.51$ ), percentage nitrophilous lichen richness ( $r = -0.76$ ), and percentage 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.

**Key words:** air pollution; ammonia; California; community analysis; epiphytic macrolichens; gradients; land use; multidimensional-scaling ordination; nitrogen dioxide; nitrophiles; ozone; sulfur dioxide.

### 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<sub>3</sub>) 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 research program to describe both spatial and temporal trends in air-quality and assess potential impacts to forest health (see Plate 1). 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., Pilegaard 1978, McCune 1988, Muir and McCune 1988, de Bakker 1989, Kubin 1990, McCune et al. 1997b, 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. Be-

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PLATE 1. Habit of four common epiphytic macrolichens in the study area. Beginning in upper left and proceeding clockwise: *Evernia prunastri*, *Phaeophyscia orbicularis*, *Physcia tenella*, and *Xanthoria polycarpa*. Photo credits: B. McCune and S. Jovan.

cause 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 ( $\text{SO}_2$ ) and the acidic deposition resulting from common anthropogenic effluents such as  $\text{SO}_2$  and nitrogen oxides ( $\text{NO}_x$ ; Gilbert 1970, 1986, Hawksworth and Rose 1970, McCune 1988, Gauslaa 1995, 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  $\text{NH}_3$  (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 ( $\text{NO}_2$ ) and ozone ( $\text{O}_3$ ) is sparse. Two studies in The Netherlands suggested that  $\text{NO}_2$  affects community composition although the data were confounded by  $\text{SO}_2$  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  $\text{O}_3$ , as field studies have

yielded conflicting results (Sigal and Nash 1983, McCune 1988, Ruoss and Vonarburg 1995).

Our primary objective was to develop a gradient model that relates epiphytic lichen community composition to air quality and climate patterns throughout the greater Central Valley region in California, USA. We explore the contribution of some of the most common pollutants in the study area,  $\text{SO}_2$ ,  $\text{NO}_2$ ,  $\text{NH}_3$ , and  $\text{O}_3$ , 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 (Fig. 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 (Fig. 1) was based upon a gradient analysis of epiphytic-lichen community data from FIA (USDA Forest Inventory and Analysis) plots spanning northern and

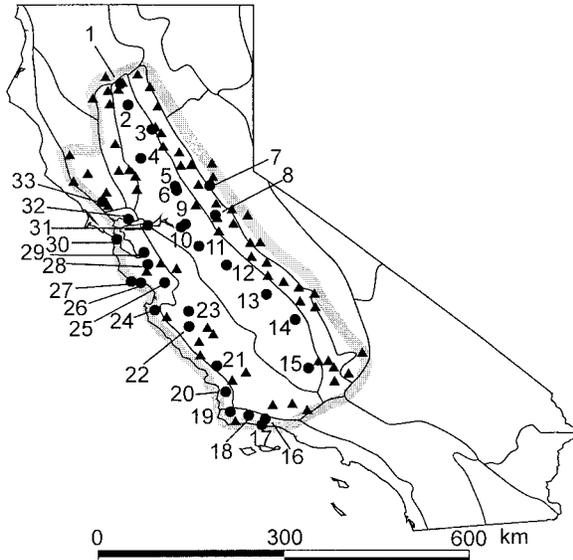


FIG. 1. Map of greater Central Valley, California, USA, model area; the model boundary is delineated by the thick gray line; the boundaries of Bailey's ecoregions are indicated by thinner black lines; solid triangles indicate on-frame plots while solid circles indicate off-frame plots. Off-frame plots are 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.

central California (Jovan and McCune 2004). Our analysis identified regions with lichen communities and climate that were relatively homogeneous, at least in comparison to variability present in the entire FIA data set. 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, thereby enhancing our ability to detect and isolate the effects of air quality. Remaining climate variability in the greater Central Valley model area primarily relates to 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: ~150–850 mm/yr) and high mean annual temperatures (16–19°C). Precipitation is higher in the Sierra Nevada foothills (450–1100 mm/yr), and 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. chry-*

*solepis*, *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*, and *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; Fig. 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  $\text{NH}_3$  in rural areas while automobile exhaust is an important  $\text{NH}_3$  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  $\text{SO}_2$  and  $\text{NO}_x$ , which contribute to acidic deposition. Acidic deposition and  $\text{SO}_2$  levels have remained relatively low throughout most of northern and central California for over two decades while  $\text{NO}_x$  emissions have declined by almost 30% since 1990 (Takemoto et al. 1995, California Air Resources Board [CARB] 2002). Ambient concentrations of  $\text{NO}_x$  compounds remain problematic, however, as evidenced by the infamous smog problems in central and southern California. Ozone ( $\text{O}_3$ ), which results from the photochemical transformation of  $\text{NO}_x$  and volatile organic hydrocar-

bons 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<sub>3</sub> non-attainment areas because hourly measurements of O<sub>3</sub> levels consistently exceeded the state standard of 0.09 ppm.

## METHODS

### *Field data*

*Sampling on-frame plots.*—USDA Forest Inventory and Analysis (FIA) field crews collected lichen community data from 66 permanent 0.38-ha circular plots on FIA's hexagonal sampling grid (Messer et al. 1991: Fig. 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 ~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. 1997a). 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 <50% of all boles and branches), and 4 = abundant (>10 thalli present and species occurs on >50% of all boles and branches). Surveys lasted a minimum of 30 min and a maximum of two h or until 10 min passed before encountering a different species. Field workers were typically nonspecialists but were trained to differentiate among species in the field. Professional lichenologists identified all specimens and conducted periodic audits of field-crew performance (Jovan and McCune 2004).

*Urban off-frame plots.*—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 (Fig. 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 (SO<sub>2</sub>) and none regularly measuring ammonia (NH<sub>3</sub>). Monitors measuring SO<sub>2</sub> 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.

*Specimen identification and location.*—Voucher specimens reside at the Oregon State University herbarium (Corvallis, Oregon, USA). 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 <4% of the plots were excluded from the analysis to reduce noise in the data. The inconspicuous species *Hyperphyscia adglutinata* and *Leprogium 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 1).

*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 wet days, and relative humidity. Climate estimates were averaged over 1961 to 1990. As lichens are poikilohydric, fog and even moisture from nonsaturated air (Matthes-Sears et al. 1986) 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 percentage basal area in live hardwoods, and species richness and percentage 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 percentage 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, James et al. 1977, Gauslaa 1995). The other indices were omitted for cyanolichens, however, because they were very infrequent throughout the study area. Nitrophilous species are indicated in Table 1. Designations of nitrophily were guided by the observations

TABLE 1. Summary of species found in USDA Forest Inventory and Analysis plots ( $n = 65$  on-frame plots) and urban plots ( $n = 33$  off-frame plots), in northern and central California, USA (see Fig. 1).

Species†	Off-frame plots		On-frame plots	
	Freq. (%)	Abund.	Freq. (%)	Abund.
<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
<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 soredica</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
<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

TABLE 1. Continued.

Species†	Off-frame plots		On-frame plots	
	Freq. (%)	Abund.	Freq. (%)	Abund.
<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
<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

Notes: Frequency (Freq.) of lichen occurrence is reported as the percentage of plots where the species occurred. Abundance (Abund.) of lichen species is reported as the average of four abundance classes (1 = rare, <3 thalli; . . . 4 = abundant, >10 thalli and occurs on >50% of all boles and branches) per plot. See *Methods: Field data: Sampling . . .* for details.

†“(N)” means that the species is considered nitrophilous.

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 California Air Resources Board (CARB) monitors were available for the 33 urban plots. Most monitors measured ambient levels of O<sub>3</sub> ( $n = 30$  monitors, maximum 1-h value; range: 68–139 ppb), and NO<sub>2</sub> ( $n = 22$  monitors, annual arithmetic mean; range: 3–25 ppb), while few measured SO<sub>2</sub> ( $n = 14$  monitors,

annual arithmetic mean; range: 1–5 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 O<sub>3</sub> levels at all FIA plots (T. Pritchard, *unpublished data*). Kriged data were “SUM60” values, which are sums of all hourly O<sub>3</sub> concentrations at or above 60 ppb from 1 June to 31 August 2002 (range: 21–7.81 × 10<sup>4</sup> ppb-hours).

It is important to note that kriged data are interpolations, and thus may deviate somewhat from actual deposition. The ambient-O<sub>3</sub> measurements are certainly more accurate although 139 ppb, the highest maximum 1-h value recorded from within the model boundaries, is probably considerably lower than concentrations experienced at eastern FIA plots in the Sierra foothills. CARB monitors were mostly located in large urban areas yet O<sub>3</sub> concentrations are expected to peak downwind to the east, where the prevailing winds transport its photochemical precursors. We know ambient O<sub>3</sub> 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 O<sub>3</sub> concentration, however, since CARB monitors were sparse in the Sierra Nevada foothills.

As no direct NH<sub>3</sub> measurements were available, we approximated deposition for all lichen community plots in two ways, using (1) high-resolution land-use maps and (2) modeled NH<sub>3</sub>-emissions estimates. Emissions should be a reasonable approximation of deposition since NH<sub>3</sub> 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 (GAP; 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 NH<sub>3</sub>-emissions data consisted of 1 × 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 NH<sub>3</sub> 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 data set 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. Nonmetric 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 data sets of NO<sub>2</sub>, O<sub>3</sub>, and SO<sub>2</sub> 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 three (the number of data points bearing on the weighted estimate; the Gaussian kernel function weights data points nearer the target point in the predictor space more heavily). The standard deviation (tolerance) of the kernel function was optimized by maximizing cross-validated coefficients of determination *R*<sup>2</sup>.

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 three-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

TABLE 2. Summary of NPMR (nonparametric multiplicative regression) models for each lichen species in the analytical data set.

Species	R <sup>2</sup> †	Neighb.‡	Var	Tolerance	Var	Tolerance
<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
<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

Notes: Possible predictor variables (Var) are designated by either 1 (axis 1 scores) or 2 (axis 2 scores). Tolerance is the standard deviation of the preceding variable. The “—” column entries indicate that the corresponding variable was not a good predictor for that particular species.

† Cross-validated coefficient of determination.

‡ Average neighborhood size.

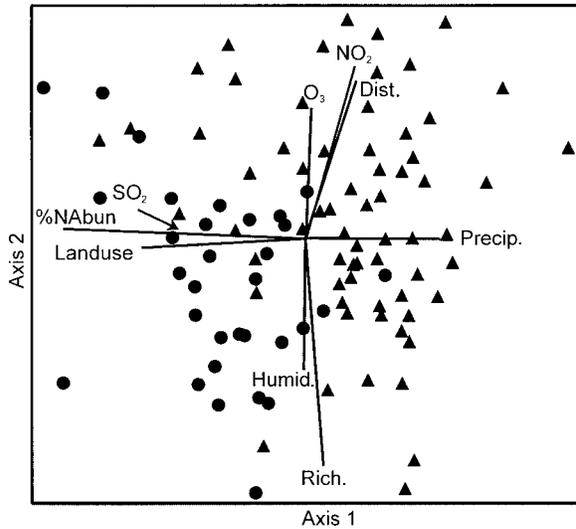


FIG. 2. Ordination joint plot with environmental variables overlaid. Solid triangles indicate on-frame plots; solid circles indicate off-frame plots. Vector lengths and directions indicate correlations with the ordination. Most vectors with  $r > 0.55$  are shown. Abbreviations for environmental vectors are: Dist., distance from the coast; Precip., mean annual precipitation; Rich., total lichen species richness; Humid., relative humidity; Landuse, percentage urban and agricultural land; %Nabun, percentage nitrophile abundance; SO<sub>2</sub>, sulfur dioxide; O<sub>3</sub>, ozone; and NO<sub>2</sub>, nitrogen dioxide. The end of the SO<sub>2</sub> vector is indicated by an arrow. Percentage nitrophile richness and sum of agricultural land are not pictured due to crowding. Both vectors align closely with axis 1. The O<sub>3</sub> vector represents the correlation of both SUM60 kriged estimates (sums of all hourly O<sub>3</sub> concentration  $\geq 60$  ppb, 1 June–31 August 2002) and CARB (California Air Resources Board) measurements with axis 2.

analyses were conducted with HyperNiche (Version 1.00.60 beta, McCune and Mefford 2004).

RESULTS

The NMS (nonmetric multidimensional scaling) 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 three-dimensional solution with real data was lower than would be expected by chance ( $P < 0.01$ ). The final stress and instability of the three-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 nonparametric multiplicative regression (NPMR) models, most species distributions were only weakly to moderately related to the two ordination axes (Table 2 and Fig. 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 (Figs. 3 and 4).

Relationship of axis 1 to NH<sub>3</sub> and nitrophile indices

The first axis in community composition was negatively correlated with all variables indicating NH<sub>3</sub> deposition (Fig. 2 and Table 3). Percentage agricultural and urban land ( $r = -0.63$ ) and total NH<sub>3</sub> emissions from the CalGAIMS (California gridded ammonia inventory modeling system) data ( $r = -0.51$ ) were both negatively correlated with axis 1. Several subcategories from the GAP (California gap-analysis project) land-use and CalGAIMS data sets 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<sub>3</sub> emissions from mobile ( $r = -0.51$ ) and domestic ( $r = -0.43$ ) sources.

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 (Figs. 2 and 5). Off-frame plots located in small urban areas with

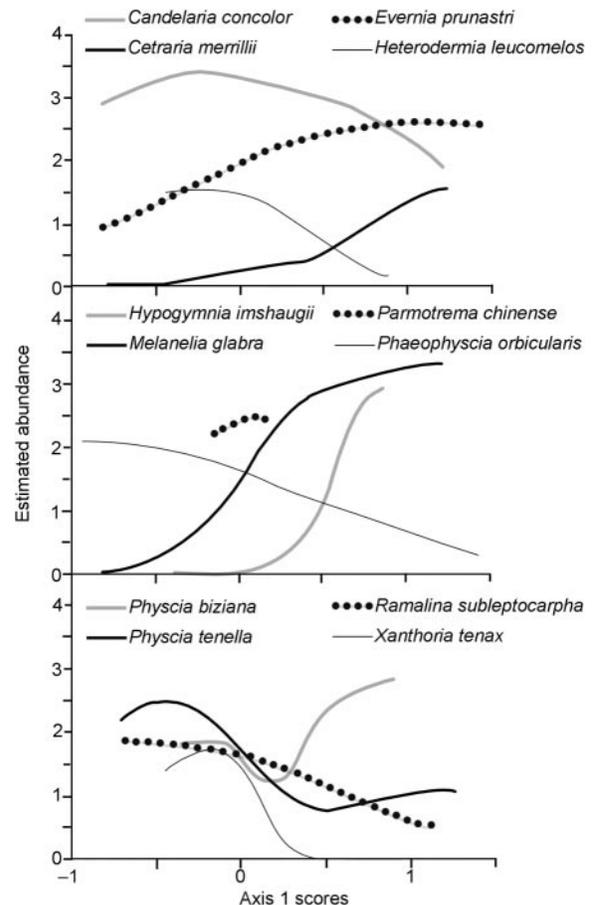


FIG. 3. Nonparametric multiplicative regression response curves for selected species along axis 1.

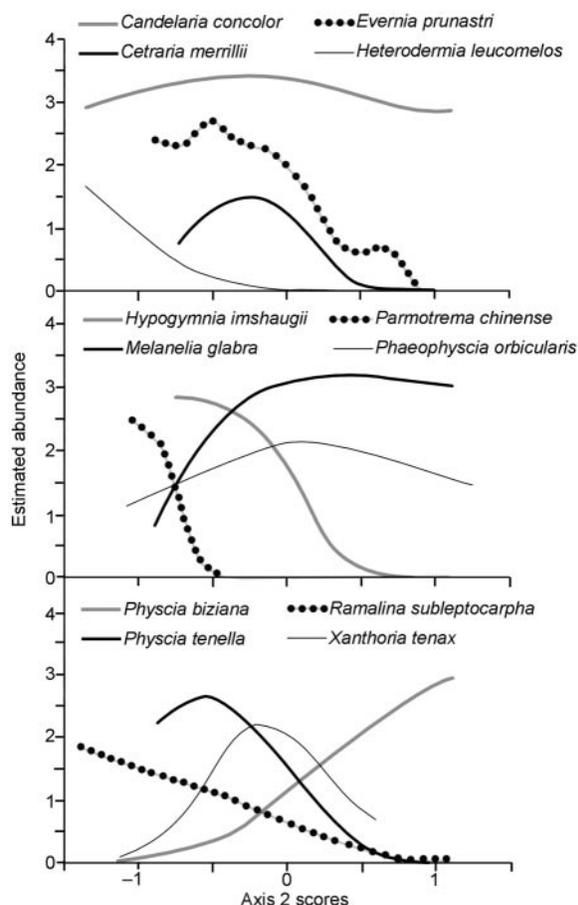


FIG. 4. Nonparametric multiplicative regression response curves for selected species along axis 2.

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, percentage nitrophile abundance and percentage nitrophile richness, were also negatively linearly correlated with axis 1 ( $r = -0.78$  and  $-0.76$ , respectively). Their corresponding vectors aligned closely with the  $\text{NH}_3$  deposition variables in the nonmetric multidimensional scaling (NMS) solution (Fig. 2). The unrelativized indices, nitrophile diversity and abundance, were more strongly correlated with axis 2 (Table 3). Species distributions had a wide variety of relationships to axis 1 (Fig. 3). Nearly all nitrophile distributions had maxima at low axis scores (Fig. 3; e.g., *Candelaria concolor*, *Phaeophyscia orbicularis*, *Physcia tenella*, *Ramalina subleptocarpha*, and *Xanthoria tenax*), including species with relatively weak models (Table 2). Contrastingly, the abundances of species in genera considered  $\text{NH}_3$  sensitive by van Herk (1999, 2001; "acidophytes"), such as *Cetraria*, *Evernia*, and *Hypogymnia*, tended to increase at higher axis scores (Fig. 3).

#### Relationship of axis 1 to other variables

Two moisture variables, mean annual precipitation ( $r = 0.58$ ) and number of wet days ( $r = 0.51$ ), were also correlated with axis 1, roughly opposite of  $\text{NH}_3$  deposition variables and the relativized nitrophile indices (Fig. 2 and Table 3). Pollutant data for  $\text{NO}_2$  and  $\text{O}_3$  show a lack of alignment although the partial  $\text{SO}_2$  data were negatively correlated with axis 1 ( $r = 0.59$ ; Fig. 2 and Table 3).

#### Relationship of axis 2 to humidity, $\text{O}_3$ , and $\text{NO}_2$

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 (Fig. 6), and is consistent with the PRISM data (Daly et al. 1994, 2001, 2002). The NMS solution also suggested a possible correlation be-

TABLE 3. Coefficients of determination for correlations between environmental variables and ordination axes.

Variable†	<i>r</i>	
	Axis 1	Axis 2
Longitude	-0.19	0.43
Latitude	0.46	0.05
Elevation	0.30	0.35
<b>Distance from the coast</b>	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
<b>Precipitation</b>	0.58	-0.09
<b>Humidity</b>	-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
<b>Lichen species richness</b>	0.19	-0.76
<b>Total lichen abundance</b>	0.22	-0.71
Cyanolichen richness	0.36	-0.31
Nitrophile richness	-0.28	-0.53
<b>% Nitrophile richness</b>	-0.76	0.22
Nitrophile abundance	-0.26	-0.48
<b>% Nitrophile abundance</b>	-0.78	0.12
<b>Landuse</b>	-0.63	-0.19
<b>Sum of agricultural land</b>	-0.56	-0.17
Sum of urban land	-0.48	-0.05
Total $\text{NH}_3$	-0.51	-0.01
$\text{NH}_3$ -Area sources	-0.36	0.09
$\text{NH}_3$ -Domestic sources	-0.43	-0.11
$\text{NH}_3$ -Fertilizer	-0.26	-0.16
$\text{NH}_3$ -Mobile sources	-0.51	-0.01
$\text{NH}_3$ -Soil	-0.30	-0.02
$\text{NH}_3$ -Stationary sources	-0.17	0.05
$\text{NH}_3$ -Wood burning	-0.24	-0.21
<b>Ozone (SUM60)</b>	0.06	0.57
<b>Ozone (max. 1hr value)</b>	0.14	0.58
<b><math>\text{NO}_2</math> (annual mean)</b>	-0.33	0.63
<b><math>\text{SO}_2</math> (annual mean)</b>	0.59	0.10

† Variables with  $r > 0.55$  or  $r < -0.55$  are in boldface type.

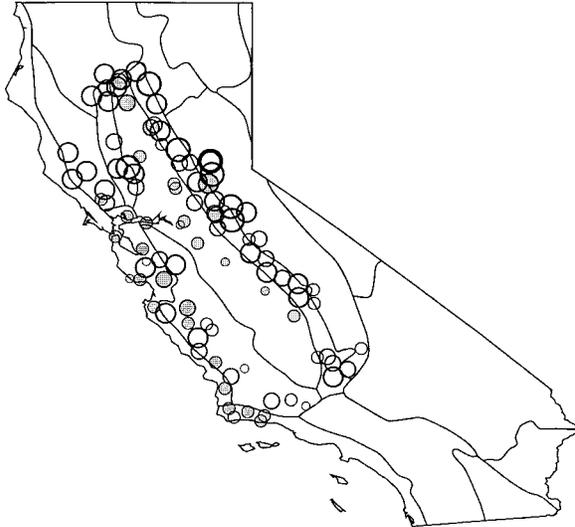


FIG. 5. Map of air-quality scores from axis 1 of the ordination. Circular symbol sizes are proportional to scores on axis 1. Off-frame plots are shaded in gray.

tween axis 2, kriged  $O_3$  estimates ( $r = 0.57$ ), CARB  $O_3$  measurements ( $r = 0.58$ ) and CARB  $NO_2$  measurements ( $r = 0.63$ ). The pollutant and humidity gradients opposed one another, indicating increasing  $O_3$  and  $NO_2$  concentrations with decreasing humidity as one proceeds eastward across the study area (Figs. 2 and 6 and Table 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 (Fig. 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 fewer. 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).

Several species with known oceanic affinities had maxima at low axis scores, steeply declining at higher scores (e.g., *Heterodermia leucomelos* and *Parmotrema chinense*; Fig. 4). Species characteristic of more continental but moist, lowland habitats, such as *Evernia prunastri* (Fig. 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 (e.g., *Xanthoria tenax*) maxima 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*).

#### DISCUSSION

##### *Ammonia deposition in the greater Central Valley*

The strong relationship between axis 1,  $NH_3$  deposition data, and the relativized nitrophile indices (Fig. 2 and Table 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  $SO_2$  levels coincided with plots in more highly developed areas, as suggested by the similar position of the  $SO_2$  and land-use vectors in the ordination biplot (Fig. 2). However,  $SO_2$  was probably not a major factor driving axis 1 despite the correlation (Table 3). The CARB (California Air Resources Board) data show extremely low  $SO_2$  levels throughout the study area with annual arithmetic means rarely

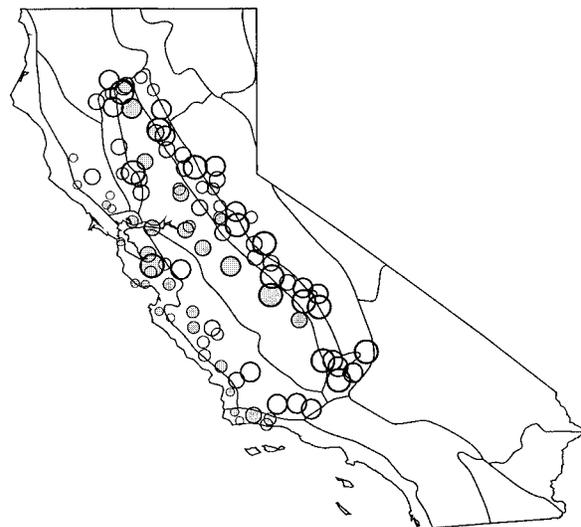


FIG. 6. Map of scores from axis 2 of the ordination. Circular symbol sizes are proportional to scores on axis 2. Off-frame plots are shaded in gray.

surpassing 3 ppb in major urban centers. The most SO<sub>2</sub>-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 SO<sub>2</sub> levels are considered SO<sub>2</sub>-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 SO<sub>2</sub> along axis 1, depression of species richness (van Haluwyn and van Herk 2002: Fig. 2). Wet deposition of related pollutants, like sulfate, are comparably low. National Atmospheric Deposition Program monitoring sites in Davis and Pinnacles National Monument (both in California, USA) 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 United States than in the east (Takemoto et al. 1995).

Our results were broadly consistent with the work of van Herk (1999, 2001), who correlated a nitrophile index (Nitrofile Indicatie Waarde, NIW; mean number of nitrophilous species per tree at plots of 10 clustered trees) with NH<sub>3</sub> 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 (Figs. 2 and 3). We speculate that the strong correlation between the relativized indices and the NH<sub>3</sub> calibration data is due to two factors, (1) the positive association of nitrophiles with NH<sub>3</sub> and (2) NH<sub>3</sub> intolerance by certain non-nitrophilous species, acidophytes (Fig. 3).

Van Herk (2001) found that an index based upon acidophytes, the AIW (Acidofiele Indicatie Waarde), related to NH<sub>3</sub> 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<sub>3</sub> so we lack research indicating what species fit into this group. According to the AIW, candidates from our data set include *Cetraria* spp., *Evernia prunastri*, *Hypogymnia* spp., *Platismatia glauca*, and some *Usnea* spp (Fig. 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 United States. Likewise, the San Joaquin Valley produces over half the estimated NH<sub>3</sub> emissions from fertilizers and confined cattle operations in California (California Air Resources Board 1999, Potter et al. 2000). 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<sub>3</sub>, not moisture patterns (Figs. 2 and 5).

#### *Correlation between humidity, NO<sub>2</sub>, and O<sub>3</sub>*

There are amazingly few field studies that investigate effects of photochemical pollutants on lichen communities. Without any clear information describing lichen responses to NO<sub>2</sub> and O<sub>3</sub> under natural conditions, our interpretation of the second model axis necessarily remains exploratory. Generally, the inverse correlation of humidity with NO<sub>2</sub> and O<sub>3</sub> is unsurprising. The geographic distribution of O<sub>3</sub> 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<sub>3</sub>, explaining the observed close relationship of decreasing O<sub>3</sub> with increasing humidity. Likewise, NO<sub>2</sub> is a chemical precursor to O<sub>3</sub>, hence the similar geographic distribution. As O<sub>3</sub> is a secondary pollutant, concentrations tend to peak downwind to the east of major urban areas where the majority of O<sub>3</sub> precursor pollutants are emitted.

#### *NO<sub>2</sub>*

Nitrogen dioxide was negatively related to species richness in The Netherlands (van Dobben and de Bakker 1996, van Dobben and ter Braak 1998) although NO<sub>2</sub> measurements in their study were confounded by correlations with SO<sub>2</sub>. The results are thus ambiguous since SO<sub>2</sub> 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 NO<sub>2</sub> along axis 2 although the pattern could be easily attributed to humidity (see discussion in *Humidity*, below).

Research shows nitrogen dioxide does affect lichen physiology, but exactly how is still unclear. Short-term fumigations with extraordinarily high levels of NO<sub>2</sub> 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 NO<sub>2</sub> levels, but, again, NO<sub>2</sub> was confounded by SO<sub>2</sub>. Regardless, nonlethal effects on lichen physiology and morphology would not be detected with the given study protocol. Clearly, there is a great need for investigations of NO<sub>2</sub> toxicity to lichens in their natural habitats, and, most importantly, we need unambiguous evidence that NO<sub>2</sub> affects lichen communities via the differential mortality or promotion of species.

Nitric acid vapor (HNO<sub>3</sub>) may actually be more ecologically important than NO<sub>2</sub> 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  $\text{HNO}_3$  concentrations can cause foliar lesions on common California tree species such as *Quercus kelloggii* and *Pinus ponderosa* (Bytnerowicz et al. 1999). In contrast,  $\text{NO}_2$  is known to be phytotoxic only at exceptionally high concentrations (Bytnerowicz et al. 1998). Nitric acid, like  $\text{NH}_3$ , 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  $\text{HNO}_3$  deposition with a lichen-gradient model. However, supporting studies typically document impacts of bark acidification via  $\text{SO}_2$ , acid precipitation of unknown chemical composition, or acidic deposition wherein sulfuric acid ( $\text{H}_2\text{SO}_4$ ) is likely the predominant constituent (e.g., Skye and Hallberg 1969, O'Hare 1974, Robitaille et al. 1977, Gilbert 1986, Gauslaa 1995). Even though both are strong acids, we can not confidently assume  $\text{H}_2\text{SO}_4$  and  $\text{HNO}_3$  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  $\text{HNO}_3$  from our analysis due to the lack of direct monitoring data and the absence of research specifically documenting  $\text{HNO}_3$  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  $\text{HNO}_3$  and an attempt to identify unequivocal indicator species.

### $\text{O}_3$

It remains debatable under what circumstances lichen communities respond to  $\text{O}_3$ . The few existing field studies present different results: Sigal and Nash (1983) potentially found a relationship between  $\text{O}_3$  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  $\text{O}_3$  does reach at least 155 ppb (maximum 1-h value) in our southeastern plots, as suggested by measurements at CARB monitors downwind of the San Joaquin Valley. Unfortunately, our  $\text{O}_3$  data are not directly comparable with Sigal and Nash (1983) as we used different  $\text{O}_3$  measurements.

Fumigation studies have documented various forms of physiological impairment from  $\text{O}_3$ , 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  $\text{O}_3$  damage. Ruoss and Vonarburg (1995) argued that lichens are insensitive to  $\text{O}_3$  under natural conditions because physiological activity ceases during daily  $\text{O}_3$  peaks when humidity levels are typically low. If severity of  $\text{O}_3$  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- $\text{O}_3$  episodes studied by Sigal and Nash (1983). As summer fog is relatively rare in our study area, particularly at inland eastern areas where  $\text{O}_3$  levels are high, lichens could be better protected from  $\text{O}_3$  damage. In any case, the current state of lichen- $\text{O}_3$  research leaves us with little basis to differentiate among  $\text{O}_3$ ,  $\text{NO}_2$ , and moisture effects along axis 2 (see *Humidity*; 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 (Fig. 4 and Table 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  $\text{O}_3$  and  $\text{NO}_2$  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  $\text{HNO}_3$  patterns with community indices, much like the nitrophile indices we used for  $\text{NH}_3$ , 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 in 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  $\text{NH}_3$ . Development of  $\text{NH}_3$  monitoring programs are particularly important for the United States since deposition is not typically monitored by state or federal agencies. Ecological effects of  $\text{NH}_3$  and excess nitrogen deposition are a growing concern for the western United States where emissions are high and continue to rise (Fenn et al. 2003a, b). 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 1991, van der Eerden et al. 1992), alteration of ectomycorrhizal community structure (Lilleskov et al. 2001, 2002), induction 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  $\text{NH}_3$  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  $\text{NH}_3$ .

We have presented here the first lichen-based model for indication of  $\text{NH}_3$  patterns in the United States. Additional lichen communities may be sampled within the defined study area, incorporated into the model, and assigned air-quality scores with NMS (nonmetric multidimensional scaling) to indicate relative, local  $\text{NH}_3$  deposition. In the absence of a multivariate lichen-community model, percentage nitrophile richness or abundance may be used as a rough but nonetheless useful estimate of  $\text{NH}_3$  deposition. Most species that we designated as nitrophiles, such as *Candelaria concolor*, and species from *Phaeophyscia*, *Physcia*, and *Xanthoria*, are widely accepted among lichenologists. The next advancement in  $\text{NH}_3$  biomonitoring research will ideally involve close calibration of lichen community data with direct  $\text{NH}_3$  measurements.

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