Environ Monit Assess (2007) 129:243–251
DOI 10.1007/s10661-006-9357-8

Nitrogen Content of *Letharia vulpina* Tissue from Forests of the Sierra Nevada, California: Geographic Patterns and Relationships to Ammonia Estimates and Climate

Sarah Jovan · Tom Carlberg

Received: 14 March 2006 / Accepted: 14 June 2006 / Published online: 21 October 2006

Abstract Nitrogen (N) pollution is a growing concern in forests of the greater Sierra Nevada, which lie downwind of the highly populated and agricultural Central Valley. Nitrogen content of *Letharia vulpina* tissue was analyzed from 38 sites using total Kjeldahl analysis to provide a preliminary assessment of N deposition patterns. Collections were co-located with plots where epiphytic macrolichen communities are used for estimating ammonia (NH_3) deposition. Tissue N ranged from 0.6% to 2.11% with the highest values occurring in the southwestern Sierra Nevada (range: 1.38 to 2.11). Tissue N at 17 plots was elevated, as defined by a threshold concentration of 1.03%. Stepwise regression was used to determine the best predictors of tissue N from among a variety of environmental variables. The best model consisted only of longitude (r^2 = 0.64), which was reflected in the geographic distribution of tissue values: the southwestern Sierra Nevada, the high Sierras near the Tahoe Basin, and the Modoc Plateau, are three apparent N hotspots arranged along the tilted north–south axis of the study area. Withholding longitude and latitude, the best regression model suggested that NH_3 estimates and annual number of wetdays interactively affect N accumulation ($r^2 = 0.61$; % N ~ NH_3 + wetdays + (NH_3 × wetdays)). We did not expect perfect correspondence between tissue values and NH_3 estimates since other N pollutants also accumulate in the lichen thallus. Additionally, other factors potentially affecting N content, such as growth rate and leaching, were not given full account.

Keywords Air pollution · Ammonia · Agriculture · Bioindication · California · Forest health · *Letharia vulpina* · Lichens · National Parks · Nitrogen · Nitrophytes · Sierra Nevada

1 Introduction

Elemental analysis of lichen tissue is one of the most extensively applied bioindication tools for air quality mapping and monitoring (i.e., Addison & Puckett, 1980; Bargagli & Mikhailova, 2002; Bruteig, 1993; Geiser, 2004; Gombert, Asta, & Seaward, 2003; Søchting, 1995). Lichens efficiently accumulate pollutants delivered by both wet and dry deposition. As elegantly stated by Geiser (2004; p. 3): "Lichens undergo rapid hydration and dehydration. These processes alternately concentrate and leach pollutants, maintaining a dynamic equilibrium with atmosphere

S. Jovan (✉)
Department of Botany and Plant Pathology,
Oregon State University,
2082 Cordley Hall,
Corvallis, OR 97331-2902, USA
e-mail: jovans@science.oregonstate.edu

T. Carlberg
USDA Forest Service, Six Rivers National Forest,
Eureka, CA 95501, USA

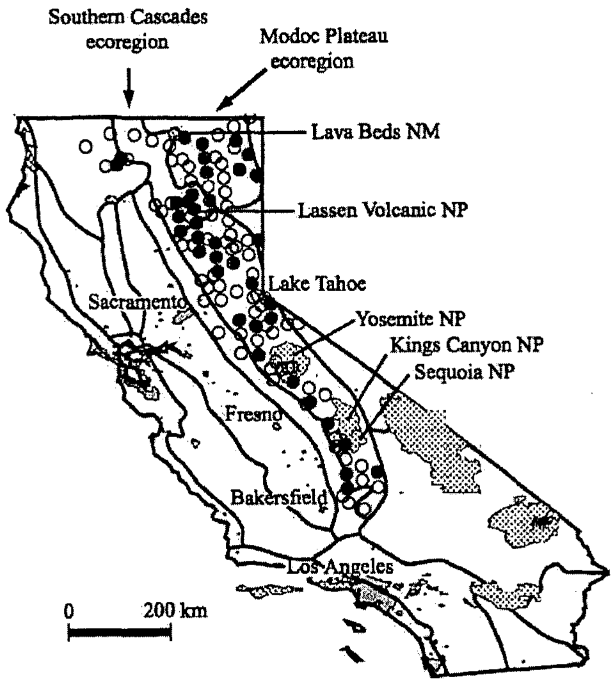

Figure 1 Map of Forest Inventory and Analysis plots where lichen communities were surveyed for the greater Sierra Nevada model. *Plot symbol is blackened* if *Letharia vulpina* tissue was also collected. *Thick black lines* delineate Bailey's (1983) ecoregions. Major urban areas are *shaded in solid gray* while National Parks (*NP*) and National Monuments (*NM*) are *dotted* and, in some cases, *labeled.*

and substrate sources of chemicals." Tissue concentrations of macronutrients like nitrogen (N) and sulfur (S), for instance, may be well-correlated with deposition measurements (Blett, Geiser, & Porter, 2003; Bruteig, 1993).

Tissue analysis is sometimes used to facilitate or augment interpretation of lichen gradient models (Geiser, 2004; Geiser & Neitlich, 2006), a community-based biomonitoring tool utilized by the Forest Inventory and Analysis Program (FIA; USDA Forest Service). These models are based on the premise that the presence and abundance of indicator species can be correlated with air quality gradients. Tissue data can help investigators link these community responses to a particular pollutant or pollutant class, which is especially useful when direct pollutant measurements are unavailable for calibration of the gradient model.

Our primary objective was to characterize N deposition to forests of the greater Sierra Nevada in California (Figure 1), much of which lies downwind of the urbanized and intensely agricultural Central Valley. Eutrophication of forest and aquatic systems is a growing concern for much of the region, but most especially in the Lake Tahoe Basin and southwestern Sierra Nevada (reviewed by Fenn et al., 2003a; Fenn, Poth, Bytnerowicz, Sickman, & Takemoto, 2003b). We analyzed the N content of a common epiphytic lichen, *Letharia vulpina* (L.) Hue, from 38 sites. We identified stands at greatest risk of eutrophication by mapping where tissue N is elevated above background levels.

Tissue collections were co-located with permanent plots where ammonia (NH_3) deposition is currently monitored by FIA, using lichen data and a lichen gradient model (Figure 1; Jovan & McCune, 2006). We included NH_3 estimates among a variety of environmental and lichen community variables to determine the best predictors of tissue N. Locally high NH_3 deposition should reflect in high tissue N. High tissue N, however, need not be accompanied by high NH_3 estimates. While we know NH_3 is a major component of total N deposition in the region, oxidized N pollutants like nitrates (NO_3^-) and nitrogen oxides (NO_x) contribute to varying degrees (Bytnerowicz & Fenn, 1996; Bytnerowicz & Riechers, 1995; Bytnerowicz et al., 2002; Fenn et al., 2003a; 2003b). Moreover, local climate may also affect N accumulation (Blett et al., 2003; Bruteig, 1993), an important consideration for studies with a large geographic scope. The potential for climatic heterogeneity to impact our data is discussed briefly.

2 Materials and Methods

2.1 Study area

The study area encompasses the Southern Cascades, Modoc Plateau, Northwestern Basin and Range, and Sierra Nevada ecoregions of California (Bailey, 1983; Figure 1). Climatic conditions and forest stand structure vary widely depending on elevation (370–2,895 m) and latitude. Most forests are mixed conifer with hardwoods common along riparian areas and in the Southern Cascades and Sierra Nevada foothills. The Modoc Plateau, which lies in the rain shadow of the Klamath Mountains, is a cool high-elevation desert supporting open stands of *Juniperus occidentalis*. As summarized in Jovan and McCune (2006), long-term averages (1961 to 1990) for annual precipitation and temperature vary considerably from 256 to 2,261 mm and from 2 to 15.7°C, respectively.

The westernmost boundary of the study area lies along the Central Valley, an important upwind source of agricultural and vehicular N emissions. The greater Sierra Nevada encompasses several notable tourist attractions such as the famous Yosemite and Sequoia National Parks (NP; Figure 1), which draw large crowds during the summer months. Forest fires are also an important local source of emissions. Tissue was analyzed from plots near the NPs but we did not collect within park boundaries.

2.2 Origin of NH_3 estimates

Jovan and McCune (2006) derived the NH_3 bioindication model using lichen community data from 115 circular, 0.38 ha FIA plots. Plots span all land-use types and lie on a permanent hexagonal sampling grid, excepting a few plots ($n = 24$) installed in areas of special concern like NPs and urban recreation areas. Field workers conducted one time-constrained survey of the lichen community at each plot between 1998 and 2001 using the standardized FIA protocol (McCune et al., 1997). The relative abundance of each epiphytic macrolichen species was estimated using four broad abundance codes: 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).

The lichen community response to NH_3 was detected using an index of known NH_3 indicator species, the proportion of nitrophyte abundance (PNA; Jovan & McCune, 2005). The PNA is technically defined as the summed abundance codes of nitrophytes relativised by total lichen abundance per plot. Nitrophytes are well-known for their positive association with NH_3 (De Bakker, 1989; Jovan & McCune, 2005; van Herk, 1999; 2001). Local nitrophytes include: *Candelaria concolor*, *Flavopunctelia flaventior*, *Parmelia hygrophila*, *Phaeophyscia orbicularis*, *Physcia adscendens*, *P. aipolia*, *P. dimidiata*, *P. stellaris*, *P. tenella*, *P. tribacia*, *Physconia americana*, *P. enteroxantha*, *P. fallax*, *P. isidiigera*, *P. perisidiosa*, *Punctelia perreticulata*, *Ramalina subleptocarpha*, *Xanthoria candelaria*, *X. fallax*, *X. fulva*, *X. hasseana*, *X. oregana*, *X. parietina*, and *X. polycarpa*.

When applied to plots in the neighboring Central Valley, the PNA was strongly, positively associated with synthetic variables for estimating NH_3 deposition. These include agricultural intensity, urbanization, and GIS-modeled NH_3 emissions estimates (Jovan & McCune, 2005). In the mountainous greater Sierra Nevada, however, it was apparent that nitrophyte abundance was also affected by the steep climatic gradients. To isolate NH_3 effects, Jovan and McCune (2006) used nonlinear regression to extract the influence of elevation and associated climatic variability from the PNA. The unstandardized residuals thus serve as modeled estimates of relative NH_3 deposition.

2.3 Tissue data

We selected *L. vulpina* for tissue analysis because this species is fairly pollutant tolerant (McCune & Geiser, 1997) and widespread throughout inland montane forests in the western Unites States. *L. vulpina* is also being used, to a limited extent, for bioaccumulation studies in Oregon, Washington (Geiser & Neitlich, 2006), and California (Geiser, unpublished data; Jovan, unpublished data). We used a cut-off of 1.03% dry weight in N (reported as % N) to define sites exposed to elevated deposition. This preliminary threshold was developed for use by the USDA Forest Service Region 6 Air Program, based on *L. vulpina* tissue collected at remote sites in Alaska, Oregon, and Washington (Geiser, web-published data, http://airlichen.nacse.org/cgi-bin/qml/usair/region5/area5.qml?qml_screen=threshold). Comparable information is not yet available for California.

Tissue was collected between August and September 2004 from 38 FIA plots included in the NH_3 bioindication model. Plots were intentionally selected to span a wide range of NH_3 estimates. The only other factors considered for site selection were: (1) the plot needed to occur on public land to avoid accessibility issues, (2) we wanted plots to have broad geographic coverage, and (3) plots needed to be close enough to roads that tissue could be collected in less than one day.

2.3.1 Field protocol

Tissue sampling closely followed the protocol by Geiser (2004). At least 10 g of dry, healthy *L. vulpina*

Table I Origin of predictor variables included in the regression analysis

Variable	Units	Source
Longitude	Decimal degrees	Standard FIA plot data
Latitude	Decimal degrees	Standard FIA plot data
Elevation	m	Standard FIA plot data
Maximum temperature	°C	Annual, averaged over 1961 to 1990
Mean temperature	°C	Annual, averaged over 1961 to 1990
Minimum temperature	°C	Annual, averaged over 1961 to 1990
Relative humidity	%	Annual, averaged over 1961 to 1990
Wetdays	Count	Annual, averaged over 1961 to 1990
Precipitation	cm	Annual, averaged over 1961 to 1990
Total basal area	m^2/ha	Standard FIA plot data
Percent of hardwood basal area	%	Derived from standard FIA plot data
Lichen species richness	Count	Derived from standard FIA plot data
Total lichen abundance	–	Summed abundance codes
Nitrophyte abundance	–	Summed abundance codes
PNA	Proportion	Jovan & McCune, 2006
NH_3 estimates	%	From lichen gradient model (Jovan & McCune, 2006)

PNA Proportion of nitrophyte abundance.

tissue were collected from woody substrates or from the litter in each plot. Tissue was taken from a minimum of six individual trees or shrubs. A replicate tissue sample was collected at about every sixth plot visited (n = 7) to assess measurement error and within-plot variability, making a total of 45 tissue samples. Replicate values were averaged for mapping tissue N. Nearby potential sources of pollutants or dust were noted. The collector wore unpowdered vinyl gloves that were changed between samples. Care was taken not to touch any man-made materials. Tissue was stored for about three months in air-tight Kapak polyester bags. Dead, dirty, and discolored fragments of thalli were discarded. After this 'high-grading', samples typically weighed 4 to 7 g.

2.3.2 Lab protocol and quality control

Thalli were re-sealed in bags and sent to the Research Analytical Laboratory at University of Minnesota. As described in Geiser (2004), samples are finely ground and dried for 2 h at 65°C. Percent dry weight in N is determined using total Kjeldahl N analysis. Lab accuracy was assessed by analyzing a reference material of known N content obtained from the National Institute of Standards and Technology (NIST

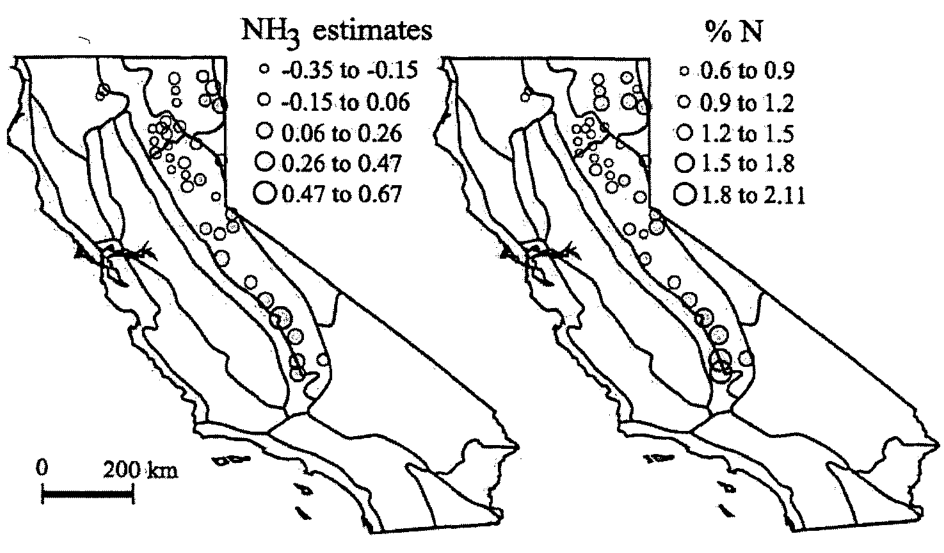

Figure 2 Maps depicting NH_3 estimates (Jovan & McCune, 2006) and percent tissue N (% N). Ammonia estimates are technically the deviation of nitrophyte abundance, taken as a percentage of total lichen abundance at a plot, from what is expected for a given elevation. *Black lines* are Bailey's (1983) ecoregions. Tissue N was elevated in *Letharia vulpina* collections from *gray plots* as defined by a threshold of % N > 1.03.

Table II Correlation coefficients for all predictor variables available as main effects for model-building

Predictor	Regression coefficient	r^2
Longitude	0.30	0.64
Latitude	−0.16	0.52
Elevation	0.00	0.03
Maximum temperature	−0.01	0.00
Mean temperature	0.01	0.01
Minimum temperature	0.03	0.03
Relative humidity	0.00	0.00
Wetdays	−0.01	0.32
Precipitation	0.00	0.09
Total basal area	0.00	0.00
Percent of hardwood basal area	0.49	0.04
Lichen species richness	−0.01	0.02
Total lichen abundance	0.00	0.02
Nitrophyte abundance	0.02	0.11
PNA	0.99	0.24
NH_3 estimates	1.29	0.39

PNA Proportion of nitrophyte abundance.

1515; apple leaves). To determine laboratory precision, the first tissue sample and every 10th sample thereafter were re-analyzed for N (n = 5).

2.4 Analysis

We used the statistical program S-Plus (Insightful Corporation, 2000) to investigate which environmental and lichen community-based variables were the best predictors of % N (Table I). Relationships were modeled using forward stepwise linear regression wherein predictors are added to the model as long as they improve goodness-of-fit, evaluated by Mallows' C_p statistic. All climate data were extracted as annual averages from the Precipitation–elevation Regressions on Independent Slopes Model (PRISM; Daly, Neilson, & Phillips, 1994; Daly et al., 2001; Daly, Gibson, Taylor, Johnson, & Pasteris, 2002). We allowed the regression to select any two-way interaction terms between climate variables, elevation, and NH_3 estimates. Two three-way interactions were also included as possible predictors (NH_3 estimates × wetdays × mean temperature, and NH_3 estimates × precipitation × mean temperature).

3 Results

Lab measurements were adequately precise, having an average deviation of 0.02% N between repeat measurements on the same tissue sample. Lab accuracy was also high as determined by only a slight overestimation of 0.02% for the standard reference material. Analysis of replicate tissue samples yielded an acceptable standard measurement error of 0.1% (mean absolute difference between replicate samples = 0.20%; standard deviation = 0.14%).

Figure 2 shows % N, which ranged from 0.6% to 2.11%. Tissue from 17 plots had N concentrations above the Region 6 Air Program threshold (1.03% N). The six southernmost plots in the study area had the highest N (range: 1.38 to 2.11). Most collections from the Modoc Plateau (0.60 to 1.32) also had elevated N,

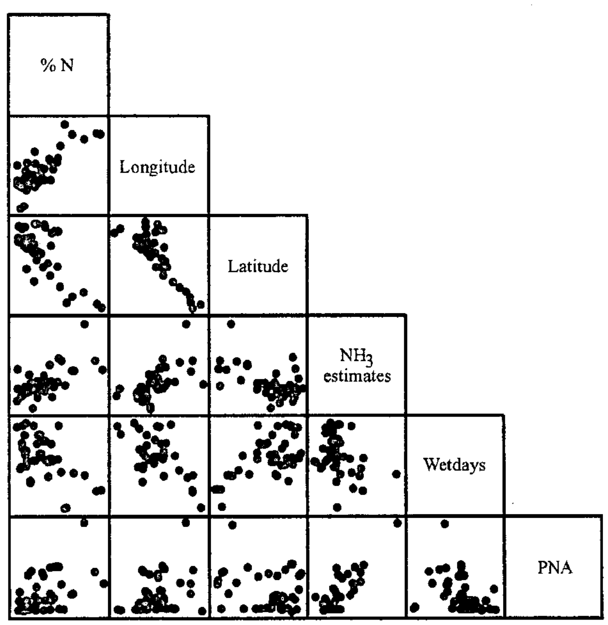

Figure 3 Bivariate scatterplots between select environmental variables.

Table III Results of stepwise linear regression (r^2 = 0.61) for nitrogen accumulation in lichen tissue after removing longitude and latitude from the dataset

Parameter	Coefficient	SE	t value	P value
Intercept	1.99	0.23	8.84	0.0000
NH_3 estimates	4.58	1.39	3.30	0.0023
Wetdays	−0.01	0.00	−4.14	0.0002
(NH_3 × wetdays)	−0.05	0.02	−2.62	0.0131

SE Standard error, *NH_3* ammonia estimates.

as did collections from plots in the middle Sierras (0.77 to 1.34). All tissue from the Southern Cascades and almost all plots from the northern half of the Sierra Nevada had comparatively low N content (0.68 to 0.90 and 0.73 to 1.04, respectively). The two plots at the northwestern extreme of the study area near Mt. Shasta also had low tissue N (0.67 and 0.71).

When considered independently as main effects, several predictors had appreciable linear correlations with tissue N (Table II and Figure 3), including longitude (r^2 = 0.64), latitude (r^2 = 0.52), NH_3 estimates (r^2 = 0.39), and wetdays (r^2 = 0.32). The best regression model, given all the data, consisted of a single predictor, longitude. After removal of longitude and latitude from the dataset, the second best regression model (r^2 = 0.61; Table III) included three variables: % N ~ 4.6(NH_3) − 0.01(wetdays) − 0.05(NH_3 × wetdays).

4 Discussion

The geographic variables longitude and latitude turned out to be strong predictors of % N (Table II and Figure 3). This result is evident from the distribution of tissue values (Figure 2) wherein the southwestern Sierra Nevada, a small area in the high Sierras near the Tahoe Basin, and the Modoc Plateau, are three apparent N hotspots arranged along the tilted axis of the study area. The majority of collections from these areas had N above the designated threshold value with the greatest exceedances occurring at the southernmost plots (which are, coincidentally, also the easternmost plots).

We did expect at least a moderate, positive relationship to estimates of NH_3 since it is a major N pollutant in much of the region (Bytnerowicz & Fenn, 1996; Bytnerowicz & Riechers, 1995; Bytnerowicz et al., 2002; Fenn et al., 2003a; 2003b). Minus the two geographic variables, NH_3 estimates made the next best predictor (Table II and Figure 3). The same basic geographic pattern was observed for NH_3 estimates and % N (Figure 2).

4.1 Sierra Nevada and Southern Cascades

The observed distribution of % N is generally in agreement with past N measurements from the Sierra Nevada and Southern Cascades (Figure 2). Monitoring data, although few, suggest highest deposition to southwestern forests bordering the intensely agricultural San Joaquin Valley and considerably lower N at more northerly sites (Blanchard & Michaels, 1994; Fenn et al., 2003a; 2003b; Jovan & McCune, 2006). Of particular concern is the high N content of tissue collected near Kings Canyon and Sequoia National Parks. Epiphytic macrolichen communities surveyed in and near the parks show evidence of elevated NH_3 (Jovan & McCune, 2006) while monitoring data from Sequoia detected elevated concentrations of several N pollutants (Bytnerowicz et al., 2002). Tissue from the site nearest Yosemite National Park was beneath the N threshold and NH_3 was estimated to be moderate, at worst. The lichen gradient model did suggest, however, relatively high NH_3 at more northern sites in and near the park for which we have no co-located tissue data.

4.2 Modoc Plateau

Nitrophyte-rich lichen communities suggest high NH_3 is reaching several plots in the Modoc Plateau, which may well be the primary contributor to the enhanced tissue N observed in this study (Figure 2; Jovan & McCune, 2006). Modoc forests are relatively remote from Central Valley emissions although there are local N sources from agriculture, a major industry in the region (Momsen, 2001). Unfortunately there are no direct N measurements to inform our interpretation, which is especially problematic since certain aspects of desert-like conditions affecting Modoc forests could hypothetically confound the lichen biomonitoring data. The dominance of nitrophytes, for instance, could be promoted via alkaline dust, an understudied phenomenon discussed by Jovan and McCune (2006). 'Enhanced' N accumulation could likewise be promoted via the exceptionally dry conditions or, more generally, stressful climatic conditions (discussed further in the "Sources of noise in the data Section 2"). As such, these data must be interpreted with utmost caution until corroborated by direct measurements.

4.3 Tahoe region

It's unclear how closely high tissue N at the two alpine sites (>2,400 m) in the mid Sierras is linked to pollution emissions from the nearby Lake Tahoe area (Figure 2). Atmospheric N is generally expected to be low in high-elevation Sierra forests (Fenn et al., 2003a; 2003b). Yet total N measured in the Tahoe Basin is on par with levels at southern Sierra forests that experts consider moderately polluted (Tarnay, Gertler, Blank, & Taylor, 2001). One site is near the city of South Lake Tahoe (% N = 1.16) but the second is approximately 40 km to the south in wilderness (1.34). Corresponding NH_3 estimates are fairly low (Figure 2; Jovan & McCune, 2006) possibly because oxidized N pollutants are dominant, at least in the basin (Tarnay et al., 2001). On the other hand, these were the two highest elevation sites in our sample and tissue condition at both was poor. A reasonable alternative explanation, thus, may be that stressful climatic conditions induced high N accumulation.

4.4 Sources of noise in the data

Environmental factors besides ambient concentration of N can affect accumulation in the thallus. Perhaps the most salient issue when dealing with such a large geographic scope is how local climate varies between sites. Bruteig (1993) proposed that favorable climatic conditions promoting faster lichen growth have a 'diluting' effect on % N. In such cases tissue N would be lower than expected for a given level of deposition. It is possible, then, that stressful conditions at the alpine sites near Tahoe may have biased % N high. It is also possible that there is an upward bias in % N at dry sites (e.g., forests of the Modoc Plateau), perhaps reflected by (1) the appreciable correlation of annual wetdays and (2) suggestion from the second regression model that wetdays and NH_3 interact to influence N accumulation (Table III).

We must consider that moisture regime, while certainly a key component of climatic favorability for lichens, may be important for a second reason. As N is mobile in the lichen thallus, major moisture differences could result in differential levels of N-leaching among plots. As noted by Blett et al. (2003) tissue collections are ideally collected from within the same precipitation regime. We probably evaded much of the short-term seasonal variability between sites by collecting during the dry season. Precipitation and number of wetdays both varied minimally across the study area around the time of tissue collection. If anything, it seems more likely that long-term moisture differences would be a more important source of noise via influence on growth rate as proposed by Bruteig (1993).

5 Conclusions

We do expect that tissue N is reflecting at least the coarser N deposition patterns in the greater Sierra Nevada. But without any co-located N deposition measurements to calibrate tissue data, we cannot fully investigate the importance of climate as suggested by our models. Thus, these data should be regarded as a preliminary assessment intended to steer more focused study of N enrichment. Results will serve as baseline data for tracking N trends with *L. vulpina* tissue.

Lichen gradient models used in tandem with tissue analysis can help land managers rapidly evaluate stand exposure to poor air quality and assess the risk of ecological degradation. Without collections from urban areas, we may be missing the most extreme N deposition hotspots. Still, an important consideration is that the capacity for a forest ecosystem to assimilate additional N inputs varies widely. The greatest ecological impacts from N fertilization need not occur where deposition is highest. Alpine and sub-alpine stands, for instance, are expected to be much more sensitive due to lower biotic activity (Fenn et al., 2003a; 2003b).

Acknowledgments We gratefully acknowledge Trent Proctor and the Region 5 Air Quality Program of the United States Forest Service for advising and providing financial support for this project. The Pacific Northwest Research Station gave additional support and Station employee Erica Hansen provided us with FIA site data. Lisa Hoover of Six Rivers National Forest adjusted work schedules so the second author could participate in field work. We thank Bruce McCune, Sally Campbell, and Sue Willits for giving feedback on drafts of the manuscript.

References

Addison, P. A., & Puckett, K. J. (1980). Deposition of atmospheric pollutants as measured by lichen element content in the Athabasca oil sands area. *Canadian Journal of Botany, 58*, 2323–2334.

Bailey, R. G. (1983). Delineation of ecosystem regions. *Environmental Management, 7*, 365–373.

Bargagli, R., & Mikhailova, I. (2002). Accumulation of inorganic contaminants. In P. L. Nimis, C. Scheidegger, & P. A. Wolseley (Eds.), *Monitoring with lichens–Monitoring lichens*, NATO Science Series. IV. Earth and Environmental Sciences (pp. 65–84). Dordrecht, The Netherlands: Kluwer.

Blanchard, C. L., & Michaels, H. (1994). *Regional estimates of acid deposition fluxes in California.* Final Report no. A132–149. Air Resources Board, Sacramento, California, USA, 98 pp.

Blett, T., Geiser, L., & Porter, E. (2003). *Air pollution-related lichen monitoring in national parks, forests, and refuges: Guidelines for studies intended for regulatory and management purposes.* Technical Report, NPS-D2292, US Department of the Interior National Park Service Air Resources Division and US Fish and Wildlife Service Air Quality Branch, US Department of Agriculture, US Forest Service.

Bruteig, I. E. (1993). The epiphytic lichen *Hypogymnia physodes* as a biomonitor of atmospheric nitrogen and sulphur deposition in Norway. *Environmental Monitoring and Assessment, 26*, 27–47.

Bytnerowicz, A., & Fenn, M. (1996). Nitrogen deposition in California forests: A review. *Environmental Pollution, 92*, 127–146.

Bytnerowicz, A., & Riechers, G. (1995). Nitrogenous air pollutants in a mixed conifer stand of the western Sierra Nevada, California. *Atmospheric Environment, 29*, 1369–1377.

Bytnerowicz, A., Tausz, M., Alonso, R., Jones, D., Johnson, R., & Grulke, N. (2002). Summer-time distribution of air pollutants in Sequoia National Park, California. *Environmental Pollution, 118*, 187–203.

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

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

Daly, C., Taylor, G. H., Gibson, W. P., Parzybok, T. W., Johnson, G. L., & Pasteris, P. (2001). High-quality spatial climate data sets for the United States and beyond. *Transactions of the American Society of Agricultural Engineers, 43*, 1957–1962.

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

De Bakker, A. J. (1989). Effects of ammonia emission on epiphytic lichen vegetation. *Acta Botanica Neerlandica, 38*, 337–342.

Fenn, M. E., Haeuber, R., Tonnesen, G. S., Baron, J. S., Grossman-Clarke, S., Hope, D., et al. (2003a). Nitrogen emissions, deposition, and monitoring in the Western United States. *Bioscience, 53*, 391–403.

Fenn, M. E., Poth, M. A., Bytnerowicz, A., Sickman, J. O., & Takemoto, B. K. (2003b). Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. In A. Bytnerowicz, M. J. Arbaugh, & R. Alonso (Eds.), *Ozone air pollution in the Sierra Nevada–Distribution and effects on forests* (pp. 111–155). Oxford, UK: Elsevier.

Geiser, L. (2004). *Manual for monitoring air quality using lichens on national forests of the Pacific Northwest.* Technical Paper, R6-NR-AQ-TP-1-04, USDA Forest Service Pacific Northwest Region, 126 pp.

Geiser, L. H., & Neitlich, P. N. (2006). Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens. *Environmental Pollution* (in press).

Gombert, S., Asta, J., & Seaward, M. R. D. (2003). Correlation between the nitrogen concentration of two epiphytic lichens and the traffic density in an urban area. *Environmental Pollution, 123*, 281–290.

Insightful Corporation (2000). S-Plus, Professional Release 3, Seattle, Washington, USA.

Jovan, S., & McCune, B. (2005). Air-quality bioindication in the greater Central Valley of California, with epiphytic macrolichen communities. *Ecological Applications, 15*, 1712–1726.

Jovan, S., & McCune, B. (2006). Using epiphytic macrolichen communities for biomonitoring ammonia in forests of the greater Sierra Nevada, California. *Water, Air, and Soil Pollution, 170*, 69–93.

McCune, B., Dey, J. P., Peck, J. E., Cassell, D., Heiman, K., Will-Wolf, S., et al. (1997). Repeatability of community data: Species richness versus gradient scores in large-scale lichen studies. *The Bryologist, 100*, 40–46.

McCune, B., & Geiser, L. (1997). *Macrolichens of the Pacific Northwest.* Corvallis, Oregon, USA: Oregon State University Press, p. 386.

Momsen, J. H. (2001). Agriculture in the Sierra, in *Status of the Sierra Nevada*, US Geological Survey Digital Data Series, Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II, University of California Centers for Water and Wildland Resources, Davis, California, USA, pp. 497–528. http://ceres.ca.gov/snep/pubs/web/PDF/VII_C17.PDF.

Søchting, U. (1995). Lichens as monitors of nitrogen deposition. *Cryptogamic Botany, 5*, 264–269.

Tarnay, L., Gertler, A. W., Blank, R. R., & Taylor, G. E. Jr. (2001). Preliminary measurements of summer nitric acid and ammonia concentrations in the Lake Tahoe Basin air-shed: Implications for dry deposition of atmospheric nitrogen. *Environmental Pollution, 113*, 145–153.

Van Herk, C. M. (1999). Mapping of ammonia pollution with epiphytic lichens in The Netherlands. *Lichenologist, 31*, 9–20.

Van Herk, C. M. (2001). Bark pH and susceptibility to toxic air pollutants as independent causes of changes in epiphytic lichen composition in space and time. *Lichenologist, 33*, 419–441.