Ecological Effects of Nitrogen Deposition in the Western United States

MARK E. FENN, JILL S. BARON, EDITH B. ALLEN, HEATHER M. RUETH, KOREN R. NYDICK, LINDA GEISER, WILLIAM D. BOWMAN, JAMES O. SICKMAN, THOMAS MEIXNER, DALE W. JOHNSON, AND PETER NEITLICH

In the western United States vast acreages of land are exposed to low levels of atmospheric nitrogen (N) deposition, with interspersed hotspots of elevated N deposition downwind of large, expanding metropolitan centers or large agricultural operations. Biological response studies in western North America demonstrate that some aquatic and terrestrial plant and microbial communities are significantly altered by N deposition. Greater plant productivity is counterbalanced by biotic community changes and deleterious effects on sensitive organisms (lichens and phytoplankton) that respond to low inputs of N (3 to 8 kilograms N per hectare per year). Streamwater nitrate concentrations are elevated in high-elevation catchments in Colorado and are unusually high in southern California and in some chaparral catchments in the southwestern Sierra Nevada. Chronic N deposition in the West is implicated in increased fire frequency in some areas and habitat alteration for threatened species. Between hotspots, N deposition is too low to cause noticeable effects or has not been studied.

Keywords: nitrogen saturation, streamwater nitrate, eutrophication, lichens, biotic communities

Anthropogenic sources of fixed nitrogen (N) are having unintended consequences in terrestrial, freshwater, and marine ecosystems across the globe. Nitrogen inputs to the United States from human activity doubled between 1961 and 1997, mainly from inorganic N fertilizer use and emissions of nitrogen oxides (NO_x) from fossil fuels; most of the increase occurred in the 1960s and 1970s (Howarth et al. 2002). Chronic N deposition to forests causes a syndrome of ecosystem responses described by the N saturation hypothesis (Aber et al. 1989). Nitrogen saturation can be defined as the long-term removal of N limitations on biotic activity, accompanied by a decrease in the capacity for N retention. Excess available N contributes to major environmental problems such as reduced drinking water quality, eutrophication of estuaries, nitrate-induced toxic effects on freshwater biota, changes in plant community composition, disruptions in nutrient cycling, and increased emissions from soil of nitrogenous greenhouse gases (Fenn et al. 1998).

In the northeastern United States, atmospheric deposition is largely a regional problem (Driscoll et al. 2001). In the western United States, however, vast acreages of land are exposed to low levels of atmospheric deposition, with interspersed hotspots of elevated N deposition downwind of large and expanding metropolitan centers or large agricultural

---

Mark E. Fenn (e-mail: mfenn@fs.fed.us) is a research plant pathologist at the US Department of Agriculture (USDA) Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507. Jill S. Baron is a research ecologist for the US Geological Survey and a researcher at the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523. Edith B. Allen is a professor of plant ecology in the Botany and Plant Sciences Department and the Center for Conservation Biology, University of California, Riverside, CA 92521. Heather M. Rueth is a postdoctoral scientist at the Ecosystems Center, Marine Biological Laboratory, 7 Water Street, Woods Hole, MA 02543. Koren R. Nydick is a postdoctoral fellow in the Aquatic, Watershed, and Earth Resources Department at Utah State University, Logan, UT 84322. Linda Geiser is an ecologist and air resource specialist at the USDA Forest Service, Siuslaw National Forest, PO Box 1148, Corvallis, OR 97339. William D. Bowman is director of the Mountain Research Station at the Institute of Arctic and Alpine Research and an associate professor in the Department of Environmental, Population, and Organismic Biology at the University of Colorado, Boulder, CO 80309. James O. Sickman is a research scientist with the Institute for Computational Earth System Science at the University of California, Santa Barbara, and an environmental scientist with the California Department of Water Resources, Division of Environmental Services, PO Box 942836, Sacramento, CA 95814. Thomas Meixner is an assistant professor of hydrology in the Department of Environmental Sciences at the University of California, Riverside, CA 92521. Dale W. Johnson is a research scientist in the Department of Environmental and Resource Sciences at the University of Nevada, Reno, NV 89557. Peter Neitlich is an ecologist for the Western Arctic National Parklands, 41A Wandling Road, Winthrop, WA 98862.

operations. Wildlands in the West range from large areas with near-background levels of air pollution to areas with the highest air pollution exposure in all of North America, with the possible exception of forests downwind of Mexico City (Fenn et al. 2002). In some parts of the West, air pollution impacts take on a regional aspect, as evidenced by impaired visibility and regional haze in a number of national parks (Fenn et al. 2003a).

Many forests, shrublands, grasslands, and other ecosystem types of the western United States are N limited and likely to show growth responses to increased N deposition. Nitrogen deficiencies have been noted in the Pacific Northwest, and N fertilization at rates much greater than N deposition has been found to cause increases in forest growth, carbon (C) sequestration, and stand health in general (Gessel et al. 1990, Canary et al. 2000). In the Sierra Nevada, water is often the factor most limiting to forest growth, but N fertilization has also been found to produce significant tree growth responses in many cases (Powers and Reynolds 1999). In Europe, where N deposition rates are much higher than in most areas of the western United States, the alleviation of N deficiencies through atmospheric deposition is seen as a major cause for the increase in forest growth observed in recent decades (EFRI 2002). Growth increases from N deposition may be deemed desirable by some forest managers and plantation owners, but undesirable ecological effects from N enrichment and co-occurring ozone (O_3) pollution can negate such positive tree growth responses.

The geographic focus of this paper will be the 11 contiguous states of the United States located entirely west of the 100th meridian (figure 1). Over an area this large, climatic conditions and ecosystem types vary widely. Some regions receive more than 1000 millimeters of precipitation, namely the Pacific coastal areas, the Sierra Nevada, the Colorado Rockies, and northern Idaho. But large areas of the West are arid or semiarid, with more than 300 clear days per year (Riebsame et al. 1997), a fact that points to the importance of atmospheric dry deposition. Our primary objective is to assess current understanding of N deposition effects on ecosystems of western North America. A major premise of this analysis is that estimated thresholds for ecological effects, estimated emissions reductions needed for ecosystem protection or recovery, and models of ecosystem responses for forests and watersheds in other geographic regions are frequently not applicable to the West (table 1).

Western ecosystems influenced by nitrogen deposition

Western ecosystems affected by N deposition generally fall into one of three categories: (1) sites downwind of large urban source areas; (2) regions with a mix of emissions sources that may include urban, mobile, agricultural, and industrial sources; and (3) sites near a large point source of N (e.g., an industrial complex or a coal-burning power plant). The latter sites are few in number, and the geographic zone affected by a point source is usually small, although its ecological and environmental effects can be locally severe.

The Interior West is distinguished by its sparse population. Ironically, this region is more urbanized (in terms of the percentage of the population living in urban areas) than even the mid-Atlantic region of the United States, with 86% of Westerners living in cities (Riebsame et al. 1997). The Interior West grew faster than the United States as a whole in the 1970s and 1980s, and the pace quickened in the 1990s. Spatial patterns of urbanization largely define the areas where air pollution impacts are most severe (figure 1). We expect that N deposition levels are low (1 to 4 kilograms [kg] N per hectare [ha] per year [yr]) over large areas of forest and other ecosystem types. The main effect of this deposition is a chronic, inadvertent low-level fertilization that may cause slight increases in available N and plant growth. However, sensitive ecosystem components (e.g., lichen species, diatoms, and streamwater nitrate [NO_3^-] levels) can be substantially influenced, in some instances, by N deposition levels as low as 3 to 8 kg per ha per yr.

Ecological effects of N deposition reported in the West are listed in table 2. In several locations, federal Class I areas are affected by N deposition. Class I areas are designated federal wilderness areas that were given special protection from degradation by air pollution under the Clean Air Act Amendments of 1977. High NO_3^- concentrations in streamwater are the most obvious symptom of ecosystem N overload in the Colorado Front Range, in montane watersheds in southern California, and in parts of the southwestern low-elevation Sierra Nevada. Chronic N deposition is likely to affect other, unstudied ecosystems downwind of urban centers in the West. NO_x emissions are typically high in western cities because of widespread reliance on private transportation, but few N deposition data are available for wildlands downwind of these urbanized regions. Enhanced NO_3^- concentrations in high-elevation lakes adjacent to and downwind of a number of western cities indicate the potential for ecosystem N enrichment (figure 2). Recent data from the Central Arizona–Phoenix Long Term Ecological Research site demonstrate that agricultural and desert ecosystems downwind of Phoenix receive nearly 30 kg N per ha per yr at the most exposed sites (Fenn et al. 2003a), but effects on the desert ecosystem have not been studied. Wet deposition data suggest that elevated N deposition may also occur outside Las Vegas (Nilles and Conley 2001).

Köchy and Wilson (2001) reported evidence that N deposition may be accelerating expansion of aspen stands *(Populus tremuloides* Michx.) into grasslands within the northern edge of the Great Plains in western Canada (figure 1). This is an example of a region where N deposition was previously believed to be unimportant. An example of a point source of N emissions is the Nikiski Industrial Complex in the Kenai Peninsula in south-central Alaska. Bulk N deposition ranged from less than 1 to 21 kg per ha per yr over a 13-kilometer gradient. Plant and soil data suggest that this site is N saturated. Spruce trees near the facility have chlorotic foliage and

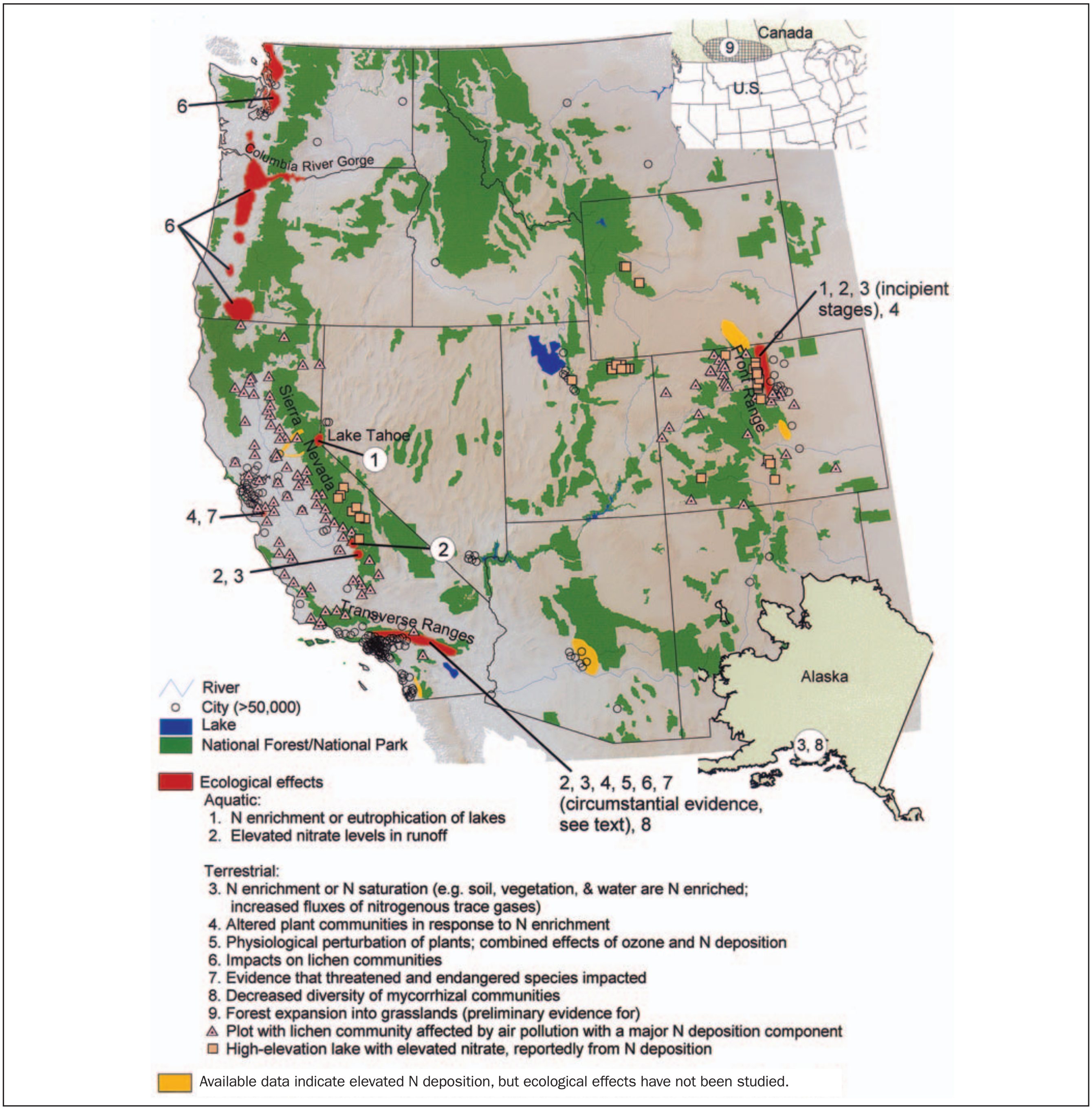

Figure 1. Map of the western United States showing the primary geographic areas discussed in this article and areas where nitrogen (N) deposition effects have been reported. Note that eutrophication effects are more widespread and of greater importance than acidification effects in western North America. Areas where effects of air pollution on lichen communities have been reported in California (Sarah Jovan, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, personal communication, 2003) and in Colorado (McCune et al. 1998; Eric Peterson, Nevada Natural Heritage Program, Department of Conservation and Natural Resources, Carson City, NV, personal communication, 2003) are represented by pink triangles. The plots in north-central Colorado where lichen community changes were observed are exposed to emissions of both N and sulfur from two large power plants in Craig and Hayden, Colorado (Peterson and Neitlich 2001). The areas shown in red in Oregon and Washington (lichen communities affected by N deposition) are kriged data (Geiser and Neitlich 2003). Only lakes at an elevation greater than 1000 meters and with a nitrate (NO_3^-) concentration of more than 5 microequivalents per liter (measured in fall surveys or on an annual volume-weighted basis) are shown in this figure. Other high-elevation lakes in the West also had elevated NO_3^- concentrations but were excluded, because N sources other than N deposition may have contributed to the elevated concentrations of NO_3^-.

Table 1. A generalized comparison of environmental characteristics in forests of the western and eastern United States. All the characteristics listed here relate directly or indirectly to ecosystem responses to atmospheric deposition.

Characteristic	Western United States	Eastern United States
Base cation saturation of soils	Base cation saturation is high.	Soils have low cation-exchange capacity and are highly weathered.
Forest stand characteristics	Except for the dense forests of the humid coastal Pacific Northwest, stands tend to be relatively open, although this is changing with long-term fire suppression; conifer species are commonly the dominant component of forest stands.	Closed canopy forests are common. Deciduous species are commonly the dominant component of forest stands.
Climate	Except for the coastal Pacific Northwest, there is summer drought in many areas; arid or semiarid climates predominate.	Precipitation occurs year-round; mesic climates predominate.
N:S ratio of deposition	Nitrogen deposition predominates in most areas.	Sulfur deposition has historically been higher than N deposition, but S deposition has decreased.
Wet versus dry deposition	Areas of high pollution exposure are dominated by dry deposition, except in areas of common fog occurrence, in which case both wet and dry deposition are major sources of N input.	Available data suggest that dry deposition is often not as dominant as in the West.
Deposition gradients	Pollution inputs are high in exposed sites, but pollution gradients decline steeply with distance from the pollutant source area.	Atmospheric pollution is more regional, but with some hotspots (e.g., sites with high fog or cloud deposition).
Major pollutant sources	Mobile sources (motor vehicles) are the largest category of NO_x emissions.	Stationary sources are major SO_x and NO_x emitters. Mobile sources of NO_x are also important.
Pollutant with the most severe impacts on forests	Ozone causes the most severe air pollution injury to forests, well documented only for California. Ozone is the major pollutant causing plant physiological disturbance, in combination with chronic N deposition.	Ozone affects a few highly sensitive species in some locations; injury may be more chronic than acute. Soil chemical changes as a result of acidic deposition (N and S) are believed to be an important factor in declining tree growth in some areas.
Direct toxicity effects on plants of nitrogenous pollutants	There is evidence for toxicity from HNO_3 vapor to plants in wildland areas in southern California.	No concentrations of HNO_3 high enough to cause toxic effects have been reported from forested areas.

Note: HNO_3, nitric acid; N, nitrogen; NO_x, nitrogen oxides; S, sulfur; SO_x, sulfur oxides.

thinning crowns (Whytemare et al. 1997), and the species richness of ectomycorrhizal fungi has been reduced by 70% (Lilleskov et al. 2002).

Chemical alterations caused by nitrogen deposition

Emissions of N pollutants result in N enrichment and altered chemical composition of the atmosphere, hydrologic system, soil, and biota of recipient ecosystems.

Southern California ecosystems. Field studies and simulation modeling (NuCM, a nutrient cycling model) indicate that N deposition inputs of 20 to 35 kg per ha per yr lead to elevated NO_3^- leaching beyond the primary rooting zone, to decreasing base cation pools in soil, and to increasing soil acidity (Fenn et al. 1996). Soils in both chaparral and mixed conifer forest sites with high air pollution exposure have acidified significantly in the past 30 years (Fenn et al. 1996). Yet the base cation saturation of these soils (65% to 80%) is still an order of magnitude higher than in highly polluted sites in the eastern United States, even in sites that received 30 to 45 kg N per ha per yr for the past 50 years (Fenn et al. 1998). High net nitrification rates relative to net N mineralization in California soils are a key factor in the mobilization and export of excess N. High runoff fluxes during the winter wet season, when biotic N demand is lowest, also predispose these ecosystems to N loss. High base cation saturation, low soil C:N ratios, and the aerobic condition of these coarse-textured soils favor high nitrification rates. As a result, the N cycle is strongly NO_3^- dominated. This is illustrated by extremely high NO_3^- concentrations in soil solution (1500 to 4500 microquivalents [μeq] per liter [L]) of N-saturated forests, while ammonium (NH_4^+) concentrations are minimal, usually at the lower end of the 0 to 60 μeq per L range (Fenn et al. 1996, Fenn and Poth 2001). Annual fluxes of nitric oxide (NO) from high-deposition chaparral and forested areas of the San Gabriel and San Bernardino Mountains in the Los Angeles air basin, produced during the process of nitrification, rival those of fertilized croplands (Fenn et al. 1996). Nitric oxide emissions are in large part reemissions from soil of atmospherically deposited N, just as the large fluxes of NO_3^- in runoff waters are the result of excess N deposition.

Table 2. Ecological effects of nitrogen deposition described for study sites in the western United States.

Ecological or environmental impact	Location	Level of uncertainty	Possibility of broader occurrence (at other sites)	Reference
Effects in aquatic systems				
Elevated NO_3^- in runoff; most severe in southern California and in chaparral catchments in the southwestern Sierra Nevada	Transverse ranges of southern California; low-elevation catchments in the Sierra Nevada; high-elevation catchments in the Colorado Front Range	Well-documented response	It is unclear how widespread this phenomenon is outside the ecosystems listed, because there is little information from low-elevation systems in the Sierra Nevada and elsewhere.	Williams et al. 1996a, Fenn and Poth 1999, Fenn et al. 2003b
N enrichment and shifts in diatom communities in alpine lakes	Colorado Front Range; Lake Tahoe (California/Nevada border)	Documented for two lakes east of the Continental Divide and Lake Tahoe	These effects seem likely in other N-enriched lakes but have not been investigated.	Baron et al. 2000, Wolfe et al. 2001, Goldman 1988
Reduced lake water clarity and increased algal growth	Lake Tahoe (California/Nevada border); high-elevation lakes throughout central and southern Sierra Nevada	Well-documented response; N and P deposition believed to be important factors	Lake Tahoe is an unusual case because of its renowned lake clarity; extent of occurrence elsewhere in northern Sierra Nevada is unknown.	Jassby et al. 1994, Sickman et al. 2003b
Increased NO_3^- concentrations in high-elevation lakes	Several regions, mainly downwind of urban centers	Fairly well established from lake surveys, but more data needed for improved definition of frequency and severity	Evidence suggests that urban plumes and agricultural emissions affect lake NO_3^- levels. There is also evidence of impacts on low-elevation lakes.	Figure 2; Sickman et al. 2002
Effects in terrestrial systems				
N enrichment of soil and plants	Forests and chaparral ecosystems in the Transverse Ranges of southern California and in the southwest Sierra Nevada; coastal sage scrub in southern California; incipient responses reported for forests in the Colorado Front Range	Well-established response	Nitrogen enrichment seems likely in other areas of emissions sources because of the expectation of high atmospheric inputs (e.g., deposition data for the Phoenix, Arizona, region in Fenn et al. 2003a).	Fenn et al. 1996, Allen et al. 1998, Fenn and Poth 1999, Padgett and Allen 1999, Baron et al. 2000, Rueth and Baron 2002, Fenn et al. 2003b
Increased fluxes of nitrogenous trace gases from soil	Forests and chaparral in southern California; alpine soils in the Colorado Front Range	Documented response in southern California chaparral and forests; experimentally shown in Colorado with N additions	This is a likely response from soils receiving chronic N deposition inputs.	Neff et al. 1994, Fenn et al. 1996, Fenn and Poth 2001
Decreased diversity of mycorrhizal communities	White spruce in Kenai Peninsula, Alaska; coastal sage scrub and chaparral in southern California	Documented response	This is a likely response from soils and plants receiving chronic N deposition inputs, but it has not been studied elsewhere.	Egerton-Warburton and Allen 2000, Sigüenza 2000, Egerton-Warburton et al. 2001, Lilleskov et al. 2002
Alpine plant community changes	Colorado Front Range	Supported by long-term monitoring data and manipulative experiments; moderate level of uncertainty	It is not known if this effect occurs elsewhere in alpine plant communities in the West.	Bowman and Steltzer 1998, Bowman 2000

Table 2. (continued)

Ecological or environmental impact	Location	Level of uncertainty	Possibility of broader occurrence (at other sites)	Reference
Enhanced growth of invasive species	Coastal sage scrub, southern California; San Francisco Bay area	N deposition, fertilization studies, and plant community data supportive, but moderate uncertainty remains	It is not known if this effect occurs elsewhere, but it is expected that nitrophilous species will be selected for if N accumulates in soil.	Allen et al. 1998, Weiss 1999, Allen et al. forthcoming
Lichen community changes	Parts of the Pacific Northwest; many areas in California; north and central Colorado	Well-established response; a highly sensitive air pollution indicator	Because of the sensitivity of many lichen species, it is likely that this effect occurs elsewhere.	McCune et al. 1998, Nash and Sigal 1999, Peterson and Neitlich 2001, Geiser and Neitlich 2003
Deleterious effects on threatened and endangered species	San Francisco Bay area; southern California	Supportive evidence, but high degree of uncertainty about the precise role of N deposition	There is a high likelihood of effects in some habitats where N accumulates in soils.	Weiss 1999, USFWS 2002, Brooks 2003
Altered fire cycle	Coastal sage scrub in southern California	Hypothesis based on observations, fertilization studies, and N deposition and N cycling data; high level of uncertainty	Because it has not been studied elsewhere, it is uncertain whether this effect occurs in other areas.	Allen et al. forthcoming
Altered forest C cycling and fuel accumulation	San Bernardino Mountains	Documented response	It is uncertain whether this effect occurs in other areas.	Grulke and Balduman 1999, Fenn and Poth 2001
Physiological perturbation of overstory species	San Bernardino Mountains	Documented response	This effect has not been widely studied but is expected for sensitive plant species exposed to O_3 and adapted to N limitation but growing in N-enriched soils.	Grulke et al. 1998, Grulke and Balduman 1999, Takemoto et al. 2001
Forest expansion into grasslands	Great Plains of western Canada	Supportive evidence found, but high degree of uncertainty as to the role of N deposition	It is not known whether this effect occurs in other areas.	Köchy and Wilson 2001
N emissions as a major contributor to regional haze problem	National forests and parks throughout California, the Pacific Northwest, and some sites in the Interior West	Well-established effect; contribution from nitrogenous pollutants has been quantified	This is known to occur in areas far removed from emissions sources because of long-range transport.	Fenn et al. 2003a, IMPROVE data (4 March 2003; *http://vista.cira.colostate.edu/improve)*
NO_x emissions as precursors for phytotoxic levels of O_3, leading to O_3 injury to sensitive plant species	Southern California; Sierra Nevada	Well-established effect	Significant O_3 injury to vegetation has not been reported from other sites downwind of urban centers but cannot be ruled out as urban regions expand.	Miller and McBride 1999, Carroll et al. 2003

C, carbon; N, nitrogen; NO_3^-, nitrate; NO_x, nitrogen oxides; O_3, ozone; P, phosphorus.
Note: Summary includes the degree of uncertainty regarding the role of N deposition in each effect and the likelihood that these effects may occur elsewhere in the West.

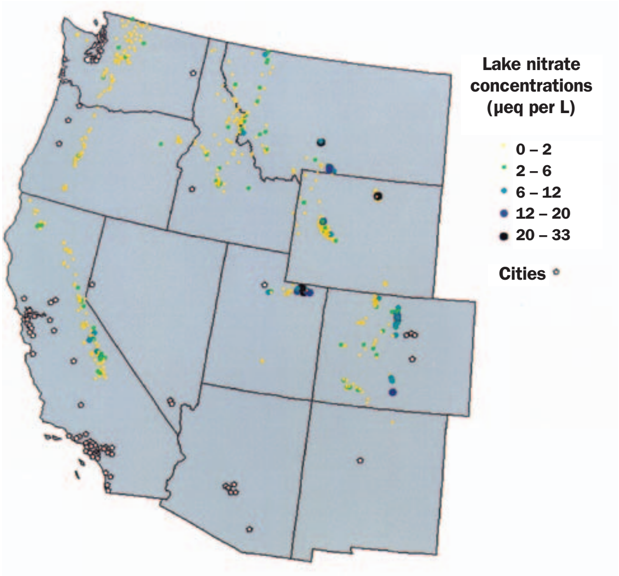

Figure 2. Nitrate concentrations (microequivalents per liter) in high-elevation lakes in western North America. Stars represent cities with a population greater than 100,000.

Streamwater NO_3^- concentrations from montane watersheds downwind of greater Los Angeles are the highest in North America. Some streams from high-elevation Class I areas in the San Gabriel and San Bernardino Mountains export high levels of NO_3^-, with peaks as high as 370 µeq per L (Fenn and Poth 1999). Nitrate concentrations in springs also correspond to N deposition levels, with relatively constant concentrations year round (i.e., 70 µeq per L in a spring in the western San Bernardino Mountains), indicating that N deposition is affecting NO_3^- levels in groundwater.

Sierra Nevada. With the exception of biomes at elevational extremes, N retention is high in most regions of the Sierra Nevada, with NO_3^- levels in streams typically below 1 µeq per L. High-elevation watersheds in the Sierra Nevada export NO_3^- during early snowmelt, even with relatively low N deposition inputs. In a recent review, Sickman and colleagues (2002) report springtime NO_3^- peaks of up to 38 µeq per L for lakes at extreme elevation and for talus-dominated catchments. In most midelevation coniferous and lower-elevation oak woodland catchments, nearly all inorganic N loading is consumed, and organic N forms dominate N export. Catchments in the Mountain Home area of the southwestern Sierra Nevada appear to be an exception to this generalization, because they receive higher N deposition (about 14 kg per ha per yr), which is reflected in slightly elevated streamwater NO_3^- values during the growing season (4 to 19 µeq per L). Streamwater NO_3^- concentrations are highly variable in Chamise Creek, an ephemeral stream in a small, low-elevation chaparral catchment in Sequoia National Park with N deposition of about 15 kg per ha (Fenn et al. 2003b). Extremely high concentrations occur during certain periods (figure 3). The volume-weighted mean NO_3^- concentration at Chamise Creek (1986–1998) was 24 µeq per L, with annual means as high as 180 µeq per L (Fenn et al. 2003b). Chaparral watersheds are the most N-saturated ecosystems in the Sierra Nevada; high rates of N deposition result from their proximity to N emissions sources and from atmospheric inversions that concentrate pollutants below an elevation of 1000 to 2000 meters (m). During the long, dry summer, N accumulates in the soil, followed by flushing events characterized by unusually high NO_3^- concentrations (Riggan et al. 1985, Fenn and Poth 1999, Padgett et al. 1999).

In the Emerald Lake watershed (2800 m in elevation) in Sequoia National Park, N mass balance studies, patterns of stream chemistry, and isotopic analyses indicate that stream NO_3^- patterns are the net result of NO_3^- flushed from soils and of snowpack NO_3^- that escapes biological cycling (Sickman et al. 2003a). This suggests that stream NO_3^- concentrations in the high Sierra Nevada would respond to increasing levels of inorganic N in the seasonal snowpack. Thus, greater winter N deposition would increase the acidification potential of snowmelt, decrease the already low acid-neutralizing capacity (ANC) of surface waters (about 10 to 50 µeq per L), and possibly alter the trophic status of the many oligotrophic, N-limited lakes in the Sierra Nevada (Sickman 2001). With the continuing urbanization of California's Central Valley, with increasing livestock operations, and with the possibility of transpacific N transport from Asia, it is probable that N deposition and its ecosystem effects in the High Sierra will increase in the next several decades.

Colorado Front Range. Annual N deposition is estimated to be 4 to 8 kg per ha in high-elevation sites east of the Continental Divide and 1 to 2 kg per ha on the west side of the divide (Baron et al. 2000). High-elevation alpine zones exhibit a relatively low capacity to sequester N derived from atmospheric deposition, because of the steep slopes, shallow soils, high cover of talus, sparse vegetation, short growing season, snowmelt-dominated hydrology, and low rates of N cycling and primary production (Baron et al. 1994, Williams et al. 1996a, 1996b). Empirical and modeling approaches indicate that the capacity of Rocky Mountain alpine catchments to sequester N is exceeded at less than 10 kg per ha per yr (Baron et al. 1994, Williams and Tonneson 2000). Evidence for this low threshold includes elevated NO_3^- concentrations, episodic loss of ANC during the summer in lakes of the upper Green Lakes Valley of the Colorado Front Range, and elevated soil solution NO_3^- concentrations in experimental plots receiving low inputs of N (20 kg per ha per yr; Williams et al. 1996a, Bowman 2000, Rueth et al. 2003).

Comparative studies and N fertilization experiments on the western (low-deposition) and eastern (higher-deposition) sides of the Continental Divide suggest that relatively small increases in N inputs can alter biogeochemistry in high-elevation old-growth Engelmann spruce *(Picea engelmannii)* forests and soils. Engelmann spruce needles and the organic soil layer are more N enriched in the eastern sites.

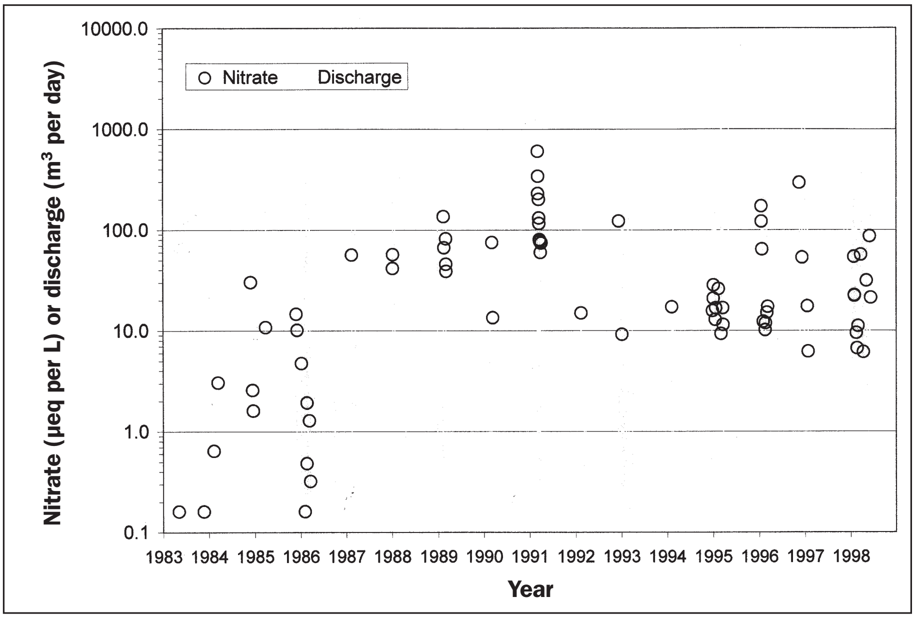

Figure 3. Nitrate concentrations (microequivalents per liter) and stream discharge (cubic meters per day) from 1983 to 1998 in Chamise Creek, an ephemeral chaparral catchment in Sequoia National Park, California.

Nitrification rates and NO_3^- losses, while low, are also higher in the eastern sites (Rueth and Baron 2002). The initial organic soil characteristics of the eastern and western sites influenced how the two sites responded to fertilization at a rate of 25 kg N per ha per yr for 4 years. Soils of the eastern fertilization site had a lower C:N ratio than soils of the western site (24 versus 36) in the organic horizon and a higher N concentration (1.5% versus 0.9%) and content (991 versus 605 grams [g] per m^2). Following fertilization at the eastern site, there were minimal changes in foliar chemistry, percent N in soils, and C:N and lignin:N ratios, while N mineralization rates, soil extractable NH_4^+ and NO_3^-, and inorganic soil N increased dramatically. In contrast, at the western site foliar N and nutrient ratios increased and the soil C:N ratio decreased with fertilization (Rueth et al. 2003). This suggests that further increases in regional N deposition east of the Continental Divide in northern Colorado will stimulate N loss from high-elevation forest ecosystems. The short growing season, evergreen habit, and old-growth status of these forests limit N demand. Thus, small increases in N inputs can result in detectable changes in N pools and processing rates.

Lake chemistry trends in the Colorado Front Range also reflect differences in atmospheric deposition. A survey of 44 lakes sampled in late summer in the mid- to late 1990s found significantly higher NO_3^- concentrations in lakes east of the Continental Divide (average 10.5 µeq per L, standard deviation 5.0), compared with lakes on the west side (average 6.6 µeq per L, standard deviation 4.3; Baron et al. 2000). In the Colorado Front Range, which is just west of the urban–agricultural corridor from Denver to Fort Collins, lake NO_3^- concentrations of up to 16 µeq per L have been commonly measured since sampling began in the early 1980s (Baron 1992), although values as high as 40 µeq per L have also been reported (Campbell et al. 2000).

Biological effects of nitrogen deposition

Nitrogen enrichment of aquatic and terrestrial ecosystems can have considerable effects on sensitive organisms or communities, sometimes at unexpectedly low levels of atmospheric deposition.

Aquatic ecosystems. There are approximately 16,000 high-elevation lakes in the western states. In contrast, few eastern lakes are alpine or even subalpine (Bahls 1992). These generally oligotrophic western mountain lakes are especially sensitive to the effects of atmospheric deposition. Many western mountain regions, including the Colorado Front Range, the Sierra Nevada, and portions of the Cascade Range, are close to urban and agricultural sources of emissions and are underlain by crystalline bedrock with little potential for buffering acidity (Omernik and Griffith 1986). The productivity of more than 20% of undisturbed high-elevation western lakes is limited by N availability, making them susceptible to eutrophication from rising N inputs (Nydick 2002). Nitrogen limitation is rather common among North American lakes, and the mean response to experimental N enrichment (average N enrichment was 46.3 µeq per L, based on a literature review including 62 lakes) was a 79% increase in phytoplankton biomass (Elser et al. 1990).

Spatial patterns of lake NO_3^- concentrations suggest that clusters of high-NO_3^- lakes are located adjacent to certain western cities. For example, two clusters of high-NO_3^- lakes are located west of urban and agricultural areas in the Colorado Front Range (figure 2). High-NO_3^- lakes have also been found east of Salt Lake City in the Uintah Mountains. Thus, "islands" of western lakes with high NO_3^- concentrations appear to be found at high elevations close to and downwind of polluted air mass trajectories. While NO_3^- concentrations in Sierra Nevada lakes are about half of those measured in the Front Range of Colorado, mean annual NO_3^- concentrations range up to 13 µeq per L in small lakes in the upper Rock Creek Canyon of the eastern Sierra (figure 1; Sickman et al. 2002). In western mountain lakes NH_4^+ is nearly undetectable, because NH_4^+ is taken up and nitrified by soil microbes higher in the watershed (Campbell et al. 2000, Sickman et al. 2003a).

Some western high-elevation lakes have already responded to increased N deposition. In Lake Tahoe, mean annual primary productivity has doubled, Secchi disk transparency has decreased substantially, and the eutrophic to mesotrophic diatom *Fragilaria crotonensis* has increased sharply, mostly as a result of N deposition (Goldman 1988, Jassby et al. 1994). In Emerald Lake, phytoplankton biomass has increased during the past two decades, while NO_3^- concentrations have remained stable or declined during the growing season (Sickman et al. 2003b). Evidence suggests that the lake has experienced increased levels of phosphorus (P) loading, which has caused mild eutrophication and a shift from P to N limitation of phytoplankton productivity. Synoptic lake surveys indicate that similar trophic changes have occurred in more than two dozen Sierra Nevada lakes between 1985 and 1999 (Sickman et al. 2003b). Similarly, *F. crotonensis* and *Asterionella formosa* now dominate the flora of two eastern Colorado Front Range lakes, whereas before 1950 the lake flora was characterized by oligotrophic assemblages (Baron et al. 1986, Wolfe et al. 2001). Diatom cell concentrations and biovolumes, proxy indicators of productivity, also increased greatly after 1950.

Nutrient amendment experiments in several high-NO_3^- lakes in the Colorado Front Range showed either no response or negative response to NO_3^- additions but strong response to P additions or to combined N and P (N + P) additions, suggesting there is a surplus of N. In low-NO_3^- lakes of the Wyoming Snowy Range, however, phytoplankton responded strongly both to N enrichment and to N + P enrichment (but not to P enrichment alone), showing increased photosynthetic rate, chlorophyll *a,* and cell density. N and N + P enrichment also led to more alkaline and light-limited environments (a manifestation of eutrophication) and to a shift in phytoplankton composition from chrysophytes to cyanophytes, chlorophytes, and diatoms, all of which are algae commonly found in mesotrophic and eutrophic environments (Nydick 2002).

Further increases in biomass and productivity in high-elevation lakes are often hindered by P availability (e.g., Lake Tahoe), putting a limit on the degree of eutrophication that can be caused by excess N alone. Although this upper limit to eutrophication can be viewed as a fortunate biological roadblock, it also limits acid neutralization through biological alkalinity production, because the acid-consuming process of N uptake by phytoplankton is limited by the availability of P (Kelly et al. 1990). A model that estimates buffering capacity from biological denitrification (Kelly et al. 1987) was applied to 481 low-ANC drainage lakes characterized in the Western Lake Survey (Landers et al. 1986). Despite the importance of biological alkalinity generation in certain well-studied lakes (Schindler et al. 1986), results suggest that nearly 70% of the lakes had only limited ability to biologically neutralize acidity, thus providing only limited in-lake buffering capacity. Western mountain lakes are highly unproductive, and low algal productivity means limited nitrate removal (and limited ANC production) in the water column. Instead, alkalinity generation occurs mostly in the sediments, where microbial processes dominate NO_3^- uptake; but NO_3^- uptake, denitrification, and ANC generation are limited by short hydraulic retention that is typical of these lakes. Seventy-two lakes (12%) were projected to be extremely prone to acidification because of inefficient biological alkalinity production combined with ANC of less than 50 μeq per L. The Sierra Nevada in California and the southern Rockies contained the greatest number of extremely acid-sensitive lakes (22 and 16, respectively), followed by the Pacific Northwest (14), the northern Rockies (13), and the central Rockies (9).

Terrestrial ecosystems. The most severe ecological effects of N deposition reported for terrestrial systems in the West are those in southern California (Takemoto et al. 2001). Ozone causes premature abscission of pine foliage in south California, while increased N fertility as a result of long-term N deposition causes more rapid foliar growth. Nitrogen deposition in the San Bernardino Mountains offsets the negative effects of O_3 on aboveground wood and foliage production of ponderosa pine (Fenn and Poth 2001, Takemoto et al. 2001). However, fine root biomass and carbohydrate allocation belowground are dramatically reduced in stands with high O_3 exposure and N deposition, indicating that the combination of these two pollutants causes major physiological disruption (Grulke et al. 1998). The net effect of O_3 and N deposition is greater foliar biomass production and turnover, resulting in enhanced litter accumulation on the forest floor and C storage in aboveground woody biomass. This may increase the risk of severe fire damage as a result of stand densification and fuel buildup in woody biomass and litter. Direct phytotoxic effects of nitric acid vapor (HNO_3), a component of photochemical smog, are also possible. The integrity of the cuticle can be affected without the occurrence of visible injury symptoms. Recent controlled exposure and field studies demonstrate that HNO_3 causes foliar injury to wildland shrub and tree species at near-ambient doses in the Los Angeles Basin (Bytnerowicz et al. 2001).

Mycorrhizal fungi are important mutualistic species associated with the health of many, if not most, terrestrial plants. Soil N eutrophication affects both the diversity and the functioning of mycorrhizal fungi. At an industrial site in the Kenai Peninsula, Alaska, the diversity of sporocarps and the number of ectomycorrhizae species declined from 30 to 9 with increasing N deposition (Lilleskov et al. 2002). Diversity and density of arbuscular mycorrhizal fungal spores declined from 19 to 12 species with increasing soil N in southern California coastal sage scrub (CSS) along an N deposition gradient (Egerton-Warburton and Allen 2000). The large-spored fungi of the genera *Scutellospora, Gigaspora, Acaulospora,* and *Entrophospora* were the primary species to decline or disappear with elevated N; their decline was accompanied by an increase in some species of small-spored *Glomus.* A similar pattern was found in archived soils of the San Dimas Experimental Forest in the Los Angeles air basin, where large-spored species declined as soil N increased from 1937 to the present (Egerton-Warburton et al. 2001). The percentage of arbuscular mycorrhizal fungal colonization of native California shrub roots, but not of exotic grass roots, declined with elevated N (Egerton-Warburton and Allen 2000, Sigüenza 2000). The arbuscular mycorrhizal fungi colonizing CSS in sites with high N deposition were poor mutualists in promoting growth of the native *Artemisia californica,* a phenomenon reported elsewhere (Corkidi et al. 2002). The exotic *Bromus madritensis* was not adversely affected by the type of mycorrhizal inoculum because it was associated preferentially with *Glomus tenue,* a mycorrhizal species that was not negatively affected by N (Sigüenza 2000). Thus, mycorrhizal feedbacks under N deposition may contribute to the decline of the dominant CSS shrub and its replacement by an abundant exotic grass.

Lichen communities in the San Bernardino Mountains have also been dramatically changed by the disappearance of up to 50% of the species that occurred in the region in the early 1900s. A disproportionate number of the locally extinct species are cyanolichens. Ozone was initially considered the main pollutant causing these effects, but it is now recognized that N pollutants are also likely to be important in causing these community changes (Nash and Sigal 1999). Community composition of epiphytic lichens is readily altered by small increases in N deposition, an effect that seems to be widespread in the West (figure 1), and alteration of bark pH is probably an important intermediary in this response (van Herk 1999). Most epiphytic lichens meet their N nutritional requirements from atmospheric deposition (Nash 1996) and can store N in excess of their nutritional needs (Søchting 1995).

In contrast to the San Bernardino Mountains, the Pacific Northwest has widespread populations of pollution-sensitive lichens (figure 4). Standardized surveys and chemical analyses of epiphytic macrolichens were carried out at over 2000 sites between 1993 and 2001 by the US Department of Agriculture's Forest Service Pacific Northwest Air Resource Program (24 February 2003; *www.fs.fed.us/r6/aq)* and the national Forest Inventory Assessment programs (24 February 2003; *http://fia.fs.fed.us/lichen).* Nitrogen concentrations in lichen tissue and lichen community composition data show similar patterns of N-enhanced locations in Oregon and Washington (figure 4). In the most N-enriched areas (red circles), weedy, nitrophilous species (e.g., *Xanthoria polycarpa* sensu lato, *Physcia adscendens,* and *Candelaria concolor)* are common, whereas populations of pollution-sensitive species, especially some of the most ecologically important—epiphytic forage lichens (e.g., *Alectoria sarmentosa, Bryoria fuscescens, Sphaerophorus globosus, Usnea filipendula)* and N-fixing cyanolichens (e.g., *Lobaria oregana)*—are small or nonexistent. Sparsity of sensitive lichen species and high N concentrations in lichen tissue are common in urban areas, in intensive agricultural zones such as the Willamette Valley, and downwind of major urban and industrial centers, such as the Columbia River Gorge National Scenic Area. Mean N concentrations in *Platismatia glauca* were significantly higher in urban–industrial or agriculturally influenced zones than in national forest sites (table 3).

Replacement of sensitive lichens by nitrophilous species has undesirable ecological consequences. In late-successional, naturally N-limited forests of the Coast Range and western Cascades, epiphytic cyanolichens make important contributions to mineral cycling and soil fertility (Pike 1978, Sollins et al. 1980, Antoine 2001) and, together with other large, pollution-sensitive macrolichens, are an integral part of the food web for large and small mammals, insects, and birds (McCune and Geiser 1997). It is expected that these lichens will be largely replaced by N-tolerant species where N inputs increase and urban boundaries expand in western Oregon and Washington.

Alpine vegetation of the southern Rockies responds to greater N availability by increasing production, but this increase is associated with changes in species composition and abundance rather than uniform increases in the growth of existing species (Bowman et al. 1993). Many of the dominant plant species do not respond to additional N, and thus subdominant species, typically grasses and some forbs, increase in abundance when N availability is increased. This differential response of alpine species to N availability is important for ecosystem function, because plant species exert significant control on temporal variation in production (Walker et al. 1994) and spatial variation in N cycling in some communities (Steltzer and Bowman 1998). The changes in species composition associated with increased N availability tend to increase rates of N cycling (Bowman and Steltzer 1998). This results in a positive feedback that can influence soil N availability as well as the chemistry of lakes and streams that receive leachates from altered alpine systems (Bowman 2000).

Approximately one-half of the annual N deposition in the Colorado Front Range occurs during the 9-month winter period. Because snow is blown across the alpine landscape and accumulates in lee areas, some areas get more N than others (Bowman 1992). As much as 10 kg per ha may leach through the snow during the initial phase of snowmelt, and a significant amount of this N can be taken up by plants even while they are covered in snow (Bilbrough et al. 2000). The areas receiving this leached N from the snow (e.g., moist meadow communities) may be most affected by N deposition, and these areas show the greatest feedbacks to enhanced N input, such as changes in species composition and subsequent impacts on N cycling (Bowman and Steltzer 1998).

Significant changes in alpine species composition have been recorded over the past two to five decades on Niwot Ridge, Colorado. Increased cover of species that are responsive to N fertilization has occurred in long-term monitoring plots (Korb and Ranker 2001). While these changes are suggestive of a biological response to six decades of elevated N deposition, consistent with changes in diatom assemblages in nearby lakes (Baron et al. 2000, Wolfe et al. 2001), the influences of changes in precipitation (Williams et al. 1996b) and pocket gopher disturbance (Sherrod and Seastedt 2001) cannot be ruled out. Continued monitoring of plant species diversity will facilitate detection of biological response to N deposition.

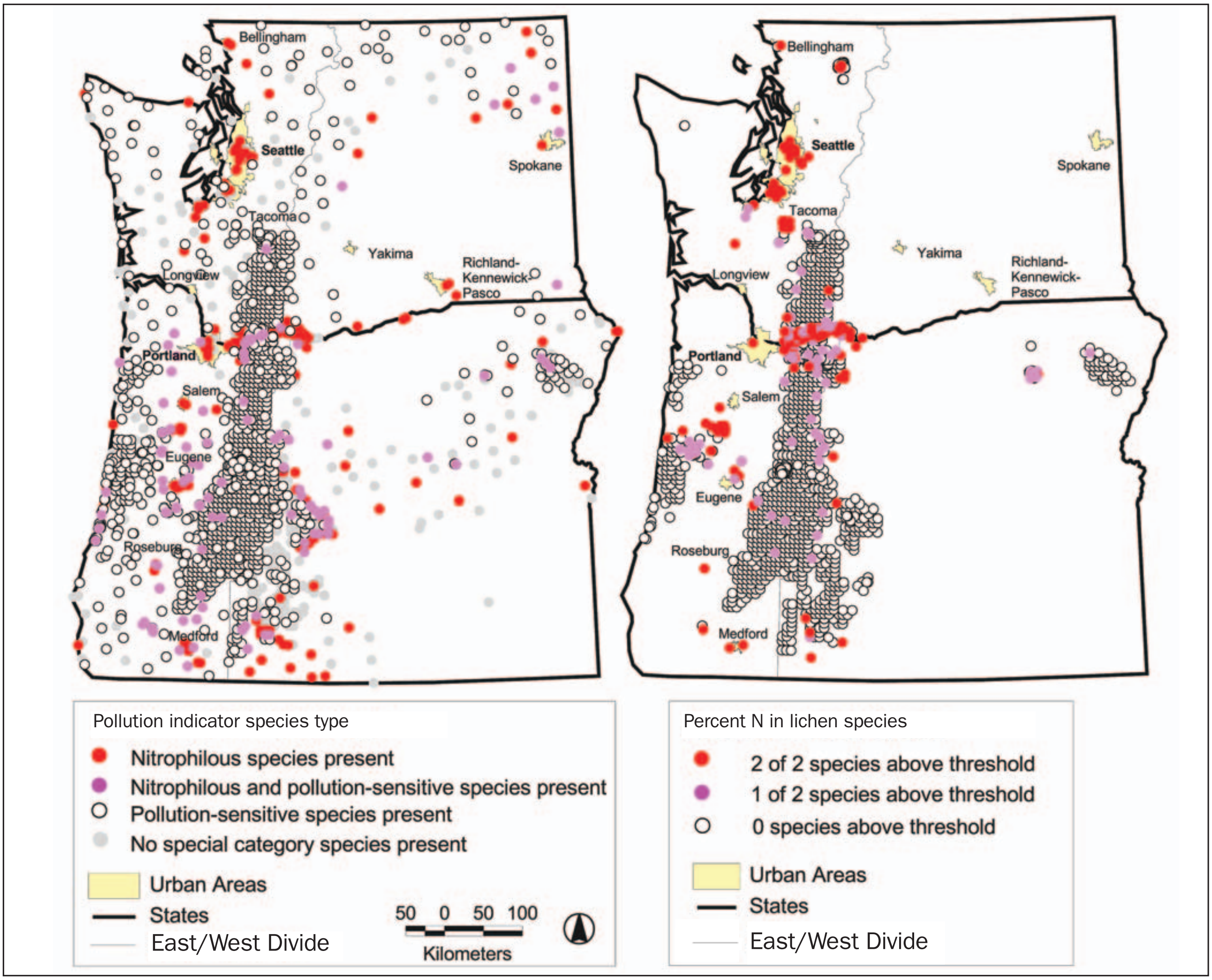

Figure 4. Locations of nitrophilous versus air-pollution-sensitive lichens in Oregon and Washington (left) are contrasted with locations in which percent nitrogen (N) in lichen tissue was above or below regional thresholds (right). Thresholds are the 97.5% quantiles for N concentration in samples from remote forest sites. Percent N values above thresholds indicate enhanced N accumulation; two species were tested at each site. Sensitive species were found in areas where percent N in lichen tissue was below thresholds (open circles); nitrophilous lichens were found in areas where percent N was above thresholds (red circles). Pink circles indicate intermediate sites. Together, the maps show that greatest N enhancement is present in urban areas, in the Columbia River Gorge National Scenic Area west of Portland, and in agricultural parts of western Oregon between Portland and Medford and eastern Oregon and Washington. This work was sponsored by the US Forest Service between 1993 and 2001. Highest sampling density occurred in selected national forests.

Indirect effects of nitrogen deposition

When N deposition alters plant or microbial communities, this can lead to cascading effects on other ecosystem processes (e.g., fire) and on organisms that depend on the affected plant community.

Nitrogen deposition enhances nonnative species invasions. Many studies on N fertilization and N deposition have shown that grasses, either native or exotic, generally increase to the detriment of herbs in mixed grasslands and shrublands (Huenneke et al. 1990, Inouye and Tilman 1995, Bowman and Steltzer 1998, Brooks 2003). Southern California CSS vegetation has been experiencing invasions of Mediterranean grasses and large-scale conversion to grassland for the past 30 years. The invasion appears to have a complex etiology, although N deposition may be a causal factor (Allen et al. 1998, Minnich and Dezzani 1998). The remaining CSS fragments are now protected for their rare and endangered species, but the conversion to grassland continues.

The CSS areas with highest N deposition have up to 87 micrograms (µg) per g extractable N in surface soil, more than five times the concentration in low-deposition sites (Padgett et al. 1999). These unusually high concentrations may contribute to the growth of invasive grasses (Allen et al. 1998,

Table 3. Mean concentrations of tissue nitrogen (percent dry weight) in 938 samples of the epiphytic lichen **Platismatia glauca** *from national forests of the Oregon and Washington Cascades, the Columbia River Gorge National Scenic Area, and rural and urban areas of the Willamette Valley and Puget Trough, 1993–2000.*

Area	Location	Number of samples	Standard mean	Standard deviation	Standard error	Tukey pairs
Umpqua NF	West Cascades, S OR	115	0.35	0.08	0.01	a
Willamette NF	West Cascades, C OR	226	0.39	0.08	0.01	a
Gifford–Pinchot NF	West Cascades, S WA	159	0.41	0.09	0.01	a, b
Deschutes NF	East Cascades, C OR	23	0.42	0.07	0.02	a, b
Mt. Hood NF	West Cascades, N OR	203	0.46	0.12	0.01	b
Columbia River Gorge NSA	OR/WA boundary	94	0.73	0.19	0.02	c
Willamette Valley and Puget Trough	W OR and WA, rural	86	0.77	0.27	0.03	c
Urban Areas	W OR and WA, cities	32	0.98	0.22	0.04	d

C, central; N, north; NF, national forest; NSA, national scenic area; OR, Oregon; S, South; WA, Washington.

Padgett et al. 1999). A field N fertilization experiment in CSS showed that exotic annual grasses increased in productivity, especially during wet years, but the shrubs did not increase in biomass in the field after 8 years of fertilization with 60 kg N per ha per yr (Allen et al. forthcoming). Plants of arid and semiarid regions are generally more limited by moisture than by nutrients, so plant productivity is increased by N only during wet years (Rapport and Whitford 1999).

Exotic grasses are also invading Mojave and Sonoran desert sites near urban areas, but the role of N deposition in this invasion is unclear. Nitrogen deposition is known to be elevated in the desert downwind of Phoenix; estimated rates are 29 kg per ha per yr in the most exposed sites (Fenn et al. 2003a). Similar scenarios probably occur downwind of other urban areas such as Las Vegas, Salt Lake City, and Tucson. Extractable inorganic soil N is high in the desert near Palm Springs, California, which receives N deposition from Los Angeles, but is low in soil from Twentynine Palms, which has cleaner air than Palm Springs (29 versus 2 µg N per g; Michael F. Allen, Center for Conservation Biology, University of California–Riverside, personal communication, 2002). The invasive annuals, *B. madritensis* ssp. *rubens* and *Schismus barbatus,* have recently invaded portions of the Mojave and Sonoran Deserts (Pake et al. 1995, Brooks 1999, Holzapfel and Mahall 1999, Brooks 2003). Field experiments have shown that these grasses are highly responsive to elevated soil N, more so than most native species (Rillig et al. 1998, DeFalco et al. 2001, Brooks 2003). The recent increases in N deposition are correlated with the increased productivity of these grasses. This correlation has not been shown to be the result of a causal relationship, but the field fertilization studies suggest that in southwestern desert sites with elevated N deposition, increased N fertility will enhance grass invasion.

Nitrogen deposition alters native fire cycles in some areas. Several lines of evidence suggest that N deposition may be contributing to greater fuel loads and thus altering the fire cycle in a variety of ecosystem types, although further studies are needed to more thoroughly evaluate the importance of N deposition and the geographic extent of this putative effect. Invasive grasses promote a rapid fire cycle in many locations (D'Antonio and Vitousek 1992). The riparian invasive *Arundo donax,* introduced from Asia, promotes the spread of fire through southern California riparian areas. This causes replacement of stands of the riparian woodland species (sycamores, willows, and cottonwoods) that are not fire adapted (Bell 1997). *A. donax* invades riparian areas preferentially where soil N is high, and it grows rapidly with elevated nutrients (Decruyenaere 2000). Frequent fire may similarly cause conversion of CSS shrubland to annual grassland. The increased productivity of flammable understory grasses increases the spread of fire and has been hypothesized as one mechanism for the recent conversion of CSS to grassland (Minnich and Dezzani 1998). Field fertilization has caused a greater increase in biomass of *B. madritensis* and other exotic species than in associated native species (Brooks 2003, Allen et al. forthcoming). Grass fuel loads of 0.5 to 1.0 kg per ha promote fire in CSS (Richard A. Minnich, Department of Earth Sciences, University of California–Riverside, personal communication, 2002).

We propose a model that compares the fire cycle in desert, CSS, chaparral, and mixed coniferous forest of southern California under N deposition (figure 5). Fire was relatively rare in the Mojave Desert until the past 10 to 15 years, but now it occurs frequently in areas of exotic grass invasion, especially that of *B. madritensis* and *B. tectorum* (Brooks 1999). Because many desert shrub species are poorly adapted to fire, burned areas take a long time to recover and may become dominated by exotic grasses. The conversion of CSS to annual grassland occurs very rapidly when two sequential fires, a few years apart, burn through the area (Minnich and Dezzani 1998; Richard A. Minnich, Department of Earth Sciences, University of California–Riverside, personal communication, 2002). In contrast, chaparral has been relatively stable under N

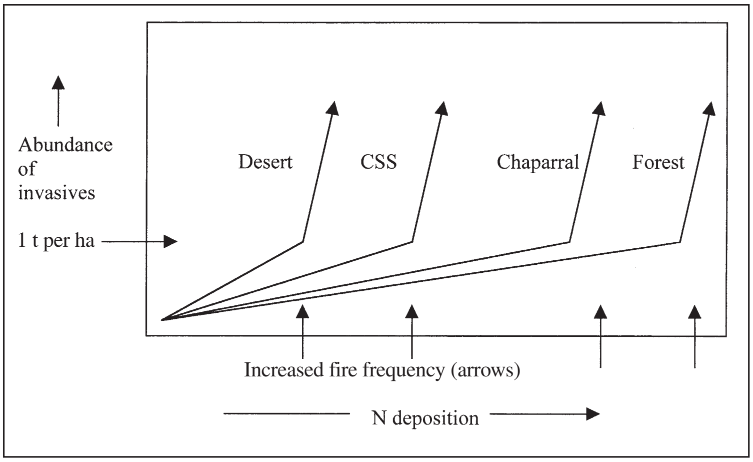

Figure 5. Conceptual thresholds of vegetation conversion to exotic annual grassland following nitrogen (N) accumulation and fire in four ecosystem types. As the productivity of annual grasses (in metric tons per hectare) increases, the fire frequency increases. These putative thresholds are shown by a rapid increase in percent exotic species, promoted by increased fire frequency. Thresholds are higher for chaparral and forest than for desert and coastal sage scrub (CSS). Thresholds in forest and chaparral may also be influenced by increased stand productivity under elevated N.

deposition (Minnich and Chou 1997). In forests, N deposition probably accelerates the process of stand densification, caused largely by fire suppression. The time needed to reach the threshold at which N deposition increases the fuel load sufficiently to cause stand-replacing fires will be different for each vegetation type.

Threatened and endangered species. Nitrogen deposition can contribute to the severe decline of some populations of the rare and threatened bay checkerspot butterfly *(Euphydryas editha bayensis),* native to the San Francisco Bay area. The bay checkerspot butterfly is restricted to outcrops of serpentinite rock. These soils are low in N and support a diverse native grassland with more than 100 species of forbs and grasses (Murphy and Ehrlich 1989), including a number of host species for the bay checkerspot butterfly as well as other plant species that supply the butterfly with nectar (Weiss 1999). The bay checkerspot butterfly primarily depends on one host plant, *Plantago erecta,* while in the larval stage. Exotic grasses are replacing native forbs, and the bay checkerspot butterfly has been declining steadily, with local extirpations in some reserves over the past decade (Weiss 1999).

Several populations of the bay checkerspot butterfly crashed after cattle grazing ceased in south San Jose, California, where N deposition to grasslands is conservatively estimated at 10 to 15 kg per ha per yr. The immediate cause of the population crash appears to have been rapid invasion by introduced annual grasses, particularly *Lolium multiflorum,* that crowded out the larval host plants of the butterfly. Low levels of soil N normally limit grass invasion in serpentinitic soils, but in ungrazed areas with experimental N fertilization or high N deposition, the introduced grasses crowd out many native species (Huenneke et al. 1990). Leaching losses of N are small in these grassland ecosystems, allowing chronic atmospheric N inputs to accumulate over several years and leading to N enrichment of the soil. Cattle grazing is believed to help maintain the native plant species, because cattle select grasses over forbs, and grazing leads to a net export of N as cattle are removed for slaughter. Thus, as Weiss (1999) points out, this case study of the checkerspot butterfly illustrates how three major global change factors (enhancement of the N cycle, land-use alterations, and invasive species) interact to threaten local biological diversity.

Another checkerspot butterfly subspecies, *E. editha quino* (Quino checkerspot butterfly), occurs in southern California in the CSS vegetation. This was once one of the most abundant species of butterflies in southern California but is now rare. Its host plant, *P. erecta,* was at one time abundant in the interspaces among the shrubs, but these sites are increasingly occupied by exotic grasses. The Quino checkerspot butterfly has become locally extirpated in the southern edge of its range by a combination of drought, grass invasion, and N deposition (USFWS 2002). This butterfly probably will not survive unless the problem of exotic grass invasion and decline of the *P. erecta* food plant can be solved by restoration, but restoration may be a continual process under N deposition and other anthropogenic influences that promote grass invasion and productivity (USFWS 2002).

The desert tortoise of the southwestern US deserts is listed as threatened by the US Fish and Wildlife Service and has declined because of grazing, habitat destruction, drought, disease, and a declining food base. Invasive grasses dominate the desert shrub interspaces where native forbs once flourished, reducing the nutritional quality of foods available to the tortoise (Nagy et al. 1998). While the annual grasses would occur in the desert even without N deposition, the productivity and density of N-fertilized grasses increase at the expense of native forbs (Brooks 2003).

California has many species that occur in shrub, forb, and grasslands affected by N deposition, with up to 200 sensitive plant species in southern California CSS alone (Skinner and Pavlik 1994). Some 25 plant species are already extinct in California, most of them annual and perennial forbs that occurred in sites now subject to vegetation type conversion to annual grassland. As CSS converts more extensively to annual grassland dominated by invasive species, loss of rare species may be inevitable. Some invasive species have been identified as threats to rare species, and N deposition has been related to increased productivity of invasive species. Thus, protection of endangered species will require increased exotic grass control, but local land management strategies to protect these endangered species may not succeed unless they are accompanied by policy changes at the regional or national level that reduce air pollution.

Nitrogen deposition effects in the West: Certainty and uncertainty. In some ways, research on the ecological effects of N deposition in western North America is in an adolescent stage. Findings from the most studied areas have been presented in this review (table 2), but studies are nonexistent in many western ecosystems downwind of urban, industrial, and agricultural sources of emissions. Thus, the spatial extent of N deposition effects in the West is only partially and crudely defined (figure 1), and the degree to which effects such as those reported herein also occur in unstudied western ecosystems is uncertain, particularly for arid and semiarid ecosystems (table 2).

The best information on the geographic coverage of areas in the West affected by N deposition is from surveys of NO_3^- concentrations in lakes and streams and from surveys of lichen communities and chemistry. Stimulation of net N mineralization and nitrification and increased soil NO_3^- levels in high-deposition sites have been demonstrated in California and in the Colorado Front Range, but little is known of plant growth responses over the range of ambient N deposition inputs that occur in the West. It seems a safe assumption that over the large acreages in western North America that are far removed from major anthropogenic N sources, the effects of N deposition would be difficult to detect. However, western demographic trends, increases in large concentrated animal feeding operations, and studies in the Sierra Nevada, the Pacific Northwest, and the Colorado Front Range all suggest that the areal extent of wildlands affected by N deposition is increasing. Much of the uncertainty in evaluating the effects of N deposition in the West arises from the chronic, subtle, and nonvisible (as opposed to foliar O_3 injury) nature of these responses. Responses such as altered root:shoot ratio, reduced fine root biomass, increased bole growth, and altered composition of plant and microbial communities are sometimes difficult to quantify because of their natural variability, except in areas with highly elevated N deposition, such as southern California.

In summary, we can say with certainty that N deposition is enriching terrestrial and aquatic ecosystems in a number of western regions and resulting in a variety of ecological perturbations, including altered microbial and plant communities (table 2). There is also strong evidence that increased NO_3^- concentrations in soil, and particularly in surface waters, result from chronic N deposition. Research is needed to more fully evaluate the geographic scope and ecological and environmental effects of N deposition in unstudied or understudied regions in the West.

Summary

Air pollution impacts in the West span the range from sparsely inhabited regions with no detectable effects to the most heavily polluted ecosystems in North America. Chronic N deposition in southern California, in the southwestern Sierra Nevada, and in the Colorado Front Range leads to increased net N mineralization and nitrification rates in soil and to elevated NO_3^- concentrations in lakes and streams. These symptoms occur in low- and midelevation high-deposition areas (> 15 kg N per ha per yr) and in high-elevation sites with relatively low N deposition (4 to 8 kg per ha per yr) but little capacity to assimilate and retain added N. These studies also indicate that the effects of N enrichment or eutrophication are generally more important in western terrestrial systems than soil acidification and associated effects. This is often true in western aquatic systems as well, but acidification is an important risk factor in many high-elevation western lakes and streams.

Biological response studies in western North America demonstrate that some aquatic and terrestrial plant and microbial communities are significantly altered by N deposition. As illustrated by the case study of the checkerspot butterfly in central California, the impacts of N deposition on plant communities can also affect the organisms, including threatened and endangered species, that depend on these plant communities as a food source. Nitrogen deposition is suspected of causing similar effects in other western sites, but definitive studies are lacking. Evidence suggests that chronic N deposition is probably increasing N cycling rates and plant growth. In some areas this may be seen as a positive response to N deposition, but simultaneous effects on water quality and sensitive organisms or ecosystem processes must also be considered.

Normally N-limited coastal sage scrub, chaparral, and forest ecosystems in southern California have become N saturated in high-deposition areas, resulting in reduced water quality, increased greenhouse gas emissions, perturbation of C and N cycling processes, and increased risk of catastrophic fire because of enhanced fuel accumulation. Nitrogen emissions also lead indirectly to severe physiological disruption of ponderosa pine through the formation of O_3 from NO_x and hydrocarbon precursors. Circumstantial evidence and fertilization studies suggest that N deposition may be contributing to vegetation type conversion and the invasion of exotic plant species in some CSS habitats. Nitrogen pollutants contribute to haze-induced visibility impairment in recreational areas and, along with O_3, present serious human health hazards in wildlands and urban areas. Nitrate concentrations in streamwater and groundwater from montane watersheds in southern California are the highest reported in North America, with concentrations as high as 370 μeq per L. These watersheds supply drinking water for hundreds of thousands of people in the adjoining urban areas. Although the drinking water standard for NO_3^- is rarely exceeded in the local watersheds except following fire (Riggan et al. 1994), elevated NO_3^- levels in water from these national forests exacerbate the problem of maintaining acceptable water quality when this water is blended with other sources of drinking water.

In the Pacific Northwest and the Colorado Front Range, sensitive organisms and communities respond to much lower inputs of N than expected (i.e., 3 to 8 kg N per ha per yr). Changes in plant communities have occurred in the

Colorado alpine, and N deposition adversely affects lichen communities—a sensitive air pollution indicator—in the Pacific Northwest, Colorado, and California. Nitrate concentrations are often greater in high-elevation lakes downwind of urban areas. Long-term monitoring, paleolimnological studies, and experimental manipulations have linked increased N availability with eutrophication, decreased water clarity, and phytoplankton species changes.

Ecological impacts of N deposition are likely in ecosystems adjacent to major urban areas such as Phoenix, Salt Lake City, Las Vegas, Tucson, Albuquerque, Houston, and Dallas–Fort Worth, but impacts in these ecosystems have not been studied. Data on N deposition rates are also lacking in most of these areas. Because of the continuing rapid population increase in the West, significant additional emissions reductions from motor vehicles, agriculture, and stationary sources may be needed to protect sensitive ecosystems and enhance the recovery of disturbed ecosystems.

Priority research needs

Some aspects of N deposition studies are in the early stages of development. For example, N deposition data, particularly of dry deposition, are lacking in most of the key Western areas discussed in this report (Fenn et al. 2003a). Nitrogen deposition data are particularly needed to determine the input levels at which effects occur and to predict where impacts can be expected. Long-term catchment studies in the alpine West have demonstrated the importance of interannual variability and its impact on watershed biogeochemical processes. Similar long-term studies are needed from other ecosystems in the West, particularly in light of wide interannual variability in precipitation and in N deposition. Interactions between N and P loading to aquatic systems should also be addressed. Experimental and manipulative studies of N deposition and processing in arid and semiarid ecosystems exposed to atmospheric N deposition are needed to further our understanding of mechanisms and thresholds for effects. Studies of N deposition and its impacts in desert or other semiarid zones downwind of urban areas in the West are particularly lacking, considering that the probability of ecological effects in these areas seems high. Field testing of potential land management practices is needed in areas where it may be possible to reduce the impacts of N deposition and to improve water quality in terrrestrial watersheds. For example, can silvicultural practices such as prescribed fire, mechanical thinning, or various harvesting regimes be used to reduce the impacts of decades of N accumulation? We expect that ongoing and future studies on these and other aspects of N deposition effects in the West will provide land managers and policymakers with improved tools and information to manage and protect the valuable natural resources of this large and unique region.

Acknowledgments

We thank Susan Schilling for invaluable assistance in the preparation of figures and Sarah Jovan, Eric Peterson, and Bruce McCune for providing data from lichen community studies in the West. We also gratefully acknowledge the reviews of an earlier version of the manuscript by George Vourlitis, Mike Allen, and Joseph Terry, and the helpful comments of three anonymous reviewers.

References cited

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM. 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39: 378–386.

Allen EB, Padgett PE, Bytnerowicz A, Minnich R. 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. Pages 131–139 in Bytnerowicz A, Arbaugh MJ, Schilling SL, eds. Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems, February 5–9, 1996, Riverside, California. Albany (CA): Pacific Southwest Research Station, USDA Forest Service. General Technical Report PSW-GTR-166. (25 February 2003; *www.rfl.psw.fs.fed.us/pubs/psw-gtr-164/fulltext/allen/allen.html#anchor1473574)*

Allen EB, Sirulnik AG, Egerton-Warburton L, Kee SN, Bytnerowicz A, Padgett PE, Temple PJ, Fenn ME, Poth MA, Meixner T. In Kus BE, Beyers JL, eds. Proceedings of the Symposium, Planning for Biodiversity: Bringing Research and Management Together. California Polytechnical University, Pomona, California; 29 February–2 March 2000. Albany (CA): Pacific Southwest Research Station, USDA Forest Service. Forthcoming.

Antoine ME. 2001. Ecophysiology of the cyanolichen, *Lobaria oregana.* Master's thesis. Oregon State University, Corvallis.

Bahls P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science 66: 183–193.

Baron JS. 1992. Biogeochemistry of a Subalpine Ecosystem: Loch Vale Watershed. Ecological Studies 90. New York: Springer-Verlag.

Baron J, Norton SA, Beeson DR, Herrmann R. 1986. Sediment diatom and metal stratigraphy from Rocky Mountain lakes with special reference to atmospheric deposition. Canadian Journal of Fisheries and Aquatic Sciences 43: 1350–1362.

Baron JS, Ojima DS, Holland EA, Parton WJ. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems. Biogeochemistry 27: 61–82.

Baron JS, Rueth HM, Wolfe AM, Nydick KR, Allstott EJ, Minear JT, Moraska B. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. Ecosystems 3: 352–368.

Bell GP. 1997. Ecology and management of *Arundo donax,* and approaches to riparian habitat restoration in southern California. Pages 103–113 in Brock JH, Wade M, Pysek P, Green D, eds. Plant Invasions: Studies from North America and Europe. Leiden (Netherlands): Backhuys.

Bilbrough CJ, Welker JM, Bowman WD. 2000. Early spring nitrogen uptake by snow-covered plants: A comparison of Arctic and Alpine plant function under the snowpack. Arctic, Antarctic, and Alpine Research 32: 404–411.

Bowman WD. 1992. Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. Arctic and Alpine Research 24: 211–215.

———. 2000. Biotic controls over ecosystem response to environmental change in alpine tundra of the Rocky Mountains. Ambio 29: 396–400.

Bowman WD, Steltzer H. 1998. Positive feedbacks to anthropogenic nitrogen deposition in Rocky Mountain alpine tundra. Ambio 27: 514–517.

Bowman WD, Theodose TA, Schardt JC, Conant RT. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. Ecology 74: 2085–2097.

Brooks ML. 1999. Alien annual grasses and fire in the Mojave Desert. Madroño 45: 13–19.

———. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology. Forthcoming.

Bytnerowicz A, Padgett PE, Parry SD, Fenn ME, Arbaugh MJ. 2001. Concentrations, deposition, and effects of nitrogenous pollutants in selected California ecosystems. Pages 304–311 in Galloway J, Cowling E, Erisman JW, Wisniewski J, Jordan C, eds. Optimizing Nitrogen Management in

Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference on Science and Policy. Lisse (Netherlands): A. A. Balkema Publishers. (4 March 2003; *www.thescientificworld.com)*

Campbell DH, Baron JS, Tonnessen K, Brooks P, Schuster P. 2000. Controls on nitrogen flux in alpine/subalpine watersheds. Water Resources Research 36: 37–48.

Canary JD, Harrison RB, Compton JE, Chappell HN. 2000. Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington. Forest Ecology and Management 138: 225–232.

Carroll JJ, Miller PR, Pronos J. 2003. Historical perspectives on ambient ozone and its effects on the Sierra Nevada. In Bytnerowicz A, Arbaugh MJ, Alonso R, eds. Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests, Vol. 2: Developments in Environmental Sciences. Amsterdam (Netherlands): Elsevier. Forthcoming.

Corkidi L, Rowland DL, Johnson NC, Allen EB. 2002. Nitrogen fertilization alters the functioning of arbuscular mycorrhizas at two semiarid grasslands. Plant and Soil 240: 299–310.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses: The grass-fire cycle and global change. Annual Review of Ecology and Systematics 23: 63–87.

Decruyenaere JG. 2000. Seasonal and site effects on the vegetative reproduction and demography of *Arundo donax* L. (Poaceae). Master's thesis. University of California, Riverside.

DeFalco LA, Detling JK, Tracy RC, Warren SD. 2001. Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. Plant and Soil 234: 1–14.

Driscoll CT, Lawrence GB, Bulger AJ, Butler TJ, Cronan CS, Eager C, Lambert KF, Likens GE, Stoddard JL, Weathers KC. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. BioScience 51: 180–198.

[EFRI] European Forest Research Institute. 2002. Relationships between recent changes of growth and nutrition of Norway spruce, Scots pine and European beech forests in Europe. (25 February 2003; *www.efi.fi/projects/recognition)*

Egerton-Warburton LM, Allen EB. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecological Applications 10: 484–496.

Egerton-Warburton L, Graham RC, Allen EB, Allen MF. 2001. Reconstruction of historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition. Proceedings of the Royal Society of London, B 1484: 2479–2848.

Elser JJ, Marzolf ER, Goldman CR. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: A review and critique of experimental enrichments. Canadian Journal of Fisheries and Aquatic Sciences 47: 1468–1477.

Fenn ME, Poth MA. 1999. Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California. Journal of Environmental Quality 28: 822–836.

———. 2001. A case study of nitrogen saturation in western U.S. forests. Pages 433–439 in Galloway J, Cowling E, Erisman JW, Wisniewski J, Jordan C, eds. Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference on Science and Policy. Lisse (Netherlands): A. A. Balkema Publishers. (4 March 2003; *www.thescientificworld.com)*

Fenn ME, Poth MA, Johnson DW. 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. Forest Ecology and Management 82: 211–230.

Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemly AD, McNulty SG, Ryan DF, Stottlemyer R. 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecological Applications 8: 706–733.

Fenn ME, de Bauer LI, Hernández-Tejeda T. 2002. Urban Air Pollution and Forests: Resources at Risk in the Mexico City Air Basin. Ecological Studies 156. New York: Springer-Verlag.

Fenn ME, et al. 2003a. Nitrogen emissions, deposition, and monitoring in the western United States. BioScience 53: 391–403.

Fenn ME, Poth MA, Bytnerowicz A, Sickman JO, Takemoto B. 2003b. Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. In Bytnerowicz A, Arbaugh MJ, Alonso R, eds. Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests, Vol. 2: Developments in Environmental Sciences. Amsterdam (Netherlands): Elsevier. Forthcoming.

Geiser L, Neitlich P. 2003. Air quality gradients in western Oregon and Washington indicated by lichen communities and chemical analysis of lichen tissue. (4 March 2003; *www.fs.fed.us/r6/aq)*

Gessel SP, Miller RE, Cole DW. 1990. Relative importance of water and nutrients on the growth of Douglas fir in the Pacific Northwest. Forest Ecology and Management 30: 327–340.

Goldman CR. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California–Nevada. Limnology and Oceanography 33: 1321–1333.

Grulke NE, Balduman L. 1999. Deciduous conifers: High N deposition and O_3 exposure effects on growth and biomass allocation in ponderosa pine. Water, Air and Soil Pollution 116: 235–248.

Grulke NE, Anderson CP, Fenn ME, Miller PR. 1998. Ozone and nitrogen deposition reduces root biomass of ponderosa pine in the San Bernardino Mountains, California. Environmental Pollution 103: 63–73.

Holzapfel C, Mahall BE. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80: 1747–1761.

Howarth RW, Boyer EW, Pabich WJ, Galloway JN. 2002. Nitrogen use in the United States from 1961–2000 and potential future trends. Ambio 31: 88–96.

Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM. 1990. Effects of soil resources on plant invasion and community structure in Californian [USA] serpentine grassland. Ecology 71: 478–491.

Inouye RS, Tilman D. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. Ecology 76: 1872–1887.

Jassby AD, Reuter JE, Azler RP, Goldman CR, Hackley SH. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California–Nevada). Water Resources Research 30: 2207–2216.

Kelly CA, Rudd JWM, Hesslein RH, Schindler DW, Dillon PJ, Driscoll CT, Gherini SA, Hecky RE. 1987. Prediction of biological acid neutralization in acid-sensitive lakes. Biogeochemistry 3: 129–140.

Kelly CA, Rudd JWM, Schindler DW. 1990. Acidification by nitric acid—future considerations. Water, Air and Soil Pollution 50: 49–61.

Köchy M, Wilson SD. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. Journal of Ecology 89: 807–817.

Korb JE, Ranker TA. 2001. Changes in stand composition and structure between 1981 and 1996 in four Front Range plant communities in Colorado. Plant Ecology 157: 1–11.

Landers DH, et al. 1986. Characteristics of Lakes in the Western United States, Vol. 1: Population Descriptions and Physicochemical Relationships. Washington (DC): US Environmental Protection Agency. Report no. EPA 600/3-86/054a.

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83: 104–115.

McCune B, Geiser L. 1997. Macrolichens of the Pacific Northwest. Corvallis: Oregon State University Press.

McCune B, Rogers P, Ruchty A, Ryan B. 1998. Lichen communities for forest health monitoring in Colorado, USA. (11 March 2003; *http://fia.fs.fed.us/lichen)*

Miller PR, McBride JR, eds. 1999. Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains. Ecological Studies 134. New York: Springer-Verlag.

Minnich RA, Chou YH. 1997. Wildland fire patch dynamics in the chaparral of southern California and northern Baja California. International Journal of Wildland Fire 7: 221–248.

Minnich RA, Dezzani RJ. 1998. Historical decline of coastal sage scrub in the Riverside–Perris Plain, California. Western Birds 29: 366–391.

Murphy DD, Ehrlich PR. 1989. Conservation biology of California's remnant native grasslands. Pages 210–222 in Huenneke LF, Mooney HA, eds. Grassland Structure and Function: The California Annual Grassland. Dordrecht (Netherlands): Kluwer Academic.

Nagy KA, Henen BT, Vyas DB. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32: 260–267.

Nash TH III. 1996. Nitrogen, its metabolism and potential contribution to ecosystems. Pages 121–135 in Nash TH III, ed. Lichen Biology. New York: Cambridge University Press.

Nash TH, Sigal LL. 1999. Epiphytic lichens in the San Bernardino mountains in relation to oxidant gradients. Pages 223–234 in Miller PR, McBride JR, eds. Oxidant Air Pollution Impacts on the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains. Ecological Studies 134. New York: Springer-Verlag.

Neff JC, Bowman WD, Holland EA, Fisk MC, Schmidt SK. 1994. Fluxes of nitrous oxide and methane from nitrogen-amended soils in a Colorado alpine ecosystem. Biogeochemistry 27: 23–33.

Nilles MA, Conley BE. 2001. Changes in the chemistry of precipitation in the United States, 1981–1998. Water, Air and Soil Pollution 130: 409–414.

Nydick KR. 2002. Mountain lake responses to elevated nitrogen deposition. PhD dissertation. Colorado State University, Fort Collins.

Omernik JM, Griffith GE. 1986. Total Alkalinity of Surface Waters: A Map of the Western Region. Corvallis (OR): Environmental Protection Agency. Report no. EPA-600/D-85-219.

Padgett PE, Allen EB. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology 144: 93–101.

Padgett PE, Allen EB, Bytnerowicz A, Minnich RA. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. Atmospheric Environment 33: 769–781.

Pake CE, Venable L, Lawrence D. 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success? Ecology 76: 246–261.

Peterson EB, Neitlich P. 2001. Impacts of two coal-fired power plants on lichen communities of northwestern Colorado. Report to the USDA Forest Service, Forest Health Monitoring Program. (20 March 2003; *http://fia.fs.fed.us/lichen)*

Pike LH. 1978. The importance of epiphytic lichens in mineral cycling. Bryologist 81: 247–257.

Powers RF, Reynolds PE. 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Canadian Journal of Forest Research 29: 1027–1038.

Rapport DJ, Whitford WG. 1999. How ecosystems respond to stress. BioScience 49: 193–203.

Riebsame WE, Robb JJ, Gosnell H, Theobald D, Breding P, Hanson C, Rokoske K. 1997. Atlas of the New West: Portrait of a Changing Region. New York: W. W. Norton.

Riggan PJ, Lockwood RN, Lopez EN. 1985. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. Environmental Science and Technology 19: 781–789.

Riggan PJ, Lockwood RN, Jacks PM, Colver CG. 1994. Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition. Environmental Science and Technology 28: 369–375.

Rillig MC, Allen MF, Klironomos JN, Chiariello NR, Field CB. 1998. Plant-species specific changes in root-inhabiting fungi in a California annual grassland: Responses to elevated CO_2 and nutrients. Oecologia 113: 252–259.

Rueth HM, Baron JS. 2002. Differences in Engelmann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA. Ecosystems 5: 45–57.

Rueth HM, Baron JS, Allstott EJ. 2003. Responses of old-growth Engelmann spruce forests to nitrogen fertilization in the Colorado Rocky Mountains. Ecological Applications. Forthcoming.

Schindler DW, Turner MA, Stainton MP, Linsey GA. 1986. Natural sources of acid neutralizing capacity in low alkalinity lakes of the Precambrian Shield. Science 232: 844–847.

Sherrod SK, Seastedt TR. 2001. Effects of the northern pocket gopher *(Thomomys talpoides)* on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55: 195–218.

Sickman JO. 2001. Comparative analyses of nitrogen biogeochemistry in high elevation ecosystems of the Sierra Nevada and Rocky Mountains. PhD dissertation. University of California, Santa Barbara.

Sickman JO, Stoddard JL, Melack JM. 2002. Regional analysis of inorganic nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains. Biogeochemistry 57–58: 341–374.

Sickman JO, Leydecker A, Chang CCY, Kendall C, Melack JM, Lucero DM, Schimel JP. 2003a. Mechanisms underlying export of N from high-elevation catchments during seasonal transitions. Biogeochemistry 64: 1–24.

Sickman JO, Melack JM, Clow DW. 2003b. Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California, USA. Limnology and Oceanography. Forthcoming.

Sigüenza C. 2000. Nitrogen deposition and soil microorganisms of *Artemisia californica* and exotic grasses in southern California. PhD dissertation. University of California, Riverside.

Skinner MW, Pavlik BM. 1994. CNPS Inventory of Rare and Endangered Vascular Plants of California. Sacramento: California Native Plant Society.

Søchting U. 1995. Lichens as monitors of nitrogen deposition. Cryptogamic Botany 5: 264–269.

Sollins P, Grier CC, McCorison FM, Cromack K Jr, Fogel R, Fredriksen RL. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs 50: 261–285.

Steltzer H, Bowman WD. 1998. Differential influence of plant species on soil N transformations within the alpine tundra. Ecosystems 1: 464–474.

Takemoto BK, Bytnerowicz A, Fenn ME. 2001. Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests. Forest Ecology and Management 144: 159–173.

[USFWS] US Fish and Wildlife Service. 2002. Quino Checkerspot Butterfly *(Euphydryas editha quino)* Draft Recovery Plan. Portland (OR): USFWS. (25 February 2003; *http://carlsbad.fws.gov/rules/quino documents/quinopdfs/outline_of_quino_recovery_plan.pdf)*

van Herk CM. 1999. Mapping of ammonia pollution with epiphytic lichens in the Netherlands. Lichenologist 31: 9–20.

Walker MD, Webber PJ, Arnold EA, Ebert-May D. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology 75: 393–408.

Weiss SB. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conservation Biology 13: 1476–1486.

Whytemare AB, Edmonds RL, Aber JD, Lajtha K. 1997. Influence of excess nitrogen deposition on a white spruce *(Picea glauca)* stand in southern Alaska. Biogeochemistry 38: 173–187.

Williams MW, Tonnessen KA. 2000. Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA. Ecological Applications 10: 1648–1665.

Williams MW, Baron JS, Caine N, Sommerfeld R, Sanford R. 1996a. Nitrogen saturation in the Rocky Mountains. Environmental Science and Technology 30: 640–646.

Williams MW, Losleben M, Caine N, Greenland D. 1996b. Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. Limnology and Oceanography 41: 939–946.

Wolfe AP, Baron JS, Cornett RJ. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology 25: 1–7.