CHAPTER 7.

Climate Effects on Lichen Indicators for Nitrogen

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INTRODUCTION

The Lichen Communities Indicator is a sensitive indicator of forest health changes caused by air quality, climate change, and other stressors. To date, more than 8,000 epiphytic lichen surveys have been collected across the Nation by the Forest Inventory Analysis (FIA) and Forest Health Monitoring (FHM) Programs and their partners (table 7.1; Phelan and others 2012). These data are currently used in several national Forest Service initiatives, including the Chief's Wilderness Challenge, the Watershed Condition Framework, the Terrestrial Ecosystem Condition Framework, and the amended Planning Rule.

The Indicator has been instrumental in developing critical loads (CLs) for nitrogen (N) in North American forests (Pardo and others 2011a). By definition, CLs are the maximum amount of N deposition that a sensitive indicator can tolerate before being "harmed." Regulators and managers use these values to negotiate pollution emissions levels that preserve the function of sensitive ecosystems. For example, the U.S. Environmental Protection Agency used lichen and other CLs to propose the first secondary standards for nitrogen oxide (NO_x) pollutants for the United States (EPA 2008), although the standard has not yet been implemented (Pardo and others 2011b). At a smaller scale, land and air managers use CLs to guide pollution permitting near ecosystems of concern.

For lichen CLs, "harm" is typically defined in terms of a shift from N-sensitive species (oligotrophs) to the moderately sensitive mesotrophs or the N-loving eutrophs.

Table 7.1—Overview of location and timeframe for all Forest Inventory and Analysis-style lichen surveys collected up to 2011

Sponsor	FIA region	Number of surveys	On frame?	Years	States
FIA	IW	1,856	Y	1994–97, 1999–2010	AZ, CO, ID, MT, NM, NV, UT, WY
R6 ARM[a]	IW	45	N	2000, 2003, 2008, 2010	ID, MT
FIA	IW	68	N	2008–11	ID, MT, WY
FIA	North	97	N	1994, 2004	CT, MA, ME, NH, NY, PA, RI, VT
FIA	North	1,307	Y	1994–95, 1998–2005	CT, DE, IL, IN, OH, MA, MD, ME, MI, MN, NH, NJ, NY, PA, RI, VT, WI, WV
FIA	North	85	I	1999–2002	DE, PA, RI
FIA	PNW	33	N	2011	Interior AK
Tongass NF	PNW	302	N	1989–94, 2002–05, 2009, 2011	AK
Chugach NF	PNW	41	N	1993–94	AK
R6 ARM[a]	PNW	795	N	1993–2011	CA, OR, WA
R6 ARM[a]	PNW	1,698	I	1994–2011	OR, WA
FIA	PNW	1,023	Y	1998–2001, 2003–07	AK, CA, OR, WA
FIA	PNW	255	N	1999–2000, 2003–04, 2008–09	AK, CA, OR, WA
FIA	South	24	N	1993	GA, SC, TN
FIA	South	442	Y	1993–95, 1998–99	AL, GA, NC, SC, TN, VA

ARM = Air Resources Management; FIA= Forest Inventory and Analysis; IW = Interior West; NF = National Forest; North = Northern; PNW = Pacific Northwest; R6 = Region 6; South = Southern.

[a] Over 2,000 lichen surveys in PNW are provided by the Forest Service, Region 6. For ARM group data, please visit http://gis.nacse.org/lichenair/.

N measurements are compared with response indices, which quantify the dominance or relative abundance of lichens in these N indicator groups (Fenn and others 2008, Geiser and others 2010, Jovan and others 2012). An ideal lichen response index would correlate with N alone, although in practice climate may be a confounding factor to lichen indices applied across mountainous terrain or large geographic areas (Grenon 2012, Jovan and McCune 2004, Will-Wolf and others 2006).

There are many statistical approaches for extracting climate effects from a lichen-N response index (e.g., Geiser and Neitlich 2007, Grenon 2012, Jovan and McCune 2006). Studies focus so much on *correcting* for climate, however, that we rarely investigate the nature of climate interactions with lichen responses to N (although, see Grenon 2012). A better understanding of these interactions will enable the development of multifactored CL models that can cover larger, more climatically heterogeneous landscapes. Likewise, climate change has the potential to skew long-term N trends tracked using lichen-based indicators. Understanding the role of climate will help practitioners detect and correct for these biases.

The purpose of this study was to investigate climate effects on lichen indices used to develop N CLs for California's forests (table 7.2). Lichen Communities Indicator data were combined across dry, oak-dominated forests (fig. 7.1) from the Los Angeles Basin model area (LAB; Jovan and others 2012) and the southern

Table 7.2—Species list for the study region classified by nitrogen (N) indicator groups used in the lichen-N response indices

Genus	Species	Common name	Count	Indicator group
Candelaria	*concolor*	Candleflame lichen	80	Eutroph
Cetraria	*merrillii*	Blackened thornbush	8	Oligotroph
Collema	*furfuraceum*	Blister tarpaper lichen	17	N/A
Collema	*nigrescens*	Broadleaf tarpaper	15	N/A
Evernia	*prunastri*	Antlered perfume	43	Mesotroph
Flavoparmelia	*caperata*	—	9	Mesotroph
Flavopunctelia	*flaventior*	—	41	Mesotroph
Heterodermia	*leucomela*	Centipede lichen	4	N/A
Hypogymnia	*imshaugii*	Forking bone	19	Oligotroph
Hypogymnia	*inactiva*	Forking bone	3	Oligotroph
Hypogymnia	*physodes*	Monk's hood	3	Oligotroph
Leptogium	*lichenoides*	Tattered vinyl lichen	6	N/A
Letharia	*columbiana*	Wolf lichen	10	N/A
Letharia	*vulpina*	Wolf lichen	13	N/A
Melanelixia	*fuliginosa*	Abraded brown lichen	5	Mesotroph
Melanelixia	*glabra*	Smooth Melanelia lichen	51	Mesotroph
Melanelixia	*subargentifera*	Powdered brown lichen	9	Mesotroph
Melanohalea	*elegantula*	Elegant brown lichen	12	Mesotroph
Melanohalea	*subolivacea*	Eyed brown lichen	37	Mesotroph
Niebla	*cephalota*	Powdery sea-fog lichen	6	N/A
Nodobryoria	*abbreviata*	Tufted foxtail	2	Oligotroph
Parmelia	*hygrophila*	Salted shield	3	Mesotroph
Parmelia	*sulcata*	Powdered shield	12	Mesotroph
Parmelina	*quercina*	—	31	N/A
Parmotrema	*arnoldii*	Powdered scatter-rug	3	N/A
Parmotrema	*austrosinense*	Unwhiskered ruffle lichen	4	N/A

continued

Table 7.2 (continued)—Species list for the study region classified by nitrogen (N) indicator groups used in the lichen-N response indices

Genus	Species	Common name	Count	Indicator group
Parmotrema	*chinense*	Powdered scatter-rug	11	N/A
Peltigera	*collina*	Tree pelt	4	N/A
Phaeophyscia	*hirsuta*	Powdered shadow	10	Eutroph
Phaeophyscia	*orbicularis*	Granulated shadow	51	Eutroph
Physcia	*adscendens*	Hooded rosette	71	Eutroph
Physcia	*aipolia*	Grey-eyed rosette	28	Eutroph
Physcia	*biziana*	Frosted rosette	39	Eutroph
Physcia	*dimidiata*	Frosted rosette	19	Eutroph
Physcia	*stellaris*	Black-eyed rosette	19	Eutroph
Physcia	*tenella*	Fringed rosette	48	Eutroph
Physconia	*americana*	Fancy frost lichen	36	Eutroph
Physconia	*enteroxantha*	Bordered frost lichen	35	Eutroph
Physconia	*fallax*	—	13	Eutroph
Physconia	*isidiigera*	—	59	Eutroph
Physconia	*perisidiosa*	Bordered frost lichen	50	Eutroph
Pseudocyphellaria	*anthraspis*	Dimpled specklebelly	3	N/A
Xanthomendoza	*fallax*	Powdered orange lichen	22	Eutroph
Xanthomendoza	*fulva*	—	24	Eutroph
Xanthomendoza	*galericulata*	—	8	Eutroph
Xanthomendoza	*hasseana*	—	29	Eutroph
Xanthomendoza	*oregana*	—	49	Eutroph
Xanthoria	*candelaria*	Shrubby orange lichen	8	Eutroph
Xanthoria	*parietina*	—	5	Eutroph
Xanthoria	*polycarpa*	Pincushion orange lichen	54	Eutroph
Xanthoria	*tenax*	—	19	Eutroph

— = no common name; N/A= not applicable because species sensitivity to N is poorly understood.

three-fourths of the Greater Central Valley model area (GCV; Jovan and McCune 2005). Lichen communities in these two regions are described by independent models that use the FIA/FHM Lichen Communities Indicator for monitoring N. Within the combined study region, N deposition varies considerably, as do tree species composition, elevation, precipitation, temperature, and dewpoint (table 7.3).

METHODS

Sampling design

Lichens were surveyed in the GCV between 1998 and 2003 (n = 71; fig. 7.1), and all LAB plots were surveyed in 2008 (n = 22). Data were combined for all analyses. Survey methods have been described in detail (Woodall and others 2010) but, briefly, a specially trained crew person spends up to 2 hours surveying for epiphytic macrolichens (i.e., excluding crustose and leprose growth forms) within a 0.4-ha plot centered on FIA subplot #1 (fig. 7.2). Most plots in the GCV occur on the systematic FIA phase 3 grid, although 28 plots were established in urban and heavily agricultural areas throughout the region. All LAB plots are "off frame" and are colocated with long-term monitoring sites for air quality and lichens originally established in the mid 1970s (Riddell and others 2011). Each lichen species encountered was assigned a broad abundance code, which follows a logarithmic scale: 1 = Rare (1 to 3 individuals in area), 2 = Uncommon (4 to 10 individuals in area), 3 = Common (> 10 individuals in area but less than half of the boles and branches have that

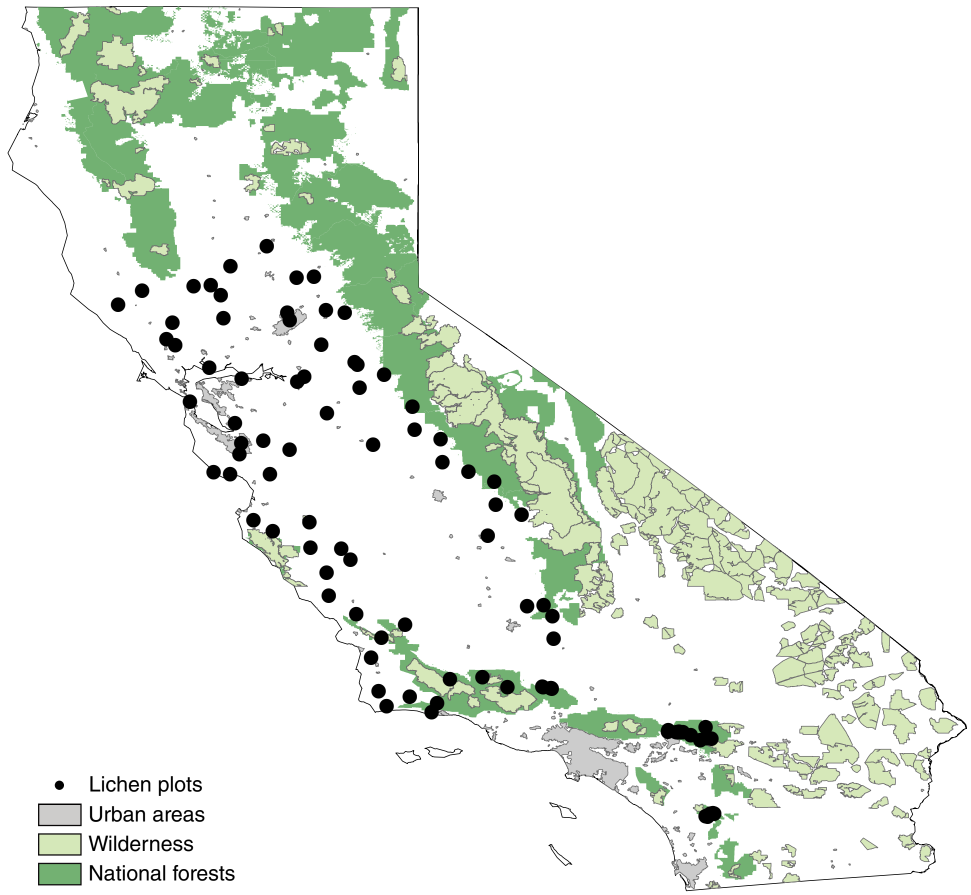
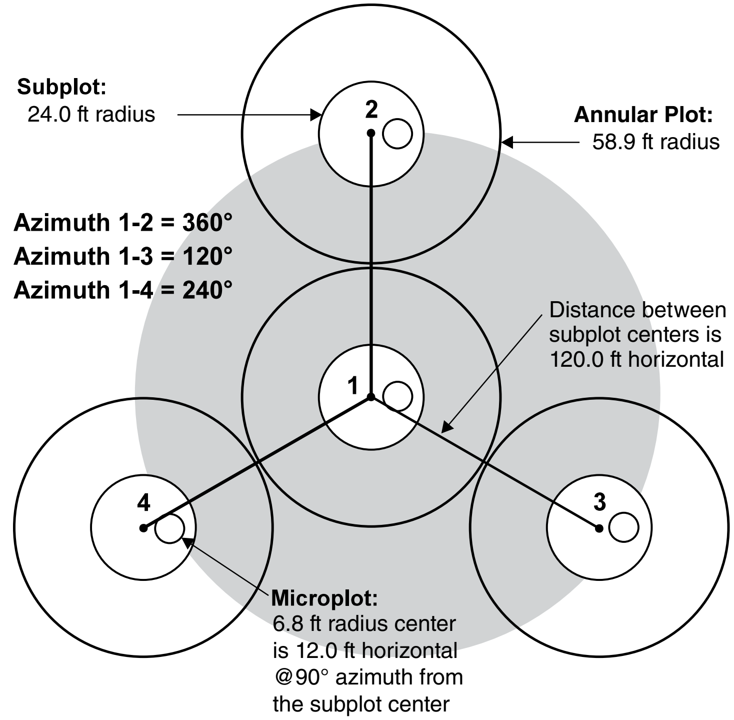


Figure 7.1—Map of the study region showing approximate locations of Forest Inventory and Analysis plots surveyed for lichens. Greater Central Valley plots all lie north of the Los Angeles metropolitan area.

Table 7.3—Variation in environmental variables across the study region and subregions

	Average		Standard deviation		Range	
Variable	GCV	LAB	GCV	LAB	GCV	LAB
Elevation (m)	397.5	1758.9	380.5	195.0	5.4–1650.0	1493.0–2327.0
Percent hardwood BA	0.8	0.5	0.3	0.3	0.0–1.0	0.1–1.0
Dry NH_x (kg N ha^{-1} yr^{-1})	0.2	1.4	0.2	0.9	0.1–1.1	0.3–3.5
Dry NO_x (kg N ha^{-1} yr^{-1})	2.6	5.7	0.8	1.8	1.1–4.5	2.2–9.2
Total N (kg N ha^{-1} yr^{-1})	4.4	8.2	1.4	3.1	2.1–8.4	3.3–15.6
Max temp. (°C)	22.5	17.9	1.8	1.2	15.7–25.3	16.1–19.7
Average temp. (°C)	15.0	11.8	1.3	1.7	10.8–18.1	7.8–13.8
Precipitation (mm)	580.2	825.3	239.8	210.2	224.0–1327.0	549.3–1150.7
Dew point (°C)	5.5	- 0.8	2.5	2.8	- 2.9–9.2	- 6.6–2.2

BA = basal area; GCV = Greater Central Valley; LAB = Los Angeles Basin; NH_x = reduced nitrogen; NO_x = oxidized nitrogen.
Note: Hardwood BA was measured in the field. Climate and nitrogen variables (NH_x and NO_x) are modeled estimates.



Reprinted from USDA Forest Service. 2011. Forest inventory and analysis national core field guide, volume 1: field data collection procedures for phase 2 plots, version 5.1. USDA Forest Service, Washington Office. Internal report. On file with: USDA Forest Service, Forest Inventory and Analysis, Rosslyn Plaza, 1620 North Kent Street, Arlington, VA 22209.

Figure 7.2—Diagram of the Forest Inventory and Analysis plot with the 0.4-ha area searched for epiphytic macrolichens overlaid in gray.

species present), and 4 = Abundant (more than half of boles and branches have the subject species present). Vouchers were collected for each unique species and sent to experts for identification and archiving.

Analysis

Lichen response indices for oligotrophs, mesotrophs, and eutrophs are based on Jovan (2008), who adapted van Herk's (1999) ammonia (NH_3) bioindication indices to fit FIA-style data and West Coast lichen species (table 7.2). An index value for a site is calculated by summing abundance codes for the N indicator group in consideration and relativizing by the summed abundance codes of all lichens found at that site.

I used HyperNiche 2.2 (McCune and Mefford 2009) to build nonparametric multiplicative regression (NPMR) models for the three lichen response indices. NPMR can resolve complex response surfaces. The model-building process automatically considers possible interactions among all predictors (Lintz and others 2011, McCune 2006). Model building is an iterative search for the best possible combination of predictors given user-defined rules to prevent overfitting. I chose strict settings, requiring a minimum data-to-predictor ratio of 10 to 1 and a minimum average neighborhood size of 25 plots. I used the local linear estimator to assign weights to observations. This estimator resolved similar but stronger and more parsimonious models than the Gaussian kernel estimator, which is typically favored for modeling species' responses to environmental gradients. Model strength is evaluated using leave-one-out cross validation, yielding an xR^2 value that estimates percent variance explained just like a coefficient of determination, but penalized by cross validation. In order to be included in the model, additional predictors were required to improve the variance explained by at least 5 percent. Model significance is evaluated using randomization tests. Confidence bands are determined by bootstrap resampling.

Predictor variables included long-term estimates (1971–2000; 800-m resolution) of average temperature, maximum temperature, dew point temperature, and precipitation extracted from the PRISM model (PRISM Group 2004; table 7.3). Percent basal area of hardwoods was calculated using the variable radius method. Estimates of total N deposition, dry deposition of reduced N (NH_x) and dry deposition of oxidized N (NO_x) were obtained from version 4.4 of the Community Multiscale Air Quality model (4-km^2 resolution). These estimates are based on N emissions inventories and meteorological conditions from 2002. See Tonnesen and others (2007) for more information on model construction and validation.

RESULTS AND DISCUSSION

The best NPMR models for all three indices included two predictors: precipitation plus one of the N deposition variables (table 7.4; xR^2 = 0.48–0.63). Total N deposition was a strong predictor of mesotroph abundance, while oligotrophs and eutrophs appeared more closely correlated with NO_x deposition. Response surfaces show how the proportion of lichens in each of the three indicator groups varies across the full range of precipitation and N values across the study area (fig. 7.3).

There was not a strong direct relationship between precipitation and the N deposition estimates (fig. 7.4). Data points were well spread along the precipitation and N axes, except for a few outliers representing high N and moderately wet plots. A dataset that is well distributed with respect to the important NPMR predictors gives confidence that the model describes real patterns and not just artifacts of the predictors' sampling distributions.

Table 7.4—Parameters of the best nonparametric multiplicative regression models for each lichen response index

Response index	xR^2	Avg. neigh.	Predictor 1	Tolerance	Predictor 2	Tolerance
Percent oligotrophs	0.48	26.4	Dry NO_x	0.81	Precipitation	275.75
Percent mesotrophs	0.53	26	Total N	2.67	Precipitation	165.45
Percent eutrophs	0.63	26.1	Dry NO_x	1.22	Precipitation	220.6

Avg. neigh. = average neighborhood size; NO_x = oxidized nitrogen.

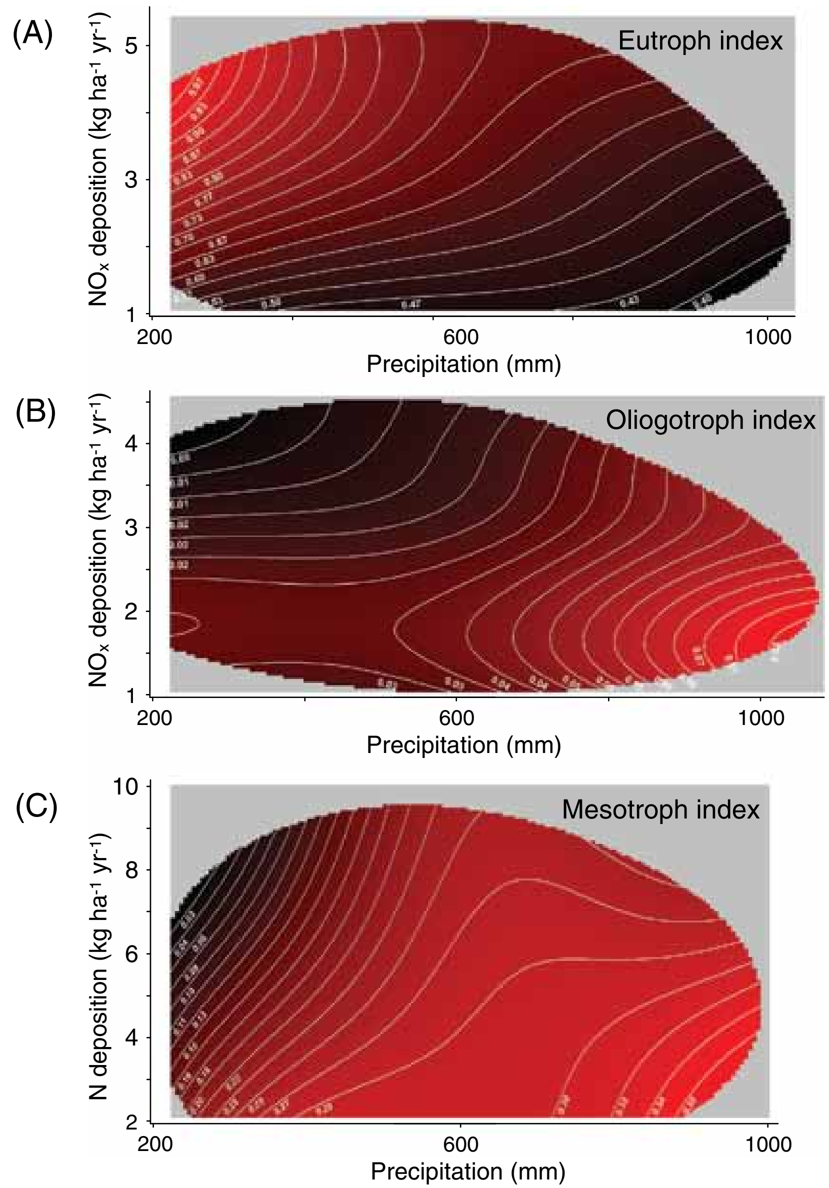


Figure 7.3—Response surfaces for the three nonparametric multiplicative regression models. White contour lines provide estimates of what proportion of lichen abundance is in eutrophs (A), oligotrophs (B), or mesotrophs (C) at different combinations of precipitation and N deposition.

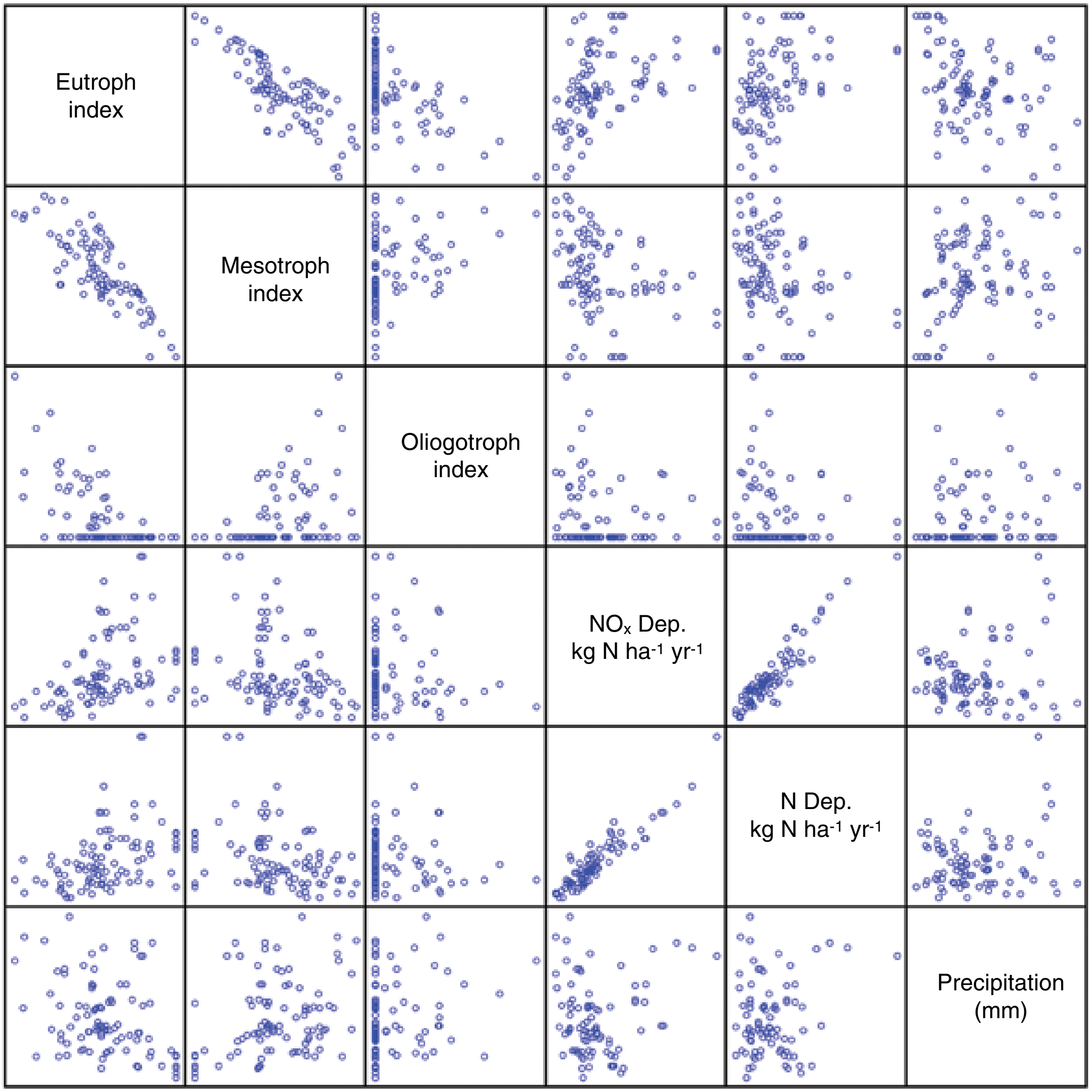


Figure 7.4—Scatterplot matrix showing 1:1 relationships between response indices and the environmental predictors identified by nonparametric multiplicative regression.

Precipitation clearly explains different variability in the lichen response indices than do the N deposition variables (fig. 7.4). The NO_x and total N deposition variables, however, were highly correlated with each other. Jovan and others (2012) found that eutrophs in the LAB do not discriminate among N forms, meaning that eutroph abundance links more closely to total N deposition. The results of this study do not necessarily conflict, because the NO_x and total N variables are almost interchangeable (fig. 7.4). Oxidized N is the dominant component of N deposition in both the LAB and the GCV (table 7.3).

The eutroph and oligotroph indices responded oppositely with respect to N and also precipitation (fig. 7.3A and B). Overall lichen communities across the study area were highly eutrophic; under the least favorable conditions for eutrophs in the study area (the wettest and lowest N sites), eutrophs still contributed ≥ 40 percent of lichen abundance. Eutrophic species comprised ≥ 97 percent of lichen abundance at plots that were dry and high in N. By contrast, oligotrophs were sparse in the study region, providing 0 percent to only about 8 percent of lichen abundance under the most favorable conditions for this group (wettest and lowest N sites; fig. 7.3B).

The mesotroph response to N and precipitation was directionally similar to the oligotroph response, suggesting the same preference for wet conditions and low N levels. Mesotrophs made a more substantial contribution to lichen communities, however, ranging from 2 to 36 percent at optimal conditions (fig. 7.3C). The model suggests precipitation has a moderating effect on how the mesotroph index responds to N except, curiously, at sites receiving 400–700 mm. The broadening contour lines in figure 7.3C indicate that mesotroph decline is less severe under these conditions even at the highest deposition levels (~10 kg N/ha/year).

Precipitation also appeared to moderate the oligotroph-N response at all but the lowest levels of precipitation and N deposition (fig. 7.3B). The NPMR model suggested an initial, slight positive effect of N (an increase in oligotroph abundance of < 0.5 percent) with a decline beginning between 1.5 and 2.0 kg N/ha/year. In contrast, more eutrophs tended to accumulate at drier sites than wetter sites for a given level of N.

Nearly all FIA-style lichen studies in the Western United States show some evidence that dry climate and N deposition have similar effects on lichen community composition (Geiser and Neitlich 2007, Geiser and others 2010, Grenon 2012, Jovan 2008, Jovan and McCune 2004, Jovan and McCune 2005, Jovan and McCune 2006), although the consistency of this phenomenon has not been explicitly recognized before now. Can it be concluded, then, that moisture levels affect lichen susceptibility to N level? This is likely because N is a mobile nutrient in the lichen thallus; water delivers dissolved N pollutants, but a high volume of water also leaches mobile pollutants out of the thallus. Thus, precipitation exerts major control over the concentration of pollution "pulses" received by the lichen.

On the other hand, lichenologists working in Mediterranean and other dry forest types long ago recognized that many of the eutrophs included in this study behave as "xerophytes" (e.g., Barkman 1958, Frati and others 2008) even in the absence of obvious N inputs. Likewise, evidence of the high moisture requirements of oligotrophs is found in several studies (e.g., Geiser and Neitlich 2007, Jovan 2008, Rambo 2010). Thus it is unclear to what degree moisture levels actually modify lichen responses to N as opposed to what degree moisture affects lichen communities in independent but similar ways as N.

The nature of this interaction has important implications for critical loads research and conservation practitioners. It may well be that N-sensitive oligotroph and mesotroph species living in dry habitats are more easily extirpated by N deposition. The vulnerability of these species to extirpation in currently habitable areas may also increase if climate shifts towards drier or hotter conditions.

From an operational standpoint, the importance of precipitation means that moisture differences across monitoring sites can skew N biomonitoring results, making drier habitats appear more polluted than they actually are. Recent research in the LAB shows it is possible to accurately predict annual N deposition levels using only a simple response index, eutroph percent cover (Jovan and others 2012), although sites in that study share a similar moisture regime. The NPMR models developed here suggest that indices designed for larger, more heterogeneous landscapes must explore possible precipitation effects. An index that is both simple and accurate can save forest managers and air quality regulators from costly investments in monitoring instrumentation.

CONCLUSIONS

Each NPMR response surface revealed interesting nonlinearities (fig. 7.3). Three features of particular note include (1) low NO_x levels seem to have a weak positive effect on oligotroph abundance, (2) mesotrophs appear relatively insensitive to N at midrange precipitation levels, and (3) eutroph abundance appears to accumulate more quickly at dry sites for a given level of N deposition. The first two findings are especially surprising, and supporting observations have not been reported in other lichen-N studies. Further study may reveal that these response features are simply artifacts of model overfitting. It is clear, however, that all three response indices showed some level of sensitivity to precipitation and that the interaction between precipitation and N response is nonlinear. Modeling techniques applied in large-scale lichen bioindication studies for N must be able to accommodate this complexity.

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