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**DISSERTATION**

**ENGLEMANN SPRUCE FOREST RESPONSES TO NITROGEN DEPOSITION  
IN NORTHERN COLORADO**

**Submitted by**

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**Graduate Degree Program in Ecology**

*In partial fulfillment of the requirements*

**For the Degree of Doctorate of Philosophy**

**Colorado State University**

**Fort Collins, Colorado**

**Fall 2001**

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COLORADO STATE UNIVERSITY

August 27, 2001

WE HERBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY HEATHER MARIE RUETH ENTITLED: ENGLEMANN SPRUCE FOREST RESPONSES TO NITROGEN DEPOSITION IN NORTHERN COLORADO, BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTORATE OF PHILOSOPHY.

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## ABSTRACT OF DISSERTATION

### ENGLEMANN SPRUCE FOREST RESPONSES TO NITROGEN DEPOSITION IN NORTHERN COLORADO

Atmospheric nitrogen (N) deposition to high-elevation sites in northern Colorado is greater east of the Continental Divide compared to the west (3-5 vs. 1-2 kg N ha<sup>-1</sup> y<sup>-1</sup>). Three approaches were used to address the effects of elevated N deposition on high-elevation old-growth Englemann spruce forests: a fertilization experiment, comparative study, and modeling exercise.

Ammonium-nitrate fertilizer was applied (25 kg N ha<sup>-1</sup> y<sup>-1</sup>) at two sites, one west and the other east of the Continental Divide over four years. We hypothesized that due to differences in atmospheric N deposition, the western site response would be minimal to fertilization due to N limitation while the eastern site would respond rapidly. The eastern site responded rapidly to fertilization. Nitrogen cycling rates and estimated N leaching losses, in particular, increased dramatically. Western sites, as expected, showed little change in N cycling rates or leaching loss estimates.

Six forested sites east and six forested sites west of the Continental Divide were compared. Higher N deposition sites had characteristics comparable to forests in the northeastern US and Europe that have been impacted by elevated N deposition. Current levels of N deposition, even though low by comparison to other regions, have caused measurable changes in forest biogeochemistry. These include increased soil and foliar N, decreased soil and foliar C:N ratios, and increased foliar N:Mg ratios and soil net mineralization rates.

CENTURY, a biogeochemical cycling model, was used to address the sensitivity of Englemann spruce forests to alterations in climate, soil texture and N inputs. The objective was to simulate potential ecosystem responses to increased annual precipitation, altered soil texture and elevated N deposition, because while field data from the comparative study indicate atmospheric N deposition has affected Englemann spruce forest biogeochemistry, variation in precipitation and soil texture between sites were plausible alternative explanations for the observed differences among sites. Similarities between model results and field data indicate elevated N inputs, not dissimilarities in precipitation or soil texture, drove the observed contrasts between high and low N deposition sites.

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**I dedicate this to my grandmother,  
Cora Tomeoni,  
Who has always and will continue  
To hold a special place in my heart and life.  
Being 97 years old she deserves it!**

**With Lots of Love, Your Granddaughter**

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## 1. Introduction

East of the Continental Divide is where a majority of Colorado's population of 4 million people resides and is an important agricultural and livestock producing region (Baron et al. 2000). The greatest concentration of nitrogen oxide ( $\text{NO}_x$ ) emissions from point and mobile sources in the state occurs in Front Range metropolitan areas (Williams and Tonnessen 2000). Local easterly winds transport some of this nitrogen (N) to high elevation watersheds east of the Continental Divide (Parrish et al. 1986, 1990, Sievering et al. 1989, Langford and Fehsenfeld 1992). Strong westerly winds in the upper atmosphere often prevent the N-enriched air masses from crossing the Continental Divide (Bossert 1990, Baron and Denning 1993). Two recent compilations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations from Colorado National Atmospheric Deposition Program/National Trends Network (NADP/NTN) monitoring stations showed that sites east of the Continental Divide had significantly greater concentrations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  than western sites (Baron et al. 2000, Heuer et al. 2000). The combination of emission sources, local easterly winds and orographic precipitation results in atmospheric N deposition rates to high-elevation ecosystems of 3-5  $\text{kg N ha}^{-1} \text{y}^{-1}$  east compared to 1-2  $\text{kg N ha}^{-1} \text{y}^{-1}$  west of the Continental Divide.

Lake chemistry data and paleolimnological research show that high-elevation aquatic systems east of the Continental Divide have been affected by N deposition (Baron et

al. 2000, Williams and Tonnessen 2000). Nitrogen deposition also influences forest biogeochemistry (Vitousek et al. 1997, Aber et al. 1998, Fenn et al. 1998, Gundersen et al. 1998). This work explores whether significant changes have occurred in Englemann spruce (*Picea engelmannii*) forests of northern Colorado.

Foliar and soil N, nitrification rates, and nitrate ( $\text{NO}_3^-$ ) leaching increase with elevated N deposition. Eventually, foliar nitrogen:nutrient imbalances occur, and foliar and soil C:N ratios decline (Vitousek et al. 1997, Aber et al. 1998, Fenn et al. 1998). If  $\text{NO}_3^-$  availability exceeds biologic demand, either directly from atmospheric  $\text{NO}_3^-$  deposition or indirectly through enhanced nitrification rates,  $\text{NO}_3^-$  leaches from terrestrial to aquatic ecosystems. Increased  $\text{NO}_3^-$  leaching has been linked to soil and stream acidification, mobilization of aluminum from terrestrial to aquatic systems, elevated cation leaching and altered nutrient cycling, all of which can adversely effect forest health and water quality (Driscoll et al. 1987, Fenn et al. 1998).

Forest ecosystems differ in their rate of response to increased N deposition (Aber et al. 1998). For example, the Harvard forest hardwood stand as of 1998 has received approximately  $900 \text{ kg N ha}^{-1}$  over 6 years without initiating significant nitrification or N leaching (Aber et al. 1998). On the other hand, McNulty and Aber (1993) observed significant biogeochemical responses in Vermont spruce-fir forests following three years of N additions ranging from  $15\text{-}31 \text{ kg ha}^{-1} \text{ y}^{-1}$ . It is not completely understood what factors control these differences. Land-use history, soil N pool size, species composition, stand age and growing season length, are important factors determining the rate at which forests respond to increased N inputs (Stoddard 1994, Nadelhoffer et al. 1995, Fenn et al. 1998, Lovett and Rueth 1999). These factors play an important role in determining the balance between N availability and demand.

The old-growth status, evergreen habit and short growing season of high-elevation Englemann spruce forests reduces ecosystem N demand which translates to less additional N is required before N availability exceeds plant and microbial demand. Low N demand may predispose Colorado Englemann spruce forests to the effects of elevated N inputs because once N availability exceeds biologic demand the negative impacts of N deposition on forest ecosystems begin to occur.

I used a fertilization experiment, comparative study, and modeling exercise to address the potential impacts of atmospheric N deposition on high-elevation old-growth Englemann spruce forest biogeochemistry in Colorado. Fertilization experiments establish a cause and effect relationship but the disadvantage is that often unrealistically high doses of N are applied in order to produce measurable responses within a few years. The benefit of comparative studies is that sampling occurs in natural undisturbed ecosystems and the drawback is that it is difficult to control all the potentially confounding factors between sites that influence N dynamics. Such factors include species composition, elevation, aspect, parent material, site history and climate. Models control potentially confounding factors, allowing a focus on the factor of interest, in this case N inputs. However, a model is just that and it is often difficult to ascertain how well model output compares to reality. Independently none of the methods can conclusively determine whether N deposition has altered forest biogeochemical processes. However, applying all three approaches leads to a more thorough understanding.

Nitrogen fertilizer was applied at the rate of 25 kg N ha<sup>-1</sup> y<sup>-1</sup> at Loch Vale and Fraser Experimental Forest, which are located east and west of the Continental Divide, respectively. The objectives of the fertilization experiment were to determine whether initial differences existed in forest biogeochemical processes and N pools between the two sites and how the

two sites responded to N fertilization. We hypothesized due to differences in atmospheric N deposition, the western site would show a limited response to fertilization due to N limitation while the eastern site would respond rapidly.

Comparative studies by others have demonstrated gradients in forest responses across regions of increasing N deposition (McNulty et al. 1991, Tietema and Beier 1995, Aber et al. 1998, Gundersen et al. 1998, Lovett and Rueth 1999). I established twelve sites in my comparative study; six west and six east of the Continental Divide. The two sites Fool Creek and Loch Vale (FC and LV) correspond to the sites used in the fertilization experiment. I tried to control potentially confounding factors during site establishment; species composition, elevation, aspect, parent material, site history and climate were matched as closely as possible. Nevertheless, there were differences. Eastern sites received 21% greater annual precipitation and had an average of 5% higher soil clay content. CENTURY, a biogeochemical cycling model, was used to address the response of forest processes to alterations in climate, soil texture and N inputs. My primary objective was to simulate potential ecosystem responses to increased annual precipitation, altered soil texture and elevated N deposition, to explore whether differences in precipitation and soil texture confounded the interpretation of the comparative study.

It has been hypothesized that climate warming could counter the impacts of greater N inputs on leaching losses through enhanced N retention in soil and vegetation (Baron and Campbell 1997, Fenn et al. 1998). The ability to predict forest responses to climate change is important for understanding the processes influencing the global carbon budget and determining the capacity of forests to offset fossil fuel emissions (Schimel et al. 2000, Joyce and Birdsey 2000). And forest responses to climate change will be strongly constrained by nutrient availability and soil moisture (Ryan et al. 1996). Therefore, a second objective of the

modeling exercise was to examine potential interactions between projected future N deposition rates and climate change on forest ecosystem processes.

The results of these three approaches to address forest biogeochemical responses to N deposition are detailed in the following three chapters. Chapter 2 examines the response of forest vegetation and soil to fertilization. Chapter 3 describes the comparison of forest conditions east and west of the Continental Divide. Chapter 4 uses a modeling approach to address the influence of alterations in climate, soil texture and N inputs on ecosystem properties.

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## 2. Response of old-growth Englemann spruce forests to nitrogen fertilization

### 2.1 Abstract

We fertilized high-elevation old-growth Englemann spruce stands in Colorado with 25 kg N ha<sup>-1</sup> y<sup>-1</sup> from 1996-1999. Nitrogen (N) was applied at two sites, one west of the Continental Divide that receives 1-2 kg N ha<sup>-1</sup> y<sup>-1</sup> as atmospheric deposition inputs, and another east of the Continental Divide that receives at least 3-5 kg N ha<sup>-1</sup> y<sup>-1</sup> from deposition. Our objectives were to determine whether initial differences existed in forest biogeochemical processes and N pools between the two sites (initial conditions determined with control plots) and how the two sites responded to N fertilization. We hypothesized soil mineralization rates and N leaching at the western site would respond little to fertilization due to N limitation while the eastern site would respond rapidly. The east site had significantly higher initial soil %N, mineralization rates, and nitrification rates, and lower soil C:N and lignin:N ratios. Following fertilization mineralization rates, soil water NO<sub>3</sub><sup>-</sup>, resin bag NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, and foliar %N increased significantly at the east site. In comparison to the east site, the west site was relatively unresponsive to fertilization. The strong response of the east site suggests either that these high elevation forest are extremely responsive to chronic low levels of N additions so that they were close to N saturation before fertilization began, or that wet and dry N deposition has been grossly underestimated in the Colorado Front Range.

## 2.2 Introduction

The Colorado Front Range east of the Continental Divide is where the majority of Colorado's population resides and is an important agricultural and livestock producing region (Baron et al. 2000). The combination of anthropogenic N sources, local easterly winds and orographic precipitation causes greater N deposition at high-elevation sites east of the Continental Divide compared with western sites (Parrish et al. 1986, 1990, Sievering et al. 1989, Langford and Fehsenfeld 1992, Williams and Tonnessen 2000). Estimated total (wet plus dry) N deposition to Loch Vale, an eastern NADP/NTN monitoring station, is 3.2-5.5 kg N ha<sup>-1</sup> y<sup>-1</sup> (years 1992-1997, Campbell et al. 2000). Wet inorganic N deposition at Fraser Experimental Forest, a western site, averaged 1.7 kg N ha<sup>-1</sup> y<sup>-1</sup> for 1984-1986 and was 1.1 kg N ha<sup>-1</sup> in 1990 (Stottlemyer and Troendle 1992, Stottlemyer et al. 1997). Human activity along the Colorado Front Range has contributed an estimated cumulative 160 kg N ha<sup>-1</sup> since 1900 to eastern high-elevation ecosystems (Rueth and Baron, in press). Aquatic ecosystems in the Front Range have responded to N additions with altered algal composition and productivity, and east compared to west side forest stands show significantly lower soil and foliar C:N ratios, elevated soil and foliar N as well as greater foliar N:Mg ratios and soil net mineralization rates (Baron et al. 2000, Wolfe et al. 2001, Rueth and Baron, in press).

Forest ecosystems differ in their rate of response to increased N deposition (Aber et al. 1998). A Harvard forest hardwood stand has received approximately 900 kg N ha<sup>-1</sup> over 6 years, without evidence of significant nitrification or N leaching (Aber et al. 1998). On the other hand, McNulty and Aber (1993) observed significant biogeochemical responses in Vermont spruce-fir forests following three years of N additions ranging from 15-31 kg ha<sup>-1</sup> y<sup>-1</sup>. It is not completely understood what factors control these differences. Land-use history, soil N pool size, species composition, stand age and growing season length are some of the

important factors determining the balance between N availability and demand (Stoddard 1994, Nadelhoffer et al. 1995, Fenn et al. 1998, Lovett and Rueth 1999).

We hypothesize that high-elevation old-growth Englemann spruce forests would respond to low N additions. Old-growth forests have reduced biologic N demand due to low net ecosystem production compared to younger forests (Swank and Vose 1997, Goodale and Aber 2001). The rate at which forests respond to increased N inputs has been linked to the capacity of the soil system to immobilize incoming N either through microbial uptake or adsorption (Tietema et al. 1995). A critical soil C:N ratio exists where below 24 or 25 increased nitrification rates and  $\text{NO}_3^-$  leaching occurs (Gundersen and Rasmussen 1990, Tietema and Beier 1995, McNulty et al. 1996, Emmett et al. 1998, Lovett and Rueth 1999). The C:N ratio threshold can be reached quickly when N accumulates faster than C and/or C inputs are reduced. Old-growth forest C inputs and N demand are reduced resulting from low productivity and elevated N inputs can accelerate the rate at which the critical C:N ratio is attained (Goodale and Aber 2001).

Here we report results from a fertilization experiment of high-elevation old-growth Englemann spruce forests in Colorado. The study is unusual in that ambient levels of N deposition are low ( $1\text{-}5 \text{ kg N ha}^{-1} \text{ y}^{-1}$ ) compared to other fertilization experiments. Beginning in 1996,  $25 \text{ kg N ha}^{-1} \text{ y}^{-1}$  was applied as  $\text{NO}_3\text{NH}_4$  pellets at Fraser Experimental Forest west of the Continental Divide, and at Loch Vale watershed in Rocky Mountain National Park east of the Continental Divide. Our objectives were to compare ambient forest biogeochemical processes and N pools between the sites, and measure how the sites responded to N fertilization. We hypothesized Fraser would show little response due to N-limitation, while Loch Vale would respond rapidly to fertilization. We used soil and foliar characteristics, soil N cycling rates, and N leaching as our response variables.

## 2.3 Materials and methods

### 2.3.1 Site description

Two research sites were established in 1996, Loch Vale watershed, Rocky Mountain National Park, east of the Continental Divide, and Fraser Experimental Forest, west of the Continental Divide. Mean annual precipitation is 112 cm at Loch Vale and 86 cm at Fraser. Up to 80% of annual precipitation occurs as snow and snow-melt dominates the hydrologic regime at both sites (Baron and Denning 1993, Stottlemyer et al. 1997). Average winter precipitation (October – May) at Loch Vale and Fraser is 82 and 62 cm while summer precipitation (June - September) is 30 and 24 cm, respectively. Mean January, July and annual temperatures are  $-7.8$ ,  $12.3$  and  $1.1^{\circ}\text{C}$  at LV and  $-10.7$ ,  $13.8$  and  $0.8^{\circ}\text{C}$  at Fraser (Loch Vale unpublished data; Fraser unpublished data, USFS Rocky Mountain Research Station, Mike Ryan).

Sites are northeast facing, old-growth closed-canopy Englemann spruce-subalpine fir (*Picea engelmannii* – *Abies lasiocarpa*) forests at approximately 3100 m elevation. These are mesic forests characterized as cool, sheltered, well drained, with relatively deep soils (Peet 1981). A few overstory lodgepole pine (*Pinus contorta*) occur in some Fraser plots and the understory of all plots is dominated by *Vaccinium spp.* Parent material is Precambrian granite, schist and gneiss (Lovering and Goddard 1950). Soils are shallow and coarse-textured with an overlying organic layer averaging 5 cm deep.

Three pairs of co-located 30x30 m plots were established at each site. One plot of each pair served as a control. Ammonium-nitrate ( $\text{NH}_4\text{NO}_3$ ) pellets were applied with a fertilizer spreader at a rate of  $25 \text{ kg N ha}^{-1} \text{ y}^{-1}$  from 1996 to the present. Fertilizer was

applied to simulate the seasonal timing of N deposition inputs. Two and a half kg N ha<sup>-1</sup> was applied monthly from April – October and 7.5 kg N ha<sup>-1</sup> was added during November as an over-winter application. Samples were collected within the inner 15x15 m of each plot.

### 2.3.2 Soil and vegetation measurements

Net N mineralization and nitrification measurements were conducted in 1997, 1998 and 1999 using *in situ* buried bags (Binkley and Hart 1989). Five 6.5 cm diameter plugs of organic horizon soil were collected in each plot and placed in poly-ethylene bags beneath the organic horizon for approximately 30 days during the growing season and nine months over winter (winter samples were collected in 1998 and 1999 only). Five adjacent samples were taken to determine initial NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> concentrations. In an attempt to extract soil N as soon as possible samples were brought back to the parking lot and homogenized (rocks and roots removed). A 10 g sub-sample was immediately extracted with 100 ml KCl. Water content and soil percent C and N were measured on the remainder. Upon return to the laboratory samples were shaken for 45 min and placed in a cooler overnight. Samples were filtered (Whatman 41) and frozen within 18 hours of initiating the extraction. An Alpkem auto-analyzer was used to analyze KCl extracts for NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> (Alpkem Corporation, Perstorp Analytical Company, Wilsonville, OR, USA, 3500 Series). Mineralization and nitrification rates were calculated by the difference in NO<sub>3</sub><sup>-</sup> plus NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, respectively, between incubated and initial extracts. Sub-samples were dried, ground with a ball mill and analyzed using a dry combustion auto-analyzer for percent C and N (LECO Corporation, St. Joseph, MI, USA, CHN-1000).

Leaching losses of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were estimated using soil ion-exchange resin bags (Binkley and Hart 1989). The resin bags consisted of ten grams each of anion and cation exchange resin in nylon stockings. Growing season measurements were taken in 1996 and year round measurements began in 1997. Three strings of five bags each spaced 20 cm apart were placed in each plot below the organic horizon (15 bags per plot) at the initiation of each sample period. Resin bags remained in the field for approximately 30 days during the growing season and nine months over-winter. Collected resin bags were brought back to the laboratory where the resin was extracted with 100 ml KCl, shaken for 45 min, placed in the cooler overnight, filtered, and frozen. An Alpkem auto-analyzer was used to analyze extracts for  $\text{NO}_3^-$  and  $\text{NH}_4^+$ .

Soil water samples were collected from five ceramic cup tension lysimeters per plot at 10 cm depth. Lysimeters were installed in 1996, and samples were collected weekly beginning in mid-June 1997 – 1999. Soil water volume was typically abundant to sufficient mid-June through mid-August and again in late-September through early-October. Samples were collected approximately 24 hours after tension was applied to reduce microbially mediated changes in chemistry. Filtering took place immediately in the field through a 0.2  $\mu\text{m}$  membrane filter (Supor® – Gelman). Dissolved organic carbon (DOC) was determined using wet-chemical oxidation; phosphoric acid was added to remove dissolved inorganic carbon, and sodium persulfate was used to oxidize the DOC to  $\text{CO}_2$ .  $\text{CO}_2$  was measured using an infrared detector (OI Analytical, Model 700 TOC Analyzer; Aiken 1992). Samples were refrigerated until analyzed for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  using an Alpkem auto-analyzer.

Current year foliage was sampled in September 1999 from 5 canopy spruce trees per plot. Needles were sampled at a height of 10 m from the south facing tree aspect, rinsed with de-ionized water, dried at 25°C and ground with a ball mill. Percent C and N were

determined using a dry combustion auto-analyzer. Samples were digested with nitric and perchloric acids to determine percent Ca, Mg, K and P and analyzed using ICP (Self and Rodriguez 1998).

Stand characterization and a second set of soil measurements were collected from the plots in August 1998 as part of a regional study of N dynamics; these methods are reported briefly (for details see Rueth and Baron, in press). Potential organic horizon net mineralization and nitrification rates were determined in the laboratory (Binkley and Hart 1989). Soils were brought to field capacity and incubated at 20°C for 35 days. Organic and mineral horizon soil samples were analyzed for percent C and N using a dry combustion auto-analyzer. Percent lignin was determined from organic horizon soils using the Van Soest fiber determination method (Goering and Van Soest 1970). Ten ion exchange resin bags per plot were placed in the field in 1998 and collected one year later.

General soil characterization measurements included soil texture (hydrometer method, Klute 1986), organic and mineral horizon soil pH (1:5 soil to de-ionized water ratio), and extractable mineral soil cations and P (ammonium acetate extraction, Page 1982). To determine species basal area we recorded diameter at breast height (d.b.h. 1.3 m) and species for each live tree greater than 5 cm d.b.h.. Three tree cores per plot were collected with an increment borer at breast height from canopy trees to determine site age. Cores were collected until complete cores were obtained in which the pith was intercepted and rotten sections were absent. They were processed following standard dendrochronological methods (Stoke and Smiley 1986, Phipps 1985).

### 2.3.3 Statistical analyses

Samples were grouped into spring April 15 – July 14, summer July 15 – September 30 and winter October 1 – April 14 seasons based primarily on the hydrologic cycle of high-elevation watersheds. Data from each plot were combined by season, and statistical calculations were performed on the means. For measurements which were conducted only once, lysimeter cations, foliar chemistry, 1998 soil measurements and stand characterization measurements, statistical calculations were performed on raw data.

We determined whether data transformations were necessary based on scatter plots of the residuals. If a pattern was detected in the residual plot, such as increasing error variance with predicted values, data were transformed.

Site effects, treatment effects, site by treatment interactions and site by treatment interactions that depended on year, were tested using an analysis of variance (ANOVA) split-split plot design. We had two sites (Fraser and Loch Vale), two treatments (control and fertilized) and year. Measurements performed only once were analyzed in a similar fashion with an ANOVA split plot design (without year). The SAS Proc Mixed procedure was used (SAS 1989). Site was considered a fixed effect. For continuous measurements, plot, treatment by plot, year by plot and treatment by plot by year were all random effects nested within site. For one time measurements, effects containing year were dropped. Statistical comparisons between sites and treatments were determined using least squared mean. To decrease Type I error only biologically meaningful comparisons were made. We made the following comparisons within a year or year by season: Fraser control with fertilized, Loch Vale control with fertilized, Fraser fertilized with Loch Vale fertilized, and Fraser control with Loch Vale control. Across years were compared only between similar site by treatment

combinations. For instance, we compared Fraser control 1997 with 1998 and 1999. For measurements broken down by season only similar seasons were compared across years. Differences were considered significant at  $P < 0.05$ .

We tested whether the response in one year depended on the response in the previous year using auto-regression. Auto-regression could be ecologically relevant in this experiment in two regards: 1) climatic conditions of the previous year could influence ecosystem characteristics; and/or 2) the response to fertilization was a gradual step-wise function.

## 2.4 Results

### 2.4.1 Statistical calculations

Data requiring natural-log transformations to produce residual scatter plots with no distinct pattern included lysimeter  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . No significant auto-regressive terms were found in the data set. The seasonal variation (spring, summer and winter) in measurements provided few additional insights in interpreting site effects, treatment effects or site by treatment interactions, therefore, in most cases only annual averages were reported.

### 2.4.2 Fraser and Loch Vale stand characteristics

Site effect characteristics are reported because we were testing whether the sites Fraser and Loch Vale were similar. Treatment effects were not reported because we did not

- expect stand characteristics to respond rapidly to fertilization, and no significant treatment effects or site by treatment interactions were observed.

There were no significant differences between sites for tree age, total or spruce basal area, soil texture, organic horizon mass, soil pH and mineral soil-extractable cations and P (Table 2.1); therefore we found no indications that the comparison between Fraser and Loch Vale was invalid. Overstory spruce trees averaged 247 and 313 years of age at Fraser and Loch Vale, respectively. Average total basal area was 62 m<sup>2</sup> ha<sup>-1</sup> at Fraser (65% spruce) and 48 m<sup>2</sup> ha<sup>-1</sup> at Loch Vale (56% spruce). Soil percent sand, silt and clay were 39, 35 and 25 at Fraser and 33, 39, and 29 at Loch Vale. Organic horizon mass averaged 6801 and 6607 g m<sup>-2</sup> at Fraser and Loch Vale, respectively. Organic and mineral horizon pH at Fraser were 5.5 and 5.2 and at Loch Vale were 4.9 and 4.8. Mineral horizon extractable Ca, Mg, K and P were 2690, 418, 314, and 6.8 mg kg<sup>-1</sup> at Fraser and 1253, 208, 257 and 7.4 mg kg<sup>-1</sup> at Loch Vale.

#### 2.4.3 Soil characteristics

Soil %N and C:N collected in 1997-1999 were significantly different between sites (%N P=0.03; C:N P=0.01). Average control soil % N and C:N were 0.94 and 33.8 at Fraser and 1.29 and 25.8 at Loch Vale; no treatment response was observed (%N P=0.9; C:N P=0.1).

We observed a significant site effect, treatment effect and site by treatment interaction for 1997-1999 mineralization rates (Fig. 2.1a). Mineralization rates within year were higher, although not significantly, at Loch Vale than Fraser and the response to fertilization was greater at Loch Vale (Fig. 2.1a). Control plot mineralization rates averaged

across years were 0.36 and 0.97  $\mu\text{g N g}^{-1} \text{d}^{-1}$  at Fraser and Loch Vale, respectively. Following fertilization annual average mineralization rates more than doubled at Loch Vale and were relatively unchanged at Fraser. During 1997 and 1998 mineralization rates in Loch Vale fertilization plots were significantly greater than Loch Vale control and Fraser fertilization plots. Comparing across seasons and years, during spring 1997 and 1998 mineralization rates in fertilized plots were significantly greater at Loch Vale than Fraser (Fig. 2.2). The only other significant site and treatment differences occurred during winter. Few significant differences across year (holding site by treatment constant) were observed and only during spring and summer. The site by treatment interaction depended on year during spring but not winter. A significant site effect was observed in winter and a significant treatment effect during summer. We saw a significant nitrification rate site effect (Fig. 2.1b). Nitrification rates were generally low with little response to fertilization except during 1997 at Loch Vale.

Significant site effect, treatment effect and site by treatment interaction were observed for organic horizon %N in 1998 (Table 2.2). Control organic horizon %N was 0.89 and 1.50 at Fraser and Loch Vale, respectively. Following fertilization %N increased 17% in Fraser; there was little response in Loch Vale. Although not significant, organic horizon C:N was lower in Loch Vale control plots than Fraser control plots (24.0 vs. 36.3). Control plot lignin:N was significantly lower at Loch Vale than Fraser (20.9 vs. 31.5). Soil  $\text{NO}_3^-$  was 0.67 at Fraser and 2.16 at Loch Vale and increased to 8.85  $\mu\text{g N g}^{-1}$  with fertilization, however, there was a lot of variability, so no significant site or treatment effects were found. Soil  $\text{NH}_4^+$  behaved similarly but the differences were significant. Following fertilization  $\text{NH}_4^+$  increased from 5.87 to 9.42 in Fraser and from 11.1 to 36.8  $\mu\text{g N g}^{-1} \text{d}^{-1}$  in Loch Vale.

Control plot potential net mineralization rates were significantly greater in Loch Vale than Fraser, 1.98 compared to less than 0  $\mu\text{g N g}^{-1} \text{d}^{-1}$  (Table 2.2). Loch Vale control plot nitrification rates were 4.86  $\mu\text{g N g}^{-1} \text{d}^{-1}$  compared to 0.23  $\mu\text{g N g}^{-1} \text{d}^{-1}$  in Fraser, however this difference was only marginally significant ( $P=0.07$ ).

#### 2.4.4 Foliar chemistry

We found no significant site or treatment effects for % Ca, % Mg or N:Ca (Table 2.3). Foliar P was unchanged with fertilization, but was significantly lower at Loch Vale (0.16 vs. 0.23, site effect  $P=0.003$ ). Control plot foliar N:P was 4.85 in Fraser and 7.89 in LV (site effect  $P<0.0001$ ). Percent N, C:N, %K, N:Mg and N:K responded significantly to fertilization. Control plot foliar %N was 1.10 and 1.22 in Fraser and Loch Vale, and increased to 1.21 and 1.29 with fertilization (treatment effect  $P=0.03$ ). Foliar C:N decreased from 46.9 to 42.4 in Fraser and from 43.1 to 40.5 in Loch Vale following fertilization (treatment effect  $P=0.04$ ). Foliar %K decreased in both sites from approximately 1.75 to 1.47 and 1.64 in Fraser and Loch Vale, respectively (treatment effect  $P=0.02$ ). Foliar N:Mg increased 14% in Fraser and 5% in Loch Vale following fertilization (treatment effect  $P=0.006$ ). Fertilized compared to control plot N:K was 34% and 13% greater in Fraser and Loch Vale, respectively (treatment effect  $P=0.006$ ).

#### 2.4.5 Soil Water

For the 1996-1999 data set we found significant treatment effects and site by treatment interactions that were year dependent for lysimeter  $\text{NO}_3^-$ , and resin bag  $\text{NH}_4^+$  and

$\text{NO}_3^-$  (Figs. 2.3 and 2.4). Site and treatment effect statistics were not provided for lysimeter  $\text{NH}_4^+$  due to infinite likelihood. Control plot soil water  $\text{NH}_4^+$  was similar between sites and both sites responded to fertilization although there was substantial inter-annual variability (Fig. 2.3a). Fertilization plots were significantly greater than control plots at Fraser and Loch Vale during 1998 and 1999. Annual average lysimeter  $\text{NO}_3^-$  increased with fertilization from 0.0025 to 0.75 in Fraser and from 0.060 to 1.73  $\text{mg l}^{-1}$  in Loch Vale. The greater response at Loch Vale to fertilization is apparent in Fig. 2.3b. At both sites and in each year soil water  $\text{NO}_3^-$  in fertilized plots was greater than control plots. Average annual resin bag  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were lower in control plots at Fraser compared to Loch Vale ( $\text{NH}_4^+$  1.10 vs. 5.14,  $\text{NO}_3^-$  0.49 vs. 3.21  $\mu\text{g N bag}^{-1} \text{ d}^{-1}$ ). Resin bag  $\text{NH}_4^+$  and  $\text{NO}_3^-$  increased dramatically with fertilization at both sites (Fig. 2.4). Annual average  $\text{NH}_4^+$  and  $\text{NO}_3^-$  increased at Fraser from 1.10 to 19.8 and 0.49 to 29.3  $\mu\text{g N bag}^{-1} \text{ d}^{-1}$ , respectively with N additions. The response to fertilization at Loch Vale was greater with rates approximately double that of Fraser. Except during 1996 resin bag  $\text{NH}_4^+$  was significantly greater in Loch Vale fertilized compared to control plots (Fig. 2.4a). Only during 1998 was resin bag  $\text{NH}_4^+$  greater in fertilized than control plots in Fraser. A similar response was found for resin bag  $\text{NO}_3^-$  (Fig. 2.4b).

A significant site by treatment interaction dependent on year was observed for soil water dissolved organic carbon (DOC, Fig. 2.5). Average annual lysimeter DOC was greater in Fraser than Loch Vale and fertilization caused a reduction at Fraser while Loch Vale remained unchanged. Fraser DOC decreased from 67.3 to 46.9  $\text{mg l}^{-1}$  with fertilization. Loch Vale control and fertilization averaged 25.4 and 26.8  $\text{mg l}^{-1}$ . We found a significant treatment effect at Fraser in 1997 and 1998 and site effect between control plots in 1998 (Fig. 2.5).

## 2.5 Discussion

Our working hypothesis was that Loch Vale, which receives higher atmospheric N inputs, would respond rapidly to fertilization due to greater extant forest N pools. We expected Fraser to have a limited, if any, response to fertilization due to N limitation. It turns out we were partly correct. While soil %N, C:N, and lignin:N were unresponsive in Loch Vale fertilized plots, N cycling and leaching increased dramatically. Furthermore, N mineralization rates declined over time with fertilization. In contrast, foliar chemistry in fertilized plots at Fraser exhibited strong change; in addition, soil %N increased and soil C:N and lignin:N decreased significantly. There was a small increase in lysimeter  $\text{NO}_3^-$  and a larger response of DOC. None of these changes added up to a large alteration of N cycling or leaching rates.

Fraser foliar chemistry responded dramatically to fertilization. There were relatively large changes in %N, %K, C:N and N:P ratios and N:cation ratios (Table 2.3). The changes in Loch Vale were much less pronounced, presumably because spruce stands there have had the benefit of years of N deposition.

Lysimeter DOC in 1998 and 1999 was greater at Fraser than Loch Vale suggesting greater N availability in Loch Vale (Fig. 2.6). Labile C is required by microbes to immobilize N, and dissolved organic carbon (DOC) should decrease with greater N availability resulting from increased microbial metabolism (Aber 1992, Gundersen et al. 1998). N limited sites should therefore have elevated soil water DOC. The rapid DOC response to fertilization in Fraser compared to Loch Vale could reflect greater N limitation at Fraser.

Soil %N increased and C:N and lignin:N ratios decreased with the addition of 100 kg N ha<sup>-1</sup> to Fraser (Table 2.2). The changes did not result in measurable increases in N cycling

rates. The magnitude of change in soil water N was quite low (less than  $1 \text{ mg N l}^{-1}$ , Fig. 2.3). The larger increase in resin bag N appears to be a direct artifact of fertilization where hydrologic transport leached N down to the resin bags before biologic uptake could occur (Fig. 2.4, Moldan et al. 1995, Gundersen and Rasmussen 1995, Gundersen et al. 1998). Increased  $\text{NH}_4^+$  leaching was not expected following fertilization due to high microbial demand, plant demand and soil cation exchange capacity. If the  $\text{NH}_4^+$  was produced internally we would have observed greater mineralization rates. We observed small increases in lysimeter  $\text{NO}_3^-$  with fertilization and larger increases in resin bag  $\text{NO}_3^-$  at Fraser; again, this result appears to have been a direct fertilization effect. If elevated resin bag  $\text{NO}_3^-$  was a biogeochemical response to fertilization we would have seen increased nitrification rates and lysimeter  $\text{NO}_3^-$  as well.

In contrast to Fraser, Loch Vale soil N, C:N and lignin:N were less responsive to fertilization and soil extractable N, N cycling rates and leaching losses increased dramatically (Table 2). Differing site soil C:N ratios explain the contrasting observations with fertilization. The soil N pool is the primary sink for incoming N leading to altered N cycling (Swank and Vose 1997). Over 40% of the variation in  $\text{NO}_3^-$  export from nine watersheds in the Appalachians, for example, was explained by either the soil N pool size or the ratio of net nitrification rate to net mineralization rate (Williard et al. 1997). A relationship exists between the soil C:N ratio and the initiation of changes in N cycling. When the ratio approaches 24 changes in N cycling and leaching losses occur (Fenn et al. 1996, Williard et al. 1997, Thomas and Prescott 2000, Goodale and Aber 2001). Loch Vale control soils sit on the threshold with an average control plot ratio of 24 while Fraser control soils are well above with an average control plot ratio of 36 (Table 2.2). It is not surprising that fertilization in Loch Vale stimulated N cycling rates and leaching losses while in Fraser the

largest response was in the soil N pool. With further fertilization in Fraser we expect the soil N pool to increase reducing the C:N ratio subsequently initiating elevated N cycling rates and leaching losses.

Annual average mineralization rates declined with fertilization in Loch Vale, and spring 1999 mineralization rates were significantly lower than 1997 and 1998 rates (Fig. 2.1a and 2.2). The decline in Loch Vale fertilized plot mineralization rates cannot be attributed to climate variability because Loch Vale control rates were not significantly different across years or across years within season. Microbial processes are mediated by C and N availability versus demand, which controls the balance between gross N transformation and immobilization rates (Tietema 1998, Hobbie and Vitousek 2000, Fisk and Fahey 2001). Reduced N mineralization rates following fertilization could represent a negative feedback where a decline in below-ground C allocation following fertilization induces microbial C limitation, depressing net N mineralization rates (Thomas and Prescott 2000, Fisk and Fahey 2001). Below ground C allocation to root biomass declines following fertilization (Gower et al. 1992, Haynes and Gower 1995, Fahey et al. 1998). Fisk and Fahey (2001) observed a decline in soil net mineralization rates resulting from increased gross mineralization rates with fertilization associated with decreased fine root biomass.

Our results allow us to ask how much N is required to initiate changes in spruce forests. Fraser fertilization plots have received  $100 \text{ kg N ha}^{-1}$  compared to Fraser control plots; an estimated  $160 \text{ kg N ha}^{-1}$  has been deposited to Loch Vale control plots compared to Fraser control plots from atmospheric N deposition; we added an additional  $100 \text{ kg N ha}^{-1}$  to Loch Vale fertilized plots (total of  $260 \text{ kg N ha}^{-1}$ ). Because we did not observe significant changes in N cycling with fertilization at Fraser, we suggest  $100 \text{ kg N ha}^{-1}$  is not sufficient to initiate biogeochemical changes in Colorado Englemann spruce forests. Something begins to

happen between 100 and 160 kg N ha<sup>-1</sup>, because there were significant differences between Fraser and Loch Vale control plots. If this is correct, we should see measurable changes with three additional years of fertilization to Fraser because then the cumulative amount of added N to Loch Vale control and Fraser fertilized plots would be similar. If regional population growth continues at the rate it has since 1900 and atmospheric N deposition tracks this increase, then we expect high-elevation watersheds east of the Continental Divide to receive N inputs equivalent to Loch Vale fertilization plots within the next 75 years (Rueth and Baron, in press). The ecosystem response will be elevated soil NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> and ecosystem N loss.

## 2.6 Conclusions

Old-growth high-elevation Englemann spruce forests respond to relatively small increases in N inputs. A continuum of low N deposition unfertilized forest stands, through high N deposition fertilized stands showed progressively greater soil N pools, cycling rates and leaching responses, similar to the effects observed in forests that receive greater N inputs. Williams and Tonnessen (2000) suggest a critical load of wet deposition N inputs of 4 kg N ha<sup>-1</sup> y<sup>-1</sup> should not be exceeded in order to protect northern Colorado's high-elevation aquatic ecosystems. Our results agree that current N inputs cause measurable changes to Englemann spruce forest biogeochemistry. Increased N leaching will be one result of additional N deposition.

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Table 2.1: Stand characteristics. Site averages and one stand deviation in parentheses. Site effect P value presented.

| Parameter   | Site      | average (std) | site effect<br>P value |
|---|-----------|---------------|------------------------|
| Tree Age<br>(y)   | Fraser    | 247 (30)      | 0.4                    |
|   | Loch Vale | 313 (142)     |                        |
| Total Basal Area<br>(m <sup>2</sup> ha <sup>-1</sup> )  | Fraser    | 62 (10)       | 0.1                    |
|   | Loch Vale | 48 (9)        |                        |
| Spruce Basal Area<br>(m <sup>2</sup> ha <sup>-1</sup> ) | Fraser    | 40 (14)       | 0.4                    |
|   | Loch Vale | 27 (22)       |                        |
| % Sand  | Fraser    | 39 (11)       | 0.4                    |
|   | Loch Vale | 33 (8)        |                        |
| % Silt  | Fraser    | 35 (6)        | 0.5                    |
|   | Loch Vale | 39 (9)        |                        |
| % Clay  | Fraser    | 25 (7)        | 0.4                    |
|   | Loch Vale | 29 (5)        |                        |
| Organic Horizon<br>Mass (g m <sup>-2</sup> )            | Fraser    | 6801 (2048)   | 0.8                    |
|   | Loch Vale | 6607 (1594)   |                        |
| Organic Horizon pH                                      | Fraser    | 5.5 (0.5)     | 0.1                    |
|   | Loch Vale | 4.9 (0.3)     |                        |
| Mineral Horizon pH                                      | Fraser    | 5.2 (0.5)     | 0.2                    |
|   | Loch Vale | 4.8 (0.3)     |                        |
| Mineral Horizon Ca<br>(mg kg <sup>-1</sup> )            | Fraser    | 2690 (1540)   | 0.2                    |
|   | Loch Vale | 1253 (762)    |                        |
| Mineral Horizon Mg<br>(mg kg <sup>-1</sup> )            | Fraser    | 418 (184)     | 0.1                    |
|   | Loch Vale | 208 (69)      |                        |
| Mineral Horizon K<br>(mg kg <sup>-1</sup> )             | Fraser    | 314 (129)     | 0.3                    |
|   | Loch Vale | 257 (69)      |                        |
| Mineral Horizon P<br>(mg kg <sup>-1</sup> )             | Fraser    | 6.8 (5.0)     | 0.6                    |
|   | Loch Vale | 7.4 (3.9)     |                        |

Table 2.2: Organic horizon soil characteristics. Site by treatment averages and one stand deviation in parentheses. Site effect, treatment effect (trt) and site by treatment interaction (site\*trt) P values presented.

| Parameter  | Site      | Control average (std) | Fertilization average (std) | site effect P value | trt effect P value | site*trt interaction P value |
|--|-----------|-----------------------|-----------------------------|---------------------|--------------------|------------------------------|
| Organic Horizon % N  | Fraser    | 0.89 (0.2)            | 1.04 (0.2)                  | <b>&lt; 0.0001</b>  | <b>0.02</b>        | <b>0.04</b>                  |
|  | Loch Vale | 1.50 (0.1)            | 1.52 (0.2)                  |                     |                    |                              |
| Organic Horizon C:N  | Fraser    | 36.3 (3.8)            | 31.9 (3.2)                  | 0.1                 | 0.8                | 0.7                          |
|  | Loch Vale | 24.0 (2.8)            | 23.5 (3.1)                  |                     |                    |                              |
| Organic Horizon Lignin:N                                       | Fraser    | 31.5 (3.6)            | 27.7 (5.4)                  | <b>0.01</b>         | 0.2                | 0.4                          |
|  | Loch Vale | 20.9 (3.2)            | 19.9 (3.9)                  |                     |                    |                              |
| Soil NO <sub>3</sub> <sup>-</sup> (µg N g <sup>-1</sup> )      | Fraser    | 0.67 (0.2)            | 0.59 (0.09)                 | 0.06                | 0.09               | 0.09                         |
|  | Loch Vale | 2.16 (2.6)            | 8.85 (11)                   |                     |                    |                              |
| Soil NH <sub>4</sub> <sup>+</sup> (µg N g <sup>-1</sup> )      | Fraser    | 5.87 (3.9)            | 9.42 (5.3)                  | <b>0.001</b>        | <b>0.002</b>       | <b>0.01</b>                  |
|  | Loch Vale | 11.1 (8.1)            | 36.8 (21)                   |                     |                    |                              |
| Mineralization (µg N g <sup>-1</sup> d <sup>-1</sup> )         | Fraser    | -0.0007 (0.003)       | 0.003 (0.009)               | <b>0.02</b>         | 0.1                | 0.3                          |
|  | Loch Vale | 1.98 (2.8)            | 2.86 (4.7)                  |                     |                    |                              |
| Nitrification (µg N g <sup>-1</sup> d <sup>-1</sup> )          | Fraser    | 0.23 (0.4)            | 0.76 (0.8)                  | 0.07                | 0.6                | 0.6                          |
|  | Loch Vale | 4.86 (4.9)            | 7.88 (3.6)                  |                     |                    |                              |
| Resin Bag NO <sub>3</sub> <sup>-</sup> (mg N y <sup>-1</sup> ) | Fraser    | 0.31 (0.4)            | 128 (130)                   | 0.06                | <b>0.0003</b>      | 0.1                          |
|  | Loch Vale | 14.5 (18)             | 218 (183)                   |                     |                    |                              |
| Resin Bag NH <sub>4</sub> <sup>+</sup> (mg N y <sup>-1</sup> ) | Fraser    | 0.80 (0.6)            | 80 (116)                    | 0.2                 | <b>0.005</b>       | 0.4                          |
|  | Loch Vale | 9.23 (10)             | 124 (135)                   |                     |                    |                              |

Table 2.3: Current year foliar chemistry. Site by treatment averages and one stand deviation in parentheses. Site effect, treatment effect (trt) and site by treatment interaction (site\*trt) P values presented.

| Element or elemental ratio | Site      | Control average (std) | Fertilization average (std) | site effect P value | trt effect P value | site*trt interaction P value |
|----------------------------|-----------|-----------------------|-----------------------------|---------------------|--------------------|------------------------------|
| % N                        | Fraser    | 1.10 (0.1)            | 1.21 (0.09)                 | 0.2                 | <b>0.03</b>        | 0.5                          |
|                            | Loch Vale | 1.22 (0.1)            | 1.29 (0.08)                 |                     |                    |                              |
| C:N                        | Fraser    | 46.9 (5.2)            | 42.4 (3.0)                  | 0.3                 | <b>0.04</b>        | 0.5                          |
|                            | Loch Vale | 43.1 (4.3)            | 40.5 (2.6)                  |                     |                    |                              |
| % Ca                       | Fraser    | 0.35 (0.07)           | 0.33 (0.5)                  | 0.06                | 0.9                | 0.4                          |
|                            | Loch Vale | 0.37 (0.08)           | 0.38 (0.08)                 |                     |                    |                              |
| % Mg                       | Fraser    | 0.10 (0.01)           | 0.10 (0.009)                | 0.2                 | 0.7                | 0.3                          |
|                            | Loch Vale | 0.094 (0.01)          | 0.096 (0.01)                |                     |                    |                              |
| % K                        | Fraser    | 1.79 (0.2)            | 1.47 (0.2)                  | 0.5                 | <b>0.02</b>        | 0.09                         |
|                            | Loch Vale | 1.73 (0.2)            | 1.64 (0.2)                  |                     |                    |                              |
| % P                        | Fraser    | 0.23 (0.03)           | 0.23 (0.03)                 | <b>0.003</b>        | 0.8                | 0.6                          |
|                            | Loch Vale | 0.16 (0.02)           | 0.16 (0.03)                 |                     |                    |                              |
| N:Ca                       | Fraser    | 3.30 (0.9)            | 3.8 (0.7)                   | 0.8                 | 0.2                | 0.4                          |
|                            | Loch Vale | 3.42 (0.7)            | 3.54 (0.9)                  |                     |                    |                              |
| N:Mg                       | Fraser    | 10.6 (1.5)            | 12.1 (1.2)                  | 0.08                | <b>0.006</b>       | 0.2                          |
|                            | Loch Vale | 13.0 (1.8)            | 13.7 (1.9)                  |                     |                    |                              |
| N:K                        | Fraser    | 0.62 (0.07)           | 0.83 (0.1)                  | 0.4                 | <b>0.006</b>       | 0.1                          |
|                            | Loch Vale | 0.71 (0.09)           | 0.80 (0.1)                  |                     |                    |                              |
| N:P                        | Fraser    | 4.85 (0.6)            | 5.4 (0.5)                   | <b>&lt; 0.0001</b>  | 0.3                | 0.6                          |
|                            | Loch Vale | 7.89 (1.1)            | 8.09 (1.0)                  |                     |                    |                              |

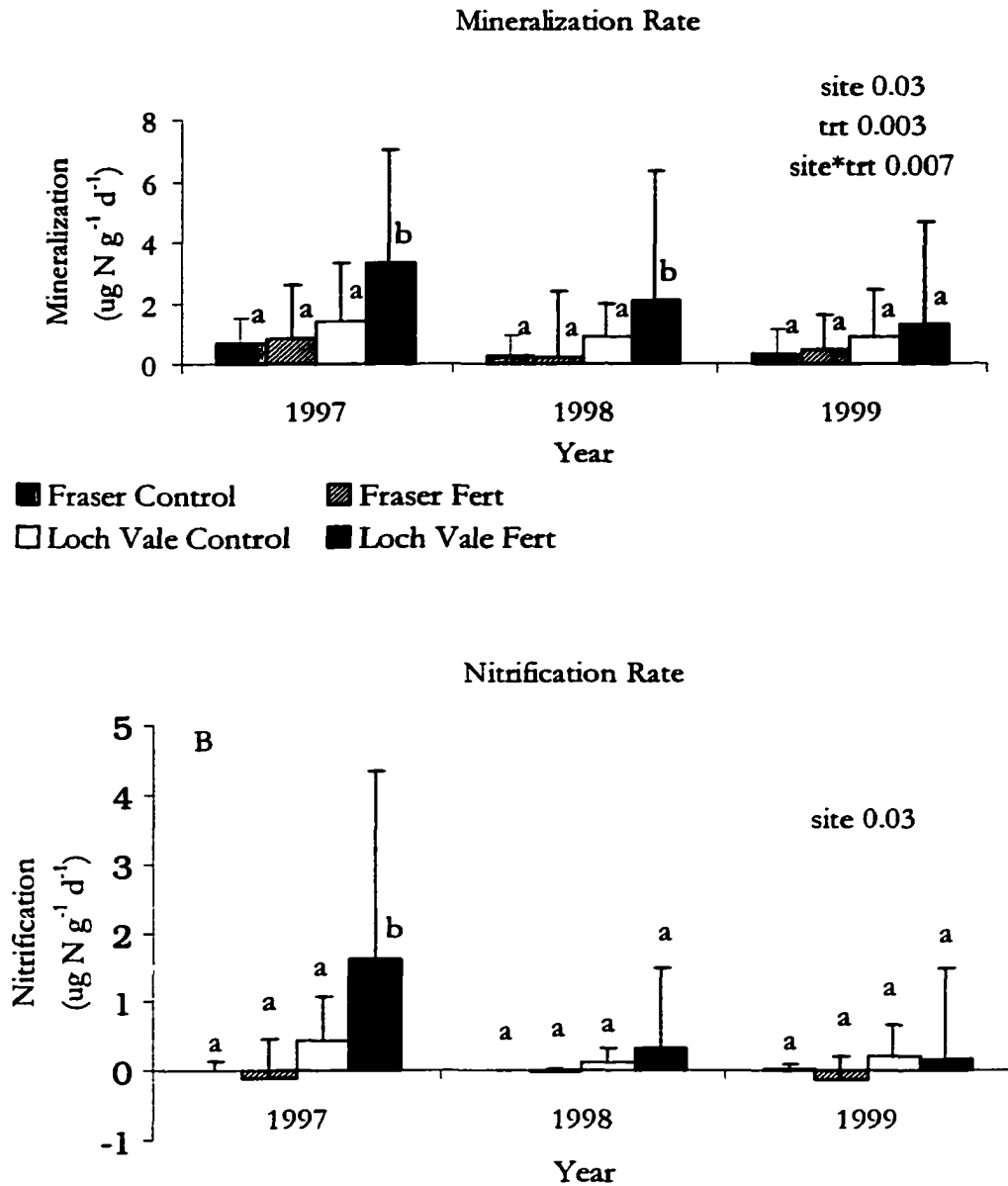


Fig. 2.1: Annual average mineralization (A) and nitrification rates (B,  $\mu\text{g N g}^{-1} \text{d}^{-1}$ ) and one stand deviation. Significant site effects, treatment effects (trt), site by treatment interactions (site\*trt) and interactions which were dependent on year (site\*trt\*y) were presented. Only biologically meaningful comparisons were made between sites and treatments across year ( $P < 0.05$ , see section 4.3.3 Statistical analyses for details).

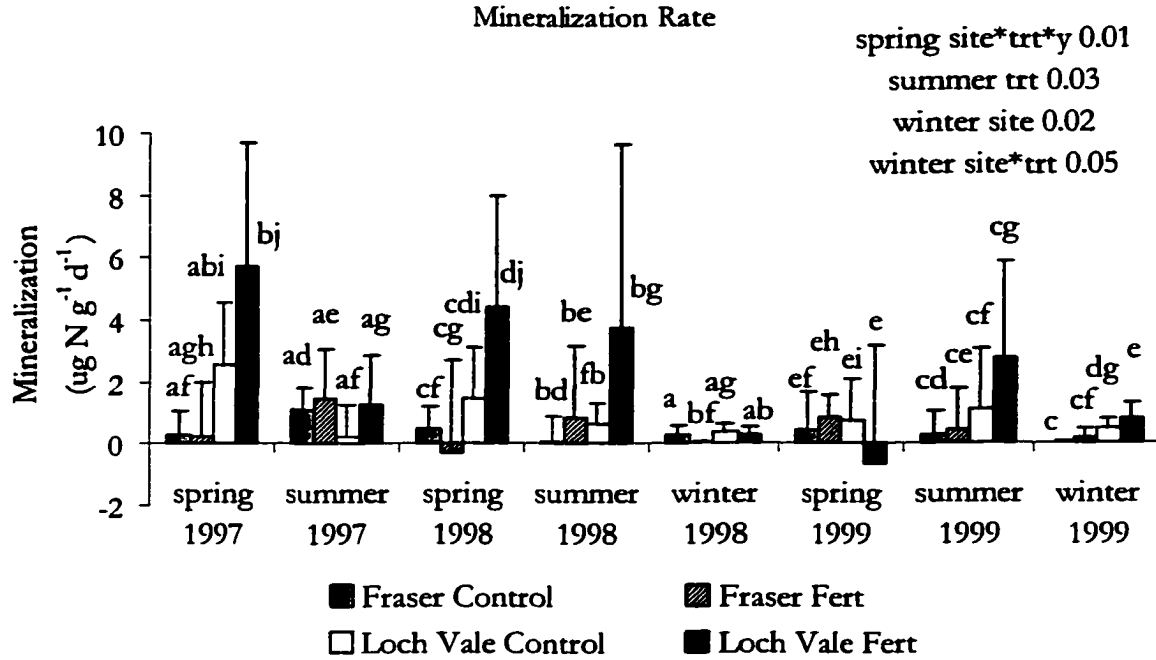


Fig. 2.2: Seasonal average mineralization rates by year ( $\mu\text{g N g}^{-1} \text{d}^{-1}$ ) and one stand deviation. Significant site effects, treatment effects (trt), site by treatment interactions (site\*trt) and interactions which were dependent on year (site\*trt\*y) were presented. Only biologically meaningful comparisons were made between sites and treatments across year ( $P < 0.05$ , see section 4.3.3 Statistical analyses for details).

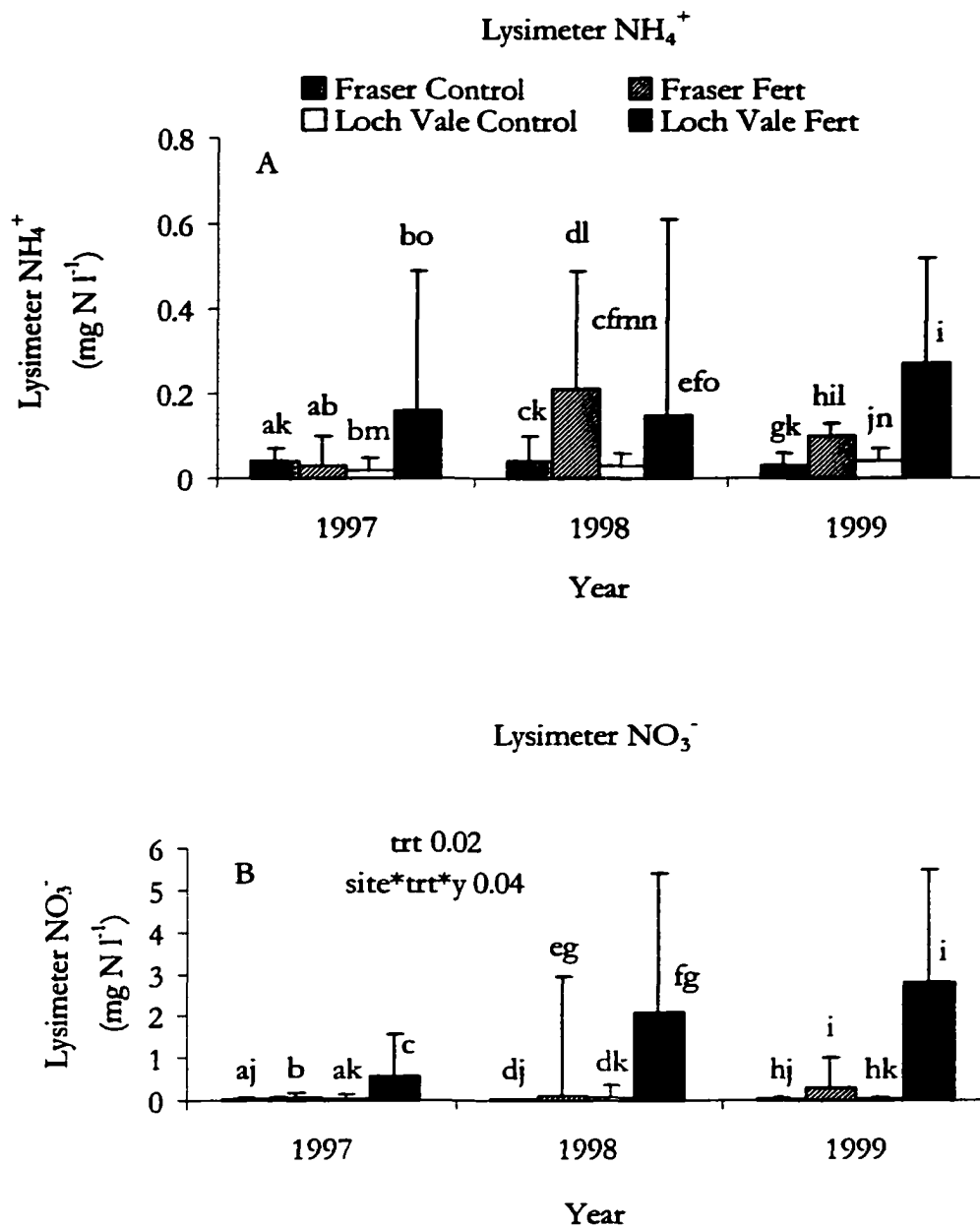


Fig. 2.3: Annual average lysimeter soil water NH<sub>4</sub><sup>+</sup> (A) and NO<sub>3</sub><sup>-</sup> (B) at 10 cm (mg l<sup>-1</sup>) and one standard deviation. Significant site effects, treatment effects (trt), site by treatment interactions (site\*trt) and interactions which were dependent on year (site\*trt\*y) were presented. Only biologically meaningful comparisons were made between sites and treatments across year (P<0.05, see section 4.3.3 Statistical analyses for details).

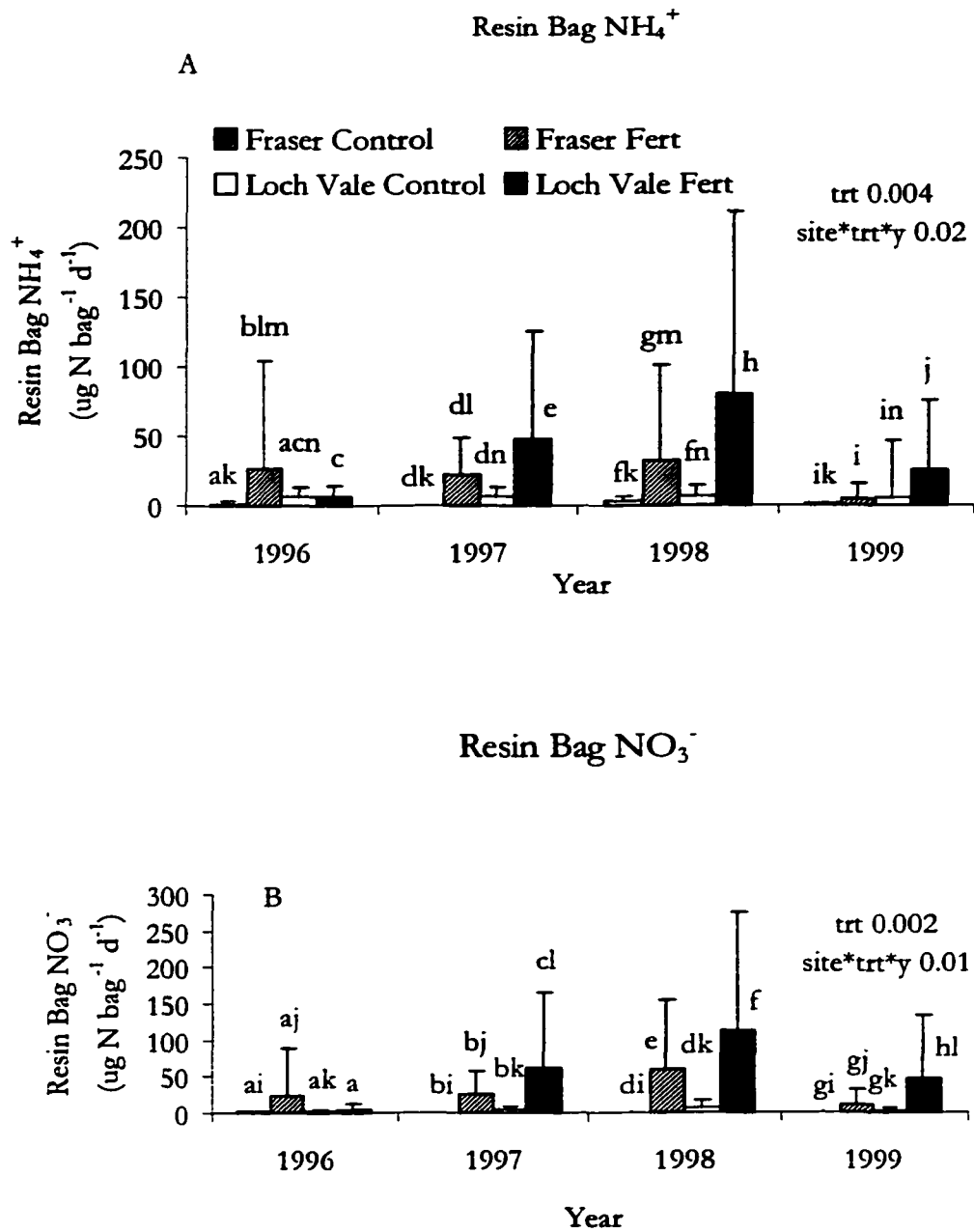


Fig. 2.4: Annual average resin bag  $\text{NH}_4^+$  and  $\text{NO}_3^-$  capture below the organic horizon ( $\mu\text{g N bag}^{-1} \text{d}^{-1}$ ) and one standard deviation. Significant site effects, treatment effects (trt), site by treatment interactions (site\*trt) and interactions which were dependent on year (site\*trt\*y) were presented. Only biologically meaningful comparisons were made between sites and treatments across year ( $P < 0.05$ , see section 4.3.3 Statistical analyses for details).

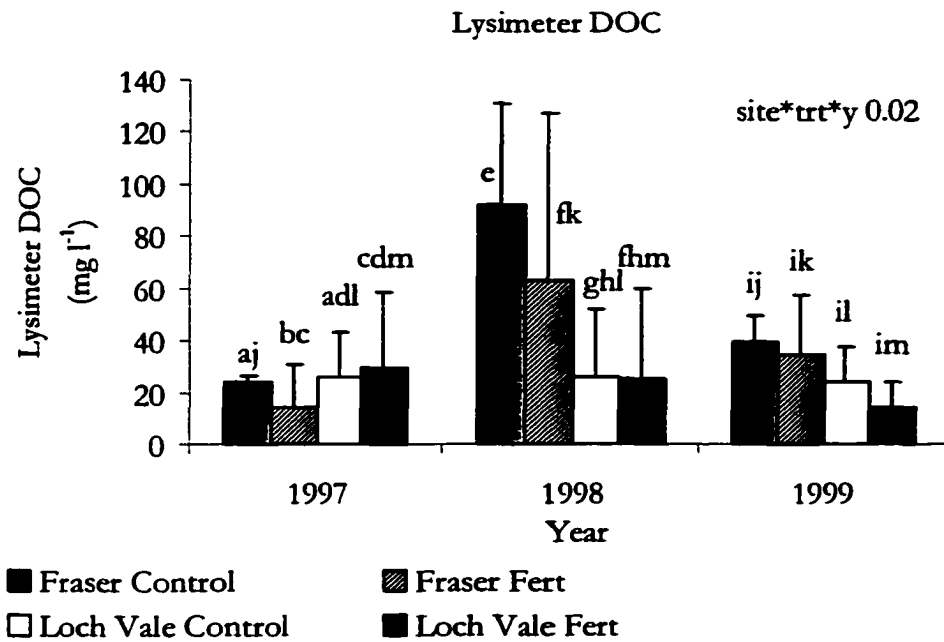


Fig. 2.5: Annual average soil lysimeter dissolved organic carbon (DOC) and one standard deviation. Significant site effects, treatment effects (trt), site by treatment interactions (site\*trt) and interactions which were dependent on year (site\*trt\*y) were presented. Only biologically meaningful comparisons were made between sites and treatments across year ( $P < 0.05$ , see section 4.3.3 Statistical analyses for details).

### 3. Differences in Englemann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA

#### 3.1 Abstract

We compared Englemann spruce biogeochemical processes in forest stands east and west of the Continental Divide in the Colorado Front Range. The divide forms a natural barrier for air pollutants such that nitrogen (N) emissions from agricultural and urban areas of the South Platte River Basin are transported via upslope winds to high elevations on the east side but rarely cross over to the west side. Far fewer emissions sources to the west cause atmospheric N deposition to be 1-2 kg N ha<sup>-1</sup> y<sup>-1</sup> on the west side, compared with 3-5 kg N ha<sup>-1</sup> y<sup>-1</sup> on the east side. Species composition, elevation, aspect, parent material, site history and climate were matched as closely as possible across six east and six west side old-growth forest stands. Higher N deposition sites had significantly lower organic horizon C:N and lignin:N ratios, and foliar C:N ratios, as well as greater %N, and N:Ca, N:Mg, and N:P ratios, and potential net mineralization rates. When C:N ratios dropped below 29, as they did in east side organic horizon soils, mineralization rates increased linearly. Our results are comparable to those from the Northeastern US and Europe that have found changes in forest biogeochemistry in response to N deposition inputs between 3-60 kg N ha<sup>-1</sup> y<sup>-1</sup>. Current levels of N deposition, even though low by comparison with more densely

populated and agricultural regions, have caused measurable changes in Englemann spruce forest biogeochemistry east of the Continental Divide in Colorado

### 3.2 Introduction

Atmospheric nitrogen (N) inputs are elevated east of the north-central Colorado Continental Divide compared to the west due to the proximity of urban and agricultural emission sources (Parrish et al. 1990, Langford and Fehsenfeld 1992). The east side of the Continental Divide is where a majority of Colorado's population of 4 million resides and is an important agricultural and livestock producing region (Baron et al. 2000b). The greatest concentration in the state of nitrogen oxide ( $\text{NO}_x$ ) emissions from point and mobile sources occur in Front Range metropolitan areas (Williams and Tonnessen 2000). Local easterly winds transport some of this N to high elevation watersheds east of the Continental Divide (Parrish et al. 1986, 1990, Sievering et al. 1989, Langford and Fehsenfeld 1992). The combination of anthropogenic N sources and orographic precipitation results in higher N deposition at high elevation sites (Williams and Tonnessen 2000). Strong westerly winds in the upper atmosphere prevent these N-enriched air masses from crossing the Continental Divide (Bossert 1990, Baron and Denning 1993). Two recent compilations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations from Colorado National Atmospheric Deposition Program/National Trends Network (NADP/NTN) monitoring stations showed that sites east of the Continental Divide had significantly greater concentrations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  than western sites (Baron et al. 2000b, Heuer et al. 2000).

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(NADP/NTN) monitoring stations east of the Continental Divide report mean annual wet inorganic N deposition of 3.6 kg N ha<sup>-1</sup> y<sup>-1</sup> for Niwot Saddle (NS, years 1984-1998) and 3.5 kg N ha<sup>-1</sup> y<sup>-1</sup> for Loch Vale (LV, years 1985-1998, Fig. 3.1, Williams et al. 1998, National Atmospheric Deposition Program 1999). These sites report the highest N deposition rates in Colorado. Total (wet plus dry) N deposition to Niwot Saddle and Loch Vale is estimated at 3.0-5.0 (years 1993-1994) and 3.2-5.5 kg N ha<sup>-1</sup> y<sup>-1</sup> (years 1992-1997), respectively (Sievering et al. 1996, Campbell et al. 2000). Reported wet inorganic N deposition at Fraser Experimental Forest, a west side site, averaged 1.7 kg N ha<sup>-1</sup> y<sup>-1</sup> for 1984-1986 and was 1.1 kg N ha<sup>-1</sup> in 1990 (Stottlemyer and Troendle 1992, Stottlemyer et al. 1997). Other west side NADP/NTN stations have wet N deposition values that range from 1.1 – 1.7 kg N ha<sup>-1</sup> y<sup>-1</sup> for the years 1988 - 1997. Dry deposition estimates are unavailable for western sites; we do not expect west site dry deposition to alter the pattern of higher deposition rates at eastern sites.

Lake chemistry data and paleolimnological research indicate that high elevation aquatic systems east of the Continental Divide have been affected by N deposition (Baron et al. 2000b, Williams and Tonnessen 2000). We explored whether there were significant changes in Englemann spruce (*Picea engelmannii*) forests from N deposition. Other researchers have found measurable changes in forest biogeochemical parameters in regions that receive elevated N deposition (Vitousek et al. 1997, Aber et al. 1998, Fenn et al. 1998, Gundersen et al. 1998). Comparison studies have demonstrated that there are gradients in responses to N deposition across regions of increasing N deposition (McNulty et al. 1991, Tietema and Beier 1995, Aber et al. 1998, Gundersen et al. 1998, Lovett and Rueth 1999). In Colorado, where N deposition ranges from 1.0 – 5.0 kg N ha<sup>-1</sup> y<sup>-1</sup>, we postulated that differences in N-

cycling parameters would be detectable in high-elevation old-growth forests because of low N demand.

### 3.3 Materials and methods

#### 3.3.1 Climate

Data from six high-elevation National Resources Conservation Service SNOTEL sites (SNOWpack TELEmetry) and two meteorological stations within the study area were compared to characterize climate conditions of north-central Colorado (Fig. 3.1, Table 3.1, National Resources Conservation Service 1999). Because most annual precipitation, 65-80%, at these sites occurs as snow, annual precipitation was divided into summer (June – September) and winter (October – May) seasons based on whether a majority of precipitation occurs as rain or snow (Baron and Denning 1993, Stottlemyer et al. 1997). We then compared climate at east and west sites by season to determine differences in precipitation that could influence forest processes.

#### 3.3.2 Study sites

Twelve, old-growth, closed-canopy Englemann spruce (*Picea engelmannii*) sites were sampled in August and September 1998 and August 1999. Old-growth stands were chosen to obviate the effects of land-use history. Site selection was based on U.S. Forest Service old-growth maps, personal communication with Dr. Veblen (University of Colorado), a 30 m resolution land cover type and stand density map of Rocky Mountain National Park, and accessibility. All stands were dominated by Englemann spruce and had a *Vaccinium spp.*

understory. Other overstory species included sub-alpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*). These were mesic spruce-fir forests characterized as cool, sheltered, well drained, with relatively deep soils (Peet 1981). Sites were northeast facing between 3000 and 3500 m elevation; slope angle averaged 10-20°. The bedrock of all stands consisted of Precambrian granite, schist and gneiss (Lovering and Goddard 1950). Soils were shallow and coarse-textured with an overlying organic layer averaging 5 cm deep. Each site consisted of three 30x30 m plots within a 0.5 km radius. Six sites were located east and six sites west of the Continental Divide (Fig. 3.1). The entire study area was 110 x 50 km.

To determine species basal area, diameter at breast height (d.b.h., 1.3 m) and species were recorded for each live tree greater than 5 cm d.b.h.. Basal area data and tree cores were collected at all sites except Granite Falls (GF), due to site accessibility constraints. Tree cores were initially collected to estimate stand age to support our old-growth classification. Growth rates were subsequently determined to address whether slight changes in climate influenced primary production. Nine cores per site were collected using an increment borer at breast height (1.3 m) from three canopy spruce trees in each plot. Cores were collected until three complete cores were obtained in which the pith was intercepted and rotten sections were absent. The cores were processed following standard dendrochronological methods (Stokes and Smiley 1968, Phipps 1985), stored in paper straws until processed, then glued to wooden mounts and sanded. Rings were counted and measured under a dissecting microscope to the nearest 0.25 mm to determine tree age at coring height and growth rates. Because the outside date of all samples was known and only complete cores were analyzed cross-dating was obtained visually. The average growth rate was determined for two 30 year time periods: 1900-1929 and 1930-1959. These time periods were chosen to compare growth rates during different regional climatic regimes (Veblen et al. 2000). 1900-1929 and

1930-1959 were characterized as cool-wet and warm-dry, respectively. Trees less than 100 years old in 1900 were removed from the statistical analysis of growth rates because younger trees with higher growth rates could confound comparisons.

### 3.3.3 Foliar sampling and analysis

Current year foliage was sampled from five canopy trees in each plot at 11 of the 12 sites (15 samples per site, East Rollins (ER) was not sampled due to inaccessibility of current year foliage in the lower canopy). Sampling occurred in August and September because full expansion of current year needles concludes in July and the end of the growing season represents stable nutrient concentrations (Fernandez et al. 1990). Lower canopy branches (height of 10 m) from the tree aspect judged to receive the greatest sunlight were collected using a tree trimmer, stored in plastic bags, and refrigerated until processed. Needles were rinsed with de-ionized water to remove particles and contamination and dried at 25°C. Needles were removed from the branch and a sub-sample was ground to fine powder.

Percent C and N were measured using a dry combustion auto-analyzer (LECO Corporation, St. Joseph, MI, USA, CHN-1000). Samples were digested using nitric and perchloric acids and analyzed by ICP for Ca, Mg, K, and P (Self and Rodriguez 1998, Thermo-Jarrell Ash, Franklin, MA, USA, model 61E).

Vector analysis was used to interpret differences in foliar nutrient concentrations between east and west sites (Timmer and Stone 1978, Haase and Rose 1995, Kiefer and Fenn 1997). Vector analysis is a method used to assess plant nutrient status and plant nutrient response to treatments such as fertilization. Needle weight often increases with fertilization, which confounds interpretations of changes in nutrient content or

concentration. Vector analysis allows simultaneous comparisons of nutrient concentration (percent dry weight) and content ( $\mu\text{g needle}^{-1}$ ), and a unit of plant weight in a graphical format. The result is an index of nutrient dilution, sufficiency, deficiency, or luxury consumption relative to a subjectively identified standard.

Nutrient and weight values were normalized to a “reference point” that has a value of 100 for all three parameters (weight, concentration and content). Vectors were drawn from the reference point to other points that represent relative changes in nutrient status and weight. The magnitude and direction of the line represents the combined response. Shifts along the diagonal 1:1 line represent no change in unit plant weight, shifts to the right or left indicate an increase or decrease in unit plant weight, respectively. Horizontal shifts represent changes in content and not concentration, and shifts along the vertical represent changes in concentration and not content.

The reference point we used was the average of all west side foliar chemistry to examine changes in nutrient status with elevated N inputs. The unit of plant weight used in all cases was average needle dry weight. To determine average east and west site needle weight five samples were randomly chosen from each site and 100 needles weighed.

#### 3.3.4 Soil sampling and analysis

Five organic horizon and five mineral horizon (to a depth of 20 cm) soil samples were collected at each plot (15 samples per site) in 1998. Organic horizon samples consisted of 4-5 adjacent 6.6 cm diameter cores to obtain enough sample for analysis. One core was taken to a depth of 20 cm to obtain a mineral horizon sample. Samples were packed in ice during transport to the laboratory, and stored at 4°C. Organic horizon samples were

homogenized through an 8 mm sieve to remove large roots and rocks, and total sample weight was recorded. A sub-sample was dried at 25°C and ground. The negative one-third bar water potential method was used to measure field capacity (Klute 1986). Mineral horizon samples were dried at 25°C; dried samples were sieved through a 2 mm sieve and a sub-sample was ground. Percent C and N were assessed on ground mineral and organic horizon samples. We measured organic horizon percent lignin with the Van Soest fiber method (Goering and Van Soest 1970). Organic horizon mass per unit area was determined using total sample dry weight and area sampled. The organic horizon N pool was calculated using %N and mass per unit area data.

Yearly leaching losses of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were estimated using soil ion exchange resin bags (Binkley and Hart 1989). The resin bags consisted of ten grams each of anion and cation exchange resin in a nylon stocking. Ten bags per plot were placed below the organic soil horizon in 1998 and collected one year later. Resin bags were extracted with 100 ml 2 M KCl-PMA and analyzed for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  using an Alpkem auto-analyzer (Alpkem Corporation, Perstorp Analytical Company, Wilsonville, OR, USA, 3500 Series).

Potential organic horizon net mineralization and nitrification rates were estimated with a laboratory soil incubation using methods modified from Binkley and Hart (1989). A moist sub-sample was brought to field capacity using de-ionized water. A plastic specimen cup containing 35 g of soil was placed in a 1 L mason jar with 30 ml of de-ionized water to maintain humidity. Another 15 g moist sub-sample was extracted with 75 ml 2 M KCl-PMA. Soils were incubated in the dark at 20°C for 35 days. We opened the jars once a week to reduce  $\text{CO}_2$  build-up, and de-ionized water was added to samples to maintain field capacity. After five weeks a 15 g sub-sample was extracted with 75 ml 2 M KCl-PMA. An Alpkem auto-analyzer was used to analyze KCl extracts for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  (Alpkem

Corporation, Perstorp Analytical Company, Wilsonville, OR, USA, 3500 Series).

Mineralization and nitrification rates were calculated by the difference in  $\text{NO}_3^-$  plus  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , respectively, between incubated and initial extracts.

General soil characterization measurements included soil texture, pH, organic matter fraction, and mineral soil extractable cations. The hydrometer method was used to assess soil texture on sieved mineral horizon samples (Klute 1986). A 1:5 soil to de-ionized water ratio was used to determine organic and mineral horizon pH; this ratio was necessary to provide enough liquid headspace for measurement. The soil-water mixer was shaken for 10 min. and allowed to settle for 20 min. before measurement. The loss on ignition method was used to measure organic matter fraction on dry organic and mineral horizon sub-samples. Samples were baked at 500°C for 6 hours and organic matter content was calculated by difference. Extractable mineral soil cations and P were estimated using ammonium acetate and analyzed by ICP (Page 1982, Thermo-Jarrell Ash, Franklin, MA, USA, model 61E).

### 3.3.5 Statistical analyses

Differences between east versus west foliar and soil analyses were tested using an analysis of variance, two-stage nested, mixed-effect model (SAS 1989). East versus west was considered a fixed effect because side was not randomly selected. Site was a random effect nested within side. Plot was a random effect nested within site and side. General linear model analysis was performed to determine the relationships between mineral soil organic matter fraction with clay content and %N. Statistical differences between east and west climate characteristics were determined with a t-test. Differences were considered significant at  $P < 0.05$  level unless otherwise stated.

### 3.4 Results

#### 3.4.1 Climate

No statistical differences were found between east and west climatic variables (Table 3.1). Both east and west forest stands are cold, with mean annual temperatures of 0.06 and 0.1°C, respectively. West sites were slightly drier, and received about 18 cm less precipitation per year than east sites (Table 3.1). The annual mean precipitation was 104 cm (range of 89 - 117) on the east and 86 cm (range of 81 - 91) on the west. We postulated differences in precipitation during the summer months will have greater biogeochemical impacts than differences during the winter months. Thirteen out of the 18 cm mean difference in precipitation between east and west sites occurred during winter and may affect snow-pack depth during spring while 5 cm occurred during the snow free season (Table 3.1).

#### 3.4.2 Stand Characteristics

There were no significant differences between stand age and spruce or fir basal area between east and west sites (Table 3.2). The average age of dominant spruce trees was 328 years (range of 113 - 506) for east and 294 years (range of 150 - 552) for west sites (Table 3.2). Total basal area averaged 58 and 52 m<sup>2</sup> ha<sup>-1</sup> for east and west sites, respectively. This supports our mesic Englemann spruce forest classification because xeric stands would have lower total basal area values of 30-40 m<sup>2</sup> ha<sup>-1</sup> (Peet 1981). Spruce and fir basal area averaged 39 and 19, and 35 and 14 m<sup>2</sup> ha<sup>-1</sup> for east and west sites, respectively. Lodgepole pine occurred at four west sites (Boreas Pass (BR), Fool Creek (FC), West Arapaho (WA) and

West Rollins (WR)) and represented from 4 to 22% of the total basal area at each site.

Growth rates were comparable between east and west sites for the two time periods analyzed suggesting that high elevation spruce stands were insensitive to the relative drought of 1930-1959 or the relative wet period of 1900-1929 (Table 3.2).

### 3.4.3 Foliar analyses

There was little variation in foliar chemical characteristics among the east and west samples (see standard deviations in Table 3.3). The mean values for all east sites showed significantly higher foliar %N and lower C:N ratios compared to west sites (Table 3.3). Foliar N:Ca, N:Mg, and N:P ratios were significantly higher at east than west sites, although foliar %Ca, %Mg, %K, and %P did not differ between east and west sites.

The average nutrient concentration and content and needle weight of all west side foliage was used as the reference point for vector analysis (Fig. 3.2). Because east side needles weighed an average of 17% more relative unit dry weight increased to 117. The decrease in Ca and P concentration and relatively unchanged nutrient content represents a dilution effect due to increased east side needle weight not being compensated by greater uptake. There was little dilution effect for Mg because content compensated for increased needle weight; therefore, we saw less of a decrease in concentration. The large increase in N and K content and slight increase in concentration indicate that N and K are available in sufficient quantities to more than compensate for increased needle weight at east sites and that N is less limiting in east forests than west. The substantial increase in N:Mg, N:Ca and N:P content at east compared to west sites indicates that the ratio of  $\mu\text{g N}$  to  $\mu\text{g Mg}$ , Ca or P per needle has increased.

#### 3.4.4 Soil analyses

Organic and mineral horizon pH and organic matter fraction did not differ between east and west sites (Tables 3.4 and 3.5). Organic horizon pH averaged 4.99 (range of 4.20 – 5.72) and 5.28 (range of 4.25 – 6.85) for east and west sites, respectively, and mean organic matter fraction was 0.65 (range of 0.39 – 0.81) for east and 0.62 (range of 0.33 – 0.83) for west sites. Mineral horizon percent sand and silt were similar between east and west sites (Table 3.4). Percent clay was greater at east than west sites; the average difference was 4.9%. No significant differences were observed in mineral soil extractable Ca, Mg, K, Na and P.

The mineral horizon soil of sites located east of the Continental Divide had marginally greater %N ( $P=0.08$ ), but no difference was found in %C between east and west sites (Table 3.4). Mineral horizon C:N ratios were significantly lower at east than west sites. Significant relationships were found between mineral soil clay content and organic matter fraction ( $P<0.0001$ ,  $R^2$  18%) as well as between mineral soil organic matter fraction and %N ( $P<0.0001$ ,  $R^2$  83%).

Organic horizon mass per unit area did not differ between eastern and western sites, and the organic horizon N pool was significantly greater at east sites (Table 3.5). East sites had significantly greater organic horizon %N. Organic horizon %C did not differ between east and west sites. Organic horizon C:N ratios were thus significantly lower at east than west sites. Organic horizon %lignin was not significantly different between east and west sites, however, lignin:N ratios were significantly lower at east than west sites because of differences in %N.

Potential net mineralization rates were significantly greater at east than west sites (Table 3.5). Potential net nitrification rates were low at all but two sites (Loch Vale (LV) and

Mills Lake (ML)) and did not differ between east and west sites. While estimated leaching losses from resin bags of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were greater at east than west sites, the differences were not significant. Two east sites (again, Loch Vale (LV) and Mills Lake (ML)) had the highest average  $\text{NO}_3^-$  losses of 1.4 and 3.1  $\text{mg N y}^{-1}$ . The range was 0-60 and 0-0.7  $\text{mg N y}^{-1}$  for east and west sites, respectively. The relationship between organic horizon %N and potential net mineralization rate shows a threshold of 1.2% N above which mineralization increases linearly (Fig. 3.3a). West sites had %N less than 1.4 and low mineralization rates; east sites had 1.3% N or greater and higher mineralization rates. Similarly, when C:N ratios were 29 or lower, mineralization rates increased linearly (Fig. 3.3b). West sites had C:N ratios greater than 29 and low mineralization rates; east sites had C:N ratios less than 29 and higher mineralization rates.

We asked whether differences in wet N deposition inputs could account for the observed differences in organic horizon N pools between east and west sites. Using the mean organic horizon mass per unit area, 7168  $\text{g soil m}^{-2}$ , and mean organic horizon %N (g N per g soil) from both sides, we found the organic horizon N pool to be 774 and 996  $\text{kg N ha}^{-1}$  on the west and east, respectively. Human population in Front Range counties has increased exponentially since 1900 (US Census Bureau 1997). Assuming increases in N deposition paralleled increases in population, after Galloway et al. (1994) and Vitousek et al. (1997), we fit an exponential curve representing increases in N deposition to the population growth curve with N deposition reaching 4.7  $\text{kg N ha}^{-1} \text{y}^{-1}$  in 1995. We assumed 95% of atmospheric N inputs end up in the organic horizon N pool (Baron et al. 1994, Nadelhoffer et al. 1999). From 1900 through the present an estimated 162  $\text{kg N ha}^{-1}$  has accumulated in east side forest soils. This accounts for 73% of the difference in organic horizon N pools between east and west sites. Emmett et al. (1998) and Lovett and Rueth (1999) performed

similar calculations and concluded N deposition inputs could account for changes in soil N. This is obviously a simplification but our estimate illustrates that a significant portion of the difference in organic horizon N pools could be explained by increased N deposition inputs.

### 3.5 Discussion

Forest ecosystems differ in their ability to respond and rate of response to increases in N deposition (Aber et al. 1998). It is not completely understood what factors control these differences. Other investigators have suggested that land-use history, the size of the soil N pool, and growing season length, are important factors in determining how fast forest stands respond to increased atmospheric N inputs (Fenn et al. 1998). These factors play an important role in determining the balance between N availability and demand. We believe that the east side Colorado Front Range forests are at the initiation point where subtle changes are being identified.

East sites had greater soil and foliar N and lower C:N ratios compared to west sites. In addition, we found significantly greater foliar N:Mg ratios at east than west sites. Other studies have presented these same results in response to elevated N deposition (Aber et al. 1998, Fenn et al. 1998).

There are many factors that can influence N cycling, N pools, and foliar chemistry, including species composition and age, elevation, aspect, parent material, site history, climate, soil texture and N deposition (Mitchell et al. 1996, Waring and Running 1998). We explore the possibility that these factors confounded our interpretations below.

Elevation, aspect, parent material, and site history were controlled during site selection, therefore these are unlikely causes for the observed differences. Stand characteristic data indicate that we effectively controlled stand age and species composition (Table 3.2). The soil properties we measured do not point to any obvious differences between east and west sites (Table 3.4).

West sites are drier than east sites (86 versus 104 cm precipitation per year), but temperatures were similar (Table 3.1). 72% (13 cm) of the difference occurs during winter months when precipitation is snow. Its greatest effect could occur by prolonging the period in spring when soils are saturated, but this should not affect nutrient cycling rates because soil moisture tends to remain high through July at both east and west sites. Could a difference of 5 cm of precipitation during the growing season influence biogeochemical processes? In mesic forests such as we studied, growth is correlated with summer temperatures, not precipitation, as in xeric forests (Peet 1989, Villalba et al. 1994). A simulation of a sub-alpine spruce-fir forest to climate change also suggested precipitation was not a major control on ecosystem processes (Baron et al. 2000a). When annual and seasonal precipitation and temperature were varied by  $\pm 10\%$  and  $\pm 2^\circ\text{C}$ , respectively, forest productivity, evapotranspiration, and soil moisture were unresponsive to changes in precipitation, but sensitive to changes in temperature. Growth rates were comparable between east and west sites for both the cool-wet and warm-dry climatic periods examined. If differences in moisture were driving the observed biogeochemical differences between east and west sites we would expect to see increased growth rates at west sites during the cool-wet period from 1900-1929 (Table 3.2). Because we did not, we conclude slight differences in climate between east and west sites have not resulted in growth rate differences between sides.

East side soil had significantly greater percent clay, with an absolute difference of 4.9% (Table 3.5). Soil texture was highly variable, and the range of values was similar for both sides. Differences in soil clay content could influence biogeochemistry through two primary mechanisms, stand productivity and soil organic matter dynamics (Burke 1989, Aber and Melillo 1991, Parton et al. 1994). Because we found no differences in tree growth rates and organic matter pools between east and west sites we conclude the estimated difference in soil clay content is not large enough to influence N dynamics (Tables 3.2, 3.4 and 3.5).

Mineral soil %N was marginally greater at east sites with an average difference of 0.11%. Organic matter stabilization increases and turnover rate decreases with greater clay content, thereby facilitating C and N accumulation in soil (Sorenson 1981, Paul 1984, Schimel et al. 1985, Parton et al. 1987). During soil development since the last glaciation (approximately 7,000 year ago; Madole 1976) greater soil clay content at east sites most likely resulted in slightly higher mineral soil N. Greater mineral soil N does not necessarily equate to higher N availability however, because clay-stabilized organic matter has low turnover rates. Gundersen et al. (1998) examined data from 5 European sites that span an N deposition gradient of 13 – 59 kg N ha<sup>-1</sup> y<sup>-1</sup> and found no relationships between either the mineral soil N pool size or C:N ratio and forest N status, vegetation variables or forest floor characteristics. Their results suggest mineral soil is not a large sink for atmospheric N deposition, and that the mineral soil N pool does not drive biogeochemical processes associated with changes in N inputs. Gundersen et al. (1998) also found, as we did, that the mineral soil N pool was correlated with clay content. Therefore, we assume that differences in mineral soil N did not result in greater N availability at east sites prior to elevated atmospheric N inputs. The influence of increased N deposition on soil properties is expected to be strongest in the organic horizon (Gundersen et al. 1998, Nadelhoffer et al.

1999). We found that 73% of the difference between east and west organic matter N pools can be accounted for by N deposition.

McNulty et al. (1991) conducted a study similar to ours examining spruce-fir N dynamics across an N deposition gradient in the Northeastern US. They observed a linear increase in net nitrification rates when forest floor %N increased above 1.4%. We saw a similar relation between potential net mineralization rates and organic horizon %N (Fig. 3.3a). As %N increased above 1.2% net mineralization rates linearly increased. No relation was seen between potential net nitrification rates and soil %N because net nitrification rates were low at most sites. Higher net nitrification rates were observed at the two sites with the lowest soil C:N ratios. Loch Vale (LV) and Mills Lake (ML) had C:N ratios of 22.4 and 24.2 and nitrification rates of 1.98 and 0.72  $\mu\text{g N g}^{-1} \text{d}^{-1}$ , respectively (Table 3.5). Others have found a nitrification threshold related to soil C:N ratios where nitrification is limited in soils with a C:N ratio greater than 25 or 24 (Gundersen and Rasmussen 1990, Emmett et al. 1998, Lovett and Rueth 1999). The low nitrification rates we observed at most sites in this study could be explained by soil C:N ratios above this threshold.

Our data suggest a positive feedback from atmospheric N additions where increased soil N pools lead to increased soil N mineralization rates, which increases plant available N (Tietema et al. 1995). The organic horizon N pool is the primary sink for incoming N (Fenn et al. 1998, Nadelhoffer et al. 1999). We found an increase in organic horizon %N and total N and a decrease in C:N and lignin:N ratios at east compared to west sites. This increase in soil N can lead to more rapid N mineralization rates (Aber et al. 1998), which we observed at east compared with west sites. Higher N mineralization rates can result in greater plant N availability. Foliar %N was greater at east than west sites. Increased foliar %N caused decreased foliar C:N ratios. Changes in foliar C and N can generate a positive feedback,

further decreasing soil C:N and lignin:N ratios through foliar litter inputs (Melillo et al. 1982). If soil C:N ratios continue to decline nitrification rates may increase (Emmett et al. 1998, Gundersen et al. 1998). The two sites with the lowest soil C:N ratios had higher potential net nitrification rates and estimated  $\text{NO}_3^-$  leaching losses (Table 3.5).

### 3.6 Conclusions

Increased N deposition results in increased foliar %N and N:Mg ratios, decreased foliar and soil C:N ratios, and changes in N mineralization rates (Aber et al. 1998, Fenn et al. 1998, Gundersen et al. 1998, Vitousek et al. 1997). Our six east sites display these characteristics, indicative of greater N availability compared to our six west sites. Other gradient studies have shown vegetation and soil responses to increased N inputs, however, the range of deposition rates in those studies was greater than in our study (McNulty et al. 1991, Tietema and Beier 1995, Lovett and Rueth 1999). Our results suggest even relatively small increases in N deposition inputs may cause measurable changes in forest biogeochemical processes.

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Table 3.1: Climate characterization from two meteorological stations and six SNOTEL sites. Mean and one standard deviation in parentheses. Standard deviations were not provided by the NRCS for the SNOTEL precipitation data.

\* Side indicates either east or west of the Continental Divide, E or W, respectively.

† Precipitation data 1961-90 for SNOTEL sites;

‡ Period indicates years used for mean temperatures.

§ Unpublished data, Baron; Precipitation data 1985-1998.

□ Unpublished data, USFS Rocky Mountain Research Station, Mike Ryan; Precipitation data 1992-1999.

| Site Name<br>(Abbreviation) | Elevation<br>(m) | Side* | Annual<br>Mean<br>Precip. (cm) | Winter<br>Precip.<br>Oct.-May<br>(cm) | Summer<br>Precip.<br>June-Sept.<br>(cm) | Period of<br>Record† | Mean<br>Jan.<br>Temp.<br>(°C) | Mean<br>July<br>Temp.<br>(°C) | Mean<br>Annual<br>Temp.<br>(°C) |
|-----------------------------|------------------|-------|--------------------------------|---------------------------------------|---|----------------------|-------------------------------|-------------------------------|---------------------------------|
| Joe †<br>Wright (JW)        | 3217             | E     | 117                            | 87                                    | 30                                      | 1989-99              | -8.4 (2.9)                    | 11.6 (5.2)                    | 0.02 (1.7)                      |
| University †<br>Camp (UC)   | 3140             | E     | 89                             | 65                                    | 24                                      | 1990-99              | -8.3 (0.8)                    | 10.8 (0.9)                    | 0.2 (0.5)                       |
| Willow Park †<br>(WP)       | 3262             | E     | 99                             | 75                                    | 24                                      | 1989-99              | -10.0 (0.9)                   | 9.2 (0.8)                     | -1.1 (0.5)                      |
| Loch Vale †<br>(LV)         | 3160             | E     | 112 (17)                       | 82 (13)                               | 30 (8)                                  | 1992-99              | -7.8 (0.8)                    | 12.3 (0.9)                    | 1.1 (0.6)                       |
| Copper Mt. †<br>(CM)        | 3201             | W     | 81                             | 61                                    | 20                                      | 1986-99              | -11.0 (3.7)                   | 9.9 (1.3)                     | -0.4 (2.1)                      |
| Lake Irene †<br>(LI)        | 3262             | W     | 91                             | 70                                    | 21                                      | 1985-99              | -10.6 (3.1)                   | 9.0 (2.7)                     | -1.4 (0.7)                      |
| Vail Mt. †<br>(VM)          | 3140             | W     | 87                             | 69                                    | 18                                      | 1986-99              | -8.9 (1.4)                    | 12.5 (1.3)                    | 1.2 (0.5)                       |
| Fraser □<br>(FC)            | 3189             | W     | 86 (16)                        | 62 (15)                               | 24 (4)                                  | 1984-93              | -10.7 (1.7)                   | 13.8 (1.4)                    | 0.8 (0.9)                       |
| East Side<br>Average        | -                | -     | 104                            | 78                                    | 26                                      | -                    | -8.6                          | 11.0                          | 0.06                            |
| West Side<br>Average        | -                | -     | 86                             | 65                                    | 21                                      | -                    | -10.3                         | 11.3                          | 0.1                             |
| P - value                   | -                | -     | 0.11                           | 0.25                                  | 0.86                                    | -                    | 0.99                          | 0.42                          | 0.67                            |

Table 3.2: Summary of forest stand characteristics by site. Mean and one standard deviation in parentheses. Side indicates either east or west of the Continental Divide, E or W, respectively. Stand age is the age of canopy spruce trees at coring height (1.3 m). Granite Falls data was not available due to inaccessibility. Sample n equals 3 per site for stand age and growth rate data. Degrees of freedom are 9 for all analyses.

| Site               | Side | Stand Age (y) | Total Basal Area (m <sup>2</sup> ha <sup>-1</sup> ) | Spruce Basal Area (m <sup>2</sup> ha <sup>-1</sup> ) | Growth Rate 1900-1929 (mm y <sup>-1</sup> ) | Growth Rate 1930-1959 (mm y <sup>-1</sup> ) |
|--------------------|------|---------------|---|--|---|---|
| Boreas Pass (BR)   | W    | 255 (36)      | 44 (6)  | 38 (8)   | 0.39 (0.24)                                 | 0.37 (0.17)                                 |
| Fool Creek (FC)    | W    | 250 (29)      | 58 (13)   | 35 (20)  | 0.29 (0.06)                                 | 0.25 (0.06)                                 |
| Byers Creek (BC)   | W    | 401 (153)     | 65 (9)  | 41 (9)   | 0.43 (0.39)                                 | 0.47 (0.46)                                 |
| West Rollins (WR)  | W    | 213 (63)      | 40 (9)  | 29 (7)   | 0.57 (0.12)                                 | 0.59 (0.37)                                 |
| West Arapaho (WA)  | W    | 358 (100)     | 51 (9)  | 31 (11)  | 0.50 (0.26)                                 | 0.58 (0.38)                                 |
| Long Lake (LL)     | E    | 422 (42)      | 80 (21)   | 60 (28)  | 0.29 (0.11)                                 | 0.33 (0.14)                                 |
| East Rollins (ER)  | E    | 238 (25)      | 65 (9)  | 44 (6)   | 0.38 (0.14)                                 | 0.41 (0.18)                                 |
| Berthoud Pass (BP) | E    | 294 (44)      | 47 (12)   | 32 (11)  | 0.55 (0.29)                                 | 0.47 (0.21)                                 |
| Loch Vale (LV)     | E    | 350 (101)     | 50 (11)   | 29 (6)   | 0.49 (0.27)                                 | 0.46 (0.26)                                 |
| Marmot Point (MP)  | E    | 313 (109)     | 61 (1)  | 39 (3)   | 0.65 (0.28)                                 | 0.58 (0.24)                                 |
| Mills Lake (ML)    | E    | 349 (133)     | 43 (1)  | 29 (6)   | 0.53 (0.34)                                 | 0.46 (0.21)                                 |
| East Side Average  | -    | 328 (100)     | 58 (16)   | 39 (16)  | 0.47 (0.26)                                 | 0.45 (0.21)                                 |
| West Side Average  | -    | 294 (111)     | 52 (12)   | 35 (11)  | 0.42 (0.25)                                 | 0.44 (0.32)                                 |
| P – value          | -    | 0.52          | 0.43  | 0.51   | 0.47  | 0.91  |

**Table 3.3: Summary of foliar chemistry of current year Englemann spruce needles. Mean and one standard deviation in parentheses, and range is minimum and maximum values. Nitrogen and nutrients are percentages of oven-dry weight. Sample n equals 75 and 90 for all analyses for east and west sites, respectively. Degrees of freedom are 9 for all analyses.**

| Analysis | East         | East        | West        | West        | P- value     |
|----------|--------------|-------------|-------------|-------------|--------------|
|          | Average      | Range       | Average     | Range       |              |
| N (%)    | 1.14 (0.1)   | 0.91 - 1.44 | 0.99 (0.1)  | 0.73 -1.32  | <b>0.02</b>  |
| C:N      | 45.6 (4.2)   | 36.3 - 55.8 | 52.1 (6.6)  | 37.7 - 68.9 | <b>0.03</b>  |
| Ca (%)   | 0.31 (0.08)  | 0.18 - 0.51 | 0.35 (0.09) | 0.14 - 0.63 | 0.26         |
| Mg (%)   | 0.097 (0.01) | 0.07 - 0.13 | 0.10 (0.01) | 0.08 - 0.14 | 0.09         |
| K (%)    | 1.34 (0.3)   | 0.79 - 2.03 | 1.19 (0.3)  | 0.74 - 2.11 | 0.42         |
| P (%)    | 0.19 (0.04)  | 0.12 - 0.28 | 0.21 (0.03) | 0.16 - 0.36 | 0.16         |
| N:Ca     | 3.83 (0.9)   | 2.17 - 6.41 | 2.99 (0.8)  | 1.59 - 6.13 | <b>0.007</b> |
| N:Mg     | 11.9 (1.7)   | 8.78 - 16.6 | 9.66 (1.6)  | 6.78 - 14.4 | <b>0.003</b> |
| N:P      | 6.34 (1.3)   | 4.39 - 9.99 | 4.77 (0.7)  | 3.00 - 7.47 | <b>0.008</b> |

**Table 3.4: Summary of mineral horizon characteristics by site. Mean and one standard deviation in parentheses. Side indicates either east or west of the Continental Divide, E or W, respectively. Nitrogen and carbon are percentages of oven-dry weight. OM is the fraction of organic matter. Sample n equals 15 per site. Degrees of freedom are 10 for all analyses.**

| Site Name (ID)     | Side | C (%)      | N (%)       | C:N        | pH         | OM           | Sand (%)   | Silt (%)   | Clay (%)   | Ca (mg kg <sup>-1</sup> ) | Mg (mg kg <sup>-1</sup> ) | K (mg kg <sup>-1</sup> ) | Na (mg kg <sup>-1</sup> ) | P (mg kg <sup>-1</sup> ) |
|--------------------|------|------------|-------------|------------|------------|--------------|------------|------------|------------|---------------------------|---------------------------|--------------------------|---------------------------|--------------------------|
| Boreas Pass (BR)   | W    | 2.85 (1.9) | 0.10 (0.06) | 27.6 (3.9) | 5.56 (0.4) | 0.079 (0.04) | 61.3 (4.6) | 20.8 (3.1) | 18.0 (2.1) | 1448 (981)                | 153 (28)                  | 281 (121)                | 60 (19)                   | 3.4 (3.5)                |
| Fool Creek (FC)    | W    | 8.11 (5.7) | 0.28 (0.1)  | 27.6 (7.9) | 5.06 (0.5) | 0.17 (0.1)   | 36.5 (13)  | 37.5 (7.8) | 26.0 (6.7) | 2848 (1513)               | 425 (179)                 | 320 (135)                | 79 (16)                   | 8.4 (6.0)                |
| Byers Creek (BC)   | W    | 5.06 (2.7) | 0.24 (0.1)  | 20.8 (3.8) | 4.86 (0.2) | 0.12 (0.06)  | 40.1 (7.2) | 34.7 (5.0) | 25.2 (2.9) | 1994 (1052)               | 326 (77)                  | 314 (115)                | 122 (23)                  | 6.3 (2.9)                |
| West Rollins (WR)  | W    | 11.5 (12)  | 0.31 (0.3)  | 31.8 (11)  | 5.11 (0.6) | 0.18 (0.2)   | 61.7 (11)  | 19.3 (8.5) | 19.0 (3.5) | 895 (613)                 | 126 (35)                  | 213 (105)                | 79 (28)                   | 6.1 (4.1)                |
| West Arapaho (WA)  | W    | 4.25 (3.9) | 0.26 (0.4)  | 24.7 (7.9) | 4.69 (0.2) | 0.088 (0.07) | 49.2 (11)  | 32.1 (6.3) | 18.7 (6.6) | 634 (420)                 | 131 (60)                  | 156 (97)                 | 70 (15)                   | 4.9 (4.1)                |
| Granite Falls (GF) | W    | 8.99 (4.0) | 0.28 (0.1)  | 32.5 (3.3) | 4.45 (0.5) | 0.18 (0.08)  | 40.6 (13)  | 32.8 (8.9) | 26.7 (9.7) | 1820 (1024)               | 271 (142)                 | 402 (169)                | 91 (24)                   | 8.5 (3.8)                |
| Long Lake (LL)     | E    | 5.64 (3.6) | 0.24 (0.1)  | 23.4 (3.7) | 4.70 (0.1) | 0.11 (0.06)  | 58.3 (15)  | 21.4 (11)  | 20.3 (5.2) | 1323 (575)                | 242 (85)                  | 211 (112)                | 87 (20)                   | 7.3 (4.6)                |
| East Rollins (ER)  | E    | 5.52 (4.1) | 0.24 (0.1)  | 21.5 (4.0) | 4.71 (0.1) | 0.12 (0.07)  | 42.2 (11)  | 33.5 (7.5) | 24.3 (3.6) | 819 (493)                 | 143 (34)                  | 189 (54)                 | 83 (16)                   | 7.4 (4.7)                |
| Berthoud Pass (BP) | E    | 8.29 (2.4) | 0.35 (0.1)  | 24.3 (4.9) | 4.76 (0.3) | 0.16 (0.04)  | 42.3 (14)  | 32.5 (8.9) | 25.2 (5.7) | 1831 (889)                | 238 (69)                  | 260 (119)                | 86 (13)                   | 7.4 (2.8)                |
| Loch Vale (LV)     | E    | 8.83 (3.9) | 0.41 (0.2)  | 22.5 (5.3) | 4.88 (0.2) | 0.17 (0.07)  | 29.8 (10)  | 38.5 (12)  | 31.6 (4.9) | 1636 (872)                | 243 (49)                  | 262 (83)                 | 80 (18)                   | 7.6 (4.5)                |
| Marmot Point (MP)  | E    | 6.58 (3.7) | 0.34 (0.1)  | 18.7 (3.2) | 4.89 (0.1) | 0.15 (0.07)  | 40.9 (4.8) | 31.3 (2.8) | 27.8 (2.6) | 1450 (480)                | 289 (75)                  | 336 (70)                 | 71 (23)                   | 6.7 (3.9)                |
| Mills Lake (ML)    | E    | 9.48 (6.5) | 0.50 (0.3)  | 18.4 (2.9) | 4.70 (0.2) | 0.18 (0.1)   | 39.1 (5.0) | 32.8 (4.2) | 28.1 (2.3) | 973 (586)                 | 185 (41)                  | 236 (80)                 | 90 (24)                   | 12 (8.8)                 |
| East Side Average  | -    | 7.29 (4.5) | 0.35 (0.2)  | 21.2 (4.9) | 4.76 (0.2) | 0.15 (0.1)   | 40.3 (12)  | 23.8 (8.4) | 26.9 (4.9) | 1281 (707)                | 220 (77)                  | 251 (94)                 | 81 (20)                   | 8.5 (5.5)                |
| West Side Average  | -    | 6.65 (6.6) | 0.24 (0.2)  | 27.2 (7.8) | 5.02 (0.5) | 0.13 (0.1)   | 48.3 (14)  | 29.7 (9.6) | 22.0 (6.4) | 15.97 (1221)              | 237 (151)                 | 274 (143)                | 82 (29)                   | 6.2 (4.5)                |
| P – value          | -    | 0.68       | 0.08        | 0.01       | 0.21       | 0.55         | 0.11       | 0.31       | 0.03       | 0.46                      | 0.83                      | 0.59                     | 0.87                      | 0.13                     |

**Table 3.5: Summary of organic horizon characteristics by site. Mean and one standard deviation in parentheses. Side indicates either east or west of the Continental Divide, E or W, respectively. Mass is the weight of organic horizon soil per square meter. Total N is the organic horizon N pool calculated using %N and the mass of the organic horizon. Nitrogen, carbon and lignin are percentages of oven-dry weight. Mineralization and nitrification rates are net potential rates. Soil ion exchange resin bags were used to estimate yearly leaching losses. Sample n equals 15 per site. Degrees of freedom are 10 for all analyses.**

| Site Name (ID)     | Side | Mass (kg m <sup>-2</sup> ) | Total N (g N m <sup>-2</sup> ) | N (%)      | C (%)       | C:N        | Lignin (%) | Lignin:N   | Mineralization Rate (μg N g <sup>-1</sup> d <sup>-1</sup> ) | Nitrification Rate (μg N g <sup>-1</sup> d <sup>-1</sup> ) | Resin Bag NO <sub>3</sub> <sup>-</sup> (mg N y <sup>-1</sup> ) | Resin Bag NH <sub>4</sub> <sup>+</sup> (mg N y <sup>-1</sup> ) |
|--------------------|------|----------------------------|--------------------------------|------------|-------------|------------|------------|------------|---|--|--|--|
| Boreas Pass (BR)   | W    | 8.4 (1.4)                  | 76 (16)                        | 0.91 (0.2) | 30.0 (5.5)  | 33.1 (2.5) | 26.4 (5.1) | 29.1 (2.6) | 0.68 (1.2)  | 0.24 (0.7)   | 0.06 (0.05)  | 0.18 (0.3)   |
| Fool Creek (FC)    | W    | 6.7 (1.2)                  | 61 (17)                        | 0.89 (0.2) | 32.1 (4.8)  | 36.3 (3.7) | 28.0 (5.6) | 31.5 (3.6) | 0.23 (0.4)  | 0 (0)  | 0.05 (0.05)  | 0.17 (0.2)   |
| Byers Creek (BC)   | W    | 6.9 (1.6)                  | 73 (20)                        | 1.00 (0.3) | 30.8 (9.1)  | 28.7 (8.0) | 28.0 (3.4) | 26.3 (2.9) | 0.94 (1.5)  | 0 (0)  | 0.13 (0.1)   | 0.25 (0.2)   |
| West Rollins (WR)  | W    | 9.7 (2.4)                  | 94 (21)                        | 1.00 (0.2) | 35.0 (7.2)  | 35.5 (7.7) | 32.2 (7.5) | 33.0 (9.5) | 0.91 (0.9)  | 0.10 (0.2)   | 0.11 (0.1)   | 0.13 (0.1)   |
| West Arapaho (WA)  | W    | 4.8 (1.2)                  | 57 (13)                        | 1.22 (0.2) | 35.5 (4.8)  | 29.6 (3.5) | 30.0 (5.6) | 24.9 (3.5) | 0.28 (0.4)  | 0 (0)  | 0.05 (0.06)  | 0.19 (0.1)   |
| Granite Falls (GF) | W    | 5.6 (1.8)                  | 75 (21)                        | 1.36 (0.2) | 39.6 (3.1)  | 29.4 (2.8) | 33.2 (3.7) | 24.7 (3.0) | 1.09 (1.0)  | 0.02 (0.01)  | 0.01 (0.02)  | 0.10 (0.1)   |
| Long Lake (LL)     | E    | 7.9 (2.0)                  | 99 (23)                        | 1.28 (0.1) | 34.0 (5.6)  | 26.5 (2.1) | 30.8 (5.2) | 24.1 (2.8) | 2.81 (1.5)  | 0.37 (0.6)   | 0.36 (0.4)   | 0.18 (0.3)   |
| East Rollins (ER)  | E    | 7.1 (1.6)                  | 93 (21)                        | 1.32 (0.2) | 34.2 (4.5)  | 25.9 (1.4) | 28.5 (3.7) | 21.7 (1.4) | 2.91 (1.5)  | 0 (0)  | 0.17 (0.3)   | 0.47 (0.4)   |
| Berthoud Pass (BP) | E    | 8.3 (2.4)                  | 107 (33)                       | 1.29 (0.1) | 36.4 (3.6)  | 28.3 (2.2) | 31.3 (4.2) | 24.3 (2.9) | 1.80 (2.1)  | 0.09 (0.1)   | 0.28 (0.3)   | 0.24 (0.3)   |
| Loch Vale (LV)     | E    | 7.7 (1.4)                  | 117 (23)                       | 1.40 (0.4) | 33.6 (10.5) | 22.4 (6.6) | 31.2 (5.0) | 20.9 (3.2) | 4.86 (4.7)  | 1.98 (2.7)   | 1.39 (1.7)   | 0.88 (1.0)   |
| Marmot Point (MP)  | E    | 7.1 (1.9)                  | 98 (24)                        | 1.29 (0.4) | 34.3 (9.7)  | 24.8 (6.9) | 30.9 (2.9) | 22.4 (1.9) | 3.84 (1.6)  | 0.27 (0.3)   | 0.22 (0.3)   | 0.21 (0.5)   |
| Mills Lake (ML)    | E    | 5.9 (1.9)                  | 91 (30)                        | 1.56 (0.2) | 37.5 (4.2)  | 24.2 (3.0) | 30.6 (3.8) | 19.8 (3.1) | 4.31 (2.4)  | 0.72 (1.8)   | 3.11 (1.2)   | 0.19 (0.3)   |
| East Side Average  | -    | 7.3 (2.0)                  | 100 (27)                       | 1.39 (0.2) | 38.8 (4.8)  | 25.9 (2.7) | 30.5 (4.2) | 22.2 (3.1) | 3.42 (2.7)  | 0.57 (1.5)   | 1.03 (5.5)   | 0.37 (0.6)   |
| West Side Average  | -    | 7.0 (2.3)                  | 73 (22)                        | 1.08 (0.2) | 34.2 (5.9)  | 32.4 (5.0) | 29.6 (5.7) | 28.3 (5.7) | 0.69 (1.0)  | 0.06 (0.3)   | 0.07 (0.1)   | 0.17 (0.2)   |
| P - value          | -    | 0.70                       | 0.002                          | 0.006      | 0.31        | 0.001      | 0.47       | 0.004      | 0.0002  | 0.12   | 0.13   | 0.13   |

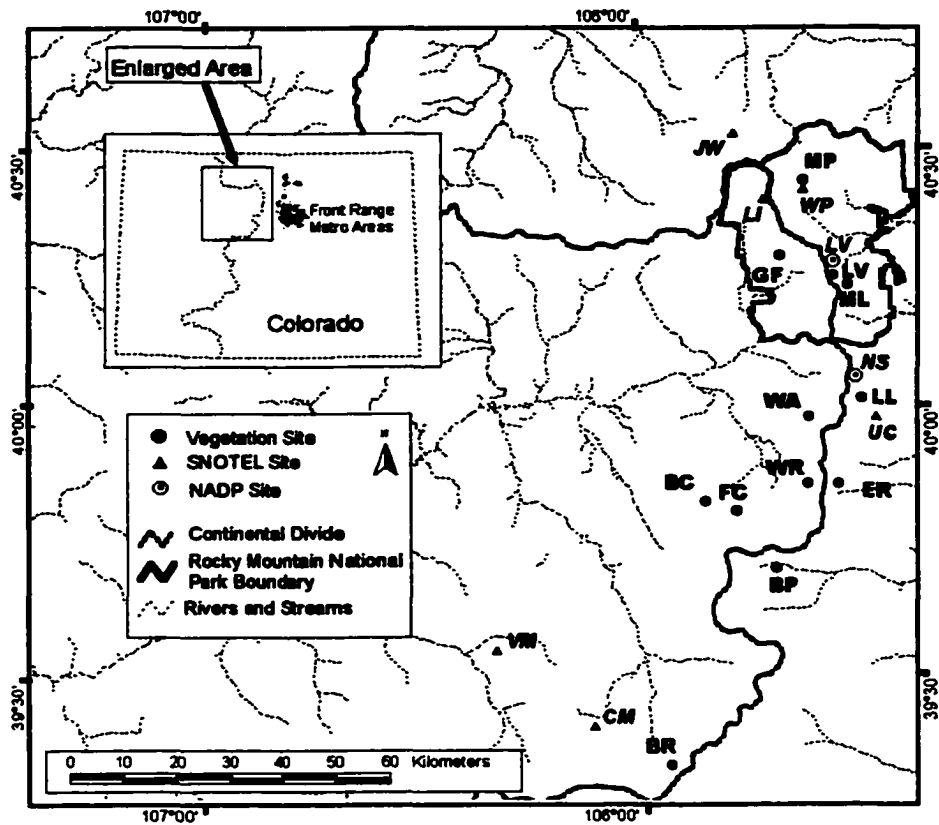


Fig. 3.1: Location of forest, SNOTEL and NADP sites. SNOTEL site abbreviations correspond to those in Table 2.1.

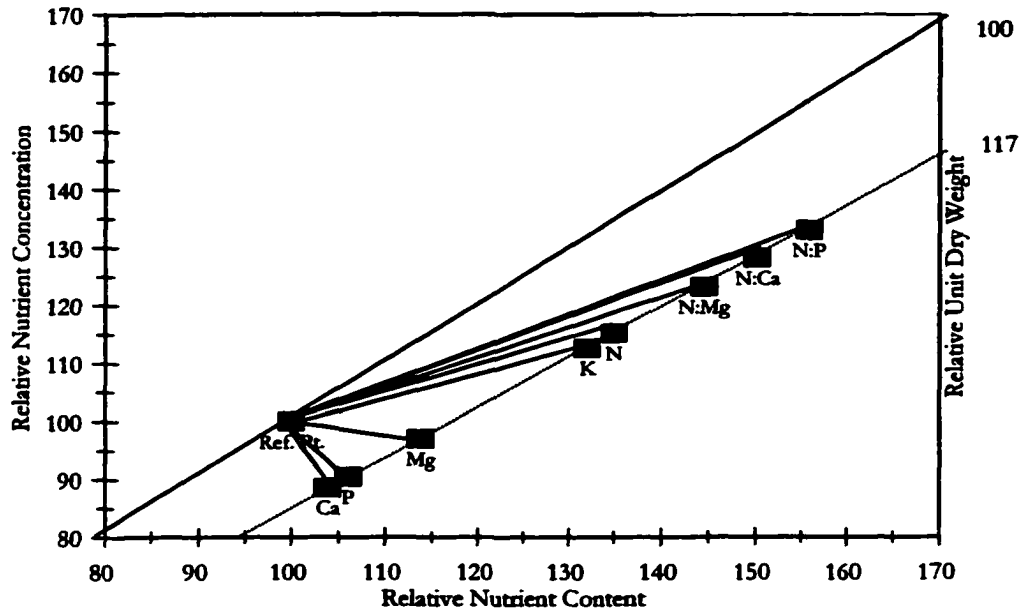


Fig. 3.2: Foliar vector analysis comparing average west to east side foliar nutrient status. Illustrates the relationship between current year nutrient concentration and content and needle dry weight. The 1:1 line represents no changes in relative unit dry weight and the dotted line represents a relative increase of 17% (or 117). The reference point (Ref. Pt.) refers to west side foliar nutrient status. For each nutrient west side foliar nutrient status was normalized to 100 for all three parameters. Vectors from the reference point represent relative changes in nutrient status and weight of east compared to west side foliage.

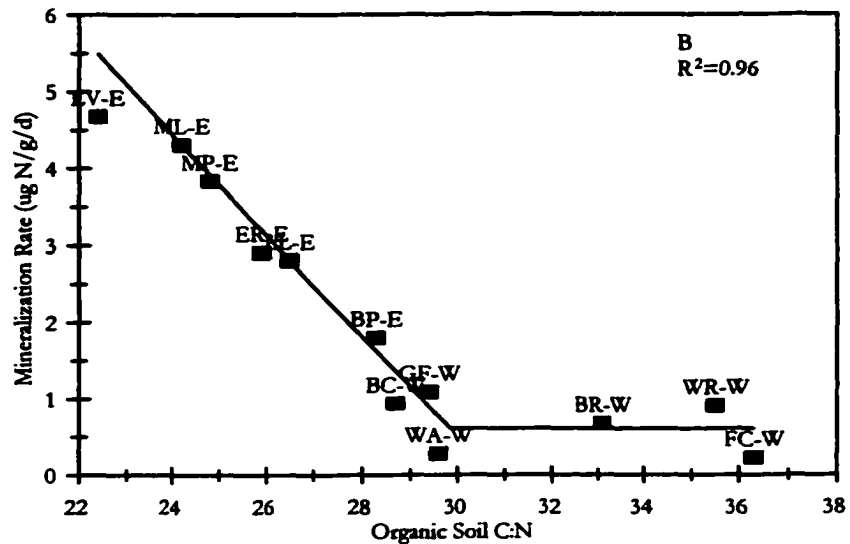
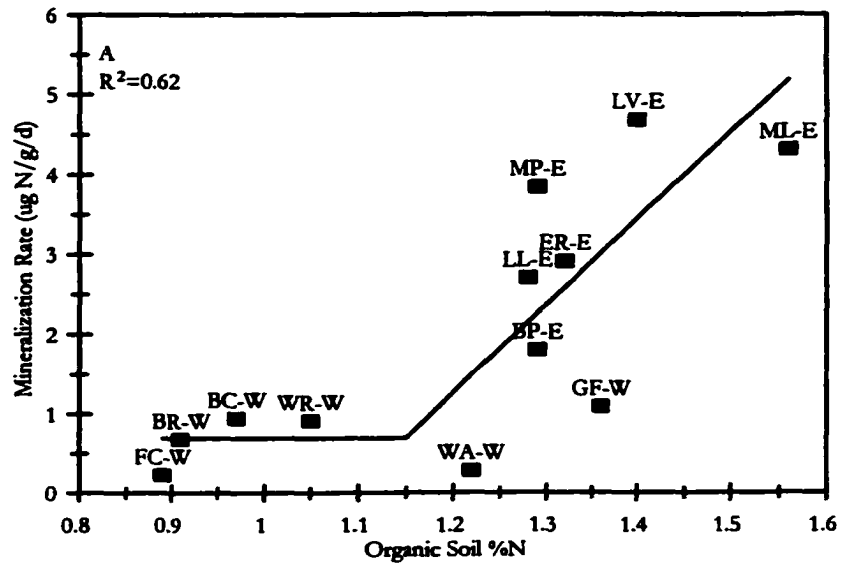


Fig. 3.3: Relationship between organic horizon potential net mineralization rates and (A) %N and (B) C:N ratios. Point labels correspond to the site abbreviations in Fig. 1 followed either by E or W indicating the site location either east or west of the Continental Divide.

## 4. Simulated effects of variation in climate, soil texture and nitrogen deposition on Englemann spruce forest biogeochemistry

### 4.1 Abstract

We applied CENTURY, a biogeochemical cycling model, to address the sensitivity of Colorado high-elevation old-growth spruce forest processes to alterations in climate, soil texture and nitrogen (N) inputs. Our objectives were: 1) to simulate potential ecosystem responses to increased annual precipitation, altered soil texture and elevated N deposition because, while field data indicate atmospheric N deposition has affected Englemann spruce forest biogeochemistry, site differences in precipitation and soil texture are plausible alternative explanations for observed differences among sites, and 2) to examine potential interactions between projected future N deposition rates and climate change on forest ecosystem processes. Simulated increased annual precipitation elevated stream N fluxes causing a decline in production and ecosystem C and N pools. The magnitude of change produced by relatively small changes in soil texture confirmed that CENTURY is highly sensitive to this parameter. Modeled forest productivity was highly sensitive to added N; however, the forests also had a limited N storage capacity. Strong hydrologic flushing, reducing N availability, caused the limited uptake capacity. Effects of precipitation, soil texture and N additions in a sensitivity analysis suggest that future increases in N deposition could have a substantial impact on N and C biogeochemistry through greater NPP and stream N fluxes. Modeled increased temperature reduced stream N fluxes by increasing

evaporation and transpiration water losses thereby reducing stream flow. The relative reduction in stream N fluxes was high while the absolute reduction was low, resulting in slightly increased NPP. We observed similarities between model results and field data from twelve similar old-growth Englemann spruce stands suggesting that elevated N inputs caused the observed differences between high and low N deposition sites in Rocky Mountain forests.

#### 4.2 Introduction

Elevated nitrogen (N) deposition rates alter catchment-scale biogeochemical cycling and can cause terrestrial ecosystems to become a source of  $\text{NO}_3^-$  to aquatic systems (Stoddard 1994, Aber et al. 1995, Vitousek et al. 1997). Increased  $\text{NO}_3^-$  leaching has been linked to soil and stream acidification, mobilization of aluminum from terrestrial to aquatic systems, elevated cation leaching and altered nutrient cycling, all of which can affect forest health and water quality (Driscoll et al. 1987, Fenn et al. 1998). The old-growth status, evergreen habit, and short growing season of high-elevation old-growth forests reduces their N demand, which may predispose them to enhanced leaching losses following elevated atmospheric N inputs (Fenn et al. 1998).

Our ability to predict forest responses to climate change is important for understanding the processes influencing the global carbon (C) budget and determining the ability of forests to offset fossil fuel emissions (Schimel et al. 2000, Joyce and Birdsey 2000). Climate change can potentially alter the function (photosynthesis, decomposition) and structure (distribution of C and N between plant and soil pools) of forest ecosystems (Melillo et al. 1990). Temperate coniferous forests are thought to be a potentially strong net

C sink due to woody tissue storage and elevated N deposition inputs may stimulate C gain (Melillo et al. 1996). The three mechanisms by which greater N availability can increase aboveground net production are increasing net photosynthesis, increasing leaf area index and reallocation of C from below- to aboveground tissues. Temperature is the main climate variable influencing coniferous forest productivity and decomposition (Brubaker and Graumlich 1989, Breymeyer 1991a, 1991b, 1993). Climate warming is thought to increase tree growth rates, photosynthesis, litter production, soil respiration rates, N mineralization rates and growing season length (Berg et al. 1993, Melillo 1996, Ryan et al. 1996). The impacts of climate warming on total ecosystem and soil C pools are unclear because inputs, production and litterfall, and respiration outputs may both increase, therefore, the net outcome will depend on the relative increases in C inputs and outputs. However, forest responses to climate change will be strongly constrained by nutrient availability and soil moisture (Ryan et al. 1996).

Our objectives in this paper are to examine the potential impacts of environmental change on forest processes. Simulations addressed increases in N deposition, comparing the magnitude of change from elevated N inputs with other abiotic variables that vary spatially such as soil texture and precipitation. We also explored forest responses to future climate change. Regional N deposition rates are currently elevated above background and will likely continue to rise with increased regional population and economic growth (Parrish et al. 1990, Langford and Fehsenfeld 1992, Baron et al. 2000, Heuer et al. 2000). We have documented the initial impacts of elevated N deposition on forest biogeochemistry (Rueth and Baron, in press). It has been hypothesized that climate warming could counter the impact of greater N inputs on leaching losses through enhanced N retention in soil and vegetation (Baron and Campbell 1997, Fenn et al. 1998). We examined how continual increases in N deposition

and the interactions between projected future N deposition rates and climate change may impact Englemann spruce forests. It is difficult to diagnose differences in ecosystems along gradients of human influences because 1) it is impossible to exactly match all conditions in more or less unaffected stands in nature, and 2) experimental simulations of impacts require decades to develop in nature and are consequently unpractical. Our approach was to compare modeled forest responses to variation in climate, soil texture, and N additions and to compare the results with field data. We used CENTURY, a plant-soil ecosystem model that represents carbon and nitrogen biogeochemistry (Fig. 4.1, Parton et al. 1987, 1988, 1993).

#### 4.3 Materials and methods

Simulations were run to portray spruce-fir forests of north-central Colorado. A field study compared similar forest stands east and west of the Continental Divide, and found the site-defining characteristics of species composition, aspect, elevation, parent material, and site history to be similar (Rueth and Baron, in press). Nitrogen deposition rates were 1-2 kg N ha<sup>-1</sup> y<sup>-1</sup> west and 3-5 kg N ha<sup>-1</sup> y<sup>-1</sup> east of the Continental Divide; precipitation was somewhat lower at west sites while soil texture was variable, but overall clay content was lower in west site soils (Rueth and Baron, in press).

Regional climate was characterized using data from six high-elevation National Resources Conservation Service SNOTEL sites within the study region (National Resources Conservation Service 1999). Regional mean January, July and annual temperatures were -9.4, 11.1 and -0.3°C, respectively. Annual precipitation averaged 104 and 89 cm east and west of the Continental Divide, respectively. Snowpack accumulates from November through May,

and represents 65-80% of annual precipitation (Baron and Denning 1993). Snowmelt processes dominate in May through July and August through October are characterized by base flow (Baron 1992).

CENTURY has been described in detail elsewhere (Metherell et al. 1993); we provide a brief overview. CENTURY contains a forest production submodel, which is linked to the soil organic matter (SOM) decomposition submodel, and a water budget model. The SOM submodel tracks the flow of elements through the forest floor and organic and inorganic soil pools. SOM C and N are divided into active, slow and passive pools with different decomposition rates, above and below ground litter pools, and a surface microbial pool. Active SOM contains soil microbes, microbial products and labile plant material, the slow pool contains more resistant plant material such as lignin compounds, and the passive pool contains physically- and chemically-stabilized SOM. Production is controlled by temperature, moisture and nutrient supply. The forest production submodel allocates C and nutrients to leaves, fine roots, fine branches, large wood and coarse roots. The water budget model calculates evaporation, transpiration, soil water content and saturated flow between soil layers.

CENTURY was parameterized based on the work of Arthur and Fahey (1992), who measured Englemann spruce forest C and N pools, turnover times and annual production in northern Colorado; during model parameterization we tuned the control simulation output to their results (Table 4.1). Site specific input variables included monthly precipitation (SNOTEL data), monthly average maximum and minimum temperatures (Baron 1992, Table 4.2, baseline), soil texture (Rueth and Baron, in press), initial SOM C pools and C:N ratios, initial forest component C:N ratios, and the lignin content of plant material (Arthur and Fahey 1992, Table 4.3). Forest component C:N ratios were allowed to float between set

minimum and maximum values. Old-growth high-elevation forests accumulate large C and N pools due to slow decomposition rates. To achieve modeled C and N pools within the range of values observed by Arthur and Fahey (1992) we adjusted the maximum decomposition rate of fine branches, wood and coarse roots, C allocation fraction to and death rate of tree components, and the temperature function for microbial decomposition (Table 4.3). CENTURY was run for 4,000 years with a medium intensity canopy fire every 500 years, comparable to the historic fire regime for Englemann spruce forests, to establish steady state (Peet 1981).

To estimate historic and project potential future increases in N deposition we estimated changes in deposition over time. Human population in Front Range counties has increased exponentially since 1950 (Fig. 4.2, US Census Bureau 1997). Assuming increases in N deposition paralleled increases in population (Galloway et al. 1994, Vitousek et al. 1997), we fit an exponential curve representing increases in N deposition to the population growth curve with N deposition reaching  $0.54 \text{ g N m}^{-2} \text{ y}^{-1}$  in the year 2000 (Fig. 4.2). The curve was extrapolated to the year 2050 and deposition levels reach  $1.5 \text{ g N m}^{-2} \text{ y}^{-1}$ . Simulated N inputs were raised every ten years.

Given our objects, three different types of simulations were performed and compared to the control. In equilibrium experiments we altered initial input variables that remained constant throughout the simulation and a new equilibrium was established. In transient experiments input variables were changed continuously therefore a new equilibrium was unlikely to be established. In some cases equilibrium and transient experiments were combined.

Simulations were run to represent the low (control) and high N deposition (combined) sites as well as changes in precipitation, soil texture and N inputs alone (Table

4.4). The control simulation was run with the average precipitation, soil texture and N deposition rates from the low N deposition sites over the entire simulation. The other simulations were compared with the control. Based on SNOTEL data annual precipitation was increased from 89 to 104 cm. To examine model sensitivity to precipitation we ran two additional simulations with the minimum and maximum SNOTEL values of 81 and 117 cm. Percent sand, silt and clay were changed from 48, 30 and 22 to 40, 33 and 27, respectively, based on data from our comparison study (Rueth and Baron, in press). To further explore the effects of soil texture on forest processes we ran a high sand/low clay and low sand/high clay simulation. We averaged the minimum and maximum percent sand and clay from each site and silt was determined by difference. Percent sand, silt and clay were 32, 37 and 31 for the low sand and 60, 22 and 18 for the high sand simulation. The precipitation and soil texture simulations were equilibrium experiments where initial input variables were changed compared to the control but remained constant throughout the simulation and a new equilibrium was established. We increased yearly N inputs from 0.15 to 0.54 g N m<sup>-2</sup> from 1950 to 2000 in ten year increments. Future N deposition increased gradually from 0.54 to 1.5 g N m<sup>-2</sup> y<sup>-1</sup> from 2000 to 2050.

Three climate change simulations were performed: a gradual 2°C increase in temperature, projected changes in temperature and precipitation from the Canadian Climate Centre General Circulation Model (GCM), and projected changes in temperature and precipitation from the Hadley Centre GCM. The Canadian and Hadley models were the two primary GCMs used to project climate change for the U.S. National Climate Change Assessment (National Assessment Synthesis Team 2000). The scenarios assume no major interventions to reduce the growth of green house gas emissions; by the year 2100 modeled CO<sub>2</sub> emissions triple and atmospheric CO<sub>2</sub> concentrations increase to over 700 parts per

million. This rate of CO<sub>2</sub> emissions increase represents a mid-range future emissions estimate of the Intergovernmental Panel on Climate Change (IPCC). Generally, the Hadley model predicts a wetter climate and the Canadian model projects a greater temperature increase (National Assessment Synthesis Team 2000). We based our Canadian and Hadley climate change simulations on the projected changes in temperature and precipitation from the two GCMs for the Estes Park grid cell. The Estes Park grid cell contains montane forests and grasslands rather than sub-alpine forest ecosystems; this is not the ideal system for projecting future changes at higher elevations but it is the best available data. Decadal changes in comparison to baseline of monthly precipitation (% change) and minimum and maximum temperatures (°C) from the Estes Park, Colorado grid cell were applied to our model climate inputs (Table 4.2). Simulations with increasing N inputs and/or changing climate conditions over time were transient experiments where input variables were changed continuously and a new equilibrium was not established.

#### 4.4 Results

##### 4.4.1 Control

Modeled ecosystem and soil N were higher and ecosystem and soil C were lower than that observed by Arthur and Fahey (1992, Table 4.1). Ecosystem and soil N differed by 96 and 85 g N m<sup>-2</sup> and ecosystem and soil C differed by 3640 and 2129 g C m<sup>-2</sup>, respectively. Ecosystem characteristics of the control simulation were within the range of observations from the literature (Table 4.1). Modeled control live biomass C and N were 6,546 and 43 g

$\text{m}^2$ , and measured values ranged from 7,250 – 7,600 and 54 – 63  $\text{g m}^{-2}$ , respectively; modeled production was 161  $\text{g C m}^{-2} \text{y}^{-1}$ , while observations ranged from 125 – 266  $\text{g C m}^{-2} \text{y}^{-1}$ .

#### 4.4.2 Precipitation

Increasing annual precipitation from 89 to 104 cm decreased productivity, ecosystem C and N pools and soil C, N, mineralization and respiration by 7 - 10% compared to the control but greatly increased stream flow and stream N fluxes (Tables 4.5 and 4.6). Stream flow and stream C and total N fluxes rose by 30%, 10% and 28%, respectively (Table 4.6). Greater stream flow in the precipitation simulation increased stream N fluxes, particularly during the peak flow months of April – June (Fig. 4.3).

Precipitation reduction from 89 to 81 cm increased production, ecosystem and soil C and N by 10-11% (Table 4.7). Stream flow declined by 18%, and total N loss also declined by 24%, compared to the control. Increasing precipitation to 117 cm led to further reductions in production and C and N pools of 19-22% and large increases in stream flow and N loss of over 55% (Table 4.7).

#### 4.4.3 Soil texture sensitivity

Ecosystem N, soil C and N, and stream N fluxes responded strongly to varying in soil texture. Production, ecosystem C and soil mineralization and respiration rates increased 10 - 12% and ecosystem N and soil C and N increased 18 - 21%, compared to the control (Table 4.5). Total (inorganic plus organic) stream N fluxes declined 19% (Table 4.6).

The low sand simulation (32% compared with 48%) resulted in greater production (19%), ecosystem C (22%) and N (34%), soil C (39%) and N (42%), and reduced stream N fluxes (51%), compared to the control. The high sand simulation produced the opposite response with decreased production, ecosystem and soil C and N pools of 16 - 24% and increased N losses of 35% (Table 4.7).

#### 4.4.4 Nitrogen additions

Increasing N inputs from 0.15 to 0.54 g N m<sup>-2</sup> y<sup>-1</sup> over 50 years produced large increases in production (29%), live biomass N (12%), mineralization rates (19%), and total stream N fluxes (75%), compared with the control (Tables 4.5 and 4.6). Elevated N deposition led to slight increases of 4% and 5% in ecosystem C and N, respectively. Greater N availability increased foliar turnover rates within CENTURY which reduced foliar C and hence C:N ratios.

#### 4.4.5 Combined precipitation, soil texture and N additions

Increasing precipitation or altering soil texture by themselves simply shifted base line ecosystem properties (Fig. 4.4). The combined simulation indicated that the precipitation, soil texture and N addition treatments were additive and there were limited modeled ecosystem interactions between the treatments (Fig. 4.4). While we only show ecosystem C and N here, other ecosystem properties such as production, live biomass C and N, and soil C and N exhibited similar patterns. The summed percent differences from the precipitation, soil texture and N addition simulations came within 1% of the combined treatment

response, in most cases (Table 4.5). The largest differences (4-8%) between the summed individual and combined simulations occurred for stream C and N fluxes (Table 4.6).

CENTURY model results suggest that different ecosystem C and N pools and processes have different sensitivities to precipitation, soil texture and N additions (Tables 4.5 and 4.6). Live biomass N, production and soil processing rates were highly influenced by N additions, whereas total ecosystem C and N were most responsive to altered soil texture driven by greater soil C and N pools. Stream N and C fluxes were driven by a combination of the three treatments. Increased precipitation actually had a negative effect on many ecosystem processes and pools.

We expected to observe decreased soil and foliar C:N, and increased soil and foliar N, net primary production, mineralization rates and inorganic N loss in the simulated high N deposition forest (combined treatment) compared to the control forest because of reported results from field studies (McNulty and Aber 1993, Tietema and Beier 1995, Aber et al. 1998, Fenn et al. 1998, Gundersen et al. 1998). We observed increased production, N mineralization rates and inorganic N loss; soil and foliar C:N ratios did not respond as expected (Tables 4.5 and 4.6). Soil C and N both increased, resulting in no net change in C:N, and foliar C:N decreased, but due to decreased C, not increased N (Table 4.5).

#### 4.4.6 Future N addition scenario

In the '2050 N Addition' treatment, we ramped N inputs up from 0.54 to 1.5 g N m<sup>-2</sup> y<sup>-1</sup> over 50 years. The model suggested future increased N deposition will substantially impact N and C biogeochemistry through greater production and stream N fluxes. Production increased from 29% to 91% and inorganic stream N fluxes increased from 60%

to over 300% (Tables 4.5 and 4.6). Comparing the '2050 N Addition' and '2050 Combined' treatments it was clear that N addition was the dominate factor influencing ecosystem pools and process rates (Tables 4.5 and 4.6).

#### 4.4.7 Climate change scenarios

The difference between the '2050 Combined' and the 'Climate Warming' scenarios was a gradual 2°C increase in temperature over 50 years. Production and live biomass N increased 3%, soil mineralization and respiration rates increased 8-9%, and foliar C and C:N decreased 6%, while other ecosystem parameters remained relatively unchanged following warming (Table 4.8). Increased temperature reduced stream flow through greater evaporation and transpiration. The 18% decline in stream flow decreased stream N fluxes dramatically, by 76% (Table 4.8, Fig. 4.5). The relationship between reduced stream flow and inorganic N fluxes is illustrated in Fig. 4.5.

The Climate Warming, Canadian and Hadley climate change simulations produced similar production rates, biomass and soil C and N pools and soil process rates (Table 4.8). The major differences between the simulations were stream flow, stream C and N fluxes and soil and air temperatures (Table 4.8). Under the Canadian model projections climate gradually dries and warms over 50 years, which resulted in decreased modeled stream flow compared to the 'Climate Warming' simulation. Inorganic stream N fluxes was reduced by 8% (Table 4.8, Fig. 4.5). Hadley model climate projections caused a 8% increase in modeled stream flow compared to the 'Climate Warming' simulation, and increased stream N fluxes.

## 4.5 Discussion

The control simulation was similar enough to reported values that we confidentially compared our modeled responses to variation in climate, soil texture and N inputs with field data. We also compared our results with those of Baron et al. (1994) who conducted a similar study; they used CENTURY to address potential forest responses to increased N deposition to explore whether observed elevated stream N resulted from terrestrial N saturation. For deposition levels ranging from 3-6 kg N ha<sup>-1</sup> y<sup>-1</sup>, Baron et al. (1994) reported forest production of 197 – 282 g C m<sup>-2</sup> y<sup>-1</sup> and total soil C of 7,900 – 10,7000 g C m<sup>-2</sup>. Our 'N Addition' treatment, which has comparable N inputs to the Baron et al. (1994) study, produced values of 208 g C m<sup>-2</sup> y<sup>-1</sup> and 4,338 g C m<sup>-2</sup>, respectively (Table 4.5). The differences can be explained by how ecosystem equilibrium was achieved in each study. For this experiment we ran the model for 4,000 years with a medium intensity canopy fire every 500 years. Baron et al. (1994) ran the model for 1,000 years without fire to establish equilibrium.

The decline in modeled production, ecosystem C and N pools and soil process rates with increased precipitation was unexpected. This decline could have resulted from a reduction in the forest energy balance or elevated N leaching losses. Research has shown that increasing the length of the snow cover period can lower forest stand temperatures, reducing photosynthesis and respiration (Kimball et al. 2000). For instance, a ten-day delay in spring thaw resulted in a 12% decrease in annual NPP for a black spruce forest in Canada (Kimball et al. 2000). An increase in the length of the snow cover period would reduce modeled soil and air temperatures but, because they remained constant following increased

annual precipitation, a decline in the forest energy balance was not responsible for the reduction in ecosystem characteristics.

Ecosystem N leaching losses depend on two processes: 1) the production of a mobile N pool from organic matter decomposition and 2) hydrologic flushing of soils to remove the mobile N pool (Creed et al. 1996). Enhanced hydrologic flushing from greater annual precipitation increases leaching losses (Creed et al. 1996). We observed a strong correlation between modeled stream flow and inorganic stream N fluxes (Fig. 4.3, Table 4.7). Raich et al. (2000) modeled tropical forest responses to changes in nutrient availability and annual precipitation with CENTURY. They, like us, found nutrient availability to be the most important factor influencing production and ecosystem C and N pools and that increasing precipitation elevated stream nutrient fluxes and hence reduced production and C and N pools.

Elevated N losses that accompanied increased precipitation resulted in the decline in production and ecosystem C and N pools. Small losses of N resulted in relatively large declines in ecosystem C, illustrating the role N plays in controlling the amount, distribution and turnover rates of C in terrestrial ecosystems (Ågren et al. 1991, Asner et al. 1997).

Slight changes in modeled soil texture produced a large forest response. CENTURY's algorithms control N loss through soil texture. Inorganic N losses increase linearly with sand content, and organic N losses are inversely proportional to clay content, because of soil hydrologic properties and simulated DOC production. Therefore, decreasing sand and increasing clay content, as we did, had a large impact on N retention.

Comparable biogeochemical responses to increased N inputs have been reported from similar forest ecosystems. McNulty and Aber (1993) observed increased inorganic and organic N leaching, tree growth and net N mineralization rates following three years of

fertilization (15-31 kg N ha<sup>-1</sup> y<sup>-1</sup>) of high elevation red spruce-balsam fir forests in Vermont. Along a N deposition gradient in Europe of 3-60 kg N ha<sup>-1</sup> y<sup>-1</sup> there was a positive relationship between N deposition rate and N leaching losses and N mineralization rates (Tietema and Beier 1995, Gundersen et al. 1998).

Carbon and nutrient allocation patterns shift with changes in nutrient and water availability. Foliar litterfall increased and belowground C allocation decreased following fertilization of red pine (*Pinus resinosa*) plantations (Haynes and Gower 1995). Gundersen et al. (1998) found as N availability increased, root biomass decreased in European coniferous forests. Fertilization of red pine increased new foliar mass and area, twig mass and total leaf area and decreased needle longevity (Gower et al. 1993). Increased new foliage area and decreased needle longevity results in a greater proportion of current year foliage and hence potentially greater photosynthetic rates. Douglas fir (*Pseudotsuga menziesii*) biomass distribution and production patterns were also affected by nutrient and water availability (Gower et al. 1992).

Allocation patterns are fixed within CENTURY; some of our results appear to be an artifact of fixed C allocation. Within CENTURY, leaf longevity decreases with greater nutrient availability but C allocation to foliage remains fixed. The reduction in leaf C following increased N inputs caused a decline in foliar C:N ratios which could have resulted from fixed allocation patterns and/or the modeled relationship between leaf longevity and N availability is misrepresented for this ecosystem. Increased modeled soil C following N addition and hence consistent C:N ratios most likely resulted from a combination of fixed allocation patterns and an underestimation of abiotic N fixation (Parton et al. 1994).

Simulations suggest that future increases in N deposition will fundamentally change ecosystem N dynamics. Relatively small increases in N inputs transformed this ecosystem

from a slow growing forest with high N retention to a faster growing forest with reduced N retention. Comparing the 'Combined' with the '2050 Combined' simulation where N deposition increased to  $1.5 \text{ g N m}^{-2} \text{ y}^{-1}$ , production increased 60% and inorganic N losses increased 258%. McNulty and Aber (1993) also observed increased production and N leaching following fertilization of high-elevation red spruce-balsam fir forests in Vermont. The continuous rise in ecosystem C and N following increased N inputs suggests that modeled maximum growth rate has yet to be achieved (Fig. 4.4).

Climate warming has been postulated to moderate the impacts of elevated N deposition (Baron and Campbell 1997, Fenn et al. 1998). Increased temperature counteracted the impacts of elevated N deposition by reducing stream N fluxes in our simulations. Comparison of the three climate change simulations suggests that ecological parameters, such as production, C and N pools and soil process rates, are relatively insensitive to the slight differences in temperature and precipitation (Table 4.8). Changes in temperature and precipitation strongly influenced stream N fluxes through changes in the water balance. The reduction in annual precipitation and greater air temperatures in the 'Canadian' simulation reduced stream flow and inorganic N loss. Greater precipitation and a slight increase in temperature in the 'Hadley' simulation resulted in elevated stream flow and N fluxes relative to the other climate change simulations (Table 4.8, Fig. 4.5). The results suggest the potential for climate change to counter the impacts of elevated N deposition will depend on the combined impacts of changes in temperature and precipitation on hydrologic processes.

The main motivation behind this work was to explore whether variation in precipitation and soil texture between sites confound our interpretation of a study suggesting current rates of N deposition have altered Englemann spruce forest biogeochemistry in

northern Colorado. The simulations illustrate that the observed variation in precipitation amount and soil texture does influence C and N biogeochemistry. But, the comparison of field data and model results suggests that N inputs were the primary factor causing the observed differences between low and high N deposition sites. If greater precipitation was the cause behind observed differences between high and low N deposition sites model results suggest we should have seen reduced soil C and N and mineralization rates at the high N deposition sites. But, in field samples, this was not so, leading us to conclude that differences in precipitation cannot be the biogeochemical driver producing the observed differences in soil properties (Rueth and Baron, in press). CENTURY results suggest a 5% difference in soil clay content should lead to a 20% increase in soil C (Table 4.5). Based on this result we would expect significant differences in measured organic and mineral horizon soil %C and organic horizon mass. However, we found no significant differences in these soil characteristics when we compared measurements from high and low N deposition sites (Rueth and Baron, in press). This leads us to conclude that precipitation and soil texture differences were not responsible for the observed differences across sites.

Simulated elevated N deposition led to increased soil N and mineralization rates. In field studies, we observed significantly greater organic horizon soil N and mineralization rates and marginally greater mineral soil N at high compared with lower N deposition sites (Rueth and Baron, in press).

The modeled differences in precipitation and soil texture operated on biogeochemical processes for the entire simulation period of 4050 years which allowed a new equilibrium to be attended; increasing N inputs was a transient experimental treatment which did not allow a new equilibrium to be established and occurred only during the last 50 years of simulation. Taking the relative impact of each simulation on ecosystem

characteristics into account, the simulated forest responded rapidly to slight increases in N inputs. The similarities between model results and field data from us and others emphasizes the role of N deposition on ecosystem processes.

#### **4.6 Conclusions**

Our CENTURY model results of Englemann spruce forest biogeochemistry were within the range of other published observations. Slight increases in precipitation enhanced stream N fluxes that caused a subsequent decline in plant production and ecosystem C and N pools. This illustrates two important linkages: 1) The balance between N retention and release depends on both hydrologic and biogeochemical processes (Creed et al. 1996), and 2) the availability of N affects the amount, distribution and turnover rates of C in terrestrial ecosystems (Ågren et al. 1991, Asner et al. 1997). Changing soil texture caused large increases in soil C and N and reduced inorganic N loss. Higher N deposition rates enhanced ecosystem productivity, even at the same time increasing N losses. Increases in temperature counteracted the negative impacts of elevated N deposition by reducing stream N fluxes. CENTURY suggests that the influence of precipitation and temperature combined on hydrologic processes will dictate the ability of climate change to counter the impacts of future elevated N deposition because of the strong correspondence of precipitation and stream N fluxes. Simulations suggest future increases in N deposition will have a substantial impact on high-elevation coniferous forest biogeochemistry and climate change could either exacerbate or alleviate the impacts dependent on changes in hydrologic processes.

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**Table 4.1: Model initialization, parameterization and simulated control values of ecosystem characteristics compared with other observations.**

| <b>Ecosystem Characteristics</b>                              | <b>Initialization Values</b> | <b>Model Parameterization Values*</b> | <b>Control Simulation</b> | <b>Other Observations</b>                        |
|---|------------------------------|---------------------------------------|---------------------------|--|
| Ecosystem C<br>(g C m <sup>-2</sup> )                         | 16,030                       | 21,000                                | 17,360                    | -  |
| Ecosystem N<br>(g N m <sup>-2</sup> )                         | 346                          | 136                                   | 232                       | 324 (1)  |
| Live Biomass C<br>(g C m <sup>-2</sup> )                      | 7,350                        | 7,550                                 | 6,546                     | 7,250 (2)<br>7,600 (3)                           |
| Live Biomass N<br>(g N m <sup>-2</sup> )                      | 51                           | 49                                    | 43                        | 63 (2)<br>54 (4)                                 |
| Production<br>(g C m <sup>-2</sup> y <sup>-1</sup> )          | -                            | 183                                   | 161                       | 219 (3); 125 - 375 (5)<br>219-266 (12); 225 (13) |
| Soil C<br>(g C m <sup>-2</sup> )                              | 4,370                        | 6,300                                 | 4,171                     | 5,700 (3); 7,500 (6)<br>4,500 (7); 3,713 (1)     |
| Soil N<br>(g N m <sup>-2</sup> )                              | 273                          | 76                                    | 161                       | -  |
| Mineralization Rate<br>(g N m <sup>-2</sup> y <sup>-1</sup> ) | -                            | -                                     | 4.3                       | 2-3 (8); 1-2 (9)<br>4 (2); 0.1-1.1 (10)          |
| Inorganic N Loss<br>(g N m <sup>-2</sup> y <sup>-1</sup> )    | -                            | -                                     | 0.048                     | 0.18 (1); 1.3 (2)<br>0.21-0.32 (11)              |

\* Arthur and Fahey 1992 - Ecosystem and soil N pools do not include the mineral soil pool.

- 1) Van Cleve et al. 1983 - White spruce, Alaska
- 2) Friedland et al. 1991 - Red spruce and balsam fir, White Mountains, New Hampshire
- 3) Prescott et al. 1989 - Englemann spruce, Canada
- 4) Gordon 1983 - Spruce, Canada
- 5) Viereck et al. 1983 - Black and white spruce, Alaska
- 6) Cole & Rapp 1981
- 7) Vogt et al. 1986
- 8) Arthur 1990 - Englemann spruce, Rocky Mountains, Colorado
- 9) Flanagan & Van Cleve 1983 - Black and white spruce, Alaska
- 10) Stump and Binkley 1993 - Englemann spruce, Rocky Mountains, Colorado
- 11) Campbell et al. 2000 - Englemann spruce, Rocky Mountains, Colorado
- 12) Gower et al. 1997, Steele et al. 1997 - Black spruce, Canada
- 13) Van Cleve et al. 1983, Oechel and Van Cleve 1986, Ruess et al. 1996 - Black spruce, Alaska

Table 4.2: Decadal modifications to monthly precipitation and minimum and maximum temperatures produced from the Canadian and Hadley GCMs.

| Parameter          | Month          | Baseline | Canadian<br>2011-2020 | Canadian<br>2021-2030 | Canadian<br>2031-2040 | Canadian<br>2041-2050 | Hadley<br>2011-2020 | Hadley<br>2021-2030 | Hadley<br>2031-2040 | Hadley<br>2041-2050 |
|--------------------|----------------|----------|-----------------------|-----------------------|-----------------------|-----------------------|---------------------|---------------------|---------------------|---------------------|
| Precipitation (cm) | Jan            | 10.10    | 9.85                  | 8.86                  | 10.90                 | 10.56                 | 11.81               | 12.43               | 14.54               | 12.62               |
|                    | Feb            | 7.66     | 6.47                  | 6.68                  | 6.89                  | 7.81                  | 8.90                | 8.35                | 9.41                | 9.67                |
|                    | March          | 10.81    | 10.79                 | 9.91                  | 11.78                 | 9.79                  | 12.05               | 12.39               | 11.00               | 11.27               |
|                    | April          | 12.35    | 13.40                 | 14.33                 | 12.71                 | 14.92                 | 13.75               | 13.81               | 13.06               | 14.07               |
|                    | May            | 10.52    | 12.10                 | 11.91                 | 9.87                  | 10.38                 | 10.86               | 11.77               | 11.01               | 10.26               |
|                    | June           | 6.00     | 5.19                  | 5.34                  | 7.93                  | 6.18                  | 6.34                | 6.67                | 6.21                | 5.76                |
|                    | July           | 7.73     | 8.23                  | 5.77                  | 7.48                  | 7.12                  | 7.65                | 6.51                | 7.29                | 7.13                |
|                    | Aug            | 5.69     | 4.51                  | 5.89                  | 7.63                  | 5.28                  | 4.70                | 5.59                | 4.76                | 3.83                |
|                    | Sept           | 6.97     | 7.21                  | 5.96                  | 5.33                  | 5.08                  | 6.74                | 8.80                | 7.98                | 6.54                |
|                    | Oct            | 7.37     | 6.40                  | 6.89                  | 6.54                  | 3.78                  | 8.75                | 7.88                | 8.24                | 4.88                |
|                    | Nov            | 10.02    | 8.89                  | 8.36                  | 8.66                  | 9.56                  | 9.19                | 10.96               | 13.64               | 10.99               |
|                    | Dec            | 8.79     | 9.94                  | 10.56                 | 8.40                  | 8.11                  | 9.80                | 9.52                | 10.09               | 8.52                |
|                    | <b>Total</b>   |          | <b>104.01</b>         | <b>102.97</b>         | <b>100.46</b>         | <b>104.13</b>         | <b>98.56</b>        | <b>110.54</b>       | <b>114.69</b>       | <b>117.23</b>       |
| Min. Temp. (°C)    | Jan            | -10.89   | -8.40                 | -7.78                 | -6.16                 | -4.59                 | -8.59               | -7.02               | -5.53               | -6.45               |
|                    | Feb            | -10.25   | -8.66                 | -8.39                 | -5.74                 | -3.83                 | -7.35               | -7.96               | -6.89               | -6.55               |
|                    | March          | -8.29    | -6.99                 | -5.92                 | -3.89                 | -3.93                 | -4.98               | -4.58               | -4.39               | -4.08               |
|                    | April          | -4.96    | -4.72                 | -3.06                 | -2.69                 | -2.17                 | -3.19               | -2.89               | -3.33               | -2.96               |
|                    | May            | -0.47    | 1.66                  | 1.76                  | 2.24                  | 2.35                  | 0.35                | 0.52                | 0.56                | 0.26                |
|                    | June           | 4.17     | 5.85                  | 5.79                  | 6.86                  | 6.48                  | 5.56                | 5.83                | 6.81                | 5.49                |
|                    | July           | 7.70     | 8.77                  | 8.58                  | 9.49                  | 9.49                  | 8.31                | 8.48                | 9.25                | 9.18                |
|                    | Aug            | 7.61     | 8.32                  | 9.13                  | 9.73                  | 9.30                  | 8.79                | 8.90                | 9.24                | 9.46                |
|                    | Sept           | 3.73     | 4.93                  | 5.05                  | 5.79                  | 5.91                  | 4.89                | 5.47                | 5.81                | 5.28                |
|                    | Oct            | -1.31    | -0.27                 | 0.18                  | -0.06                 | 0.28                  | -0.26               | 0.29                | 1.09                | 0.86                |
|                    | Nov            | -7.43    | -6.04                 | -6.49                 | -5.89                 | -5.99                 | -5.58               | -6.06               | -6.24               | -4.98               |
|                    | Dec            | -10.46   | -7.16                 | -6.62                 | -4.12                 | -3.73                 | -7.83               | -7.65               | -6.03               | -6.95               |
|                    | <b>Average</b> |          | <b>-2.57</b>          | <b>-1.06</b>          | <b>-0.65</b>          | <b>0.46</b>           | <b>0.80</b>         | <b>-0.82</b>        | <b>-0.56</b>        | <b>0.03</b>         |
| Max. Temp. (°C)    | Jan            | -2.86    | -1.83                 | -1.69                 | -1.27                 | -0.63                 | -1.55               | -1.00               | -0.56               | -0.67               |
|                    | Feb            | -1.63    | -1.13                 | -0.73                 | -0.41                 | 1.07                  | -0.18               | -0.54               | 0.15                | 0.55                |
|                    | March          | 1.96     | 2.79                  | 4.22                  | 5.17                  | 6.21                  | 3.74                | 4.50                | 4.87                | 5.03                |
|                    | April          | 6.60     | 6.98                  | 9.91                  | 10.06                 | 11.63                 | 7.60                | 8.37                | 8.18                | 7.63                |
|                    | May            | 11.18    | 13.33                 | 14.01                 | 14.65                 | 15.12                 | 11.39               | 10.93               | 11.13               | 10.96               |
|                    | June           | 16.34    | 17.71                 | 18.82                 | 19.19                 | 19.33                 | 17.44               | 17.59               | 18.59               | 17.59               |
|                    | July           | 19.45    | 19.73                 | 21.82                 | 21.13                 | 21.89                 | 19.98               | 20.91               | 20.62               | 20.72               |
|                    | Aug            | 18.65    | 19.94                 | 20.80                 | 19.80                 | 21.68                 | 20.55               | 20.65               | 21.38               | 22.39               |
|                    | Sept           | 14.11    | 15.12                 | 16.12                 | 15.76                 | 17.53                 | 15.83               | 15.19               | 16.05               | 16.11               |
|                    | Oct            | 7.65     | 9.40                  | 10.06                 | 9.27                  | 12.45                 | 7.33                | 8.13                | 9.06                | 10.90               |
|                    | Nov            | 0.21     | 2.98                  | 3.05                  | 3.71                  | 4.73                  | 1.82                | 0.82                | 0.61                | 2.60                |
|                    | Dec            | -2.01    | -0.42                 | -0.30                 | 0.35                  | 0.93                  | -0.06               | -0.28               | 0.87                | 0.63                |
|                    | <b>Average</b> |          | <b>7.47</b>           | <b>8.72</b>           | <b>9.67</b>           | <b>9.78</b>           | <b>10.99</b>        | <b>8.66</b>         | <b>8.77</b>         | <b>9.25</b>         |

Table 4.3: Model input parameters. The exponential decomposition function is  $a(e^{bt})$ .

| Parameter  | Soil or Forest Component | Value   |
|--|--------------------------|---------|
| Initial SOM C ( $\text{g m}^{-2}$ )                  | Surface                  | 250     |
|  | Active                   | 370     |
|  | Slow                     | 2000    |
|  | Passive                  | 2000    |
| Initial SOM C:N                                      | Surface                  | 15      |
|  | Active                   | 14      |
|  | Slow                     | 25      |
|  | Passive                  | 12      |
| Initial Forest Component C:N                         | Leaf                     | 45      |
|  | Fine root                | 50      |
|  | Fine branch              | 200     |
|  | Large wood               | 380     |
|  | Coarse root              | 170     |
| Forest Component Lignin Fraction                     | Leaf                     | 0.16    |
|  | Fine root                | 0.20    |
|  | Fine branch              | 0.25    |
|  | Large wood               | 0.35    |
|  | Coarse root              | 0.35    |
| Forest Component Minimum C:N                         | Leaf                     | 30      |
|  | Fine root                | 40      |
|  | Fine branch              | 100     |
|  | Large wood               | 300     |
|  | Coarse root              | 140     |
| Forest Component Maximum C:N                         | Leaf                     | 60      |
|  | Fine root                | 60      |
|  | Fine branch              | 300     |
|  | Large wood               | 450     |
|  | Coarse root              | 200     |
| Forest Component Maximum Decomposition Rate Constant | Dead fine branch         | 0.2     |
|  | Dead large wood          | 0.09    |
|  | Dead coarse root         | 0.1     |
| Forest Component C Allocation Fraction               | Leaf                     | 0.33    |
|  | Fine root                | 0.4     |
|  | Fine branch              | 0.13    |
|  | Large wood               | 0.115   |
|  | Coarse root              | 0.025   |
| Forest Component Monthly Death Rate Fraction         | Leaf                     | 0.95    |
|  | Fine root                | 0.012   |
|  | Fine branch              | 0.007   |
|  | Large wood               | 0.00035 |
|  | Coarse root              | 0.00035 |
| Exponential decomposition function                   | a                        | 0.08    |
|  | b                        | 0.085   |

Table 4.4: Simulation treatments. Bold numbers are changes compared with the control.

| Parameters Altered                                | Simulation |               |                          |             |             | Simulated Year 2050 |               |                 |                       |                     |
|---|------------|---------------|--------------------------|-------------|-------------|---------------------|---------------|-----------------|-----------------------|---------------------|
|   | Control    | Precipitation | Soil Textur <sup>e</sup> | N Addition  | Combined    | 2050 N Addition     | 2050 Combined | Climate Warming | Canadian <sup>†</sup> | Hadley <sup>‡</sup> |
| Annual Precipitation (cm)                         | 89         | <b>104</b>    | 89                       | 89          | <b>104</b>  | 89                  | <b>104</b>    | <b>104</b>      | <b>99</b>             | <b>106</b>          |
| Soil Percent Sand                                 | 48         | 48            | <b>40</b>                | 48          | <b>40</b>   | 48                  | <b>40</b>     | <b>40</b>       | <b>40</b>             | <b>40</b>           |
| Soil Percent Silt                                 | 30         | 30            | <b>33</b>                | 30          | <b>33</b>   | 30                  | <b>33</b>     | <b>33</b>       | <b>33</b>             | <b>33</b>           |
| Soil Percent Clay                                 | 22         | 22            | <b>27</b>                | 22          | <b>27</b>   | 22                  | <b>27</b>     | <b>27</b>       | <b>27</b>             | <b>27</b>           |
| * N Inputs (g N m <sup>-2</sup> y <sup>-1</sup> ) | 0.15       | 0.15          | 0.15                     | <b>0.54</b> | <b>0.54</b> | <b>1.5</b>          | <b>1.5</b>    | <b>1.5</b>      | <b>1.5</b>            | <b>1.5</b>          |
| † Temperature Increase (°C)                       | 0          | 0             | 0                        | 0           | 0           | 0                   | 0             | <b>2</b>        | <b>3.4</b>            | <b>2.2</b>          |
| ‡ Type of Experiment                              | EQ         | EQ            | EQ                       | TRAN        | EQ & TRAN   | TRAN                | EQ & TRAN     | EQ & TRAN       | EQ & TRAN             | EQ & TRAN           |

\* N inputs were gradually increased in the: 1) N addition and combined simulations from 0.15 to 0.54 g N m<sup>-2</sup> y<sup>-1</sup> over 50 years from 1950 to 2000, and 2) 2050 N addition and 2050 combined simulations from 0.54 to 1.5 g N m<sup>-2</sup> y<sup>-1</sup> over 50 years from 2000 to 2050.

† Temperature was gradually increased in the climate warming simulation 2°C over 50 years from 2000 to 2050.

‡ See Table 2 for detailed information on alterations to precipitation and temperature.

‡ Equilibrium experiments (EQ) altered initial input variables remained constant throughout the simulation and a new equilibrium was established. In transient experiments (TRAN) input variables were changing continuously therefore a new equilibrium was unlikely to be established. Some experiments were a combination of both equilibrium and transient responses. Transient responses to N inputs and climate change began in 1950 and 2000, respectively.

Table 4.5: Simulation results. Percent differences compared to the control are presented. Refer to Table 3.4 for specifics on each simulation.

|   | Simulated Present Day |               |              |            |          | Simulated Year 2050 |               |
|---|-----------------------|---------------|--------------|------------|----------|---------------------|---------------|
|   | Control               | Precipitation | Soil Texture | N Addition | Combined | 2050 N Addition     | 2050 Combined |
| <b>Production (g C m<sup>-2</sup> y<sup>-1</sup>)</b>   |                       |               |              |            |          |                     |               |
| Total   | 161                   | -7%           | 11%          | 29%        | 32%      | 91%                 | 92%           |
| <b>Biomass C &amp; N Pools</b>                          |                       |               |              |            |          |                     |               |
| Ecosystem C (g C m <sup>-2</sup> )                      | 17360                 | -8%           | 12%          | 4%         | 7%       | 17%                 | 20%           |
| Ecosystem N (g N m <sup>-2</sup> )                      | 232                   | -9%           | 18%          | 5%         | 14%      | 23%                 | 32%           |
| Live Biomass C (g C m <sup>-2</sup> )                   | 6546                  | -6%           | 8%           | 4%         | 7%       | 18%                 | 20%           |
| Live Biomass N (g N m <sup>-2</sup> )                   | 43                    | -5%           | 7%           | 12%        | 14%      | 40%                 | 42%           |
| Foliar C (g C m <sup>-2</sup> )                         | 898                   | 2%            | -2%          | -4%        | -5%      | -26%                | -26%          |
| Foliar N (g N m <sup>-2</sup> )                         | 19                    | 0%            | 0%           | 0%         | 0%       | 0%                  | 0%            |
| Foliar C:N  | 47                    | 2%            | -2%          | -4%        | -4%      | -25%                | -26%          |
| <b>Soil C &amp; N</b>                                   |                       |               |              |            |          |                     |               |
| C (g C m <sup>-2</sup> )                                | 4171                  | -9%           | 20%          | 4%         | 14%      | 19%                 | 29%           |
| N (g N m <sup>-2</sup> )                                | 161                   | -9%           | 21%          | 3%         | 14%      | 16%                 | 28%           |
| C:N   | 26                    | 0%            | 0%           | 0%         | 0%       | 2%                  | 1%            |
| <b>Soil Process Rates</b>                               |                       |               |              |            |          |                     |               |
| Mineralization (g N m <sup>-2</sup> y <sup>-1</sup> )   | 4.3                   | -7%           | 12%          | 19%        | 21%      | 70%                 | 72%           |
| Soil Respiration (g C m <sup>-2</sup> y <sup>-1</sup> ) | 148                   | -7%           | 10%          | 17%        | 20%      | 59%                 | 61%           |

Table 4.6: Simulation results. Percent differences compared to the control are presented for all data except soil and air temperatures where °C are given. Refer to Table 3.4 for specifics on each simulation.

|  | Simulated Present Day |               |              |            |          | Simulated Year 2050 |               |
|--|-----------------------|---------------|--------------|------------|----------|---------------------|---------------|
|  | Control               | Precipitation | Soil Texture | N Addition | Combined | 2050 N Addition     | 2050 Combined |
| <b>Water Balance</b>                               |                       |               |              |            |          |                     |               |
| Stream Flow (cm y <sup>-1</sup> )                  | 44                    | 30%           | 0%           | 0%         | 30%      | 0%                  | 30%           |
| Evaporation (cm y <sup>-1</sup> )                  | 14                    | 17%           | 1%           | 2%         | 19%      | 2%                  | 19%           |
| Transpiration (cm y <sup>-1</sup> )                | 31                    | -1%           | 0%           | 0%         | -1%      | 0%                  | -1%           |
| <b>Stream N &amp; C Fluxes</b>                     |                       |               |              |            |          |                     |               |
| Inorganic N (g N m <sup>-2</sup> y <sup>-1</sup> ) | 0.048                 | 13%           | -27%         | 60%        | 38%      | 338%                | 296%          |
| Organic N (g N m <sup>-2</sup> y <sup>-1</sup> )   | 0.013                 | 15%           | 8%           | 15%        | 31%      | 69%                 | 85%           |
| Organic C (g C m <sup>-2</sup> y <sup>-1</sup> )   | 0.21                  | 10%           | 0%           | 10%        | 24%      | 48%                 | 62%           |
| <b>Soil Temperature</b>                            |                       |               |              |            |          |                     |               |
| January (°C)                                       | 0                     | 0             | 0            | 0          | 0        | 0                   | 0             |
| July (°C)  | 10.5                  | 10.5          | 10.5         | 10.5       | 10.5     | 10.5                | 10.5          |
| Annual (°C)  | 4.2                   | 4.2           | 4.2          | 4.2        | 4.2      | 4.2                 | 4.2           |
| <b>Air Temperature</b>                             |                       |               |              |            |          |                     |               |
| January (°C)                                       | -6.2                  | -6.2          | -6.2         | -6.2       | -6.2     | -6.2                | -6.2          |
| July (°C)  | 10.3                  | 10.3          | 10.3         | 10.3       | 10.3     | 10.3                | 10.3          |
| Annual (°C)  | 2.5                   | 2.5           | 2.5          | 2.5        | 2.5      | 2.5                 | 2.5           |

Table 4.7: Simulation results comparing three precipitation levels and soil textures, only precipitation and soil texture were changed compared to the control. Percent differences compared to the control are presented. Control, low, moderate and high precipitation levels are 89, 81, 104 and 117 cm y<sup>-1</sup>, respectively. Soil texture (percent sand, silt and clay) are for the control (48, 30 and 22), low sand (32, 37 and 31), moderate sand (40, 33 and 27) and high sand (60, 22 and 18) simulations. Moderate precipitation and sand correspond to the precipitation and soil texture simulations in Tables 4.4, 4.5, and 4.6.

|   | Control | Low<br>Precip. | Moderate<br>Precip. | High<br>Precip. | Low<br>Sand | Moderate<br>Sand | High<br>Sand |
|---|---------|----------------|---------------------|-----------------|-------------|------------------|--------------|
| <b>Production (g C m<sup>-2</sup> y<sup>-1</sup>)</b>   |         |                |                     |                 |             |                  |              |
| Total   | 161     | 11%            | -7%                 | -19%            | 19%         | 11%              | -16%         |
| <b>Biomass C &amp; N Pools</b>                          |         |                |                     |                 |             |                  |              |
| Ecosystem C (g C m <sup>-2</sup> )                      | 17360   | 10%            | -8%                 | -20%            | 22%         | 12%              | -17%         |
| Ecosystem N (g N m <sup>-2</sup> )                      | 232     | 10%            | -9%                 | -21%            | 34%         | 18%              | -21%         |
| Live Biomass C (g C m <sup>-2</sup> )                   | 6546    | 9%             | -6%                 | -18%            | 15%         | 8%               | -15%         |
| Live Biomass N (g N m <sup>-2</sup> )                   | 43      | 7%             | -5%                 | -16%            | 14%         | 7%               | -12%         |
| Foliar C (g C m <sup>-2</sup> )                         | 898     | -3%            | 2%                  | -8%             | -6%         | -2%              | -5%          |
| Foliar N (g N m <sup>-2</sup> )                         | 19      | -2%            | 0%                  | -12%            | -3%         | 0%               | -8%          |
| Foliar C:N  | 47      | -1%            | 2%                  | 5%              | -3%         | -2%              | 5%           |
| <b>Soil C &amp; N</b>                                   |         |                |                     |                 |             |                  |              |
| C (g C m <sup>-2</sup> )                                | 4171    | 10%            | -9%                 | -22%            | 39%         | 20%              | -24%         |
| N (g N m <sup>-2</sup> )                                | 161     | 10%            | -9%                 | -22%            | 42%         | 21%              | -24%         |
| C:N   | 26      | 0%             | 0%                  | 0%              | -2%         | 0%               | 0%           |
| <b>Soil Process Rates</b>                               |         |                |                     |                 |             |                  |              |
| Mineralization (g N m <sup>-2</sup> y <sup>-1</sup> )   | 4.3     | 19%            | -7%                 | -16%            | 26%         | 12%              | -12%         |
| Soil Respiration (g C m <sup>-2</sup> y <sup>-1</sup> ) | 148     | 17%            | -7%                 | -15%            | 25%         | 10%              | -11%         |
| <b>Water Balance</b>                                    |         |                |                     |                 |             |                  |              |
| Stream Flow (cm y <sup>-1</sup> )                       | 44      | -18%           | 30%                 | 57%             | 0%          | 0%               | 0%           |
| Evaporation (cm y <sup>-1</sup> )                       | 14      | -2%            | 17%                 | 19%             | 1%          | 1%               | -2%          |
| Transpiration (cm y <sup>-1</sup> )                     | 31      | 0%             | -1%                 | -1%             | 0%          | 0%               | 0%           |
| <b>Steam N &amp; C Fluxes</b>                           |         |                |                     |                 |             |                  |              |
| Inorganic N (g N m <sup>-2</sup> y <sup>-1</sup> )      | 0.048   | -22%           | 13%                 | 36%             | -53%        | -27%             | 39%          |
| Organic N (g N m <sup>-2</sup> y <sup>-1</sup> )        | 0.013   | -2%            | 15%                 | 20%             | 2%          | 8%               | -4%          |
| Organic C (g C m <sup>-2</sup> y <sup>-1</sup> )        | 0.21    | -7%            | 10%                 | 17%             | -4%         | 0%               | -8%          |

Table 4.8: Results comparing the three climate change simulations with the 2050 Combined simulation. Percent differences compared to 2050 Combined are presented for all data except soil and air temperatures where °C are given. Temperature and precipitation were the only parameters changed compared to the 2050 Combined simulation (see Table 4.4 for details).

|   | 2050<br>Combined | Climate<br>Warming | Canadian | Hadley |
|---|------------------|--------------------|----------|--------|
| <b>Production (g C m<sup>-2</sup> y<sup>-1</sup>)</b>   |                  |                    |          |        |
| Total   | 309              | 3%                 | 6%       | 2%     |
| <b>Biomass C &amp; N Pools</b>                          |                  |                    |          |        |
| Ecosystem C (g C m <sup>-2</sup> )                      | 20904            | 0%                 | 0%       | 0%     |
| Ecosystem N (g N m <sup>-2</sup> )                      | 306              | 1%                 | 1%       | 0%     |
| Live Biomass C (g C m <sup>-2</sup> )                   | 7867             | 1%                 | 1%       | 0%     |
| Live Biomass N (g N m <sup>-2</sup> )                   | 61               | 3%                 | 5%       | 2%     |
| Foliar C (g C m <sup>-2</sup> )                         | 665              | -6%                | -5%      | -6%    |
| Foliar N (g N m <sup>-2</sup> )                         | 19               | 0%                 | 0%       | 0%     |
| Foliar C:N  | 35               | -6%                | -5%      | -6%    |
| <b>Soil C &amp; N</b>                                   |                  |                    |          |        |
| C (g C m <sup>-2</sup> )                                | 5385             | 0%                 | 0%       | 0%     |
| N (g N m <sup>-2</sup> )                                | 206              | 0%                 | 0%       | 0%     |
| C:N   | 26               | 0%                 | 0%       | 0%     |
| <b>Soil Process Rates</b>                               |                  |                    |          |        |
| Mineralization (g N m <sup>-2</sup> y <sup>-1</sup> )   | 7.4              | 8%                 | 11%      | 4%     |
| Soil Respiration (g C m <sup>-2</sup> y <sup>-1</sup> ) | 239              | 9%                 | 10%      | 3%     |
| <b>Water Balance</b>                                    |                  |                    |          |        |
| Stream Flow (cm y <sup>-1</sup> )                       | 57               | -18%               | -32%     | -9%    |
| Evaporation (cm y <sup>-1</sup> )                       | 17.2             | 10%                | 10%      | -1%    |
| Transpiration (cm y <sup>-1</sup> )                     | 30.2             | 28%                | 36%      | 23%    |
| <b>Leaching Losses</b>                                  |                  |                    |          |        |
| Inorganic N (g N m <sup>-2</sup> y <sup>-1</sup> )      | 0.2              | -63%               | -71%     | -35%   |
| Organic N (g N m <sup>-2</sup> y <sup>-1</sup> )        | 0.024            | -13%               | -4%      | 4%     |
| Organic C (g C m <sup>-2</sup> y <sup>-1</sup> )        | 0.34             | -15%               | -9%      | 3%     |
| <b>Soil Temperature</b>                                 |                  |                    |          |        |
| January (°C)  | 0                | -4.01              | -1.1     | -2.9   |
| July (°C)   | 10.5             | 12.5               | 13.1     | 11.8   |
| Annual (°C)   | 4.2              | 4.7                | 6.2      | 5      |
| <b>Air Temperature</b>                                  |                  |                    |          |        |
| January (°C)  | -6.2             | -4.3               | -1.4     | -3.2   |
| July (°C)   | 10.3             | 12.2               | 12.9     | 11.5   |
| Annual (°C)   | 2.5              | 4.4                | 5.9      | 4.7    |

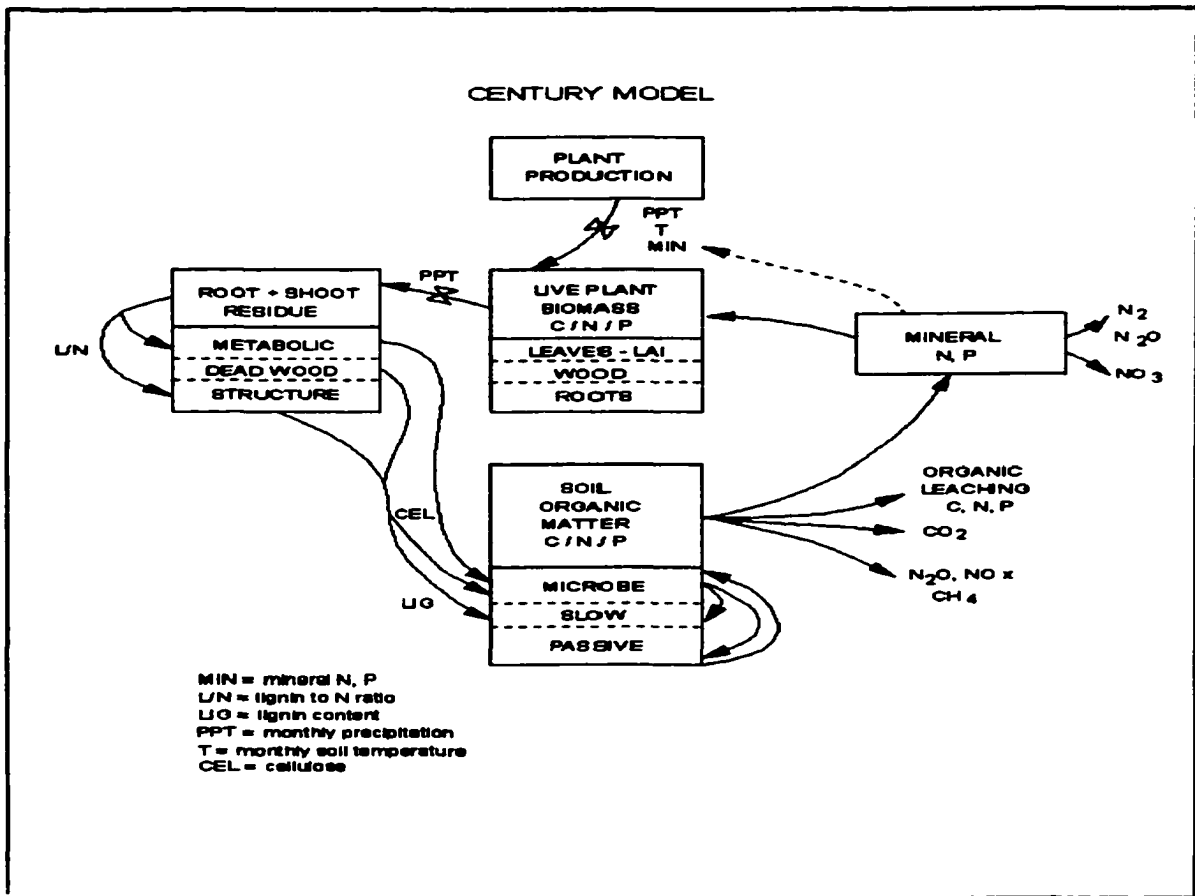


Fig 4.1: CENTURY conceptual model.

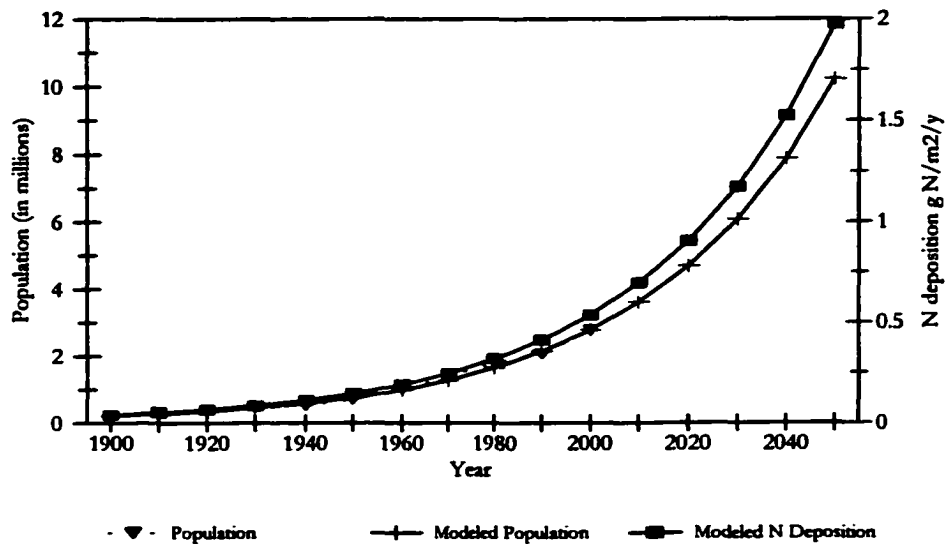


Fig. 4.2: Colorado Front Range population growth from census values from 1900 to the present. An exponential curve was fit to the population growth curve to project future increases in population. The same relationship was used to estimate past and future N deposition rates.

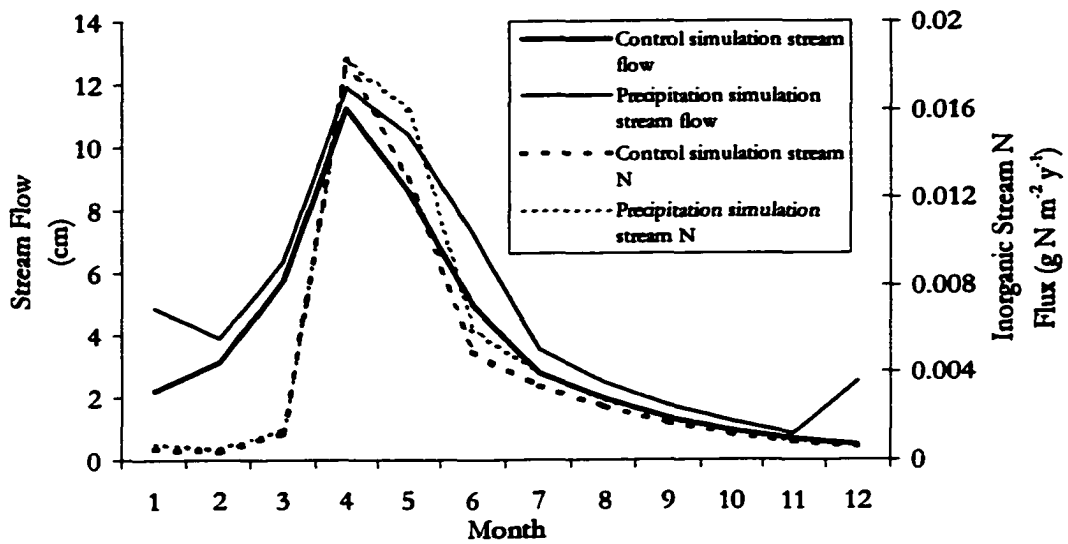


Fig. 4.3: Modeled stream flow and inorganic N leaching from the control and precipitation simulations.

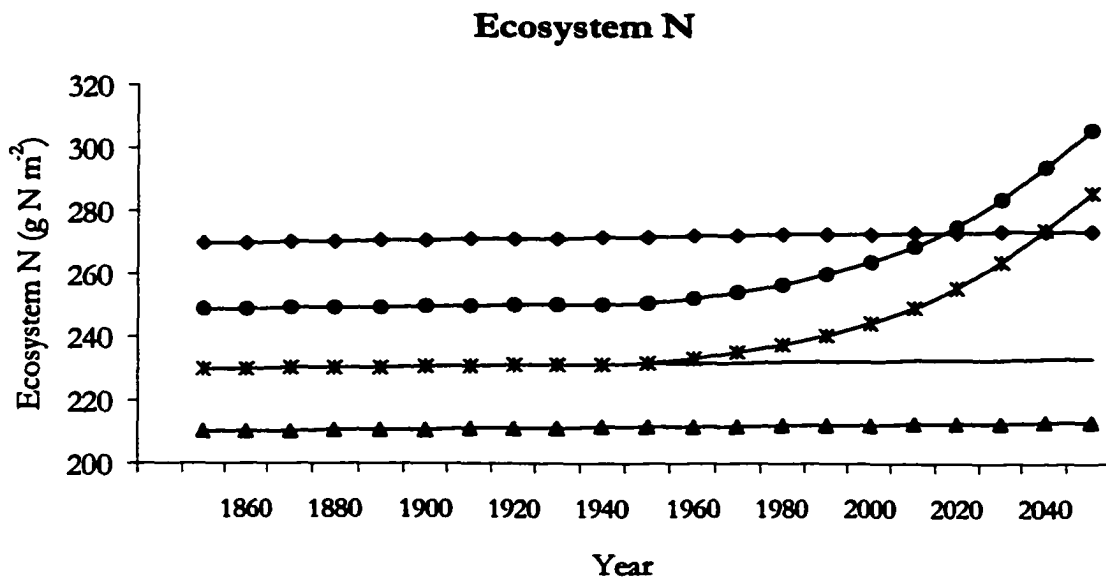
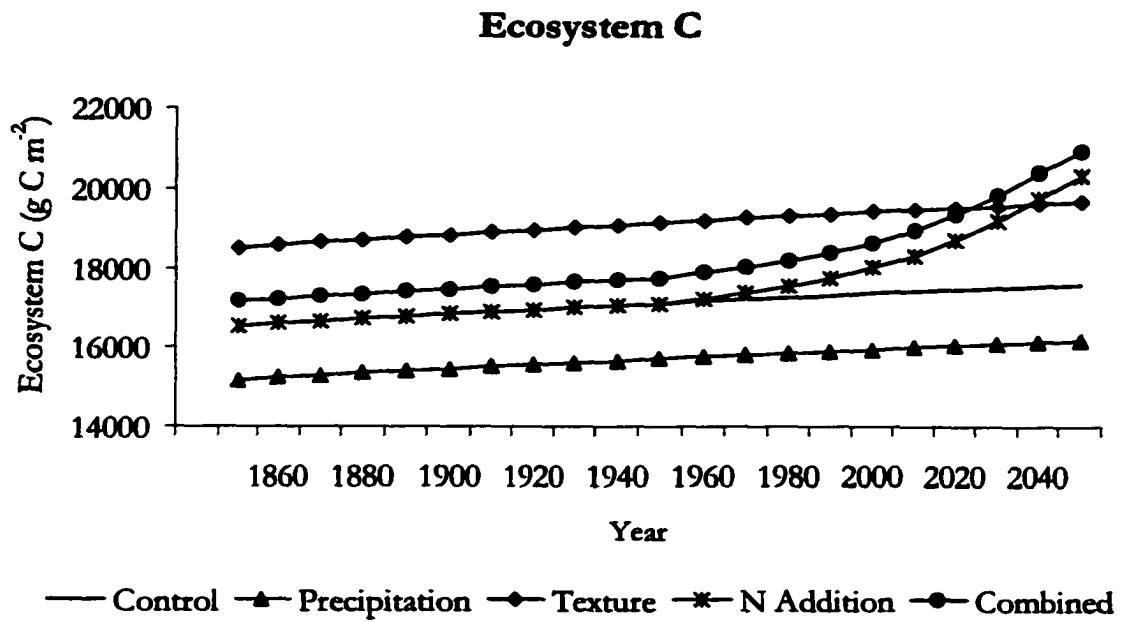


Fig. 4.4: Simulated ecosystem C and N.

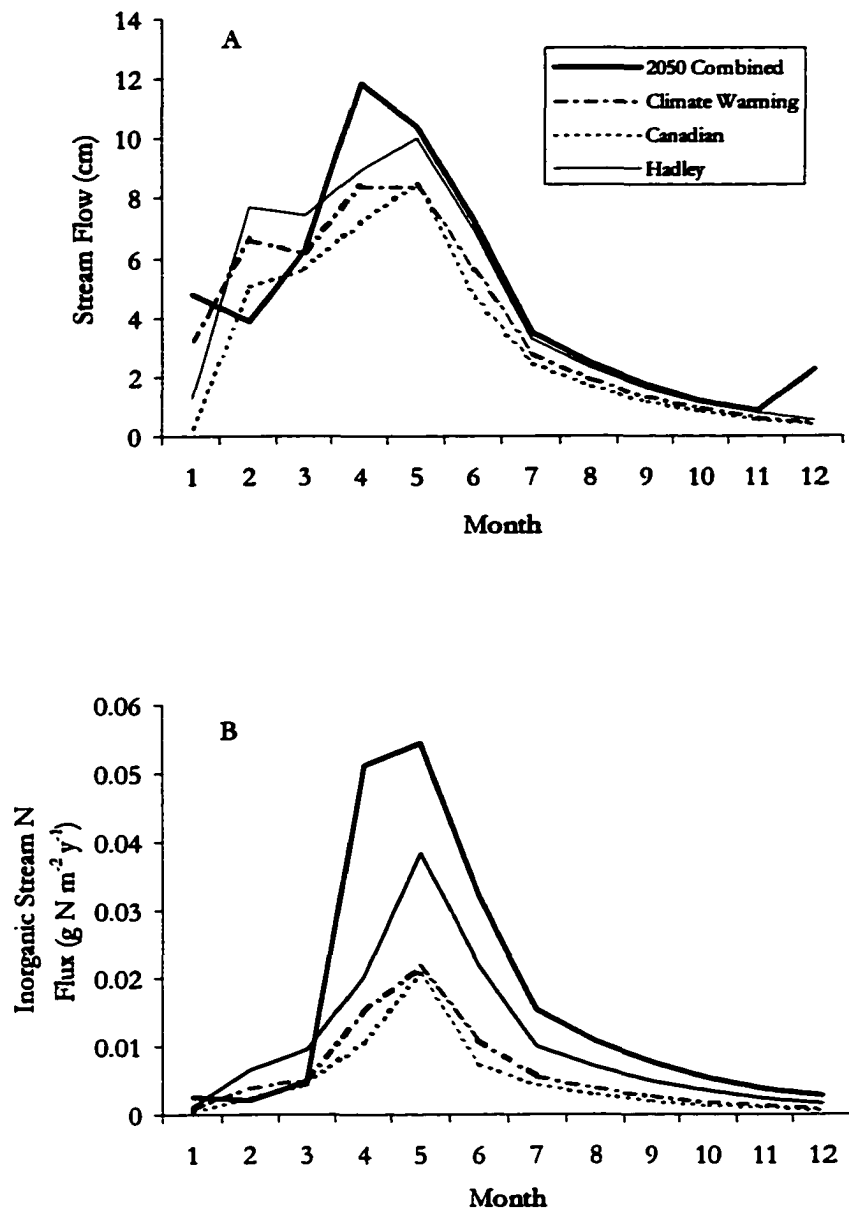


Fig. 4.5: Modeled stream flow (A) and inorganic N leaching (B) from the climate change simulations.