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Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA

Linda H. Geiser^{a,*}, Sarah E. Jovan^b, Doug A. Glavich^a, Matthew K. Porter^{c,1}^a US Forest Service Pacific Northwest Region Air Resource Management Program, Siuslaw National Forest, PO Box 1148, Corvallis, OR 97339, USA^b US Forest Service Forest Inventory and Analysis Program, Pacific Northwest Research Station, 620 SW Main St, Suite 400, Portland, OR 97205, USA^c Laboratory for Atmospheric Research, Washington State University, Pullman, WA 99164, USA*Lichen-based critical loads for N deposition in western Oregon and Washington forests ranged from 3 to 9 kg ha⁻¹ y⁻¹, increasing with mean annual precipitation.*

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ABSTRACT

Critical loads (CLs) define maximum atmospheric deposition levels apparently preventative of ecosystem harm. We present first nitrogen CLs for northwestern North America's maritime forests. Using multiple linear regression, we related epiphytic-macrolichen community composition to: 1) wet deposition from the National Atmospheric Deposition Program, 2) wet, dry, and total N deposition from the Communities Multi-Scale Air Quality model, and 3) ambient particulate N from Interagency Monitoring of Protected Visual Environments (IMPROVE). Sensitive species declines of 20–40% were associated with CLs of 1–4 and 3–9 kg N ha⁻¹ y⁻¹ in wet and total deposition. CLs increased with precipitation across the landscape, presumably from dilution or leaching of depositional N. Tight linear correlation between lichen and IMPROVE data suggests a simple screening tool for CL exceedance in US Class I areas. The total N model replicated several US and European lichen CLs and may therefore be helpful in estimating other temperate-forest lichen CLs.

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1. Introduction

About 13 years ago, Vitousek et al. (1997) focused international attention on the profound ecological consequences of increasing anthropogenic releases of nitrogen (N). An essential macronutrient, small enhancements in N availability benefit biota in N-limited ecosystems. Thresholds between harmless and harmful amounts of deposition mark critical loads (CLs), providing regulators and decision-makers with benchmarks for pollutant emission reduction strategies (Porter et al., 2005; Burns et al., 2008). This paper reports first CLs for the North American West Coast Marine Forests (WCMF) ecological region (CEC 1997; Fig. 1).

'Critical load' is defined as 'the quantitative exposure to one or more pollutants below which significant harmful effects on sensitive elements of the environment do not occur, according to present knowledge' (Nilsson and Grennfelt, 1988). N deposition CLs are usually reported in kg ha⁻¹ y⁻¹. The European 1988 Sofia Protocol

first adopted CLs as a guide to air pollution policy. Later, CLs facilitated the selection of emissions reduction targets by the UN Economic Commission Convention on Long-Range Transboundary Air Pollution. US CLs have been reported for various ecosystems (Pardo and Driscoll, 1996; Williams and Tonnessen, 2000; Baron, 2006; Bowman et al., 2006; Fenn et al., 2008; Pardo et al., in press). The first regulatory application of CLs was achieved in Rocky Mountain National Park (Porter and Johnson, 2007) and the Environmental Protection Agency now allows states CL-based management approaches to the NO₂ Increment Rule (Burns et al., 2008).

Composition or cover changes in vegetative communities indicate CL exceedance for terrestrial ecosystems (Bobbink et al., 2003; Pardo et al., in press). Among lichens, oligotrophs (a.k.a. acidophytes) are adapted to environments with low nutrient availability, mesotrophs (a.k.a. neutrophytes) have moderate N requirements, and eutrophs (a.k.a. nitrophiles) thrive in nutrient-rich environments. Their relative dominance shifts with nutrient-N deposition, allowing characterization of community effects and ecological harm (McCune and Geiser, 2009; Jovan, 2008; Sparrius, 2007; Van Herk et al., 2003; Sutton et al., 2009; Mitchell et al., 2005). In contrast, acidic and oxidizing forms of N are broadly toxic and tend to reduce species richness (Davies et al. 2007;

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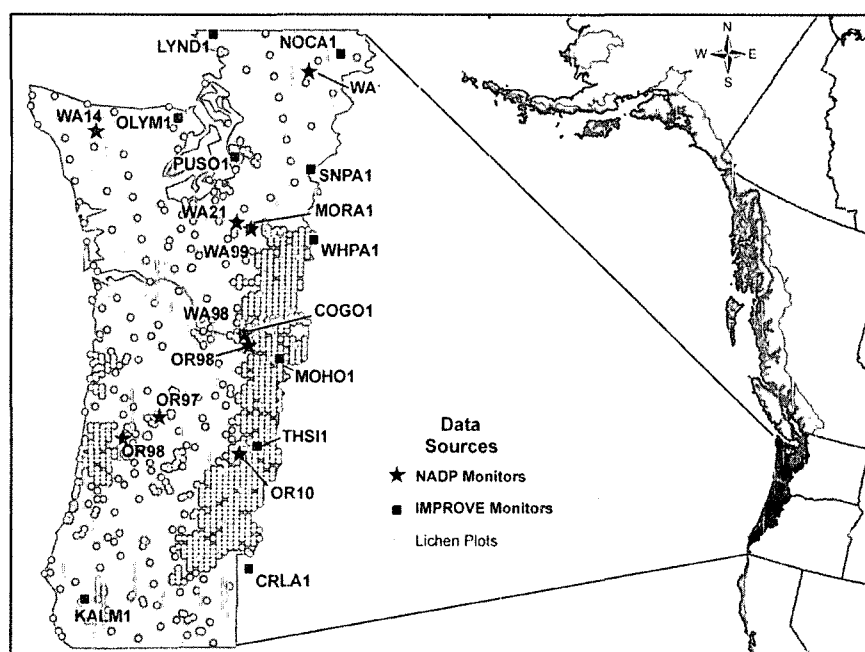


Fig. 1. Map of the study area with monitor and lichen plot locations. Modeled estimates of total N deposition were calculated for all lichen plots. The study area comprises the Oregon/Washington component of the North American West Coast Marine Forests ecological region, shaded in light and dark gray, respectively, in the map to the right. Note: IMPROVE site codes end in '1'.

Riddell et al. 2008). Because lichens are highly N-sensitive, lichen-based CLs help identify deposition targets conveying ecosystem-wide protection.

Within WCMF, epiphytic macrolichens have been widely used to monitor air quality (Geiser and Neitlich, 2007; Jovan, 2008; Dillman et al., 2007). The extensive coniferous rainforests provide ideal habitat for oligotrophs; drier valleys offer comparatively mesic environments, and nutrient-enriched habitats like animal perches,

seashores and, now, anthropogenically N-enhanced forests of urban and agricultural areas, favor eutrophs. Western Oregon and Washington lichen communities shifts from oligotroph- to eutroph-dominated across an N gradient (Geiser and Neitlich, 2007) spanning roughly $0.8\text{--}8\text{ kg total N deposition ha}^{-1}\text{y}^{-1}$ (Porter, 2007). N effects are primarily due to nutrient enrichment rather than acidification; 1994–2002 yearly mean precipitation pH at regional monitors was 5.0–5.5 (NADP, 2010).

Table 1

Summary of N deposition data sources, compounds measured, monitor locations, years of data used, and number of associated lichen survey sites.

Data source	N compounds measured	Monitor locations ^a	Monitor code	Elev. (m)	Latitude	Longitude	N data years	No. of lichen plots
NADP	Mean annual wet deposition ($\text{kg ha}^{-1}\text{y}^{-1}$) of N from NH_4^+ and NO_3^-	North Cascades NP, WA	WA19	123	48.5406	–121.4453	1994–2004	6
		Olympic NP, WA	WA14	176	47.8600	–123.9319	1994–2004	6
		UW Pack Forest, Eatonville, WA	WA21	617	46.8353	–122.2867	1994–2004	6
		Mount Rainier NP, WA	WA99	421	46.7614	–122.1217	1999–2004	6
		Mt Zion, CRGNSA, WA	WA98	238	45.5639	–122.2089	2002–2004	3
		Bull Run, Mt Hood NF, OR	OR98	267	45.4478	–122.1481	1994–2004	3
		OSU Hyslop Farm, Willamette Valley, OR	OR97	69	44.6347	–123.1900	1994–2004	6
		Alsea Guard Station, Siuslaw NF, OR	OR02	104	44.3856	–123.6153	1994–2004	6
		Andrews Exptl Forest, Willamette NF, OR	OR10	436	44.2122	–122.2558	1994–2004	6
		Lynden, WA	LYND1	28	48.9533	–122.5586	1996–1997	2
IMPROVE	Mean annual concentrations of N ($\mu\text{g m}^{-3}$) from NH_4NO_3 and $(\text{NH}_4)_2\text{SO}_4$ in ambient < 2.5 μm diameter particulates	North Cascades NP, WA	NOCA1	569	48.7316	–121.0646	2001–2004	6
		Olympic NP, WA	OLYM1	600	48.0065	–122.9727	2002–2004	6
		Seattle, WA	PUSO1	98	47.5696	–122.3119	2002–2004	7
		Snoqualmie Pass, MBS NF, WA	SNPA1	1049	47.4220	–121.4259	1997–2004	2
		Mount Rainier NP, WA	MORA1	439	46.7583	–122.1244	1994–2004	6
		White Pass, Gifford-Pinchot NF, WA	WHPA1	1827	46.6243	–121.3881	2001–2004	8
		Mt Zion, CRGNSA, WA	COGO1	179	45.6644	–121.0008	2002–2004	7
		Mt Hood W, Mt Hood NF, OR	MOHO1	1531	45.2888	–121.7837	2001–2004	5
		3 Sisters W, Willamette NF, OR	THSI1	885	44.2910	–122.0434	1995–2004	8
		Crater Lake NP, OR	CRLA1	1996	42.8958	–122.1361	1994–2004	5
CMAQ	Mean annual wet, dry and total N deposition ($\text{kg ha}^{-1}\text{y}^{-1}$) ^b	Kalmiopsis W, Siskiyou NF, OR	KALM1	80	42.5520	–124.0589	2001–2004	7
		Lichen plot coordinates overlaid on 36-km grid of modeled N deposition	—	0–2590	Study area	Study area	1990–1999	1411

^a MBS = Mt. Baker-Snoqualmie; NF = National Forest; NP = National Park; OR = Oregon; OSU = Oregon State University; UW = University of Washington; W = Wilderness; WA = Washington.

^b Sum of N from HNO_3 , NH_3 , NO_2 , PAN, NO, RNO_3 , PAN2, N_2O_5 , HONO, ANH_4I , MA-PAN, ANO_3I , PBZN, ANO_3J , and ANH_4J .

Table 2

N-indicator assignments of western Oregon and Washington lichen epiphytes following McCune and Geiser (2009).

Oligotrophs				Eutrophs			
Ahtiana		<i>metaphysodes</i>	<i>crocata</i>	Candelaria		<i>tubulosa</i>	
<i>sphaerosporella</i>	Hypotrachyna	<i>sinuosa</i>	Ramalina	Leptogium		<i>furfuraceum</i>	
Alectoria	Leioderma	<i>sorediatum</i>	<i>menziesii</i>	<i>polycarpum</i>		Letharia	
<i>imshaugii</i>	Leptogium	<i>brebissonii</i>	<i>pollinaria</i>	<i>columbiana</i>		Lobaria	
<i>sarmentosa</i>	<i>lichenoides</i>	<i>palmatum</i>	<i>roesleri</i>	<i>hallii</i>		<i>scrobiculata</i>	
<i>vancouverensis</i>	Letharia	<i>vulpina</i>	<i>thrausta</i>	Melanelixia		<i>glabra</i>	
Bryoria	Lichinodium	<i>canadense</i>	Sphaerophorus	Melanohalea		<i>exasperatula</i>	
<i>bicolor</i>	Lobaria	<i>oregana</i>	<i>globosus</i>	<i>subolivacea</i>		Nephroma	
<i>fremontii</i>	<i>pulmonaria</i>	Menegazzia	Sticta	<i>occultum</i>		<i>parile</i>	
<i>furcellata</i>	Nepiroma	<i>terebata</i>	<i>fuliginosa</i>	Nodobryoria		<i>abbreviata</i>	
<i>fuscescens</i>	<i>bellum</i>	<i>helveticum</i>	<i>limbata</i>	<i>oregana</i>		Parmelia	
<i>glabra</i>	<i>laevigatum</i>	<i>resupinatum</i>	<i>weigeli</i>	<i>hygrophila</i>		Parmeliopsis	
<i>pseudocapillaris</i>	Niebla	<i>cephalota</i>	Usnea	<i>hyperopta</i>		Peltigera	
<i>pseudofuscescens</i>	Parmelia	<i>pseudosulcata</i>	<i>cornuta</i>	<i>collina</i>		Physcia	
<i>spiralisfera</i>	Parmeliopsis	<i>squarrosa</i>	<i>filipendula</i>	<i>stellaris</i>		Physconia	
Cavernularia	<i>ambigua</i>	Parmotrema	<i>hirta</i>	<i>americana</i>		<i>isidiigera</i>	
<i>hultenii</i>	<i>arnoldii</i>	<i>chinense</i>	<i>longissima</i>	Platismatia		<i>glauca</i>	
<i>lophyrea</i>	<i>crinitum</i>	Peltigera	<i>rubicunda</i>	<i>herrei</i>		<i>stenophylla</i>	
Cetraria	<i>britannica</i>	<i>pyxidata</i>	<i>scabrata</i>	Pseudocyphellaria		<i>rainierensis</i>	
<i>californica</i>	<i>membranacea</i>	<i>umbricola</i>	<i>schadenbergiana</i>	Sulcaria		<i>badia</i>	
<i>merrillii</i>	<i>neopolydactyla</i>	Platismatia	<i>wirthii</i>	Usnea		<i>cavernosa</i>	
<i>orbata</i>	<i>lacunosa</i>	Polychidium	Vulpicida	<i>glabrescens</i>		<i>laponica</i>	
<i>pallidula</i>	<i>contortum</i>	Pseudocyphellaria	<i>canadensis</i>				
<i>platyphylla</i>	<i>anomala</i>						
Cladonia	<i>anthraspis</i>						
<i>bellidiflora</i>							
<i>carneola</i>							
<i>furcata</i>							
<i>norvegica</i>							
<i>transcendens</i>							
<i>verruculosa</i>							
Erioderma							
<i>sorediatum</i>							
Esslingeriana							
<i>idahoensis</i>							
Fuscopannaria							
<i>pacifica</i>							
Heteroderma							
<i>leucomela</i>							
Hypogymnia							
<i>apinnata</i>							
<i>duplicata</i>							
<i>enteromorpha</i>							
<i>heterophylla</i>							
<i>imshaugii</i>							

The primary objectives of this work are to:

- 1) Use existing lichen community and N deposition data to calculate empirical CLs applicable to the WCMF eco-region.
- 2) Assess the role of precipitation in epiphyte-based CLs.
- 3) Use epiphyte-based CLs derived for other temperate-forest eco-regions to test the broader applicability of our CL calculation techniques.

2. Material and methods

2.1. Study area

The study area (Fig. 1) encompasses western Oregon and Washington from the Cascades crest to the Pacific Ocean. With northwestern California, it comprises the southernmost section of the vast West Coast Marine Forests ecological region (CEC, 1997), a mountainous area containing all North America's temperate, coniferous rainforests. The oceanic influence causes high precipitation (44 to >500 cm), long growing seasons, and moderate mean annual temperatures (5–9 °C). Rainforests are dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea sitchensis*, and *Alnus rubra*; high elevation and sub-alpine dominants are *Abies amabilis*, *Abies procera*, and *Tsuga mertensiana*. In drier rain-shadows, *Quercus garryana* and *Arbutus menziesii* co-occur with *P. menziesii*. Most N emissions originate from urban, industrial, and agricultural activities in the Puget Trough and Willamette Valley. Of the pollutants affecting lichens, nutrient-N is dominant. The study area is generally representative of

N-deposition and precipitation ranges observed within the broader WCMF eco-region.

2.2. Data sources

2.2.1. Lichen community data

Lichen responses to N were derived from community surveys at 1411 circular 0.38 ha plots. Surveys were conducted from 1994 to 2002 by the US Forest Service Forest Inventory and Analysis (FIA) and Pacific Northwest Regional Air Resource Management programs. Plots are on a 23 km grid, with higher intensity sampling in some national forests and urban areas (Fig. 1). Field protocols followed FIA (2006). Briefly, each plot was surveyed for up to 2 h by a trained observer who collected each epiphytic-macrolichen species detected and assigned an ocular abundance rating. Taxonomists identified all collections. Additional environmental data included climate, air pollution, stand structure, and stand composition variables.

Patterns in lichen community composition were distilled into 'air scores' by Geiser and Neitlich (2007) using non-metric multi-dimensional scaling to ordinate plots. Vector overlays of environmental variables revealed two strong axes (i.e. gradients) in community composition that clearly separated lichen response to air quality from climatic factors, especially temperature. Close correlations to the best measures of pollution available included: lichen N (dw %N), ammonium wet deposition (mg L⁻¹), and location in an urban area. 'Air scores' are thus scores assigned to each plot based on its community composition, equal to its position along the N-based air quality axis.

2.2.2. Atmospheric data

NADP: There were nine National Atmospheric Deposition Program precipitation collection monitors in the study area (Fig. 1, Table 1). Weekly precipitation from 1994

to 2002 was analyzed at the NADP Central Analytical Laboratory. Mean annual wet deposition of inorganic N (kg ha^{-1}) data meeting quality control criteria for reporting were downloaded from the NADP (2010) website.

IMPROVE: There were twelve Interagency Monitoring of Protected Visual Environments (IMPROVE) monitors in the study area (Fig. 1, Table 1). IMPROVE measures nitrate and sulfate concentrations in fine particulates ($<2.5 \mu\text{m}$) every third day for 24 h; both cations are presumed balanced by ammonium ions (IMPROVE 1995). Data for 1994–2002 were obtained from http://vista.cira.colostate.edu/Data/IMPROVE/RHR/group_means_nia_20060306-5.csv. N concentration ($\mu\text{g m}^{-3} \text{y}^{-1}$) at each monitor was calculated by averaging mean annual concentrations of N from NH_4NO_3 and $(\text{NH}_4)_2\text{SO}_4$.

CMAQ: N deposition was simulated at Washington State University Laboratory for Atmospheric Research by Porter (2007) using the Community Multi-Scale Air Quality (CMAQ) atmospheric chemistry and transport model. CMAQ (Byun and Schere, 2006) is a community-supported modeling code applicable to various time and geographic domains. Each project uses unique meteorological simulations and emissions processing and accounts for terrain, land cover, land use, atmospheric physics and chemistry, meteorology, climate, and anthropogenic and biogenic emissions. Model output consisted of wet and dry deposition ($\text{kg N ha}^{-1} \text{y}^{-1}$) of 16 N-containing air pollutants (Table 1) for 1990–1999 on a 36-km^2 grid. Grid values were averaged by month and year to estimate mean annual deposition of wet, dry and total N for each grid cell.

Precipitation: We used output from PRISM (2009), the parameter–elevation regressions on individual slopes model (Daly et al., 2000), and ArcGIS 9.2 software (ESRI, 2007) to estimate precipitation from a 1961–1990 2-km^2 grid of mean annual precipitation at all lichen plot coordinates.

2.2.3. Data integration

Mean annual wet, dry, and total N depositions were estimated at lichen plot coordinates from CMAQ model output grids. Each NADP and IMPROVE monitor was associated with a subset of lichen plots occurring $\leq 8\text{ km}$ away (Table 1). Air scores of associated lichen plots were averaged to create one air score per IMPROVE monitor. To retain plot precipitation, air scores associated with NADP monitors were not averaged.

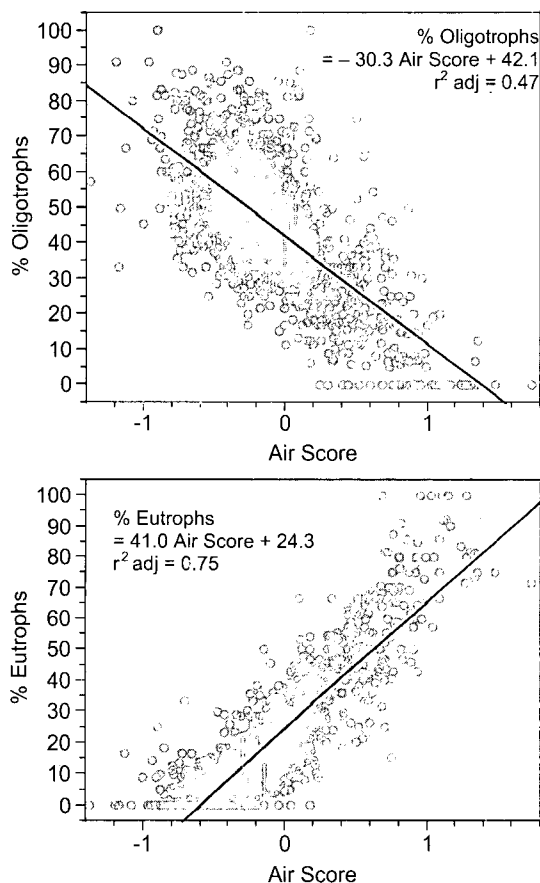


Fig. 2. Relationship between air scores and lichen community composition. As air score increases, the relative contribution (%) of oligotrophs to total species richness decreases while that of eutrophs increases.

2.3. Data analyses

To develop a CL, we followed the three step process recommended by Porter et al. (2005): 1) select a biological response and the response threshold above which a harmful effect can be demonstrated, 2) model the mathematical relationship between deposition and biological response, and 3), use the model to calculate the CL at the response threshold. Statistical analyses were performed with JMP Statistical Discovery Software 5.0 (SAS Institute Inc., Cary, NC).

2.3.1. Selecting a biological response and response threshold

We selected 'air score' as our biological response because it is a quantitative measure of lichen community composition along an N deposition gradient. To find a score marking the transition between natural 'clean-air' to N-compromised communities we compared the individual contributions of oligotrophs, mesotrophs and eutrophs (Table 2) as a mean percentage of total species richness in each of six biologically-derived divisions of air scores created by Geiser and Neitlich (2007).

2.3.2. Modeling the relationship between N and lichen response

Linear regression was used to quantify relationships between N measures and lichen response. Geiser and Neitlich (2007) reported a good correlation between air scores and ammonium wet deposition concentrations (mg L^{-1}) but not loading ($\text{kg ha}^{-1} \text{y}^{-1}$). Because loading is a function of both N concentration and precipitation volume, we tested both a simple model (Eq. (1)) and a model accounting for precipitation (Eq. (2)) for each N measure:

$$\text{air score} = \beta_0 + \beta_1 \times \text{N measure}, \text{ and} \quad (1)$$

$$\text{air score} = \beta_0 + \beta_1 \times \text{precipitation} + \beta_2 \times \text{N measure}, \quad (2)$$

where β_0 is the y-axis intercept; β_1 and β_2 are unitless regression coefficients. For 'N measure' we tested five variables: CMAQ wet, dry, and total N deposition, NADP wet N deposition, and IMPROVE fine particulate N concentration. N measurement units were $\text{kg ha}^{-1} \text{y}^{-1}$ except IMPROVE data which were $\mu\text{g m}^{-3} \text{y}^{-1}$. Precipitation units were cm. An F-test was performed and non-significant variables ($p > 0.05$) were dropped.

2.3.3. Calculating the critical load at the response threshold

To calculate the CLs, we selected the regression equation for each N measure with the best-fit (highest adjusted r^2) to lichen response. We then solved for N at the lichen response threshold (i.e., the air score we selected to best represent transition from a natural to an N-compromised community composition) and calculated 95% confidence intervals.

2.3.4. Mapping areas of critical load exceedance

We used the best regression equation for CMAQ total N deposition to calculate a CL for each 2-km^2 precipitation grid cell in the study area. We then mapped CLs across the study area for each 50 cm precipitation interval. To show areas of CL exceedance as of the year 2002, we circumscribed areas in which air scores exceeded the lichen response threshold, utilizing the kriged interpolation calculated by Geiser and Neitlich (2007).

3. Results

3.1. Lichen response threshold

Because the lichen community response to N is continuous (Fig. 2), choosing a response threshold is essentially a judgment call. Table 3 summarizes N-indicator changes across the six air score divisions. The first two divisions represent the least polluted

Table 3

Step 1: Select a biological response threshold. Air score ranges and relative contribution of oligotrophs, mesotrophs, and eutrophs to species richness within divisions assigned by Geiser and Neitlich (2007). Division 6 was divided here to distinguish highest N deposition sites. N = number of surveys; (s.d.) = standard deviation.

Division	Air score range	N	% Oligotrophs mean (s.d.)	% Oligotrophs & mesotrophs mean (s.d.)	% Eutrophs mean (s.d.)
1	−1.40 to −0.11	845	53 (13)	91 (7)	9 (7)
2	>−0.11−0.02	215	44 (11)	80 (8)	20 (8)
3	>0.02−0.21	212	41 (14)	73 (10)	27 (10)
4	>0.21−0.33	50	30 (14)	66 (11)	34 (11)
5	>0.33−0.49	55	25 (12)	53 (10)	47 (10)
6A	>0.49−1.00	117	21 (15)	43 (2)	57 (17)
6B	>1.00−2.0	25	3 (6)	17 (12)	83 (12)

Table 4

Step 2: Model the relationship between N deposition and lichen response. Best-fit linear regression models of nitrogen deposition (as estimated by CMAQ, NADP, or IMPROVE) and lichen response (air score). Number of lichen surveys used to derive models: CMAQ (1411), NADP (48), IMPROVE (69). See also Table 1.

Data Source	Eq	Model	r^2 adj.	Term	Estimate	S.e.	t Ratio	Prob > t
CMAQ	1	Air Score = $\beta_0 + \beta_1$ Precip (cm) + β_2 Total Inorg N (kg ha ⁻¹ y ⁻¹)	0.35	β_0	-0.0918	0.0323	-2.84	0.0046
				β_1	-0.0024	0.0001	-18.26	<.0001
				β_2	0.1493	0.0068	21.86	<.0001
	2	Air Score = $\beta_0 + \beta_1$ Precip (cm) + β_2 DRY Inorg N (kg ha ⁻¹ y ⁻¹)	0.37	β_0	-0.1106	0.0318	-3.48	0.0005
				β_1	-0.0021	0.0001	-16.08	<.0001
				β_2	0.2063	0.0089	23.17	<.0001
NADP	3	Air Score = $\beta_0 + \beta_1$ Precip (cm) + β_2 WET Inorg N (kg ha ⁻¹ y ⁻¹)	0.23	β_0	0.1152	0.0324	3.56	0.0004
				β_1	-0.0028	0.0001	-19.26	<.0001
				β_2	0.3149	0.0235	13.41	<.0001
	4	Air Score = $\beta_0 + \beta_1$ Precip (cm) + β_2 WET Inorg N from NO ₃ ⁻ & NH ₄ ⁺ (kg ha ⁻¹ y ⁻¹)	0.64	β_0	0.6857	0.1616	4.24	0.0001
				β_1	-0.0044	0.0005	-8.44	<.0001
				β_2	0.2133	0.0733	2.91	0.0058
IMPROVE	5	Air Score = $\beta_0 + \beta_1$ Ambient fine particulate N from AmmNO ₃ & AmmSO ₄ (μg m ⁻³ y ⁻¹)	0.93	β_0	-0.7565	0.0711	-10.65	<.0001
				β_1	1.9030	0.1604	11.86	<.0001

sites in the study region and communities were, on average, strongly dominated by oligotrophs and mesotrophs (80–91%) with only a minor eutroph component (9–20%). The last two air score divisions (5–6), primarily urban and agriculturally influenced sites, were dominated or nearly dominated by eutrophs.

Assuming that communities in the first two divisions are little affected by air pollution and that those in the last two divisions have shifted in a detrimental way, we selected the air score dividing the third and fourth divisions, 0.21, as the lichen response threshold. This range corresponds to a community composition in which the oligotroph contribution to species richness has declined by about 33–43%, combined oligotroph plus mesotroph contributions have declined 20–27% and eutroph contribution has increased 3–4-fold (but is still not the dominant component). Some may argue this threshold allows too much or too little change. But with the regression equations provided below, CL may be recalculated for any air score.

3.2. Modeled relationships between N and lichen response

Table 4 presents final regression models relating N deposition measures to air score. Accounting for precipitation improved the models for NADP and CMAQ but not IMPROVE data. T-test results for all models were highly significant ($p < 0.005$). Correlation coefficients were strongest for IMPROVE, intermediate for NADP and weakest for CMAQ data.

3.3. Critical loads

Table 5 presents CLs for depositional N and a critical level for N in ambient-air fine particulates. CLs for CMAQ estimates of total N deposition ranged from 2.7 to 9.2 kg ha⁻¹ y⁻¹, increasing over an approximately 10-fold range in mean annual precipitation. Dry

deposition CLs also increased with precipitation from 2.0 to 6.1 kg ha⁻¹ y⁻¹. Total deposition CLs were roughly twice as large as wet deposition CLs at mean to maximum precipitation ranges, but were more than twice as large at minimum precipitation. Therefore, dry deposition made a greater relative contribution to total deposition, and to the CL, in drier parts of the study area. Similar wet deposition CLs were generated by the CMAQ and NADP models at low to moderate precipitation; the NADP model predicted higher CLs at maximum precipitation. The IMPROVE model (Fig. 3) generated a critical level of 0.51 μg m⁻³ for mean annual concentration of N in ambient-air fine particulates.

3.4. Relative contribution of different N components

Across the study area, CMAQ total deposition estimates ranged from 0.8 to 8.2 kg N ha⁻¹ y⁻¹; median 2.4 (Table 6). Wet deposition contributed 21–64% of total N deposition, roughly correlated with increasing precipitation. Primary components of wet deposition were ammonium and nitrate; primary components of dry deposition were nitric acid, ammonia, and nitrogen dioxide. These five compounds contributed on average 99% and 80% of total wet and dry depositional N, respectively. Because each of the five compounds was strongly linearly correlated with at least two others ($r^2 = 0.32$ – 0.91), we did not attempt to analyze their individual contributions to lichen response other than as sums of wet, dry, and total N compounds. However, nutrient-N generally comprised 60–90% of total N deposition, and maximum deposition from HNO₃ was 1.3 kg N ha⁻¹ y⁻¹.

3.5. Geographic areas exceeding lichen-based critical loads

Fig. 4 maps CLs across the study area, applying the CMAQ total N regression model (Table 4, Eq. (1)) across 50 cm increments of

Table 5

Step 3: Calculate the critical load. Estimated critical loads/levels and 95% confidence intervals (CI) for N in western Oregon and Washington. Values were calculated from regression models (Table 4) at the lichen response threshold, air score = 0.21, for minimum (44), median (186), and maximum (451) mean annual precipitation (cm) in the study area. Sample sizes as in Table 4.

Measure	Data source	N measure	CL (95% CI)	CL (95% CI) at min. precip.	CL (95% CI) at median precip.	CL (95% CI) at max. precip.
Critical load	CMAQ	kg total N ha ⁻¹ y ⁻¹	2.7–9.2 (0–13.5)	2.7 (0–7.0)	5.0 (0.8–9.2)	9.2 (5.0–13.5)
		kg dry N ha ⁻¹ y ⁻¹	2.0–6.2 (0–9.1)	2.0 (0–5.0)	3.4 (0.4–6.4)	6.1 (3.1–9.1)
		kg wet N ha ⁻¹ y ⁻¹	0.7–4.4 (0–6.5)	0.7 (0–2.9)	2.0 (0–4.2)	4.4 (2.2–6.5)
		kg wet N ha ⁻¹ y ⁻¹	0.0–7.0 (0–9.6)	0 (0–1.3)	1.6 (0–4.2)	7.0 (4.4–9.6)
Critical level	IMPROVE	Ambient atmospheric N from AmmNO ₃ & AmmSO ₄ in PM _{2.5} (μg m ⁻³ y ⁻¹)	0.51 (0.37–0.64)	NA	NA	NA

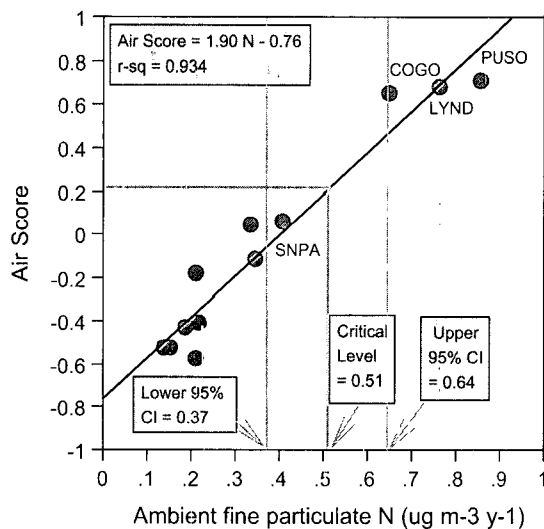


Fig. 3. Air scores, a summary of lichen community composition, were correlated with mean annual N concentrations in airborne fine particulates measured by IMPROVE in western Oregon and Washington. At the response threshold, air score 0.21, the critical level is $0.51 \mu\text{g N m}^{-3} \text{ y}^{-1}$. LYND1 near Bellingham, WA; PUSO1 in downtown Seattle; and COGO1 in the Columbia River Gorge National Scenic Area exceeded the critical level. SNPA1 at Snoqualmie Pass near Alpine Lakes Wilderness fell within the lower 95% CI.

precipitation at air score = 0.21. Highest CLs occurred in the mountains; CLs were exceeded in much of Oregon's Willamette Valley, Washington's Puget Trough, the valley floor of the Columbia River Gorge, and in and around major cities.

4. Discussion

Lichen community based CLs for CMAQ-modeled total N deposition in the Oregon and Washington portion of the MWCF eco-region ranged from 2.7 to $9.2 \text{ kg N ha}^{-1} \text{ y}^{-1}$ between 45 and 400 cm mean annual precipitation. CLs for wet and dry deposition were 1 – 4 and 2 – $6 \text{ kg N ha}^{-1} \text{ y}^{-1}$, respectively, also increasing with precipitation. The critical level for IMPROVE ambient fine particulate N was $0.51 \mu\text{g N m}^{-3} \text{ y}^{-1}$; accounting for precipitation did not improve estimates. These empirical CLs were derived by 1) selecting a biological response threshold that appears to provide protection from harm, 2) modeling the relationship between the biological response and N deposition, and 3) solving for N deposition at the response threshold across the observed precipitation range.

4.1. Comparison to other western US lichen CLs

Exceedances of CLs proposed here occurred largely in urban and agricultural corridors of Washington and Oregon (Fig. 3) affecting

Table 6
Deposition of dominant N-containing compounds and combined deposition of all 16 compounds at 1411 western Oregon and Washington lichen plots (1990–1999).

Statistic	Wet dep. ($\text{kg N ha}^{-1} \text{ y}^{-1}$)			Dry dep. ($\text{kg N ha}^{-1} \text{ y}^{-1}$)				Total all
	NO_3^-	NH_4^+	All	HNO_3	NH_3	NO_2	All	
Maximum	1.03	1.51	2.24	1.32	4.1	1.77	6.45	8.17
Mean	0.5	0.49	1	0.78	0.52	0.27	1.94	2.94
Std dev	0.17	0.27	0.41	0.27	0.39	0.27	0.94	1.24
Median ^a	0.39	0.36	0.74	0.64	0.43	0.18	1.57	2.44
Minimum	0.19	0.1	0.37	0.05	0.08	0	0.36	0.8

^a FIA data only; data from these on-frame plots have inferential value for the study area.

about 25% of the study area (Geiser and Neitlich, 2007). Within the larger WCMF eco-region (Fig. 1), we expect that only the Vancouver/Fraser River environs of British Columbia will also exceed CLs (Porter, 2007). With minimum and median N deposition of 0.8 and $2.4 \text{ kg ha}^{-1} \text{ y}^{-1}$ (Table 6), most of the study area is still within 1 – 2 kg of the 0.4 – 0.7 pre-anthropogenic N deposition loads estimated by Holland et al. (1999).

Our CLs are comparable to lichen community CLs proposed for California (Table 7). Fenn et al. (2008) estimated total annual N deposition from nitrate and ammonium in coniferous forests of the Sierra Nevada using canopy-throughfall samplers. Their CLs varied across three response thresholds:

- 1) The 100% quantile for % N in the lichen epiphyte, *Letharia vulpina*, from clean sites, corresponding to a community in which oligotrophs comprised 40% of total lichen abundance ($\text{CL} = 3.1 \text{ kg N ha}^{-1} \text{ y}^{-1}$),
- 2) Oligotroph abundance of 25% and eutroph abundance of 50% ($\text{CL} = 5.2$), and
- 3) Oligotroph extirpation ($\text{CL} = 10.2$).

To find out if our total N model (Table 4 Eq. (1)) could replicate these CLs, we inserted air score ranges corresponding to Fenn et al.'s response thresholds and appropriate precipitation. Our list of N-indicators is predominantly the same. Fenn et al.'s responses use percent abundance while our models use percent richness but these measures are intimately correlated in the Sierra Nevada study area ($r^2 = 0.92$; Jovan and McCune, 2006). For Fenn et al.'s first threshold, 40% oligotrophs, we used Table 3 Division 3 air scores, which support, on average, 41% oligotrophs. Fenn et al. did not account for precipitation but this is perhaps unobjectionable because post-hoc estimates indicate that mean annual precipitation across sites (800 m normals for 1970–2000; PRISM 2009) varied only 2-fold (79–165 cm), in contrast to the nearly 10-fold precipitation range across our study area.

At 111 cm precipitation (their median), we predict a CL of 2.5 – $3.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$, encompassing their prediction of $3.1 \text{ kg N ha}^{-1} \text{ y}^{-1}$. If we use Division 5 air scores to approximate their middle response threshold, our model predicts a CL of 4.6 – 5.7 , encompassing their prediction of 5.2 . If we use Division 6B air scores to approximate a 0% oligotroph threshold, our model predicts a CL of 9.1 – 15.8 , encompassing the Fenn et al. estimate of 10.2 . We advise however that a CL permissive of oligotroph extirpation is unacceptable because dominant regional oligotrophs (e.g. *Alectoria*, *Bryoria*, *Lobaria*, *Ramalina* and *Usnea*) comprise the bulk of lichen biomass in old-growth forests, contribute to nutrient cycling, and play integral ecological roles as nesting material, essential winter forage for rodents and ungulates, and invertebrate habitat (McCune and Geiser, 2009).

Fenn et al. (in press) proposed a lichen community CL of $5.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$ for California's Greater Central Valley (GCV). This estimate utilized air scores calculated by Jovan and McCune (2005) at 117 sites. The response threshold was set at an air score corresponding to a eutroph abundance of 50%. Although Fenn et al. did not account for it, mean annual precipitation across GCV study sites varied nearly 10-fold (17–156 cm). Using our Division 5 air scores (0.33–0.49) to approximate the GCV response threshold of 50% eutrophs, our model predicts a CL of 3.1 – 6.4 at minimum to maximum GCV precipitation, encompassing Fenn et al.'s predicted value of 5.5 . A historical flora is needed to verify this higher response threshold because much of the area is now agriculturally influenced, but the dry climate and hardwood-dominated forests naturally favor eutrophs (Jovan and McCune 2004). Hardwood dominance in MWCF stands increased air scores up to 0.32 units over co-located 100% conifer stands (Geiser and Neitlich 2007).

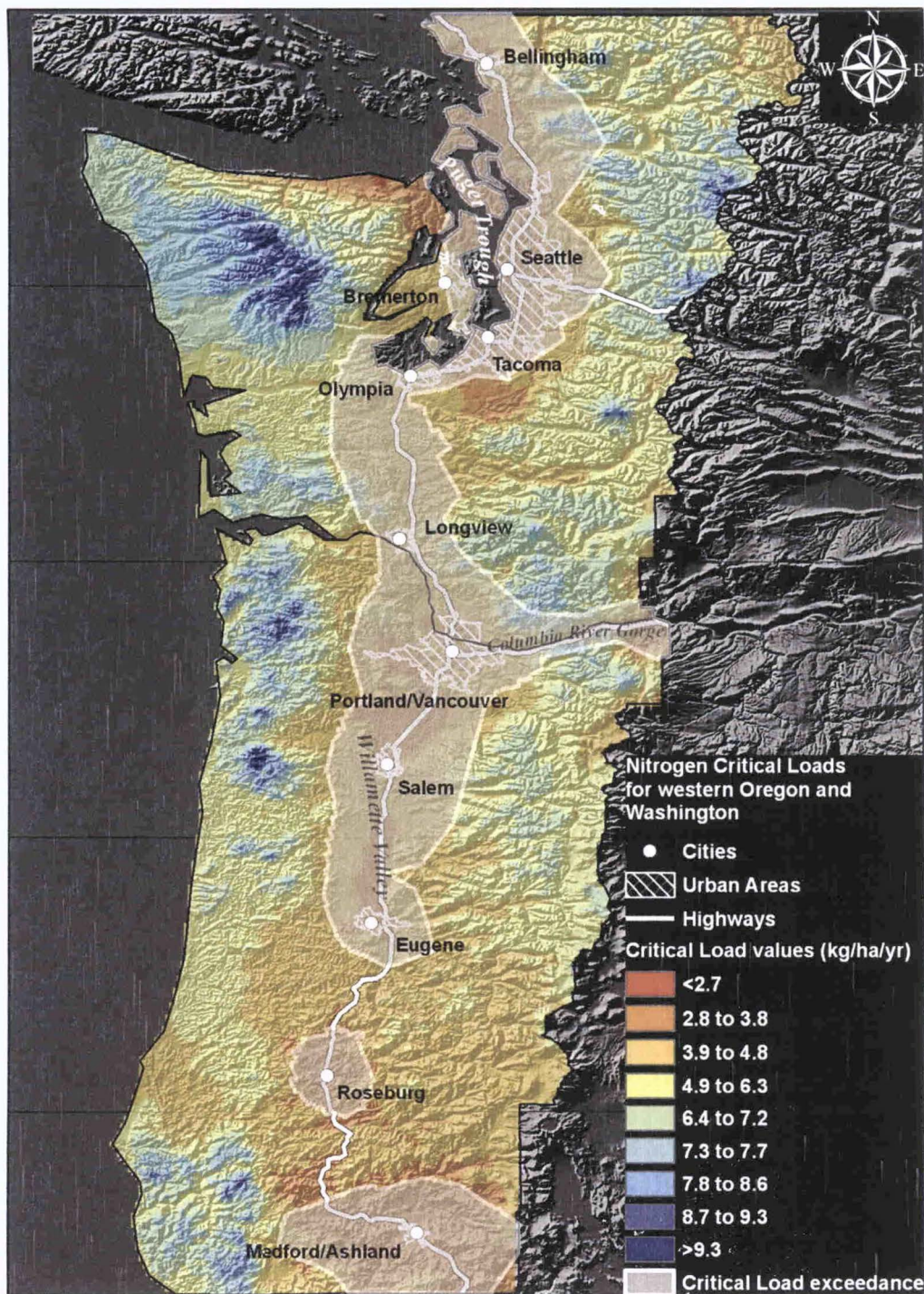


Fig. 4. Map of lichen community based critical loads (CLs) for nitrogen in western Oregon and Washington. CLs are the amount of N deposition necessary to shift epiphytic-macrolichen communities to an air score of 0.21, the point where oligotrophs comprise 30–41% of the community. CLs vary over the landscape because precipitation moderates lichen response. White shading, generally associated with largest urban and agricultural areas and low elevations, indicates CL exceedances from 1994 to 2002 (air score ≥ 0.21).

supporting a higher air score response threshold for the GCV compared to the conifer-dominated MWCF.

4.2. Comparison to European CLs

In Europe, the temperate and boreal forest N CL established by the UNECE based on algal and epiphytic lichen diversity is

10–15 kg N ha⁻¹ y⁻¹ (Bobbink et al., 2003). An anthropogenic overlay of 15–60 kg N ha⁻¹ y⁻¹ occurred over much of Europe during the 1970s–1990s; pre-1970s estimates were 2–6 kg N ha⁻¹ y⁻¹ (Lövblad and Erisman, 1992). Although N deposition has decreased over much of Europe since the 1980s (Wright et al., 2001), CL overestimates may easily result from study of cleanest-site lichen communities that have already suffered species loss. Indeed,

Table 7

Comparison of lichen community based CLs for the US and Europe. Application of the regression model developed for western Oregon and Washington (Table 3 Eq. (1)) to datasets from California and Scotland using appropriate precipitation ranges and comparable thresholds for lichen community composition yielded CLs comparable to published CLs. Applying a more protective lichen response threshold to the Scotland data yielded lower CLs (italics) than published CLs.

Study area	Threshold lichen community composition	Matching OR/WA air score	Ann precip (cm)	CL using OR/WA model ($\text{kg N ha}^{-1} \text{y}^{-1}$)	Previously published CL ($\text{kg N ha}^{-1} \text{y}^{-1}$)	Reference	N Deposition measure
Wet coniferous forest, western OR & WA, US	30–41% Oligotrophs	0.21	44	2.7		This paper	CMAQ
	30–41% Oligotrophs	0.21	186	5		This paper	CMAQ
	30–41% Oligotrophs	0.21	451	9.2		This paper	CMAQ
Mesic coniferous forest, California Sierras, US	40% Oligotrophs	0.02–0.21	111	2.5–3.8	3.1	Fenn et al., 2008	Throughfall
	25% Oligotrophs	0.33–0.49	111	4.6–5.7	5.2	Fenn et al., 2008	Throughfall
	0% Oligotrophs	1.0–2.0	111	9.1–15.8	10.2	Fenn et al., 2008	Throughfall
Mediterranean mixed hw-conifer forest, Greater Central Valley, California, US	50% Eutrophs	0.33–0.49	17	3.1–4.2	5.5	Fenn et al., in press	CMAQ
	50% Eutrophs	0.33–0.49	156	5.3–6.4	5.5	Fenn et al., in press	CMAQ
Wet Atlantic oakwoods, Scotland, UK	0% Oligotrophs	1.0–2.0	221	10.8–17.5	11–18	Mitchell et al., 2005	Stem flow
	25% Oligotrophs	0.33–0.49	221	6.4–7.4		This paper	
Boreal Sweden	↓ Diversity & cover	n.a.	n.a.	n.a.	5–10	Nordin et al., 2005	N additions
The Netherlands	↓ Diversity & cover	n.a.	n.a.	n.a.	8–9	Van Dobben et al., 2006	Simulated

deVries et al. (2007) suggested decreasing CLs for European boreal forests to $5\text{--}10 \text{ kg N ha}^{-1} \text{y}^{-1}$ based on community studies of lichens, bryophytes and vascular plants in Scandinavia (Nordin et al., 2005) where background deposition is closer to that of the WCMF (Holland et al., 2005). And vegetation modeling by Van Dobben et al. (2006) suggests a lichen CL for Netherlands forests of $8\text{--}9 \text{ kg N ha}^{-1} \text{y}^{-1}$. These new estimates are closer to CLs proposed for the western US.

We compared CLs generated by our model to those of Mitchell et al. (2005) for high rainfall Atlantic oakwoods in Scotland. The epiphyte list from their 7 sites suggests a complete absence of oligotrophic lichens (except *Lobaria pulmonaria*, detected at two sites), which is not surprising because total N deposition ranged from 10 to $53 \text{ kg N ha}^{-1} \text{y}^{-1}$. Using Division 6B air scores (1.0–2.0) to correspond to 0% oligotrophs and their mean annual precipitation of 221 cm (between-site precipitation was similar), our model predicted a CL of $10.8\text{--}17.5 \text{ kg N ha}^{-1} \text{y}^{-1}$. This is nearly identical to the 11–18 range calculated by Mitchell et al. (Table 7). Applying the more stringent GCV threshold for deciduous forests of 0.33–0.49 yields a CL of $6.4\text{--}7.4$ —closer to CLs for western US temperate forests. The ability of our model to replicate CLs outside of the WCMF region suggests a predictable relationship between deposition, precipitation and lichen community composition across temperate forests.

4.3. Precipitation effects on lichen CLs

During rain events, nutrients on canopy surfaces are solubilized and, together with solutes in bulk precipitation and solutes from lichen surfaces, passively absorbed into hydrated lichen thalli (Boonpragob and Nash, 1990). Some N accumulates on cell wall ion-exchange sites; some is transported across cell membranes and utilized or stored (Dahlman et al., 2003); some is leached if precipitation is dilute. Lichen N status thus equilibrates with temporal changes in growth, precipitation volume, and deposition concentrations (Boonpragob et al., 1989; Muir et al., 1997). Because cryptogams appear to respond more directly to N concentration than total loading (Pitcairn et al., 2006; Pearce and van der Wal, 2008; Geiser and Neitlich, 2007) precipitation presumably moderates loading effects by diluting the N concentrations to which lichens are exposed.

4.4. General considerations for estimation of lichen CLs using our model

Our total N model (for nutrient-N dominated areas) predicts lichen community composition from just two terms: N deposition

and precipitation. However we recognize that % hardwood dominance, soil fertility (%P), dust levels, and temperature also especially influence oligotroph, mesotroph, and eutroph richness. To predict lichen CLs with our model, the values of these variables should be considered during response threshold selection (e.g. by permitting higher thresholds for hardwood-dominated forests), and their range should be minimized by the study area boundaries or, otherwise controlled, as we controlled for temperature by using air scores.

Specifically, it is well-established that alkaline bark substrates usually associated with hardwoods favor mesotrophs and eutrophs (Van Herk, 2001; Otnyukova and Sekretenko, 2008). The consistently greater alkalinity and frequently higher base cation concentrations in canopy drip of hardwoods compared to conifers (Cronan and Reiners, 1983; Olson et al., 1981; Houle et al., 1999) can depress abundance of green algal oligotrophs and promote cyanolichens (Goward and Arsenault, 2000). Although soil nitrogen may have little effect on N concentrations in canopy-throughfall (Miller et al., 1976), there is convincing evidence that soil phosphorus increases P concentrations in canopy leachates, especially favoring cyanolichens (Benner & Vitousek, 2007). In dusty climates, soil aerosols favor mesotrophs and eutrophs via alkalization (Farmer 1993) or drying (Loppi and Pirintsos, 2000) of bark substrates. Hot, dry conditions give competitive advantage to stress-tolerant, smaller-sized eutrophs over the pendant oligotrophs and larger mesotrophs that thrive in cooler, more humid climates (Jovan and McCune, 2004; Will-Wolf et al., 2006). Our inclusion of a precipitation term in the model would account for any possible direct effects of precipitation on community composition in addition to the interactive effects of precipitation and N deposition.

Finally, because strongly acidifying and oxidizing pollutants were low throughout our study area and correlated to nutrient-N deposition, their separate effect on community composition was not well-addressed by our model.

4.5. Deposition measurement accuracy affects CLs

Correlations were strongest between on-site deposition measures and co-located or nearby lichen measurements (Table 4). Correlations were weaker for CMAQ-modeled data probably due to the low grid cell resolution ($36 \times 36 \text{ km}$) of deposition estimates and modeling limitations. Yet the statistical power generated by N deposition estimates at all 1411 lichen plots produced highly significant regression models that we expect are accurate on average. We note much larger confidence intervals for the wet

deposition CL generated from only 9 NADP sites (Table 5). Confidence intervals for CMAQ could be tightened by using higher resolution predictions that include cloud water as a variable. The IMPROVE network is designed to monitor US Class I areas, the Clean Air Act's most stringently protected national parks, wildernesses and wildlife refuges. The strong correlation between airborne particulate N and lichen response suggests IMPROVE data will be a reliable screening tool for CL exceedance (Fig. 3).

5. Conclusions

The majority of the MWCF eco-region currently receives deposition within 1–2 kg N ha⁻¹ y⁻¹ of pre-anthropogenic levels. This means opportunities still exist to set CLs that sustain intact natural ecosystems. We found that no single epiphyte-based CL is appropriate across land areas varying significantly in precipitation. In our study region, where mean annual precipitation ranges from 44 to 450 cm and nutrient-N is the dominant component of deposition, CLs ranged from 1 to 7 and from 3 to 9 kg N ha⁻¹ y⁻¹ in wet and total deposition, respectively. These loads are associated with declines in oligotrophic lichens and increases in eutrophs. In drier regions where dry deposition dominates or is more variable, wet deposition data are probably inadequate to define CLs. Because lichens absorb both wet and dry deposited N, wet deposition CLs should be most useful over landscapes with high, uniform precipitation.

Using our model generated from CMAQ data, we can predict N CLs at any desired lichen community composition (expressed as the percentage composition by oligotrophs or eutrophs) and precipitation level. Using ad-hoc re-calculations, we could also essentially duplicate published CL values for dry to mesic forests of California and wet forests of Scotland. The ability to apply our model more broadly suggests there is a predictable relationship between deposition, precipitation and lichen community composition across temperate forests. We note that hardwood dominance, soil fertility, dust, and temperature variability can also influence N-indicator group dominance and should be controlled or accounted for by study area boundaries and response threshold selection. All lichen-based CLs for Western North America range from 3 to 10 kg N ha⁻¹ y⁻¹, which supports efforts to lower the UNECE CL for European forests.

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