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

Sarah Jovan and Bruce McCune

Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, OR 97331-2902, U.S.A. e-mail: jovans@science.oregonstate.edu; e-mail: mccuneb@science.oregonstate.edu

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 geography, 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 diminuitive 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.

Keywords. Air pollution, California, community analysis, cyanolichens, epiphytic macrolichens, gradients, nitrophiles, non-metric multidimensional scaling.

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 & Rose 1970; McCune 1988; McCune et al. 1997a; Muir & McCune 1988; van Dobben & de Bakker 1996; van Herk 1999, 2001).

Epiphytic macrolichen communities in northern and central California are diverse, owing greatly to the topographic and climatic complexity of the 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 poses 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,b*), national or state parks (Baltzo 1989; Smith 1980, 1990; Wetmore 1985), watersheds (Ryan & Nash 1991), and broader geographic regions (Herbert & 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 an 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 & 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 was 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. 1997*b*, 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 oc-

curring 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. (1997*b*) 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 data set 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 & 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

TABLE 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.

	Total ($n = 211$) % Freq	Central Valley ($n = 67$) IV	Central Valley ($n = 67$) % Freq	SCM ($n = 85$) IV	SCM ($n = 85$) % Freq	NW Coast ($n = 59$) IV	NW Coast ($n = 59$) % Freq
Ahtiana sphaerosporella	13.27	—	1.49	**24.3**	**28.24**	—	5.08
Alectoria imshaugii	0.95	—	0.00	—	1.18	—	1.69
Alectoria sarmentosa	13.27	—	0.00	—	2.35	**43.2**	**44.07**
Alectoria vancouverensis	0.95	—	0.00	—	0.00	—	3.39
Bryoria capillaris	7.11	—	0.00	—	1.18	**22.5**	**23.73**
Bryoria fremontii	12.32	—	0.00	**12.4**	**21.18**	—	13.56
Bryoria friabilis	0.95	—	0.00	—	1.18	—	1.69
Bryoria fuscescens	1.90	—	0.00	—	2.35	—	3.39
Bryoria pseudofuscescens	1.42	—	0.00	—	1.18	—	3.39
Bryoria simplicior	1.90	—	0.00	—	2.35	—	3.39
Bryoria tortuosa	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Bryoria trichodes	0.95	—	0.00	—	1.18	—	1.69
Candelaria concolor **(N)**	43.60	**51.2**	**79.10**	—	41.18	—	6.78
Cetraria chlorophylla	11.37	—	1.49	—	8.24	**23.1**	**27.12**
Cetraria merrillii	28.91	—	14.93	**20.8**	**42.35**	—	25.42
Cetraria orbata	24.17	—	10.45	—	15.29	**44.5**	**52.54**
Cetraria pallidula	2.37	—	0.00	—	3.53	—	3.39
Cetraria platyphylla	25.59	—	2.99	—	29.41	**27.7**	**45.76**
Cetrelia cetrarioides	0.95	—	0.00	—	0.00	—	3.39
Cladonia chlorophaea	0.95	—	0.00	—	1.18	—	1.69
Cladonia coniocraea	1.42	—	1.49	—	0.00	—	3.39
Cladonia fimbriata	3.32	—	1.49	—	0.00	**8.5**	**10.17**
Cladonia furcata	0.95	—	0.00	—	0.00	—	3.39
Cladonia ochrochlora	2.84	—	2.99	—	0.00	—	6.78
C. squamosa v. subsquamosa	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Cladonia transcendens	5.21	—	0.00	—	0.00	**18.6**	**18.64**
Cladonia verruculosa	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Collema furfuraceum	10.43	**24.7**	**28.36**	—	0.00	—	5.08
Collema nigrescens	8.06	—	10.45	—	0.00	9.8	16.95
Collema subflaccidum	0.47	—	1.49	—	0.00	—	0.00
"*Dendriscocaulon*" *sp.*	0.95	—	0.00	—	0.00	—	3.39
Esslingeriana idahoensis	18.96	—	4.48	—	4.71	**48.7**	**55.93**
Evernia prunastri	32.23	**31.9**	**53.73**	—	8.24	—	42.37
Flavoparmelia caperata **(N)**	0.95	—	2.99	—	0.00	—	0.00
Flavopunctelia flaventior **(N)**	14.22	**41.5**	**43.28**	—	0.00	—	1.69
Flavopunctelia soredica	0.47	—	1.49	—	0.00	—	0.00
Fuscopannaria leucostictoides	0.95	—	0.00	—	0.00	—	3.39
Fuscopannaria mediterranea	1.42	—	1.49	—	0.00	—	3.39
Fuscopannaria pacifica	0.47	—	0.00	—	0.00	—	1.69
Fuscopannaria pulveracea	0.47	—	0.00	—	0.00	—	1.59
Heterodermia leucomelos	0.47	—	1.49	—	0.00	—	0.00
Hypogymnia apinnata	2.37	—	0.00	—	0.00	**8.5**	**8.47**
Hypogymnia enteromorpha	7.58	—	0.00	—	1.18	**24.2**	**25.42**
Hypogymnia imshaugii	58.77	—	29.85	—	68.24	**36.4**	**77.97**
Hypogymnia inactiva	8.06	—	2.99	—	0.00	**23.0**	**25.42**
Hypogymnia metaphysodes	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Hypogymnia occidentalis	6.16	—	4.48	—	1.18	**12.6**	**15.25**
Hypogymnia physodes	1.90	—	4.48	—	0.00	—	1.69
Hypogymnia tubulosa	4.27	—	5.97	—	0.00	—	8.47
Leptochidium albociliatum	1.90	—	2.99	—	0.00	—	3.39
Leptogium brebissonii	0.47	—	1.49	—	0.00	—	0.00
Leptogium cellulosum	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Leptogium corniculatum	0.95	—	2.99	—	0.00	—	0.00
Leptogium gelatinosum	0.47	—	0.00	—	0.00	—	1.69
Leptogium lichenoides	12.80	**19.0**	**28.36**	—	0.00	—	13.56
Leptogium polycarpum	0.95	—	1.49	—	0.00	—	1.69

TABLE 1. Continued.

	Total (n = 211)	Central Valley (n = 67)		SCM (n = 85)		NW Coast (n = 59)	
	% Freq	IV	% Freq	IV	% Freq	IV	% Freq
Leptogium pseudofurfuraceum	6.64	**17.6**	**19.40**	—	0.00	—	1.69
Leptogium saturninum	1.42	—	2.99	—	0.00	—	1.69
Leptogium tenuissimum	0.47	—	0.00	—	0.00	—	1.69
Leptogium teretiusculum	1.42	—	0.00	—	0.00	**5.1**	**5.08**
Letharia columbiana	38.39	—	8.96	**56.0**	**74.12**	—	20.34
Letharia vulpina	56.87	—	17.91	**47.9**	**85.88**	—	59.32
Lobaria hallii	2.37	—	1.49	—	0.00	**6.2**	**6.78**
Lobaria oregana	0.47	—	0.00	—	0.00	—	1.69
Lobaria pulmonaria	6.64	—	0.00	—	0.00	**23.7**	**23.73**
Melanelia elegantula	17.54	—	5.97	**27.2**	**35.29**	—	5.08
Melanelia exasperatula	13.27	—	5.97	**11.3**	**21.18**	—	10.17
Melanelia fuliginosa	2.84	**5.7**	**7.46**	—	0.00	—	1.69
Melanelia glabra	27.01	**67.2**	**74.63**	—	5.88	—	3.39
Melanelia subargentifera	2.37	**7.5**	**7.46**	—	0.00	—	0.00
Melanelia subaurifera	0.47	—	1.49	—	0.00	—	0.00
Melanelia subelegantula	6.16	—	0.00	—	10.59	—	6.78
Melanelia subolivacea	41.23	—	43.28	—	48.24	—	28.81
Nephroma bellum	0.47	—	0.00	—	0.00	—	1.69
Nephroma helveticum	8.53	—	1.49	—	0.00	**27.2**	**28.81**
Nephroma resupinatum	4.74	—	1.49	—	0.00	**14.7**	**15.25**
Niebla cephalota	0.47	—	1.49	—	0.00	—	0.00
Nodobryoria abbreviata	30.81	—	2.99	**25.9**	**49.41**	—	35.59
Nodobryoria oregana	20.85	—	0.00	**15.9**	**31.76**	—	28.81
Parmelia hygrophila (**N**)	11.85	—	5.97	—	3.53	**22.9**	**30.51**
Parmelia pseudosulcata	0.95	—	0.00	—	0.00	—	3.39
Parmelia saxatilis	1.42	—	1.49	—	0.00	—	3.39
Parmelia sulcata	27.01	—	22.39	—	15.29	**29.2**	**49.15**
Parmeliella triptophylla	1.42	—	2.99	—	0.00	—	1.69
Parmelina quercina	20.85	**52.1**	**58.21**	—	1.18	—	6.78
Parmeliopsis ambigua	3.79	—	0.00	—	4.71	—	6.78
Parmeliopsis hyperopta	3.79	—	0.00	—	1.18	**11.4**	**11.86**
Parmotrema arnoldii	2.37	—	2.99	—	0.00	—	5.08
Parmotrema austrosinense	0.95	—	2.99	—	0.00	—	0.00
Parmotrema chinense	1.90	**6.0**	**5.97**	—	0.00	—	0.00
Peltigera collina	9.00	—	13.43	—	0.00	—	16.95
Peltigera membranacea	0.95	—	0.00	—	0.00	—	3.39
Peltigera praetextata	0.47	—	0.00	—	0.00	—	1.69
Phaeophyscia ciliata	2.37	—	5.97	—	0.00	—	1.69
Phaeophyscia hirsuta (**N**)	0.47	—	1.49	—	0.00	—	0.00
Phaeophyscia orbicularis (**N**)	9.00	**21.8**	**23.88**	—	2.35	—	1.69
Physcia adscendens (**N**)	22.75	**39.8**	**52.24**	—	9.41	—	8.47
Physcia aipolia (**N**)	17.06	**20.4**	**32.84**	—	2.35	—	20.34
Physcia americana	0.47	—	1.49	—	0.00	—	0.00
Physcia biziana	15.64	**39.0**	**43.28**	—	1.18	—	5.08
Physcia caesia	0.47	—	1.49	—	0.00	—	0.00
Physcia dimidiata (**N**)	5.21	—	8.96	—	5.88	—	0.00
Physcia dubia (**N**)	2.37	—	4.48	—	2.35	—	0.00
Physcia stellaris (**N**)	9.48	**17.7**	**22.39**	—	4.71	—	1.69
Physcia tenella (**N**)	10.43	—	13.43	—	10.59	—	6.78
Physciella chloantha	0.95	—	2.99	—	0.00	—	0.00
Physciella melanchra	0.47	—	1.49	—	0.00	—	0.00
Physconia americana	28.44	**31.6**	**53.73**	—	5.88	—	32.20
Physconia enteroxantha (**N**)	19.43	**21.1**	**34.33**	—	9.41	—	16.95
Physconia fallax	5.69	**7.2**	**10.45**	—	4.71	—	1.69
Physconia isidiigera	26.07	**49.1**	**62.69**	—	4.71	—	15.25
Physconia leucoleiptes	1.90	—	1.49	—	1.18	—	3.39
Physconia perisidiosa (**N**)	29.86	**38.7**	**59.70**	—	5.88	—	30.51
Platismatia glauca	22.75	—	5.97	—	7.06	**55.4**	**64.41**
Platismatia herrei	7.11	—	0.00	—	0.00	**25.4**	**25.42**
Platismatia stenophylla	7.11	—	0.00	—	0.00	**25.4**	**25.42**
Polychidium muscicola	0.95	—	0.00	—	0.00	—	3.39
Pseudocyphellaria anomala	9.48	—	4.48	—	0.00	**25.3**	**28.81**

TABLE 1.   Continued.

	Total (n = 211)	Central Valley (n = 67)		SCM (n = 85)		NW Coast (n = 59)	
	% Freq	IV	% Freq	IV	% Freq	IV	% Freq
Pseudocyphellaria anthraspis	14.69	—	14.93	—	0.00	**25.0**	**35.59**
Pseudocyphellaria crocata	0.00	—	0.00	—	0.00	—	0.00
Punctelia subrudecta	6.16	**19.4**	**19.40**	—	0.00	—	0.00
Ramalina dilacerata	0.47	—	0.00	—	0.00	—	1.69
Ramalina farinacea	11.37	—	17.91	—	0.00	—	20.34
Ramalina leptocarpha	1.42	—	2.99	—	0.00	—	1.69
Ramalina menziesii	3.32	**8.4**	**8.96**	—	0.00	—	1.69
Ramalina pollinaria	0.47	—	1.49	—	0.00	—	0.00
Ramalina roesleri	0.47	—	0.00	—	0.00	—	1.69
Ramalina sinensis	0.47	—	1.49	—	0.00	—	0.00
Ramalina subleptocarpha (N)	4.74	**10.1**	**11.94**	—	2.35	—	0.00
Ramalina thrausta	0.47	—	0.00	—	0.00	—	1.69
Sphaerophorus globosus	5.69	—	1.49	—	0.00	**17.5**	**18.64**
Sticta fuliginosa	0.47	—	0.00	—	0.00	—	1.69
Sticta limbata	0.47	—	0.00	—	0.00	—	1.69
Teloschistes chrysophthalmus	0.00	—	0.00	—	0.00	—	0.00
Teloschistes flavicans	0.47	—	1.49	—	0.00	—	0.00
Tholurna dissimilis	0.47	—	0.00	—	1.18	—	0.00
Usnea arizonica	2.84	—	5.97	—	0.00	—	3.39
Usnea cavernosa	2.37	—	0.00	—	0.00	**8.5**	**8.47**
Usnea ceratina	1.42	—	0.00	—	0.00	—	5.08
Usnea chaetophora	0.47	—	0.00	—	0.00	—	1.69
Usnea cornuta	1.42	—	1.49	—	0.00	—	3.39
Usnea diplotypus	3.32	—	0.00	—	1.18	**9.1**	**10.17**
Usnea esperantiana	0.47	—	0.00	—	0.00	—	1.69
Usnea filipendula	16.59	—	0.00	—	9.41	**39.5**	**45.76**
Usnea fragilescens	0.47	—	1.49	—	0.00	—	1.69
Usnea glabrata	1.90	—	1.49	—	0.00	—	5.08
Usnea glabrescens	0.47	—	0.00	—	0.00	—	1.69
Usnea hirta	0.47	—	0.00	—	0.00	—	1.69
Usnea lapponica	1.42	—	1.49	—	1.18	—	1.69
Usnea pacificana	5.69	—	1.49	—	1.18	**16.0**	**16.95**
Usnea rubicunda	0.47	—	0.00	—	0.00	—	1.69
Usnea scabrata	7.11	—	1.49	—	2.35	**18.2**	**20.34**
Usnea subfloridana	6.16	—	1.49	—	1.18	**16.7**	**18.64**
Usnea substerilis	3.79	—	5.97	—	1.18	—	5.08
Usnea wasmuthii	0.47	—	0.00	—	0.00	—	1.69
Usnea wirthii	3.32	—	0.00	—	0.00	**11.9**	**11.86**
Vulpicida canadensis	6.16	—	2.99	—	3.53	**9.3**	**13.56**
Xanthoria candelaria (N)	12.80	—	13.43	—	18.82	—	3.39
Xanthoria fallax (N)	10.43	**12.6**	**19.40**	—	10.59	—	0.00
Xanthoria fulva (N)	9.95	—	8.96	**11.6**	**17.65**	—	0.00
Xanthoria hasseana (N)	18.48	**16.0**	**31.34**	—	8.24	—	18.64
Xanthoria oregana (N)	18.01	**17.2**	**29.85**	—	18.82	—	3.39
Xanthoria parietina (N)	1.90	**6.0**	**5.97**	—	0.00	—	0.00
Xanthoria polycarpa (N)	17.54	**33.4**	**41.79**	—	7.06	—	5.08
Xanthoria tenax (N)	2.37	—	5.97	—	1.18	—	0.00

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 con-

sidered nitrophilous in this study are indicated in Table 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*, ''*Dendriscocaulon*,'' *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).

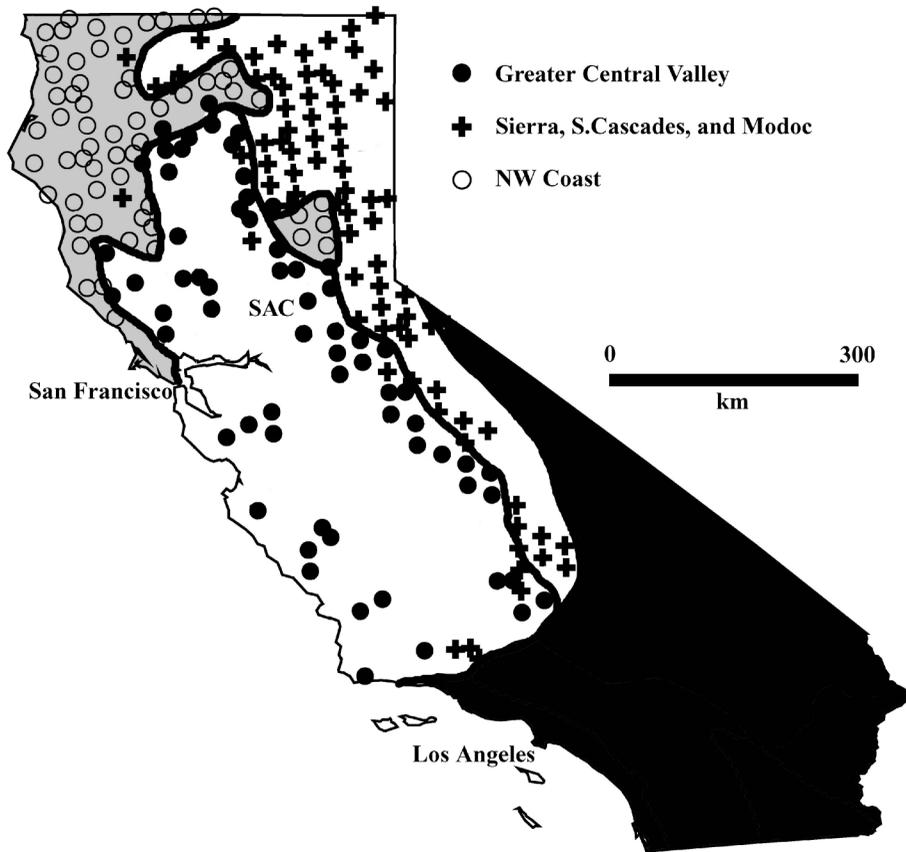All statistical analyses were conducted using PC-ORD

FIGURE 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.

software (McCune & Mefford 1999). To delineate distinctive model areas, plots were separated into preliminary groups using hierarchical, agglomerative cluster analysis with relative Sørensen 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 & 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 & 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 & 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 geography 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 model; and the Northwest Coast model (Fig. 1). The ISA identified 10 or more lichens as statistically significant indicator species for each model area (Table 1). Stronger indicators have higher indicator values, which quantify the faithfulness and exclusivity of a species to a particular group (McCune & Grace 2002).

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 (Fig. 2).
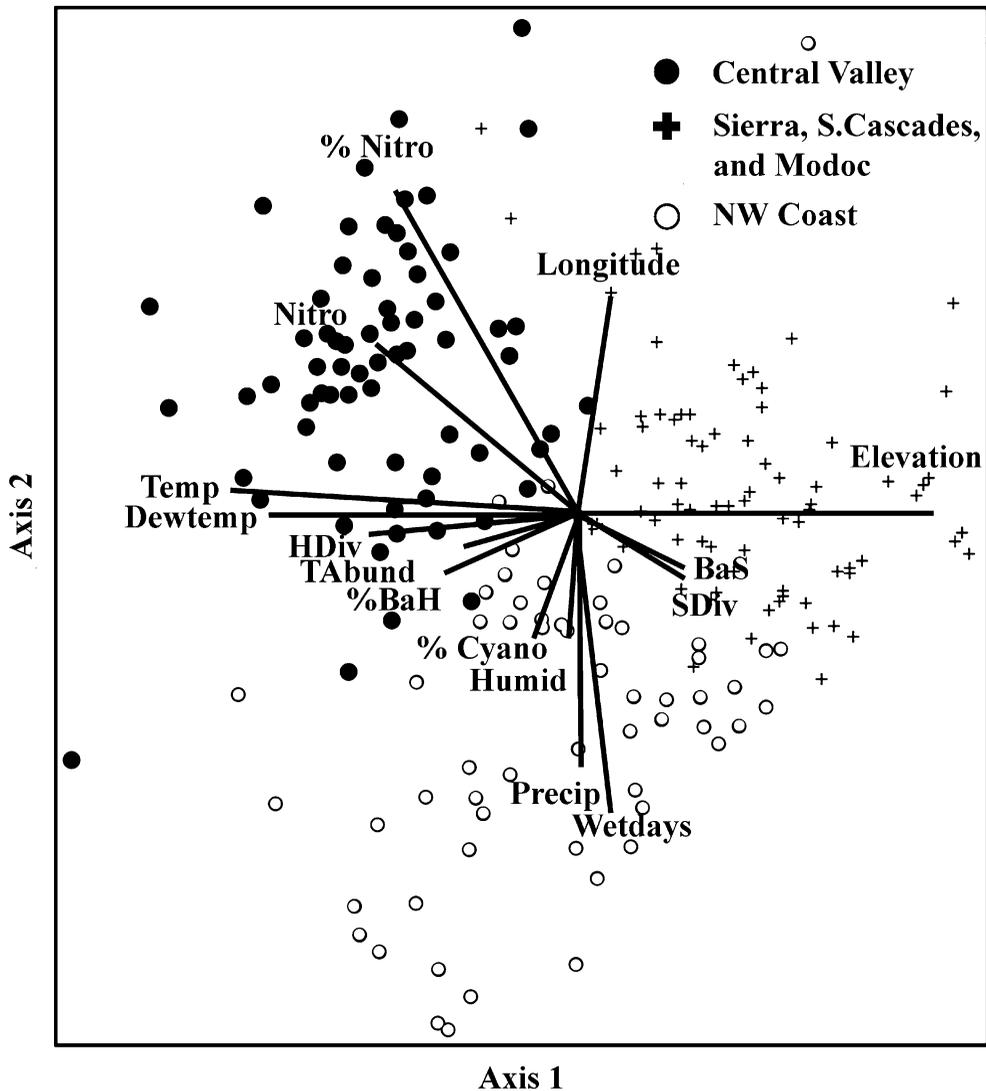
FIGURE 2. Ordination plotted to scale in a joint plot with environmental variables overlaid. Vector length and direction indicates correlations of the variable with ordination axes. Only vectors with an $-0.42 < r > 0.42$ for one axis are shown to prevent crowding. Related variables with overlapping 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.

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 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 (Fig. 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). As expected, diversity of hardwood species and % basal area in hardwoods both correlated negatively with axis 1 ($r = -0.61$ & -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

TABLE 2. Correlations between environmental variables and ordination axes and between community summary variables and ordination axes.

Variable	Axis 1 r	Axis 2 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 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
Species richness	−0.40	−0.27
Total 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

axis 2 (r = −0.71, −0.66, and 0.61, respectively; Table 2).

Cyanolichen and nitrophile indices.—Each functional group index was correlated with both macroclimatic gradients (Table 2, Fig. 2). Cyanolichen richness and percentage 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 (Fig. 1). Lichen community composition indicates regionally high temperatures and low moisture relative to the other regions in the study area, which is consistent with the PRISM climatic data (Figs. 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 1). Overall, a high proportion of indicator species for this group were nitrophilous species, including many species from the genera *Physcia*, *Physconia*, and *Xanthoria*. Most cyanolichen species were uncommon, excepting diminutive species from the genera *Leptogium* and *Collema* (Table 1). Species richness for the area was high because plots tended to have a high diversity and abundance of nitrophiles (Figs. 2–3). Over 50% of the lichen abundance was from nitrophiles in over 60% of plots from this group.

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. 2000). 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 (Fig. 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 (Fig. 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 (>1,830 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 (Figs. 2–3). This region had the lowest species richness, with a total of 70 species among all plots. No cyanolichen species were found (Fig. 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 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 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.
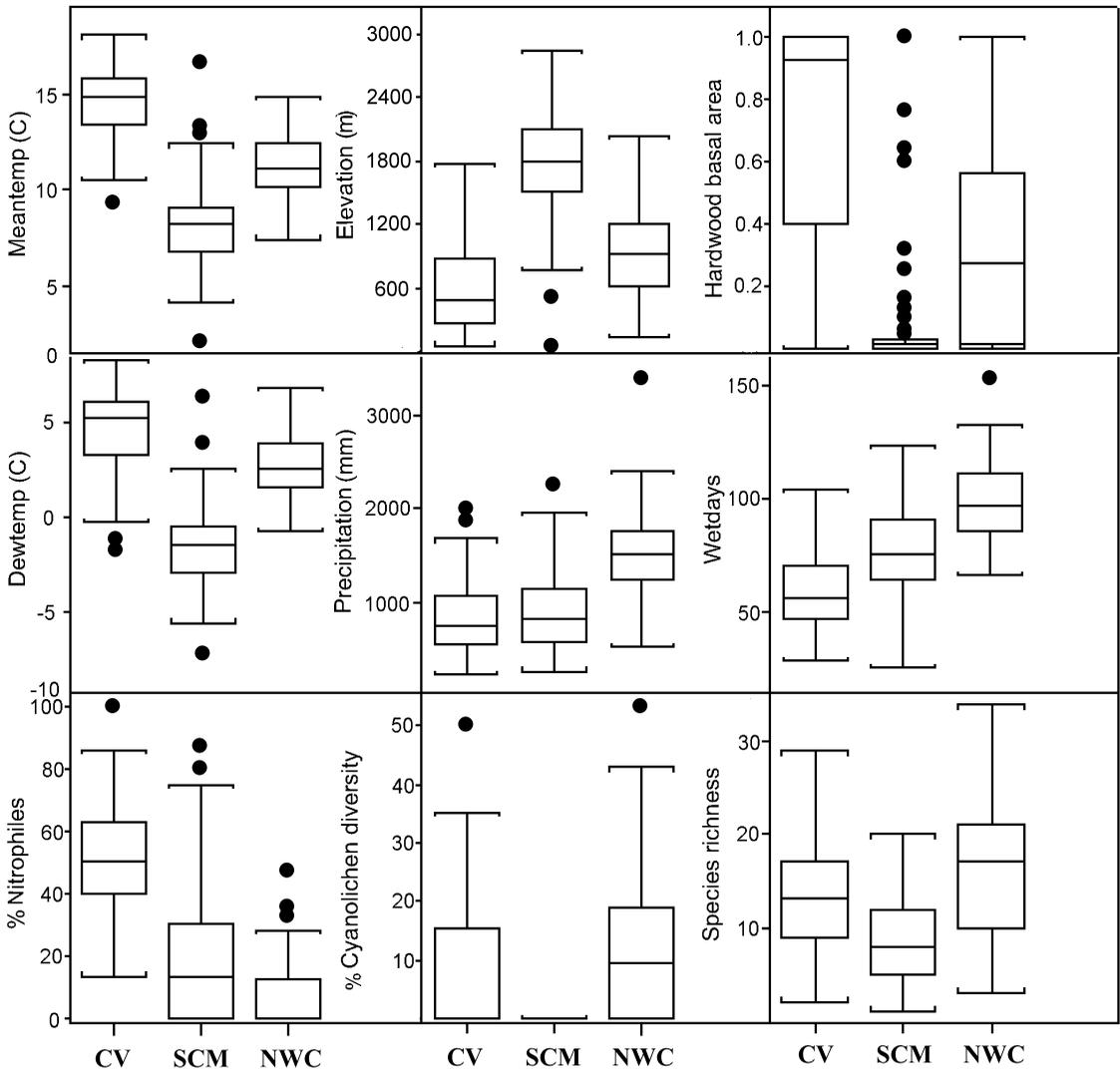
The Modoc Plateau region in northeastern Cali-

FIGURE 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.

fornia, 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 & 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 species composition of lichen, fungi, and plant communities (Fenn et al. 2003). 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 (Fig. 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 (Figs. 2–3). The NW Coast area had the highest species richness of 137 species (Fig. 3). Both cyanolichen indices showed the highest richness and abundance in this model area while nitrophilous species were relatively low (Figs. 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 (*Alectoria sarmentosa*, *Bryoria capillaris*, Table 1). The three indicator species with the highest indicator values for the model area were *Cetraria orbata*, *Esslingeriana idahoensis*, and *Platismatia glauca*.

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 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*, *Peltigera collina*, *Platismatia herrei*, and *Usnea filipendula*. These are primarily montane species, infrequent to common at elevations between 600 to 1,500 m and their known distributions in California include the western slope of the Sierra Nevada (Hale & Cole 1988). Thus, their occurrence in plots of the Oroville anomaly, which range in elevation from 530 to 1,550 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 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 & McCune, unpubl. 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 "*Dendriscocaulon*." 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 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 (1,340–2,130 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 (Fig. 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.

Literature Cited

Antoine, M. E. 2001. Ecophysiology of the lichen *Lobaria oregana*. Master of Science thesis, Oregon State University, Corvallis, OR.

Baltzo, D. E. 1989. Lichens of Mount Diablo State Park, Contra Costa County, California. Mycotaxon 34: 37–46.

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.

Daly, C., R. P. Neilson & D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 140–158.

———, W. P. Gibson, G. H. Taylor, G. L. Johnson & P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22: 99–113.

———, G. H. Taylor, W. P. Gibson, T. W. Parzybok, G. L. Johnson & 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.

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 & S. Anderson. 1977. The effects of acid rain on nitrogen fixation in western Washington coniferous forests. Water Air & Soil Pollution 8: 21–34.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

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.

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 & P. Neitlich. 2003. Ecological effects of nitrogen deposition in the western United States. BioScience 53: 404–420.

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.

Goward, T. 1994. Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada. Acta Botanica Fennica 150: 31–38.

Hale, M. E. & M. Cole. 1988. Lichens of California. University of California Press, Berkeley.

Hawksworth, D. L. & 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. & R. W. Meyer. 1984. Lichens of the San Joaquin Experimental Range, California. The Bryologist 87: 251–254.

James, P. W., D. L. Hawksworth & F. Rose. 1977. Lichen communities in the British Isles: a preliminary conspectus, pp. 295–413. *In* M. R. D. Seaward (ed.), Lichen Ecology. Academic Press, London.

Jørgenson, P. M. 2000. Survey of the lichen family Pannariaceae on the American continent, north of Mexico. The Bryologist 103: 670–704.

———. 2002. *Pannaria*, pp. 304–307. *In* T. H. Nash III, B. D. Ryan, C. Gries, F. Bungartz (eds.), Lichen Flora of the Greater Sonoran Desert Region I. Lichens Unlimited, Arizona State University, Tempe.

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.

Kruskal, J. B. 1964. Non-metric multidimensional scaling: A numerical method. Psychometrika 29: 115–129.

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.

McCune, B. 1988. Lichen communities along O_3 and SO_2 gradients in Indianapolis. The Bryologist 9: 223–228.

———, J. Dey, J. Peck, K. Heiman & S. Will-Wolf. 1997a. Regional gradients in lichen communities of the Southeast United States. The Bryologist 100: 145–158.

———, ———, ———, D. Cassell, K. Heiman, S. Will-Wolf & P. N. Neitlich. 1997b. Repeatability of community data: species richness versus gradient scores in large-scale lichen studies. The Bryologist 100: 40–46.

——— & L. Geiser. 1997. Macrolichens of the Pacific Northwest. Oregon State University Press & U.S.D.A. Forest Service, Corvallis.

——— & J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, OR.

——— & M. J. Mefford. 1999. Multivariate analysis on the PC-ORD system. Version 4. MjM Software, Gleneden Beach, OR.

Momsen, J. H. 2001. Agriculture in the Sierra, pp. 497–528. *In* Sierra Nevada Ecosystem Project: Final Report to Congress, Vol II. Assessments and scientific basis for management options. University of California, Davis.

MUIR, P. S. & B. MCCUNE. 1988. Lichens, tree growth, and foliar symptoms of air pollution: Are the stories consistent? Journal of Environmental Quality 17: 361–370.

NEITLICH, P., P. ROGERS & R. ROSENTRETER. 2003. Lichen communities indicator results from Idaho: baseline sampling. General Technical Report RMRS-GTR-103. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

POTTER, C., C. KRAUTER & S. KLOOSTER. 2000. Statewide Inventory Estimates of Ammonia Emissions from Native Soils and Chemical Fertilizers in California. Final report prepared for the California Air Resources Board, Sacramento, CA.

ROSE, F. 1976. Lichenological indicators of age and environmental continuity in woodlands, pp. 279–307. *In* D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), Lichenology: Progress and Problems. Academic Press, London.

———. 1988. Phytogeographical and ecological aspects of Lobarion communities in Europe. Botanical Journal of the Linnean Society 96: 69–79.

RYAN, B. 1990*a*. Lichens and Air Quality in the Emigrant Wilderness, California: A Baseline Study. Arizona State University, Tempe.

———. 1990*b*. Lichens and Air Quality in Wilderness Areas of California: A Series of Baseline Studies. Arizona State University, Tempe.

SMITH, C. W. 1990. Toward an inventory of lichens of Pinnacles National Monument, pp. 159–168. *In* C. Van Riper III, T. J. Stohlgren, S. D. Veirs, Jr. & S. C. Hillyer (eds.), 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, University of California, Davis. Transactions and Proceedings Series No. 8. U.S. Department of the Interior, National Park Service, Washington, D.C.

SMITH, D. W. 1980. A taxonomic survey of the macrolichens of Sequoia and Kings Canyon National Parks. Master of Science Thesis, San Francisco State University, San Francisco, CA.

TAVARES, I. I. 1997. A preliminary key to *Usnea* in California. Bulletin of the California Lichen Society 4: 19–23.

VAN DOBBEN, H. F. & A. J. DE BAKKER. 1996. Re-mapping epiphytic lichen biodiversity in The Netherlands: Effects of decreasing SO_2 and increasing NH_3. Acta Botanica Neerlandica 45: 55–71.

VAN HERK, C. M. 1999. Mapping of ammonia pollution with epiphytic lichens in the Netherlands. Lichenologist 31: 9–20.

———. 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.

WETMORE, C. M. 1985. Lichens and Air Quality in Sequoia National Park and Kings Canyon National Park. Final Report, National Park Service Contract CX 0001–2–0034, University of Minnesota, St. Paul, MN.