

The effects of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming, USA—a critical review

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“Capsule”: *The effects of nitrogen deposition will become more evident as growth increases.*

Abstract

The Rocky Mountains of Colorado and southern Wyoming receive atmospheric nitrogen (N) deposition that ranges from 2 to 7 kg ha⁻¹ yr⁻¹, and some previous research indicates pronounced ecosystem effects at the highest rates of deposition. This paper provides a critical review of previously published studies on the effects of atmospheric N deposition in the region. Plant community changes have been demonstrated through N fertilization studies, however, N limitation is still widely reported in alpine tundra and subalpine forests of the Front Range, and sensitivity to changes in snow cover alone indicate the importance of climate sensitivity in these ecosystems. Retention of N in atmospheric wet deposition is <50% in some watersheds east of the Continental Divide, which reflects low biomass and a short growing season relative to the timing and N load in deposition. Regional upward temporal trends in surface water NO₃⁻ concentrations have not been demonstrated, and future trend analyses must consider the role of climate as well as N deposition. Relatively high rates of atmospheric N deposition east of the Divide may have altered nutrient limitation of phytoplankton, species composition of diatoms, and amphibian populations, but most of these effects have been inconclusive to date, and additional studies are needed to confirm hypothesized cause and effect relations. Projected future population growth and energy use in Colorado and the west increase the likelihood that the subtle effects of atmospheric N deposition now evident in the Front Range will become more pronounced and widespread in the future.

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1. Introduction

Human activities have accelerated the global cycle of nitrogen (N), and fixation of N by humans for energy production, fertilizer production, and crop cultivation now exceeds the amount of biologically fixed N on the continents (Galloway et al., 2003). The release to the atmosphere of NO_x gas from fossil fuel combustion, NH₃ gas from agricultural production, and particulate N from a range of human activities, results in wet and dry deposition of nitrate (NO₃⁻) and ammonium (NH₄⁺) to the land surface. The rate of atmospheric N deposition has greatly increased since the beginning of the

20th century, and high rates of atmospheric N deposition have been widely documented in Europe as well as in North America (Dise and Wright, 1995; Fenn et al., 1998).

The Rocky Mountain region of Colorado and southern Wyoming generally receives about 2–5 kg ha⁻¹ year⁻¹ of atmospheric N in wet deposition and about 0.5–1.4 kg ha⁻¹ year⁻¹ of atmospheric N in dry deposition (Burns, 2003). These rates are lower than rates east of the Rockies in the United States, nonetheless, symptoms of advanced stages of N saturation have been reported in alpine ecosystems of the Front Range of the Rocky Mountains (Williams et al., 1996; Williams and Tonnessen, 2000). Thin, patchy soil and sparse vegetation at high elevations in alpine watersheds of the Colorado Rockies result in the export of a large proportion of the N in atmospheric deposition. Wet deposition of

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NO_3^- increased from about $1.8 \text{ kg ha}^{-1} \text{ year}^{-1}$ in the mid-1980s to about $4.7 \text{ kg ha}^{-1} \text{ year}^{-1}$ by the early-1990s at the Niwot Ridge NADP site, and a similar sharp increase in stream NO_3^- concentrations during the growing season was reported for the outlet of a lake near Niwot Ridge (Fig. 1; Williams et al., 1996). The increased deposition of atmospheric N in the Front Range may have adversely affected amphibian populations, and altered terrestrial plant community composition, foliar N:P in bristlecone pines, soil-bacteria and fungal communities, and phytoplankton dynamics (Morris and Lewis, 1988; Harte and Hoffman, 1989; Williams et al., 1996; Bowman and Steltzer, 1998).

An increased interest in the effects of atmospheric N deposition in the Colorado and Wyoming Rockies has

been evident among researchers based on the large number of publications on the subject during the past decade. The wealth of published studies on atmospheric N deposition in the Colorado Rocky Mountains has highlighted the spatial and temporal variability of its effects (Baron et al., 2000; Clow and Sueker, 2000; Sickman et al., 2002), but some studies have produced conflicting conclusions about the ecological effects (i.e. Harte and Hoffman, 1989; Corn and Vertucci, 1992). Additionally, it is unclear whether the N saturation model that was developed to explain the response of ecosystem processes to elevated levels of atmospheric N deposition and was based largely on data from humid forested ecosystems and catchments in eastern North America and Europe applies to semi-arid, alpine eco-

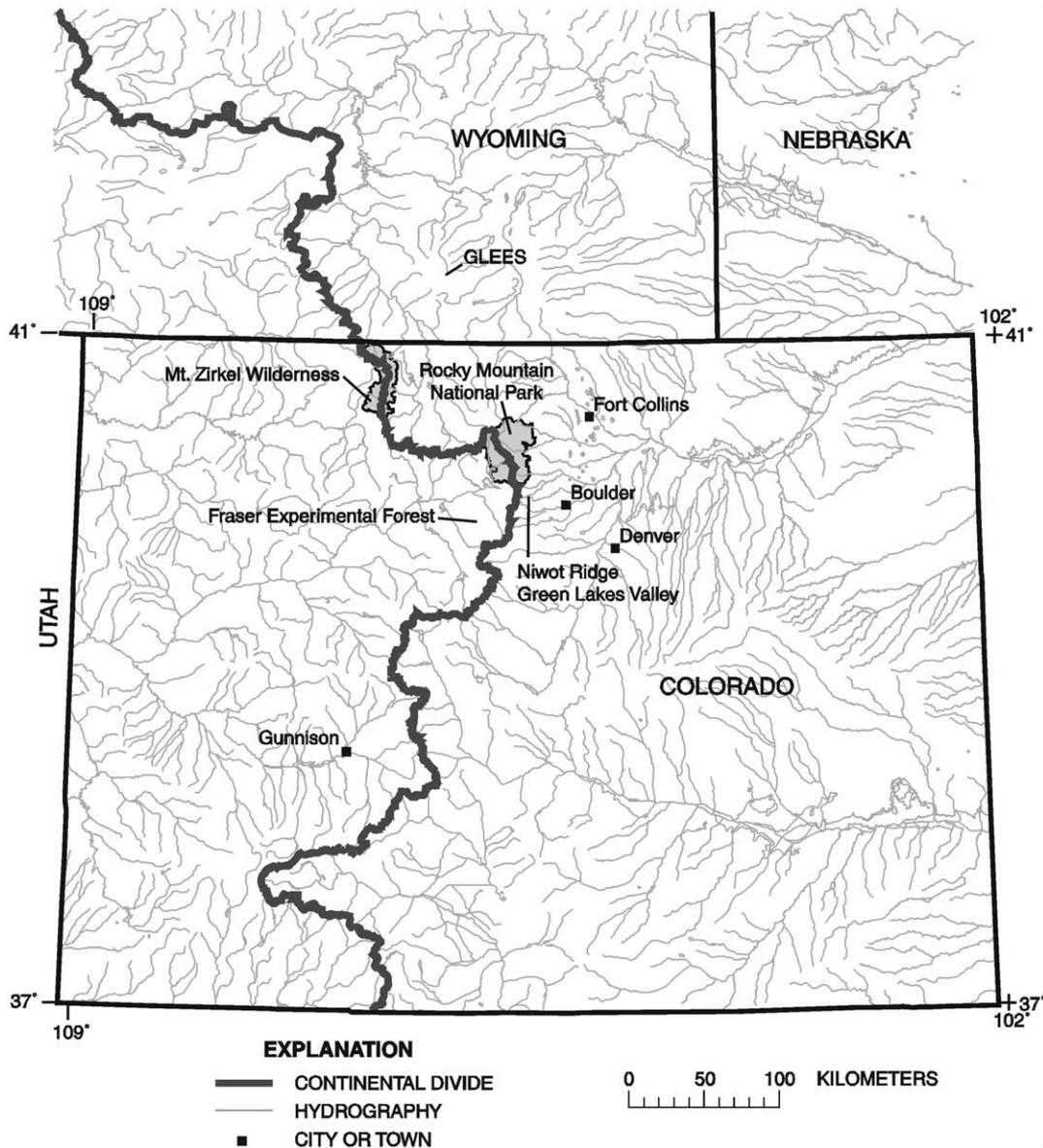


Fig. 1. Map showing field sites discussed in report, including cities, sites of intensive field studies, and the Continental Divide.

systems in the Colorado Rockies that receive lower levels of N deposition. The objective of this paper is to provide a critical review of the pertinent literature on N cycling in high-elevation ecosystems of the Rocky Mountains.

1.1. Nitrogen saturation

The prevailing paradigm until the early 1980s was that vegetation growth in undisturbed terrestrial ecosystems, particularly forested ecosystems, was N limited. This concept was first challenged by researchers in Europe, who showed atmospheric N deposition to forests to be in excess of biological demand, and proposed the variously defined concept of N saturation (Skeffington and Wilson, 1988). The N saturation concept was later formalized by Aber et al. (1989), who defined four progressive stages of forest-ecosystem response to increasing loads of atmospheric N deposition, and hypothesized the manner in which the relative rates of biogeochemical processes such as N-mineralization, nitrification, and net primary productivity would be affected at each of these four stages (Fig. 2). Stoddard (1994) later related these stages to patterns of NO_3^- concentrations observed in surface waters. Subsequent research has shown that N retention within ecosystems is affected by a combination of land-use history, dominant tree species, and soil characteristics, among several other factors (Aber et al., 1993; Aber and Driscoll, 1997; Gundersen et al., 1998).

Recent research has shown that the N saturation model, which was originally based largely on data from forested ecosystems, also describes the patterns of NO_3^- leaching observed in alpine ecosystems of the Colorado Rockies (Williams et al., 1996; Fenn et al., 1998; Sickman et al., 2002). Using the generally accepted defini-

tion that N saturation occurs when the availability of NO_3^- and NH_4^+ exceeds the total combined plant and microbial nutritional demand (Aber et al., 1989), the evidence indicates that some alpine and subalpine watersheds in the Colorado Rocky Mountains are N saturated (Williams et al., 1996; Campbell et al., 2000). In apparent contrast, however, alpine tundra and subalpine forests in the Front Range are generally N-limited ecosystems, and NO_3^- concentrations of surface waters in some parts of the Colorado Rockies are $< 10 \mu\text{mol l}^{-1}$ at baseflow (Bowman et al., 1993; Stottlemeyer et al., 1997; Campbell et al., 2000). These varying results provide an important reason for this critical review of published studies.

As N saturation advances, a series of biogeochemical responses are predicted to accompany increased NO_3^- leaching into surface waters, including elevated rates of N-mineralization and nitrification, increased fluxes of nitrous oxide (N_2O) gas from soils, and increased foliar N concentrations (Fig. 2; Aber et al., 1989; Galloway et al., 2003). At an advanced stage of 2–3, declines in fine root biomass, foliar biomass, and net primary productivity have been predicted. Results to date suggest, however, that atmospheric deposition of N at current levels may result in observable changes in plant community composition at sites in the Rockies that receive only $4\text{--}6 \text{ kg N ha}^{-1} \text{ year}^{-1}$ of atmospheric deposition (Bowman and Steltzer, 1998; Baron et al., 2000). Can we expect similar changes in biomass and net primary productivity to those observed in humid forested ecosystems at stage 2–3 of N saturation in the Colorado Rockies? If atmospheric N deposition were to increase so that ecosystems in the Front Range reached stage 3 of N saturation, would ecosystem processes decline as predicted by the N saturation model? This review will attempt to address these questions by using the lens of N saturation to view the results of published studies.

1.2. Geographic scope of review

The principal geographic focus of this review is the Front Range and surrounding mountainous region of the Colorado Rocky Mountains; the Glacier Lakes Ecosystem Experiments site (GLEES) in adjacent southeastern Wyoming (Fig. 1) is included because a wealth of publications based on data collected at this site are available. The Front Range receives the highest rate of atmospheric N deposition (as much as $6\text{--}7 \text{ kg N ha}^{-1} \text{ year}^{-1}$) of any location in the Rockies or intermountain west, and thus serves as an example of what might happen in other parts of the Rockies if future rates of atmospheric N deposition reach similar levels. Most studies of the effects of atmospheric N deposition in this region have been performed at three sites in addition to the GLEES site mentioned above: (1) the Loch Vale Watershed in Rocky Mountain National

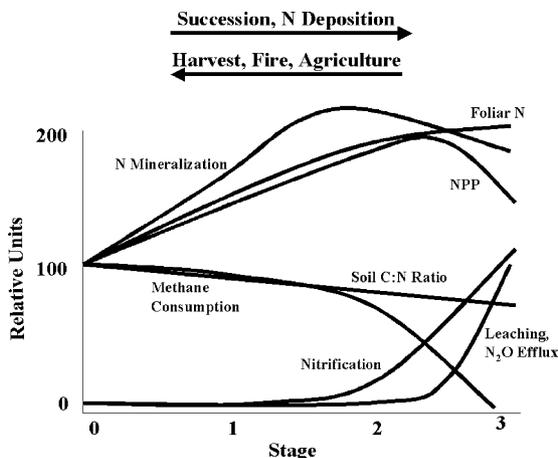


Fig. 2. Relative changes in the rates of several N cycling processes as a function of the degree of N saturation (from Galloway et al., 2003). Abbreviations: N_2O , nitrous oxide; NPP, net primary productivity.

Park, (2) the Niwot Ridge site and surrounding area northwest of Boulder, and (3) the Fraser Experimental Forest, just west of the Continental Divide (Fig. 1). Research results from these sites will be the focus of this paper.

2. Critical review

This review first discusses the effects of atmospheric N deposition on alpine tundra and alpine/subalpine forest ecosystems. After reviewing studies on the N chemistry of surface waters, the review ends with the effects of atmospheric N deposition on aquatic ecosystems—primarily algae and amphibians. A more detailed review of these topics is available in Burns (2002). The rates, sources, and trends in atmospheric N deposition are reviewed in another paper (Burns, 2003).

2.1. Alpine tundra—an ecosystem sensitive to N deposition and climate change

The alpine tundra of Colorado has lower rates of primary production than ecosystems at lower elevations in the region because of its short growing season, low temperatures, and seasonal extremes of moisture (Bowman and Fisk, 2001). Another result of the harsh climate is that only 1–2% of N storage is in living plant biomass; most living biomass is present in roots, and the majority of N use for production is by the roots (Fisk et al., 1998). Tundra ecosystems may therefore be more sensitive than forests to changes in atmospheric N deposition, because past work in Europe has shown that root biomass is sensitive to the rate of N deposition (Gundersen et al., 1998). Total N storage in tundra at Niwot Ridge ranges from 7000 to 8000 kg ha⁻¹, and 85–95% of this N is stored in soil organic matter (Fisk et al., 1998). Microbial biomass accounts for <1% of N storage in the tundra ecosystem, but accounts for a majority of the actively cycled N. Up to 5% of microbial N turns over daily (Fisk et al., 1998), and large temporal variations in the size of this pool have been noted (Fisk and Schmidt, 1995; Brooks et al., 1998).

2.1.1. Effects on the plant community

Investigators at Niwot Ridge in the Front Range have shown that the rates of N-cycling processes in alpine tundra plant communities are dependent on moisture regime (Bowman et al., 1993; Bowman, 1994; Fisk et al., 1998). Rates of N-mineralization and concentrations of NO₃⁻ and NH₄⁺ are greater in wet alpine meadow soil than in dry meadow soil (Bowman et al., 1993; Fisk et al., 1998). Tundra plants have only a limited capacity to increase growth or N content as soil N increases, so much of the observed increase in plant N uptake during experimental additions of N at Niwot Ridge has occur-

red through changes in species composition (Bowman et al., 1995; Theodore and Bowman, 1997). In wet alpine meadow, community dominance shifted from *Acomastylis* to *Dechampsia* with increasing N additions, and other experiments have shown decreases in species richness in tundra in response to N additions (Bowman et al., 1995; Seastedt and Vaccaro, 2001). Such shifts in species composition may lead to increased leaching of NO₃⁻ from soils because the favored species often has greater rates of N-mineralization and nitrification than pre-existing species (Bowman and Steltzer, 1998; Steltzer and Bowman, 1998). Nutrient addition studies to date generally support the hypothesis that long-term increases in atmospheric N deposition will likely shift alpine terrestrial-plant productivity from N-limitation to P-limitation.

Future changes in alpine vegetation if atmospheric N deposition increases in the Colorado Rockies defy simple predictions because climate change may induce unforeseen complications. Experiments that have increased the amount of snowfall in alpine tundra have found shifts in species composition and decreases in species richness attributable primarily to snow cover (Bowman, 2000; Seastedt and Vaccaro, 2001). Future changes in snowpack thickness and duration are likely to mask any changes that may result from atmospheric N deposition alone.

Interpretation of results where N additions represent from 3 to 35 years of average atmospheric N deposition (Bowman et al., 1993; Seastedt and Vaccaro, 2001) requires caution because plant-community responses to a gradual, long-term increase in atmospheric N deposition may differ from responses projected from short-term experimental data. Few studies exist of long-term plant-community changes in response to changing rates of atmospheric N deposition in the Colorado Rockies, and long-term data from plot studies are difficult to interpret because of factors such as climate and grazing by herbivores that may affect plant communities (Korb and Ranker, 2001). Nevertheless, these data may reveal whether observed long-term changes are consistent with the expected effects of atmospheric N deposition.

2.1.2. Microbial processes and the role of snow cover

Microbial N pools and associated N-cycling processes are spatially heterogeneous within alpine tundra and are controlled by a complex relationship among soil moisture and temperature, plant community type, carbon availability, and snow cover thickness (Fisk and Schmidt, 1995; Fisk et al., 1998; Brooks et al., 1999; Lipson et al., 2000).

Microbial N cycling processes under snow cover provide a key to understanding seasonal and annual dynamics of NO₃⁻ concentrations and export in soil water and surface water (Williams et al., 1998; Brooks and Williams, 1999; Brooks et al., 1999). Soil in areas

that develop consistent snow cover early in the season remain thawed throughout the winter and thus have high rates of microbial immobilization of N and do not release much NO_3^- during snowmelt. In contrast, soil in areas with inconsistent snow cover become frozen and thus have low rates of microbial N immobilization and release large amounts of NO_3^- during snowmelt (Brooks et al., 1998). Rates of net N-mineralization as high as $75 \text{ kg N ha}^{-1} \text{ year}^{-1}$ have been measured in alpine tundra, and changes in microbial biomass N under snow cover can exceed those of the snow-free season (Brooks et al., 1996; Lipson et al., 1999).

2.1.3. Talus—important source area of NO_3^-

The steep, rocky talus slopes that often extend from below flat alpine ridgetops down to the valley floor have been infrequently studied because they were formerly assumed to be inert piles of rocks and sand with little ability to actively cycle N. These talus slopes are well connected to the streamflow system, however, and recent studies have revealed that they can contain areas of sand, clay, and organic material, some of which support patches of tundra-like vegetation, and have a dynamic N cycle (Williams et al., 1997; Bieber et al., 1998). Inorganic N pools and rates of N-mineralization and nitrification in soil below these vegetation patches are comparable to those measured in alpine tundra (Williams et al., 1997; Bieber et al., 1998). Even barren patches of talus soil with little vegetation cover contain wind-deposited organic matter and measurable microbial biomass (Ley et al., 2001). Because of the direct hydrologic connection between talus slopes and surface waters, these areas are probably a major source of NO_3^- in surface waters, especially during the growing season (Campbell et al., 2000). Little is known, however, about talus hydrology, and few measurements exist. Given the potential importance of N cycling and hydrology in talus, additional studies of the contributions of N from talus to surface water NO_3^- are warranted.

2.2. Alpine and subalpine forest—generally nitrogen limited

Alpine and subalpine forests in the Rocky Mountains of Colorado and southeastern Wyoming are generally limited by the availability of N and several other factors such as temperature and light availability (Fahey et al., 1985; Prescott et al., 1992). Two recently published studies suggest, however, that forested areas east of the Continental Divide that receive the highest rates of atmospheric N deposition (generally $4\text{--}6 \text{ kg N ha}^{-1} \text{ year}^{-1}$) may not be N limited (Williams et al., 1996; Rueth and Baron, 2002). The first of these studies found higher foliar N:P ratios in Bristlecone pine at 3650 m on Mt. Evans (in the Front Range) than at two other sites on the mountain at lower elevations (Williams et al.,

1996). Atmospheric N deposition was assumed to be greater at the highest elevation site but no data were obtained to support this assumption, nor was the variation among the measurements (five trees at each elevation) reported. Thus, the significance of the reported values is difficult to evaluate. The second study reported higher foliar N and organic soil N, and lower C:N ratios in foliage and organic soil samples from six stands of Englemann spruce east of the Continental Divide than those in samples from six sites west of the Divide and attributed these differences to greater atmospheric N deposition east of the Divide (Rueth and Baron, 2002). The Bristlecone pine and Englemann spruce data, however, are within the N limitation range of forest productivity (Barrick and Schoettle, 1996); thus, these studies do not provide definitive evidence of a lack of N limitation at these sites. At present, atmospheric N deposition likely primarily enhances production in sub-alpine forests, but additional and continued studies are needed to examine the effects in areas furthest east in the Front Range that have the highest rates of N deposition.

Rueth and Baron (2002) measured net N-mineralization and nitrification rates in laboratory incubations of O-horizon soil from Englemann spruce stands. The mean net N-mineralization rate for sites east of the Continental Divide ($91 \text{ kg N ha}^{-1} \text{ year}^{-1}$) was significantly greater than the mean for sites west of the Divide ($18 \text{ kg N ha}^{-1} \text{ year}^{-1}$), but the mean net nitrification rate for sites east of the Divide ($15 \text{ kg N ha}^{-1} \text{ year}^{-1}$) was not significantly greater than the mean for sites west of the Divide ($1.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$). The five-fold difference in N-mineralization rates between these two sets of sites exceeds the approximate two-fold difference in atmospheric N deposition between the sites and suggests that other factors such as soil texture and organic matter content may play a role in the different rates as well.

2.3. Inorganic nitrogen chemistry of surface waters

Data on dissolved inorganic nitrogen (DIN) species in surface waters can identify hydrologic sources and the biogeochemical processes that may transform N during its movement through watersheds. Concentrations and loads of NO_3^- and NH_4^+ (mainly NO_3^-) in surface waters have been measured on a regular, continuous basis at only a few intensive-study sites in the Rocky Mountain study region. Surface water NO_3^- concentrations have been measured at many other sites, but primarily in water-chemistry surveys, with just one or a few values available for each site. Much of the variation in NO_3^- concentrations and loads in surface waters in the study region has been attributed to variation in atmospheric N deposition, and load data from two lakes in the Front Range provide some of the strongest evidence that high-elevation ecosystems are at stage 1–2 of the N saturation model.

2.3.1. Concentrations of DIN species in surface waters at intensively-studied sites

Nitrate concentrations in surface waters of the Rocky Mountains of Colorado and southern Wyoming show wide spatial and temporal variability. Snowmelt dominates the annual hydrograph in high-elevation watersheds, and the highest NO_3^- and NH_4^+ concentrations in surface waters commonly occur early in the snowmelt (Campbell et al., 1995; Williams and Tonnessen, 2000). Ammonium concentrations in most surface waters are $<1 \mu\text{mol l}^{-1}$ and generally much less than NO_3^- concentrations. Few measurements of dissolved organic N (DON) or particulate organic N (PON) concentrations are available in surface waters of the Colorado Rockies except for data from a recent study at Green Lake 4 near Niwot Ridge where DON plus PON was about 22% of the total N load (Williams et al., 2001).

Tributaries to Loch Vale (660 ha drainage area) generally have the highest reported surface-water NO_3^- concentrations in the Colorado Rocky Mountains with mean volume-weighted NO_3^- concentrations of 18–25 $\mu\text{mol l}^{-1}$, and highest concentrations of 40 $\mu\text{mol l}^{-1}$ during early snowmelt (Table 1; Campbell et al., 1995; 2000). Nitrate concentrations at the outlet of Green Lake 4 (220 ha drainage area), near Niwot Ridge, generally range from about 20 $\mu\text{mol l}^{-1}$ during winter baseflow to 30 $\mu\text{mol l}^{-1}$ during early snowmelt, and then decrease to $<5 \mu\text{mol l}^{-1}$ in late summer (Table 1; Williams et al., 1996, 2001; Williams and Tonnessen, 2000). In this basin, NO_3^- concentrations generally increase upvalley at smaller drainage basins, except for some variation that reflects the geomorphology and vegetation drained at the smallest basin scale (Williams and Tonnessen, 2000; Williams et al., 2001). These spatial patterns indicate that stream NO_3^- concentrations

increase as the relative amount of biomass decreases upstream.

Nitrate concentrations at the GLEES site and at Fraser Experimental Forest are much lower than at Loch Vale and Green Lakes Valley. Mean NO_3^- concentrations at the East Glacier Lake outlet (29 ha drainage area) are about 1 $\mu\text{mol l}^{-1}$, and about 5 $\mu\text{mol l}^{-1}$ at the West Glacier Lake outlet (61 ha drainage area) (Table 1; Reuss et al., 1995). The NO_3^- concentrations here, as at Loch Vale and Green Lakes Valley, increase with decreasing drainage area and increasing elevation (Williams et al., 1996). Streams at the Fraser Experimental Forest, west of the Continental Divide, have the lowest NO_3^- concentrations of any of the four intensive study locations. Stream NO_3^- concentrations are generally in the 1–2 $\mu\text{mol l}^{-1}$ range with peak concentrations as high as 10 $\mu\text{mol l}^{-1}$ during snowmelt (Table 1; Stottlemeyer and Troendle, 1992; Stottlemeyer et al., 1997).

2.3.2. Nitrate concentrations in surface-water surveys

Eight surveys that included NO_3^- concentrations in alpine and subalpine surface waters in the Colorado Rockies (Fig. 3) have assessed regional N status with respect to atmospheric N deposition (Gibson et al., 1983; Eilers et al., 1987; Turk and Spahr, 1991; Newell, 1993; Musselman et al., 1996; Baron et al., 2000; Williams and Tonnessen, 2000; Clow et al., in press). In all of these surveys, samples were collected during late summer and fall, when the remote high-elevation terrain is accessible, but NO_3^- concentrations tend to be at or near their annual minimum values (Inyan et al., 1998). Nitrate concentrations reported from the eight surface water surveys range from 0.2 to 8.5 $\mu\text{mol l}^{-1}$ (Fig. 3). Data from five of these surveys can be separated into waters east and west of the Continental Divide. The results of

Table 1

Nitrate concentrations at intensive study sites in the Rocky Mountains of Colorado and southern Wyoming. All concentrations are reported in $\mu\text{mol l}^{-1}$

Study site/watershed	Area (ha)	Elev. (m)	Reference	Years(s)	Mean	Max.	Min.
<i>Loch Vale</i>							
Icy Bk.	326	3159	Campbell et al., 2000	1992–1997	18–22	30–40	10–15
Andrews Ck.	183	3100	Campbell et al., 2000	1992–1997	22–25	40–50	10–15
Loch Vale	660	3120	Baron & Campbell, 1997	1982–1993	16	20–25	10–12
<i>Green Lakes Valley</i>							
Arikaree	9	3785	Williams & Tonnessen, 2000	1994	15–20	50	5
Martinelli	8	3415	Caine, 1995	1985–1994	15–20	35–45	5
Navajo	42	3700	Williams & Tonnessen, 2000	1994	20–25	50	15
Green Lake 4	220	3550	Williams & Tonnessen, 2000	1984–1996	10–15	25–35	1–9
Lake Albion	700	3250	Caine, 1995	1985–1994	8	20–25	0–5
<i>GLEES</i>							
East Glacier Lake	29	3282	Reuss et al., 1995	1988–1990	0.6		
West Glacier Lake	61	3276	Reuss et al., 1995	1988–1990	4.9		
<i>Fraser Forest</i>							
Fool Ck.	67	3180	Stottlemeyer & Troendle, 1992	1987–1988	1.0		
East St. Louis Ck.	803	2880	Stottlemeyer & Troendle, 1992	1987	2.0		
Lexen Ck	124	2985	Stottlemeyer et al., 1997	1990	2.5	5	0

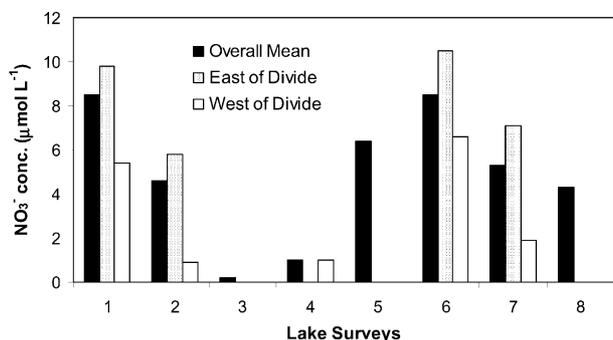


Fig. 3. Nitrate concentrations from lake surveys in the Rocky Mountains of Colorado and southern Wyoming. References and number of lakes sampled in each survey: (1) Gibson et al., 1983, $n = 127$; (2) Eilers et al., 1987, $n = 44$; (3) Turk and Spahr, 1991, $n = 50$; (4) Newell, 1993, $n = 10$; (5) Musselman et al., 1996, $n = 267$; (6) Baron et al., 2000, $n = 44$; (7) Williams and Tonnessen, 2000, $n = 54$; (8) Clow et al., in press, $n = 22$.

these surveys indicate that NO_3^- concentrations in surface waters east of the Divide are about two to six times higher than those in surface waters west of the Divide (Gibson et al., 1983; Eilers et al., 1987; Baron et al., 2000; Williams and Tonnessen, 2000; Clow et al., in press).

2.3.3. Causes of temporal variation in NO_3^- concentrations

Surface water data collected at the four intensive study locations indicate a several-fold increase in NO_3^- concentrations from late summer to early spring snowmelt (Campbell et al., 2000; Williams and Tonnessen, 2000). This seasonal pattern is typical of that observed in upland surface waters of northeastern North America and Europe (Stoddard, 1994). Nitrate concentrations in alpine ecosystems decrease in late spring as biological demand for N increases, and then increase as the short growing season ends late in the summer. The highest NO_3^- concentrations typically occur from late April to mid-May, well before peak snowmelt runoff in mid-June to early July (Campbell et al., 2000; Williams and Tonnessen, 2000).

Measurements of $\delta^{18}\text{O}-\text{NO}_3^-$ indicate that even during snowmelt, much of the NO_3^- in tributaries of Loch Vale originates from nitrification in soils (Campbell et al., 2002). This is consistent with a build-up of NO_3^- in the soil and talus under the snowpack through immobilization, N mineralization, and nitrification followed by NO_3^- flushing into surface waters during snowmelt (Brooks et al., 1996; Brooks et al., 1998).

2.3.4. Causes of Spatial Variation in NO_3^- Concentrations

Much of the spatial variation in NO_3^- concentrations among surface waters of the Colorado Rockies can be attributed to three factors: (1) precipitation tends to increase with elevation in the Rockies (Burns, 2003), (2) rates of atmospheric N deposition east of the Con-

tinental Divide tend to be greater than west of the Divide (Baron et al., 2000; Burns, 2003), and (3) variation in land cover type. Several recent studies have shown that local variation in the amount of vegetation and soil vs. bedrock and talus slopes explain a significant amount of the variation in surface water NO_3^- concentrations in high elevation watersheds of Colorado (Clow and Sueker, 2000; Sickman et al., 2002). Vegetation and soil cover promotes retention of N, and therefore, lower NO_3^- concentrations in surface waters, whereas bedrock and talus slopes allow the rapid movement of infiltrating precipitation to surface waters, have little vegetation to take up N, and are therefore associated with higher NO_3^- concentrations in surface waters

2.3.5. Are there significant temporal trends in surface water NO_3^- concentrations?

The only sites at which surface-water chemistry data are sufficient for evaluation of trends in NO_3^- concentrations are at Loch Vale and the Green Lakes Valley. Surface waters at the Loch Vale watershed show no significant temporal trends in NO_3^- concentrations, but the outlet of Green Lake 4 shows a trend of increasing annual minimum NO_3^- concentrations from 1984 to 1993 (Williams et al. 1996) and from 1985 to 1997 (Williams and Tonnessen, 2000). The entire NO_3^- record at this lake shows no significant trend, however, and the annual minimum NO_3^- concentrations at two small watersheds without lakes, and at the lake that drains the entire 700-ha Green Lakes Valley, show no temporal trend (Caine, 1995). The trend at Green Lake 4 is not consistent across the Green Lakes Valley; this suggests that some factor other than increasing N deposition (as recorded at the nearby Niwot Saddle) may be causing the upward trend in the annual minimum NO_3^- concentration at the Green Lake 4 outlet.

2.3.6. Watershed N budgets and N saturation

Elevated NO_3^- concentrations, which average as high as 15 to 25 $\mu\text{mol l}^{-1}$ in the Loch Vale and Green Lakes Valley watersheds (Campbell et al., 2000; Williams and Tonnessen, 2000) are relatively low compared to values of 50–200 $\mu\text{mol l}^{-1}$ in watersheds of eastern North America and Europe that have been affected by atmospheric N deposition (Stoddard, 1994). The proportion of atmospheric N deposition retained by the ecosystem may be more representative of N status than NO_3^- concentrations in surface waters because retention accounts for the low biological activity and high hydrologic throughput of high-elevation watersheds in the Rockies.

Nitrogen budgets at the four intensive study locations described previously indicate that retention of inorganic N from atmospheric wet deposition ranges from 25 to 50% in the Loch Vale and Green Lakes Valley watersheds to 68 to 95% in the GLEES and Fraser Forest watersheds (Table 2; Stottlemyer and Troendle, 1992;

Table 2
Percentage input of N in wet atmospheric deposition that was retained in watersheds in the Rocky Mountains of Colorado and southern Wyoming

Site	Reference	Years	Retention of DIN Input (%)
<i>Green Lakes Valley</i>			
Green Lake 4	Williams et al., 2001	1996–1998	49 ^a
Loch Vale			
Andrews Creek	Campbell et al., 2000	1992–1997	29
Icy Brook	Campbell et al., 2000	1992–1997	46
Loch Vale	Baron and Campbell, 1997	1984–1993	25
<i>Fraser Forest</i>			
East St. Louis Ck.	Stottlemeyer and Troendle, 1992	1987–1988	95
Fool Ck.	Stottlemeyer and Troendle, 1992	1987	96
<i>GLEES</i>			
East Glacier Lake	Reuss et al., 1995	1988–1990	96 ^a
West Glacier Lake	Reuss et al., 1995	1988–1990	68 ^a

^a Includes snow inputs from pits or lysimeters.

Reuss et al., 1995; Baron and Campbell, 1997; Campbell et al., 2000; Williams et al., 2001). If N in dry deposition were included, the % retention would be even greater. The spatial retention patterns among these sites are broadly consistent with those observed for NO₃⁻ concentrations in their surface waters. Sites with greatest retention have the lowest surface water NO₃⁻ concentrations.

2.4. Aquatic ecosystems—impacted by N deposition or not?

The principal aquatic biota studied in the Colorado Rocky Mountains in relation to acid precipitation and atmospheric N deposition are algae and amphibians. Little is known about the effects of atmospheric deposition on fish because many of the lakes most sensitive to acidification are fishless or have a history of stocking with non-native species (Peterson et al., 1998). Adverse effects on fish populations in high-elevation lakes and streams in the region probably are minimal, however, because these waters have not been chronically acidified by atmospheric deposition.

2.4.1. Algae—N limitation and changes in species dominance

Two major areas of study regarding the effects of atmospheric N deposition on algae and in the Colorado Rockies are whether: (1) algal production is limited by N availability in lakes and streams, and (2) algal populations have been affected by atmospheric N deposition.

A likely outcome of increasing N saturation in an ecosystem is a shift in nutrient limitation of terrestrial and aquatic biota from N to other nutrients such as P (Williams et al., 1996). Morris and Lewis (1988) studied nutrient limitation in phytoplankton at eight Colorado mountain lakes that are located mostly west of the Continental Divide, and found examples of N limi-

tation, P limitation, concurrent N and P limitation, reciprocal N and P limitation, and neither N nor P limitation. The potential role of atmospheric N deposition in this aspect of phytoplankton growth cannot be easily ascertained, however, because some of the lakes are affected by human development and its associated nutrient runoff. Toetz (1999) found N and P co-limitation in periphytic epilithon at subalpine North Boulder Creek in the Green Lakes Valley. McKnight et al. (1990) measured the response of phytoplankton photosynthesis rates to additions of either Ca(NO₃)₂ or H₂SO₄ and concluded that growth stimulation by NO₃⁻ could not be conclusively demonstrated. To date, neither the number of aquatic nutrient studies, nor the spatial extent of such studies in the Colorado Rockies, is great enough to provide general conclusions about spatial patterns of nutrient limitation among phytoplankton species. Additional aquatic nutrient research is needed that encompasses a significant spatial range in atmospheric N deposition.

Recently collected sediment cores from three Front Range lakes indicate long-term shifts in diatom populations that are consistent with increased atmospheric N deposition rates since the mid-20th century (Wolfe et al., 2001; Waters et al., in press). Sediment cores from two lakes east of the Continental Divide in Rocky Mountain National Park showed increasing amounts of two diatom species (*Asterionella formosa* and *Fragilaria crotonensis*) in sediment from 1900 to 1950 and eventual dominance of *A. formosa* between 1950 and 1970 (Wolfe et al., 2001). Both species are correlated with agricultural effects and respond quickly to N additions (McKnight et al., 1990). Wolfe et al. (2001) also found a 2–3 permil increase in δ¹⁵N at these lakes after 1950 that paralleled the changes in species composition, and attributed these changes to the effects of increasing atmospheric N deposition to these lakes from the east. Waters et al. (in press) found several changes in the

diatom community at Green Lake 4 that began about 1939, including (1) increased *Fragilaria* species, (2) increased abundance of microbial and algal humic substances, and (3) decreased species diversity. They attributed these changes to the long-term effects of increased atmospheric N deposition from increased use of ammonia-based fertilizer in the west since 1939. One puzzling aspect of these data is why the shifts indicative of N enrichment began in 1939 in Green Lake 4, and not until 1950 in the two lakes in Rocky Mountain National Park. The long-term changes in the diatom community are noteworthy, however, additional sediment studies are necessary to discern whether these changes are widespread across the Front Range.

2.4.2. Amphibians—has atmospheric N deposition caused decline?

Many species of amphibians are sensitive to acidity during their aquatic stages, and episodic acidification of small vernal pools has been suggested as a possible explanation for declines in populations of tiger salamander (*Ambystoma tigrinum*), boreal toad (*Bufo boreas boreas*), and chorus frog (*Pseudacris triseriata*) in the Colorado Rocky Mountain region (Harte and Hoffman, 1989; Carey, 1993; Kiesecker, 1996). Other studies in the Colorado Rockies, however, indicate that episodic acidification generally occurs before amphibian species lay their eggs in the spring and therefore, does not affect the aquatic stages (Corn and Vertucci, 1992; Wissinger and Whiteman, 1992; Vertucci and Corn, 1996). Atmospheric N deposition is a possible threat to amphibians because of its potential, though uncertain role in episodic acidification of surface waters in the Colorado Rockies.

Harte and Hoffman (1989) exposed tiger salamander eggs to varying pH conditions within *in-situ* microcosms in a lake in the Elk Mountains of west-central Colorado where surface waters are known to become episodically acidic in the early spring, and where tiger salamander populations were declining through the 1980s. An LD-50 pH (value at which 50% mortality occurs) of 5.6 was obtained from experiments, and 100% mortality of the zooplankton *Diatomus coloradensis* (major component of the aquatic food web) at pH 5.0 was observed. The authors did not observe any egg or larval mortality in the ponds under natural conditions, but demonstrated that the pH of some of the ponds in the area decreased to values <5.0 during early spring snowmelt, when tiger salamander eggs were assumed to have been present in pond waters. Wissinger and Whiteman (1992) monitored the tiger salamander population in the same region and found that episodic acidification associated with snowmelt occurred only before the eggs were laid in ponds, and also found no correlation between the acid-neutralizing capacity of ponds and embryonic survival. Their observations support pond drying as a

greater source of tiger salamander mortality than episodic acidification.

In summary, most of the evidence supporting acidification of habitat as a cause of amphibian-population declines in the Colorado Rockies comes from laboratory experiments or circumstantial evidence, and no field evidence is currently available to unequivocally attribute population declines to acidification.

2.5. Comparison to forested ecosystems of eastern North America

High-elevation ecosystems in the Rocky Mountains of Colorado and southern Wyoming are snow-covered for 7–9 months of the year, so snow plays a greater role in these ecosystems than those in upland areas of eastern North America. Rockies ecosystems therefore sequester much less N than those in the east. For example, only 1–2% of N storage in alpine tundra at Niwot Ridge is in the form of living biomass, and the majority of this biomass is stored in roots (Fisk et al., 1998), whereas in a hardwood forest at Hubbard Brook, New Hampshire about 30% of N is stored in living biomass that is at least 5 times greater than in the alpine tundra at Niwot Ridge, and the majority of this living biomass is stored above ground (Likens and Bormann, 1995). One consequence of these differences is that climate change and atmospheric N deposition are perhaps more tightly linked in the Rockies than in any other region of North America. Additionally, microbial N cycling processes play an even greater relative role than they do in eastern North America. The date of initiation and melting of snow cover, and the redistribution of snow by wind have large implications for microbial N cycling processes and NO_3^- production for leaching. Therefore, atmospheric N deposition alone cannot be simply related to ecosystem N indicators to determine cause and effect, as has been done in many previous studies in the region.

High-elevation ecosystems in the Rockies also have more exposed bedrock and talus than those in eastern North America. Surprisingly, however, most of the NO_3^- in alpine surface waters has been processed and nitrified at least once (Campbell et al., 2002). These observations can be reconciled in part by considering the active N cycle within talus slopes. Little is known, however, about either the total rates of N cycling processes within talus or the hydrology of talus. Talus discharge has been assumed to dominate stream baseflow, but there is little quantitative evidence to support this assumption. More research of the N and water cycles in talus is therefore recommended.

The response of high-elevation ecosystems and watersheds in the Colorado Rockies has been described previously within the context of the N saturation model (Williams et al., 1996; Fenn et al., 1998; Campbell et al.,

2000). However, watersheds in eastern North America that receive nearly double the amount of N in wet deposition than that of the eastern Front Range have retention values of 50–80% (Fenn et al., 1998)—a range comparable to that of Green Lake 4, but significantly less than that of Loch Vale. The percent retention of DIN in wet deposition at Loch Vale is comparable to values observed at Fernow Watershed 4 in West Virginia, a site considered to be at an advanced stage (2) of N saturation (Fenn et al., 1998). These comparisons indicate that alpine watersheds in the Front Range of Colorado that receive only 3–5 kg N ha⁻¹ year⁻¹ in wet deposition are at a stage of N saturation comparable to that of watersheds in eastern North America that receive 6 to 8 kg N ha⁻¹ year⁻¹ in wet deposition (stage 1 to 2; Aber et al., 1989; Stoddard, 1994), and comparable to watersheds in Europe that receive > 10 kg N ha⁻¹ year⁻¹ (Dise and Wright, 1995). This similarity is

attributed to the low biomass and short growing season in alpine watersheds of the Front Range. These N retention results, however, do not necessarily mean that root biomass, foliar biomass, and net primary productivity would be adversely affected as predicted by Aber et al. (1989) if atmospheric N deposition increased sufficiently at Loch Vale to produce stage 2–3 results. These aspects of the model remain to be demonstrated in high elevation ecosystems of the Rockies.

As studies reviewed here have shown (Bowman et al., 1993, 1995), and as Fenn et al. (1998) have previously discussed, alpine tundra plants can be N limited within a watershed such as the Green Lakes Valley that has high stream NO₃⁻ concentrations and retention of only about half of atmospheric N deposition. This response is due in part to the temporal offset between snowmelt and its associated high NO₃⁻ availability and the growing season. Therefore, the dynamics of N-mineraliza-

Table 3

Summary of several types of studies of ecosystem effects of atmospheric N deposition discussed in this review

Study type	Key references	Ecosystem affected	Effects	Critical evaluation
N additions	Bowman et al., 1995; Theodose and Bowman, 1997; Bowman and Steltzer, 1998; Steltzer and Bowman, 1998	Alpine tundra plant community	Shifts in community composition, increased NO ₃ ⁻ leaching, increased soil acidity, shift to P limitation	Climate change that affects snow cover will complicate responses
Snow cover	Brooks et al., 1998; Brooks et al., 1999	Alpine tundra microbial community	Frozen soil results in high NO ₃ ⁻ release	Pattern is different in Sierra Nevada, but Sierra soils may not freeze similarly to soils in Rockies
N availability	Williams et al., 1996; Rueth and Baron, 2002	Subalpine forest	Higher N-mineralization and foliar N, lower C:N in stands east of Continental Divide	Stands are still within range of N limitation, differences exceed deposition difference
N cycling	Williams et al., 1997; Bieber et al., 1998	Talus slopes	Active N cycle, N pools, N-mineralization and nitrification rates comparable to alpine tundra	Hydrologic connection of talus to alpine tundra and surface waters still not well understood
NO ₃ ⁻ concentrations east vs. west	Baron et al., 2000; Williams and Tonnessen, 2000	Lakes	Greater NO ₃ ⁻ concentrations east of Continental Divide	Greater atmospheric N deposition east of Divide is most likely explanation
NO ₃ ⁻ trends	Williams et al., 1996; Williams and Tonnessen, 2000	Lakes	Upward trend in seasonal minimum NO ₃ ⁻ concentrations	Trend not consistent across Green Lakes valley, atmospheric N deposition not likely cause
Watershed N retention	Baron and Campbell, 1997; Campbell, 2000; Williams et al., 2001	Alpine/subalpine watersheds	Low N retention	Values at Loch Vale, Green Lakes valley comparable to eastern North American watersheds that receive 2–3 times as much N deposition
N limitation of phytoplankton	Morris and Lewis, 1988; Toetz, 1990; McKnight et al., 1990	Lake and stream phytoplankton	Growth limited by N availability	Studies inconclusive to date
Historical changes in diatom species	Wolfe et al., 2001; Waters et al., in press	Lake diatoms	Species dominance has changed since mid-20th century	Not enough studies to determine role of N deposition across region
Amphibian decline	Vertucci and Corn, 1996; Harte and Hoffman, 1989; Wissinger and Whiteman, 1992	Vernal pools and ponds	Episodic acidification has caused declines in tiger salamander, other species	Role of acidification in amphibian decline unclear, never demonstrated by in-situ studies

tion, nitrification, and immobilization affect NO_3^- leaching rates to an even greater extent than in forested ecosystems of eastern North America. These microbial N cycling processes show high variation as a function of changes in snow cover (Brooks et al., 1998, 1999). Indeed, annual variation in snow cover alone, regardless of N content, is probably the greatest control of year-to-year variation in NO_3^- concentrations and loads in surface waters. Additional research into the effect of snow cover on surface water NO_3^- concentrations may further elucidate this point.

3. Summary

The numerous advances in scientific understanding of the effects of atmospheric N deposition on high elevation ecosystems in the Colorado Front Range and surrounding region during the past two decades that were discussed in this review are summarized in Table 3.

Nitrogen limitation of production in alpine tundra is common, among other factors such as light, moisture, and temperature. The tundra plant community responds to N additions through increased production, and a shift towards nitrophilous plants with consequent increased microbial N cycling rates and increased leaching of NO_3^- . Experimentally-increased snow cover alone, however, can produce rapid shifts in plant community composition, increased microbial immobilization, and decreased NO_3^- concentrations in drainage waters. In contrast to alpine tundra, subalpine forest vegetation is more uniformly N limited with low NO_3^- leaching rates, however, higher rates of atmospheric N deposition east of the Continental Divide appear to increase foliar and soil N content in these forests.

Surface waters in the Front Range commonly have NO_3^- concentrations $> 30 \mu\text{mol l}^{-1}$ during early snowmelt, and about $5\text{--}10 \mu\text{mol l}^{-1}$ during the growing season. In contrast, NO_3^- concentrations in surface waters west of the Continental Divide are generally, $< 2 \mu\text{mol l}^{-1}$ during the growing season. This east-west difference seems to be largely caused by atmospheric N deposition that is generally $1\text{--}3 \text{ kg ha}^{-1} \text{ year}^{-1}$ lower west of the Divide. A reported temporal trend of increasing minimum NO_3^- concentrations at Green Lake 4 since the mid-1980s was not confirmed throughout the Green Lakes Valley nor in the Loch Vale watershed, and thus, is probably not the direct result of historical increases in atmospheric N deposition.

The effects of atmospheric N deposition on aquatic ecosystems in the study region are uncertain. A widespread shift from N to P limitation of phytoplankton has not been clearly demonstrated. The results of two recent studies suggest a change in the dominance of diatom species near the mid-20th century, but widespread species changes across lakes in the region and the

role of atmospheric N deposition in these possible changes awaits further confirmation. The effects of episodic acidification by atmospheric N deposition on decline of the tiger salamander and other amphibians have never been conclusively demonstrated under natural conditions by an in situ study of a natural population.

In summary, results of research to date on the effects of atmospheric N deposition in the Colorado Rockies suggests that rates of NO_3^- leaching and NO_3^- concentrations in surface waters have increased since the mid-20th century in response to increased rates of atmospheric N deposition. Rates of microbial N cycling processes have probably also accelerated in response to increased atmospheric N deposition. Ecosystem effects on alpine tundra, subalpine forest, and aquatic ecosystems, however, are currently subtle, and clear effects resulting from atmospheric N deposition are difficult to demonstrate given natural variability and climate effects, which co-vary with N deposition. These subtle effects, however, are likely to become more prominent given current or increased rates of N deposition. Declines in net primary productivity, fine root biomass, foliar biomass, and greatly increased NO_3^- leaching are predicted by the N saturation model if alpine ecosystems in the Colorado Front Range move from the current level of stage 1–2 of N saturation to stage 2–3. It is unclear, however, if such an advance of N saturation will occur in Colorado at rates of N deposition that are about half those that would cause similar effects in forested ecosystems of eastern North America.

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