AN ABSTRACT OF THE DISSERTATION OF

Kristin L. Vanderbilt for the degree of Doctor of Philosophy in Forest Science presented on August 31, 2000. Title: Patterns of Nitrogen Fluxes in Watersheds of the H.J. Andrews Experimental Forest, OR.

Abstract approved: Signature redacted for privacy.

Frederick J. Swanson

Seasonal and annual patterns of N fluxes and concentrations in streamwater in six conifer-dominated watersheds at the H.J. Andrews Experimental Forest, OR, were studied to gain insight into the factors that influence N retention in this ecosystem. Processes affecting N flux in streamwater differed between organic (DON) and inorganic (DIN; NO_3-N and NH_4-N) forms of N. Annual DON flux increased with increasing annual discharge in all watersheds, implying that regional-level climatic fluctuations may influence DON retention. Annual DIN flux, in contrast, was not consistently related to annual stream discharge. DON concentrations in stream water peaked in winter before the peak in the hydrograph, suggesting that DON may be flushed from the soil into the stream. Concentrations of DIN were relatively constant throughout the year.

Annual and seasonal patterns of N retention were calculated using three separate estimates of N inputs to this ecosystem: (1) atmospheric DIN alone, (2) atmospheric DIN + DON, and (3) atmospheric DIN + DON + inputs from biological fixation. Vegetation demand for N had little effect on annual DIN retention, perhaps because inputs of DIN to the Andrews Forest and periods of forest growth are asynchronous. High inputs of biologically-fixed N did not result in increased nitrate leaching, suggesting that biologically-fixed N is efficiently retained in this ecosystem.

Forest harvest at the Andrews resulted in very small losses of N from the soil relative to other sites. The high C:N ratio of soil at the Andrews Forest probably

promotes immobilization of N after harvest, and little of the N released by decomposing roots or made available via reduced vegetation demand escapes the soil microbial community.

Patterns of Nitrogen Fluxes in Watersheds of the H.J. Andrews Experimental Forest, OR

by

Kristin L. Vanderbilt

A DISSERTATION

submitted to

Oregon State University

Corvallis, Oregon

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented August 31, 2000
Commencement June 2001

Doctor of Philosophy dissertation of Kristin L.Vanderbilt presented on August 31, 2000

APPROVED:

Signature redacted for privacy.

Major Professor, representing Forest Science

Signature redacted for privacy.

Chair of Department of Forest Science

Signature redacted for privacy.

Dean of Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Signature redacted for privacy.

Kristin L. Vanderbilt, Author

ACKNOWLEDGEMENTS

I gratefully acknowledge the support and guidance of my graduate committee throughout this research project. Fred Swanson, Kate Lajtha, Kermit Cromack, and Lisa Ganio all provided valuable perspectives to this study. I thank my graduate representative Steve Sharrow for review of this dissertation.

I also offer thanks to many others who assisted in various ways. Susan Stafford encouraged me to pursue my interest in information management. Manuela Huso provided invaluable statistical advice. Barbara Marks helped me write a data-processing program, and Dick Waring taught me to use the 3-PG model. Gay Bradshaw provided innovative ideas and inspiration. Cam Jones provided insights into the chemical analyses done on Andrews Forest stream samples. Gody Spycher and Don Henshaw assisted me with data management issues. Charlie Halpern generously permitted me to use his biomass data from WS10.

I offer a huge thank you to the friends and fellow grad students who supported me during the ups and downs of this journey.

Funding was provided by the USDA Forest Service, Pacific Northwest Research Station and National Science Foundation-sponsored H.J. Andrews Experimental Forest Long-Term Ecological Research Program (DEB 96-32921).

CONTRIBUTION OF AUTHORS

Dr. Kate Lajtha was involved in the interpretation of data for both manuscripts. She also edited both manuscripts.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

PATTERNS OF NITROGEN FLUXES IN WATERSHEDS OF THE H.J. ANDREWS EXPERIMENTAL FOREST, OR

1 Introduction

Human activity has altered the global N cycle by approximately doubling the rate of N inputs to the terrestrial environment via fossil fuel combustion, fertilizer application to agricultural crops, and release of nitrogen from biomass during land conversion from one use to another (Vitousek et al. 1997). Increased N availability has resulted in acidification of lakes, soils, and streams (Howarth et al. 1996), changes in biodiversity in some ecosystems (Tilman 1987), depletion of soil nutrients such as calcium (Likens et al. 1996), and increased N_20 fluxes, a greenhouse gas, from soils (Fenn et al. 1998). Although N is the key element limiting productivity of many forested ecosystems, increased N deposition has led to some forests showing signs of N excess (Dise and Wright 1995; Fenn et al. 1996).

Forests receiving N inputs exceeding biotic and abiotic retention capacity have been termed nitrogen saturated (Agren and Bosatta 1988), a condition that progresses through four stages if elevated N inputs to a forest persist (Aber et al. 1989; Stoddard 1994). Stage 0 refers to the N-limited condition. Stage 1 occurs when typical seasonal pulses of nitrate are amplified, and chronically elevated nitrate export characterizes level 2. In stage 3, forest decline occurs. Early stages of N saturation have been reported for a mixed deciduous forest in the eastern United States (Peterjohn et al. 1996), high elevation sites along the Colorado Front Range (Baron et al. 1994), chaparral near Los Angeles (Fenn et al. 1996), and at many forested sites in Europe (Dise and Wright 1995; Dise et al. 1998; Gundersen et al. 1998).

Because N saturation is a well recognized problem, a major challenge facing researchers is to determine how to predict the amount of N a forest can retain before becoming N saturated (Fenn et al. 1998). The degree of N saturation

is a function of the total N inputs to a system from the atmosphere, N-fixing organisms, and mineralization relative to the capacity of vegetation, soils, and microbes to sequester N. Although factors including successional status of forests (Pardo 1995), forest floor C:N ratio (Gundersen et al. 1998), soil texture (Lajtha et al. 1995) and climate fluctuations (Mitchell 1996) have been shown to influence N retention, prediction of N retention capacity of a forest is elusive because forests vary so widely in their ability to retain N (Johnson 1992).

The use of small watersheds to study the balance between inputs and outputs of N to forested ecosystems was popularized in the 1970's to explore how vegetation disturbance affected forest N capital (Likens et al. 1970; Feller and Kimmins 1984; Swank and Waide 1987). Presently, the long-term records from these watershed studies are being revisited with new objectives. Stream chemistry data demonstrate the range of natural variability of N export from watersheds, from which inferences are being made about the effects of ecosystem processes on N retention. Long-term records are rare, however, for areas that are free of elevated atmospheric N inputs that can be used to study the function of systems unperturbed by chronically elevated N inputs.

For this study, I examined factors controlling N retention in watersheds at the H.J. Andrews Experimental Forest, Oregon, a Long-Term Ecological Research (LTER) site little affected by anthropogenically-derived N deposition. Long-term stream and precipitation chemistry data exist for six watersheds at this site, with records spanning as much as 30 years. Stream chemistry data at the Andrews Forest are unusual because they include dissolved organic N (DON) and particulate organic N (PON), while most other stream chemistry data sets described in the literature include only dissolved inorganic nitrogen (DIN).

In Chapter 2 I report the results of an analysis of the relationships between DON and DIN fluxes from watersheds and hydrologic variables and variables representing biotic demand for N. This analysis was done to determine how strongly biotic demand and hydrologic flushing affect DON and DIN retention. In Chapter 3, DIN retention, DON + DIN retention, and retention of all N inputs,

including those from biological fixation, were calculated and related to vegetation disturbance, forest age, and estimates of forest N demand. I interpreted the results of this analysis with respect to biogeochemical theory regarding nutrient retention and vegetation succession.

2 Annual and Seasonal Patterns of Nitrogen Dynamics in Precipitation and Streams at the H.J. Andrews Experimental Forest, OR

2.1 Introduction

Although nitrogen (N) is the most commonly limiting nutrient in temperate forest ecosystems, atmospheric deposition of N has been increasing in parts of Europe, Asia, and North America to levels that may exceed forest biological demand (Vitousek et al. 1997; Fenn et al. 1998). Excess N may result in forests becoming N saturated (Agren and Bosatta 1988; Aber et al. 1989), a condition which may adversely affect forest health (Nihlgard 1985). Understanding what controls the amount of N a forest can retain before being adversely affected by N deposition is essential for appropriate forest and watershed management. Several scientists have used streamwater N records from a range of forested watersheds with different size, N deposition, vegetation, and soil characteristics to infer factors that affect N fluxes (Dise and Wright 1995; Lepisto et al. 1995). Others have examined long-term records from a few watersheds to learn how changes in N deposition or climate have affected N export (Murdoch and Stoddard 1992; Mitchell et al. 1996; Swank and Vose 1997). Few long-term records exist, however, for areas without elevated N inputs with which to assess the causes and range of natural variability of N fluxes from forested watersheds.

Unlike many areas in the United States, the H.J. Andrews Experimental Forest, OR, is almost completely unaffected by deposition of N from anthropogenic sources. The Andrews Forest has six watersheds where N fluxes and hydrology have been monitored for as much as thirty years. This is one of the longest records of N fluxes in forested watersheds from an area with little pollution in the United States. In addition, while most stream chemistry records only include dissolved inorganic N (DIN), the Andrews record also includes DON (dissolved organic N) and PON (particular organic N). These data are a rich record offering valuable insights into the natural variability of N fluxes and the processes affecting N fluxes within this N-limited ecosystem.

Each watershed's stream chemistry records represent the integrated response of many processes operating at different temporal and spatial scales throughout the watershed. Watershed geomorphology (Creed and Band 1998), hydrology (Schnabel et al. 1993; Lewis 1999), soil characteristics (Gundersen 1998; Seely et al. 1998), land-use or fire history (Pardo et al. 1995; Johnson et al. 1997), vegetation type or successional stage (Vitousek and Reiners 1975; Wigington et al. 1998), and atmospheric loading (Stoddard 1994) may all affect the quantity of N that enters a stream from the terrestrial ecosystem. Instream processes, such as cycling of N through biota, organic matter storage and the potential for particulate matter transport, also modify the concentration of N that is detected at the outlet of a watershed (Meyer et al. 1988; Burns 1998). Long-term records may provide clues about which processes most strongly control N fluxes from the watershed.

The objectives of this paper are to synthesize long-term patterns of N dynamics in precipitation and streamwater at the Andrews Forest, and to look for biotic and/or hydrologic influences on seasonal and annual patterns of N export. Many studies have reported that stream discharge influences N export, especially NO_3-N, at seasonal and annual scales (Bond 1979; Lewis and Grant 1979; Hill 1986; McDowell and Asbury 1994; Lewis et al. 1999). Hydrology can influence stream chemistry either by flushing stored nutrients (Lajtha et al. 1995; Creed and Band 1996; Andersson and Lepisto 1998) or by dilution of constantly released ions (Lewis and Grant 1979; Stottlemyer and Troendle 1987; Elwood and Turner 1989; Stohlgren et al. 1991). Extreme storm events may also have strong effects on stream chemistry (Correll et al. 1999). Other researchers have concluded that N uptake by vegetation or soil microfauna control seasonal patterns of stream N export (Likens and Bormann 1977; Vitousek 1977; Foster et al. 1989). I developed two hypotheses relating variability in N concentration to biotic and hydrologic variables:

1) Concentrations of DON in stream water are positively related to measures of the amount of water flushing through the catchment (such as stream discharge and precipitation) throughout the year because DON in stream water is thought to be recalcitrant (Hedin et al. 1995) and DON movement through soils and streams would be little affected by changes in biological activity during the year; and

2) Concentrations of inorganic N in stream water are related to factors influencing or representing soil and stream biological demand, such as air temperature, soil temperature, and forest transpiration, because of the low N availability in forests and streams at the Andrews Forest relative to N demand.

2.2 Methods

2.2.1 General Site Description

The six watersheds under study are located in the H.J. Andrews Experimental Forest in the west-central Cascade Mountains of Oregon (Table 1). This rugged, 6400-ha area is characterized by dense coniferous forests and steep slopes. Elevation ranges from 412 m to 1630 m. The Pacific Ocean lies 160 km to the west and strongly influences the climate of the Andrews Forest. Mean January and July temperatures are 2 and 18 degrees C, respectively. Annual precipitation averages 230 cm. About 80% of annual precipitation falls in the October-March period during storms of relatively long duration (12-72 hours) and low intensity. Precipitation is typically dominated by rain below 350 m, and snow above 1100 m. At elevations above 750 m, snowpack may persist for several months. Rain and snow events both occur between 400 and 1200 m elevation (Harr 1981).

2.2.2 Watershed Characteristics

Watersheds fall into two elevational categories: high elevation watersheds (WS6, WS7, WS8) and low elevation watersheds (WS2,WS9, WS10) (Table 2-1). Vegetation within all the six watersheds studied is dominated by Douglas-fir (*Pseudotsuga mensiezii*). Age classes differ between watersheds due to fires and silvicultural treatments. Less common tree species include *Tsuga heterophylla*, *Thuja plicata*, and, at high elevation, *Abies amabilis*. Understory shrub species include *Rhododendron macrophyllum*, *Acer circinatum*, and *Castanopsis chrysophylla*.

WS6 and WS7 have had high cover of *Ceanothus velutinus*, a shrub that can fix as much as 100 kg $ha^{-1}yr^{-1}$ N (Youngberg and Wollum 1976), within the last 20 years, although it has been overtopped by Douglas-fir and is presently dying out. The old-growth trees in WS8, WS9, and WS2 are host to the cyanophilous lichen *Lobaria oregana*, which may fix as much as 5 kg $ha^{-1}yr^{-1}$ N (Pike 1978).

Soils of the high elevation WS6, WS7, and WS8 are frigid Andic Dystrudepts, with fine-loamy or loamy-skeletal texture (Lammers, pers. comm). Soil depth typically ranges from one to three meters to bedrock (Dyrness and Hawk 1972).

Soils in WS2 are fine-loamy or loamy skeletal Typic Haplumbrepts, and fine-loamy Typic Dystrochrepts. WS10 soils are Typic Dystrochrepts with fine-loamy to loamy-skeletal texture, Umbric Dystrochrepts, and Typic Hamplumbrepts. Soils in WS9 are Typic Haplumbrepts with fine-loamy texture, Typic Dystrochrepts with coarse-loamy texture, and Ultic Hapludalfs of fine-silty texture. Soil depth to saprolite is probably less than 3 m in WS 9 (Fredriksen 1975), between one and two meters in WS2 (Rothacker, Dyrness, and Fredriksen 1967), and as much as six meters in WS10 (Fredriksen 1975).

Soils in all the watersheds studied have similar hydraulic characteristics (Perkins 1997). Hydraulic conductivity is high, and therefore transmission of subsurface water is rapid (Harr 1977).

Table 2-1. Characteristics of the small gaged experimental watersheds at the Andrews Forest.

Watershed	Area (ha)	Elevation (m)	Aspect	% Basal Area Logged (Year of Harvest)	Type of Harvest	Dominant Vegetation in 2000	Period of Stream Chemistry Record (water years)
WS2	60	530-1070	NW	0	Uncut	470-year-old Douglas-fir	1982-present
WS9	8.5	425-700	SW	0	Uncut	470-year-old Douglas-fir	1969-present
WS10	10.2	430-670	SW	100 (1975)	Clear-cut	25-year-old Douglas-fir	1969-present
WS6	13.0	863-1013	S	100 (1974)	Clear-cut	25-year-old Douglas-fir	1972-1987
WS7	15.4	908-1097	SSE	60 (1974) 40 (1984)	Shelterwood Cut	25-year-old Douglas-fir	1972-1987
WS8	21.4	955-1190	SSE	0	Uncut	170-year-old Douglas-fir	1972 to present

2.2.3 Precipitation and Streamwater Sampling

One precipitation sampler used in this study is located in high elevation WS7, and the other is located in a clearing near low elevation WS9. Precipitation was collected at three-week intervals prior to June 1988 and at one-week intervals thereafter. From the inception of the study until 1988, both precipitation collectors consisted of stainless steel funnels to catch bulk precipitation that was then fed through plastic tubing to an acid-washed polyethylene carboy within an insulated box for storage. In 1988, the high elevation funnel collector was replaced with an Aerochem collector that separates wet and dry deposition. The Andrews Forest has served as an NADP (National Atmospheric Deposition Program) sampling site since 1980, and the NADP's Aerochem collector is located in the same clearing as the Andrews low elevation precipitation collector.

For most of the period of record, no preservative was added to precipitation samples to prevent chemical changes during storage. Mercuric chloride was added in early years, but its use was abandoned in June, 1971, because it was interfering with phophorus analyses. Three-week composite samples of precipitation have been compared to wet-only deposition samples collected weekly for the NADP program, and only minor differences in NO_3-N concentrations were observed (Martin and Harr 1988). NH_4-N was not measured in this comparison.

Streamwater was sampled just above the weir at the outlet of each watershed. Sampling location has not changed since the inception of the study. Samples were collected by proportional water sampler (Fredriksen 1969), which samples a fixed volume of water at a frequency proportional to stream flow. Individual samples were composited in an acid-washed polyethylene carboy, stored in the dark, and collected at three-week intervals until June 1988. Since that time, carboys have been collected once a week, refrigerated, and combined at three-week intervals for chemical analysis. To test whether water chemistry changed during the three-week storage period, two grab samples were collected during each sampling period in 1981-1982, and one was left in the gage house for three weeks

and one was analyzed immediately. Martin and Harr (1988) reported that concentrations of NO_3-N and NH_4-N did not change significantly during the three-week storage period. Further testing has occurred since 1989, when a quality control procedure was implemented. Once or twice a year, one grab sample is collected and analyzed immediately, while another is collected at the same time and left in the gage house and collected with the next sample collection. Paired t-test analysis indicates that NO_3-N, NH_4-N, filtered total Kjeldahl N (DON + NH_4-N) and unfiltered total Kjeldahl N (PON + DON + NH_4-N) concentrations do not change significantly during the period they remain in the gage house ($n = 12$, NO_3-N: $p = 0.335$; NH_4-N: $p = 0.720$; DON: $p = 0.115$; PON: $p = 0.515$).

Stream discharge has been measured continuously with rectangular weirs at the high elevation watersheds (WS6, WS7, WS8) since 1963. Stream discharge has been measured continuously with trapezoidal weirs at the low elevation watersheds (WS2, WS9, WS10) since 1953.

2.2.4 Chemical Analysis

Stream and precipitation samples were filtered in the laboratory prior to analysis. Glass-fiber GF/C filters (1.2 μm pore size) were used from the inception of the study until 1983, after which GF/F (0.7 μm pore size) filters were used (Martin and Harr 1989). Filters were pre-washed with deionized water and dried at 65 °C. NO_3-N was measured from 1968 to July 1978 manually using a cadmium reduction column and a Spec 20 spectrophotometer. Since July 1978, NO_3-N has been measured using the same chemistry on a Technicon Auto-Analyzer II. From 1966 to 1978, NH_4-N was analyzed on macro-Kjeldahl equipment by distillation and Nesslerization. Since 1978, NH_4-N has been measured using the phenate procedure on a Technicon Auto-Analyzer II. The macro-Kjeldahl analysis was used to analyze DON and PON. PON was calculated as the difference between Kjeldahl N content of filtered and unfiltered samples. DON concentration was

calculated as the difference between Kjeldahl N and NH_4-N concentration in the filtered sampled.

2.2.5 Data Analysis

Patterns of N in streamwater and precipitation were examined as three-week, volume-weighted concentrations and as three-week mass fluxes (kg ha^{-1}). Three-week mass fluxes (kg ha^{-1}) were calculated by multiplying each three-week flow-weighted concentration by the total volume of discharge for the three-week interval. Annual N fluxes were calculated by summing three-week mass flux data over the water year (October 1 – September 30). Annual concentration was calculated by dividing the annual flux by total precipitation or discharge per year. All statistical analyses were done using SAS (SAS Institute Inc. 1990). Statistical significance was defined as $\alpha = 0.05$. Actual p values are reported for most analyses.

2.2.6 Annual N Concentrations and Fluxes

Temporal trends in annual N concentrations in precipitation were examined using linear regression. Linear regression was also used to relate annual N inputs (kg ha^{-1}) to annual precipitation and to relate annual N export (kg ha^{-1}) to annual stream discharge. Pearson correlation coefficients were used to relate export of N from pairs of watersheds to each other by water year.

WS6, WS7, and WS10 were harvested, and the years directly following harvest were not used to derive annual relationships because the disturbance was expected to increase annual discharge and alter nutrient exports. The number of years to be excluded from the analysis was determined by examining plots of NO_3-N and filtered Kjeldahl N export and estimating the year when export returned to approximately pre-disturbance levels. NH_4-N and PON data were not collected during the first few years following harvest. Years excluded from the annual

export analysis due to disturbance effects or missing data were: WS10: NO_3-N: 1976-1981; NH_4-N: 1971, 1974-1978; DON: 1974-1981; PON: 1969-1978. WS9: NH_4-N: 1971, 1974-1978; DON: 1974-1978; PON: 1969-1978. WS6: NO_3-N: 1975-1980; NH_4-N: 1974-1978, DON: 1974-1979; PON: 1972-1978; WS7: NO_3-N: 1975-1978; NH_4-N: 1974-1978. DON: 1974-1978. PON: 1972-1978. WS8: NO_3-N: 1975; NH_4-N: 1974-1978; 1982; DON: 1974-1978; PON: 1972-1978. WS2: PON: 1982-1988.

A few other anomalous data points were closely examined to determine whether they should be included in the regression analyses or not. NH_4-N export in 1985 in WS10 was an outlier, but one three-week interval contributed 75% of the NH_4-N flux for that year. That interval was deleted and the point used in the regression. An extreme NH_4-N flux outlier measured in 1972 at WS8 was also excluded from the regression analysis. The exceptionally high NH_4-N concentrations measured that year are suspect.

2.2.7 Data Synthesis for Intra-Annual Analysis

Variables hypothesized to affect stream chemistry (Table 2-2) were calculated from Andrews Forest data obtained from the Forest Science Data Bank (FSDB), a database maintained by the Department of Forest Science at Oregon State University. Stream discharge, precipitation, air temperature, and soil temperature were obtained from the FSDB. These data were reported in daily intervals, while the stream chemistry data were reported in three-week intervals. Total stream discharge, total precipitation, and average temperature were calculated for each three-week interval. Every effort was made to insure that data used represented the conditions on each watershed as closely as possible. For example, soil temperature data for WS6 come from a vegetation plot at the same elevation and with approximately the same vegetation type.

Calculating N loads as NO_3-N, NH_4-N, DON, and PON required examining every datum from both precipitation and stream chemistry data files to correct for

data that were collected on different dates. When the date of stream chemistry collection differed by 1-2 days from precipitation chemistry collection, which occurred for 2% of data points, dates were adjusted so that collections were synchronized. After 1988, precipitation was collected at one-week intervals, so it was necessary to add together three precipitation N load values to estimate the load for the three-week interval during which stream chemistry was measured. Dates of collection were again synchronized when they differed by 1 or 2 days.

Soil moisture was calculated for each watershed using MMS (Modular Modeling System) (CADSWES 1993). The model required inputs of daily temperature, precipitation, and solar radiation, which were obtained from the FSDB database. The model runs at a daily time-step, so soil moisture model outputs were averaged for three-week intervals.

Transpiration was modeled using 3-PG (Landsberg and Waring 1995), which requires inputs of vapor pressure deficit, precipitation, temperature, and solar radiation. These data were available from the FSDB for 1989 to 1993, so only five years of transpiration data were modeled. Model outputs were at monthly time-steps, so they were interpolated to three week intervals.

2.2.8 Definition of Intervals for Intra-Annual Analysis

Three intervals were defined based on precipitation and forest biological activity: fall, winter, and spring/summer. Fall is the months of September, October, and November. Stream low flows occur in August, and fall storms begin to increase stream discharge in September. Stream discharge rises dramatically in November. Vegetation typically begins to senesce during September. Winter includes December, January, February, and March. These are the coldest months of the year, and during this period forest vegetation is largely dormant. Soils are

Table 2-2 Definition and rationale of variables to be correlated to stream N concentration by season.

Variable	Definition (units)	Rationale
Current Stream Discharge	Discharge during the three-week sample collection period (cm).	Water may either flush N into the stream, increasing stream N concentrations, or dilute stream N concentrations.
Antecedent Stream Discharge	Discharge during the three weeks prior to the three-week sample collection period (cm)	A measure of catchment "wetness" prior to sample collection, which influences decomposition, possibly resulting in higher stream N concentrations. Alternatively, antecedent discharge may represent prior hydrologic flushing of nutrients from the soil, decreasing N pool size and stream N concentrations.
Current Precipitation	Precipitation during the three-week sample collection period (cm)	Precipitation may increase stream N concentration as throughfall enters the stream channel. Precipitation may also flush N from the soil into the stream, increasing stream N concentration.
Antecedent Precipitation	Precipitation during the three weeks prior to the three-week sample collection period (cm)	See Antecedent Discharge
Soil Temperature	Average soil temperature during the three week sample collection period (^{0}C)	During fall and spring, when soils are moist, soil temperature may be positively related to N mineralization, which may increase concentrations of N in soil water and stream water. Alternatively, soil temperature may be correlated to biotic uptake, decreasing stream N concentrations.
Air Temperature	Average air temperature during the three week sample collection period (^{0}C)	Biological demand in streams, soils, and vegetation may be positively related to ambient temperature, and therefore negatively related to N concentrations in streams. See also Soil Temperature.
Transpiration	Volume of water moving through forest vegetation (cm).	Index of N uptake through plant roots. Greater uptake of N by vegetation may decrease stream N concentrations.
Soil Moisture	Volume of water stored in soil (cm)	Greater soil water content implies that more of the soil is being flushed of N, increasing N stream concentrations. Alternatively, soil moisture may dilute N concentrations in soil water and stream water.
NO_3-N load	NO_3-N input in bulk deposition during the three week sample period (kg ha^{-1})	Direct inputs to stream may increase concentration of stream NO_3-N
NH_4-N load	NH_4-N input in bulk deposition during the three week sample collection period (kg ha^{-1})	Direct inputs to stream may increase NH_4-N and/or NO_3-Nconcentrations.

Table 2.2. (continued)

DON load	DON input in bulk deposition during the three week sample collection period (kg ha^{-1})	Direct inputs to stream may increase concentration of DON. Atmospheric inputs of DON to streams may be more labile than subsurface flow inputs, and they may therefore increase NO_3-N and NH_4-N concentrations in streams.
PON load	PON input in bulk deposition during the three week sample period (kg ha^{-1})	Atmospheric inputs of PON may be mineralized to yield increased concentrations of DON, NO_3-N and ammonium in stream water.
Stream NH_4-N Concentration	Flow-weighted NH_4-N concentration during the three week sample period (mg L^{-1}).	Nitrification of NH_4-N may yield increased stream concentrations of NO_3-N
Stream DON concentration	Flow-weighted DON concentration during the three week sample period (mg L^{-1})	Decomposition of DON may result in increased stream concentrations of NH_4-N and/or NO_3-N.
Stream PON Concentration	Flow-weighted PON concentration during the three week sample period (mg L^{-1})	Decomposition of PON may result in increased stream concentrations of NH_4-N, NO_3-N, and/or DON.

saturated (Perkins 1997) and precipitation, soil water flux, and stream flow are high. The spring/summer interval extends from April through August. By April, trees are breaking dormancy. Precipitation drops off, and soil moisture drops below saturation in April or May (Perkins 1997).

2.2.9 Statistical Analysis

Pearson correlation coefficients were calculated for all combinations of seasons and concentrations and outputs of NH_4-N, DON, and PON. Examination of scatterplots indicated that all explanatory variables, with the exception of air and soil temperature, actual evapotranspiration (AET), and soil moisture, would require a log transformation to linearize the relationship between response and explanatory variables. Response variables in the analysis were log transformed to equalize variance of residuals.

Multiple linear regression was used to identify the suite of variables explaining most variation in NH_4-N, DON, and PON. PROC MIXED (SAS Institute 1990) was employed for this purpose. Logistic regression was used to analyze NO_3-N data, because many of the values for NO_3-N concentration were 0. The data were recoded as 1 if a concentration other than zero was recorded, and 0 if a concentration of 0 was recorded. PROC GENMOD (SAS Institute 1990) was used for logistic regression.

2.2.10 Seasonal Influence of Litter Inputs on Stream N Chemistry

The effects of the timing of litter inputs and litter quality on stream N concentrations were evaluated using data on litterfall inputs of N from the old-growth forest to the channel of Watershed 10 from May 1972 to April 1974 (reported in Triska et al. 1984). Litterfall N input data were divided into N in needles, deciduous leaves, woody material (cones, twigs, bark and wood), and miscellaneous (frass, flower parts, seeds, fruit, etc.). Correlation coefficients

between NO_3-N, NH_4-N, and DON and each category of input were calculated. All variables were log transformed to equalize variance of residuals.

2.3 Results

2.3.1 Seasonal and Annual Trends in Precipitation Chemistry

Concentrations of NO_3-N, NH_4-N, DON, and PON in bulk precipitation have similar seasonal patterns at both low and high elevation (Figure 2-1 and Figure 2-2). NO_3-N and NH_4-N peak in August or September. DON and PON concentrations are generally lowest during the fall and winter. Seasonal patterns of N concentration in bulk and wet-only deposition at high elevation are similar, although concentrations of DON and PON tend to be lower in wet-only precipitation than in bulk precipitation.

Peaks in NO_3-N and NH_4-N inputs (kg ha^{-1}) occur in April at both elevations (Figure 2-3 and Figure 2-4). DON deposition peaks once in spring (April at high elevation; May at low elevation), and again in September at both elevations. PON input peaks in May at low elevation, but PON input does not seem to vary systematically by season at high elevation.

At low elevation, DON and PON have highest mean annual concentrations in precipitation, followed by NO_3-N and NH_4-N (Table 2-3). At high elevation, NO_3-N has the highest mean annual concentration in bulk precipitation, followed by NH_4-N then DON and PON .

Total annual bulk N deposition at the low elevation sampler averaged 1.63 kg ha^{-1} yr^{-1}, while at the high elevation sampler total annual bulk N deposition averaged 2.01 kg ha^{-1} yr^{-1}. Wet-only deposition of N at high elevation averaged

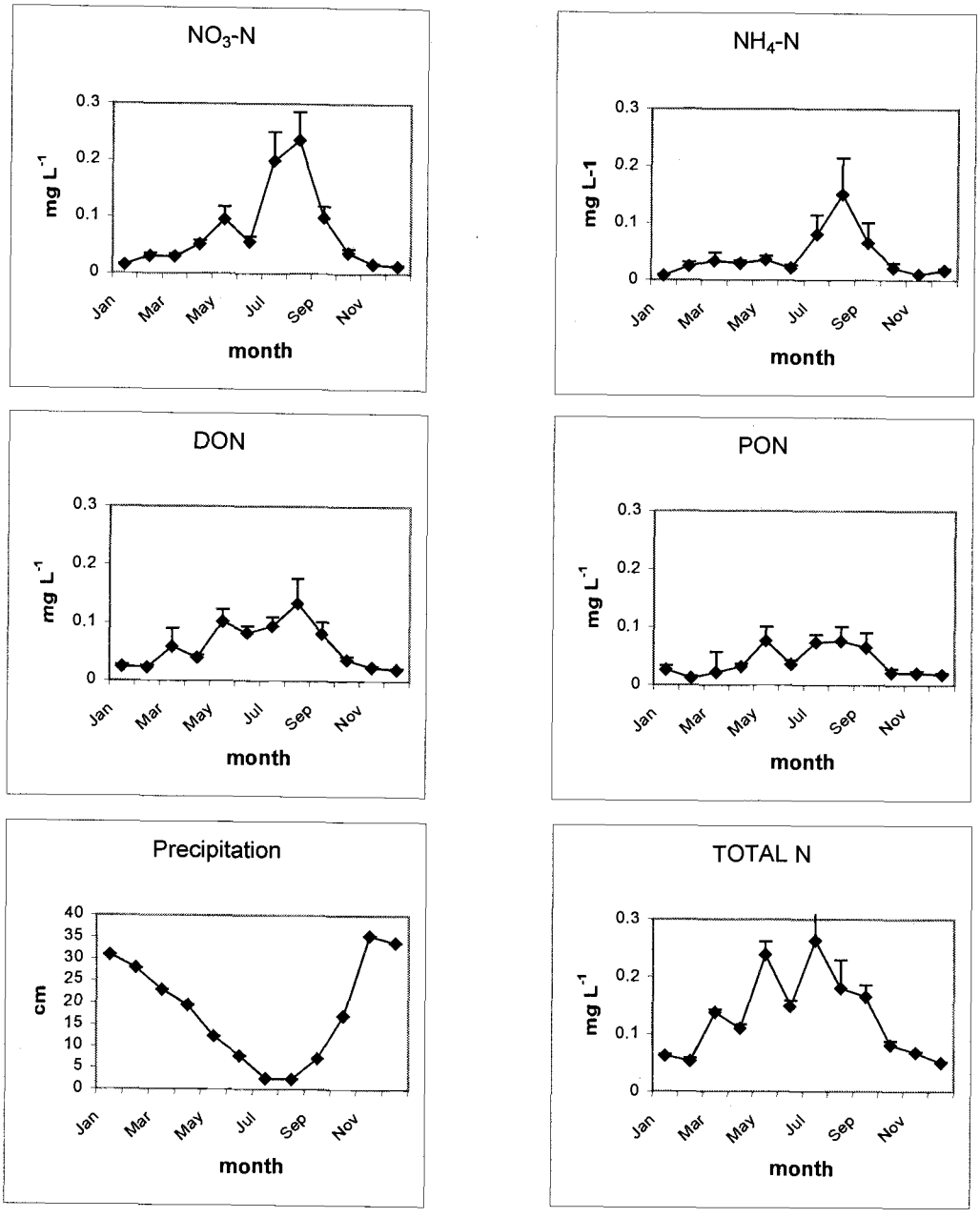

Figure 2-1 Mean monthly bulk deposition N concentrations (+1SE) and precipitation volume sampled at the low elevation precipitation collector. Water years included in averages: NO_3-N: 1969-1995; NH_4-N: 1969-1973, 1979-1995; DON: 1969-1973; 1979-1995; PON: 1979-1995

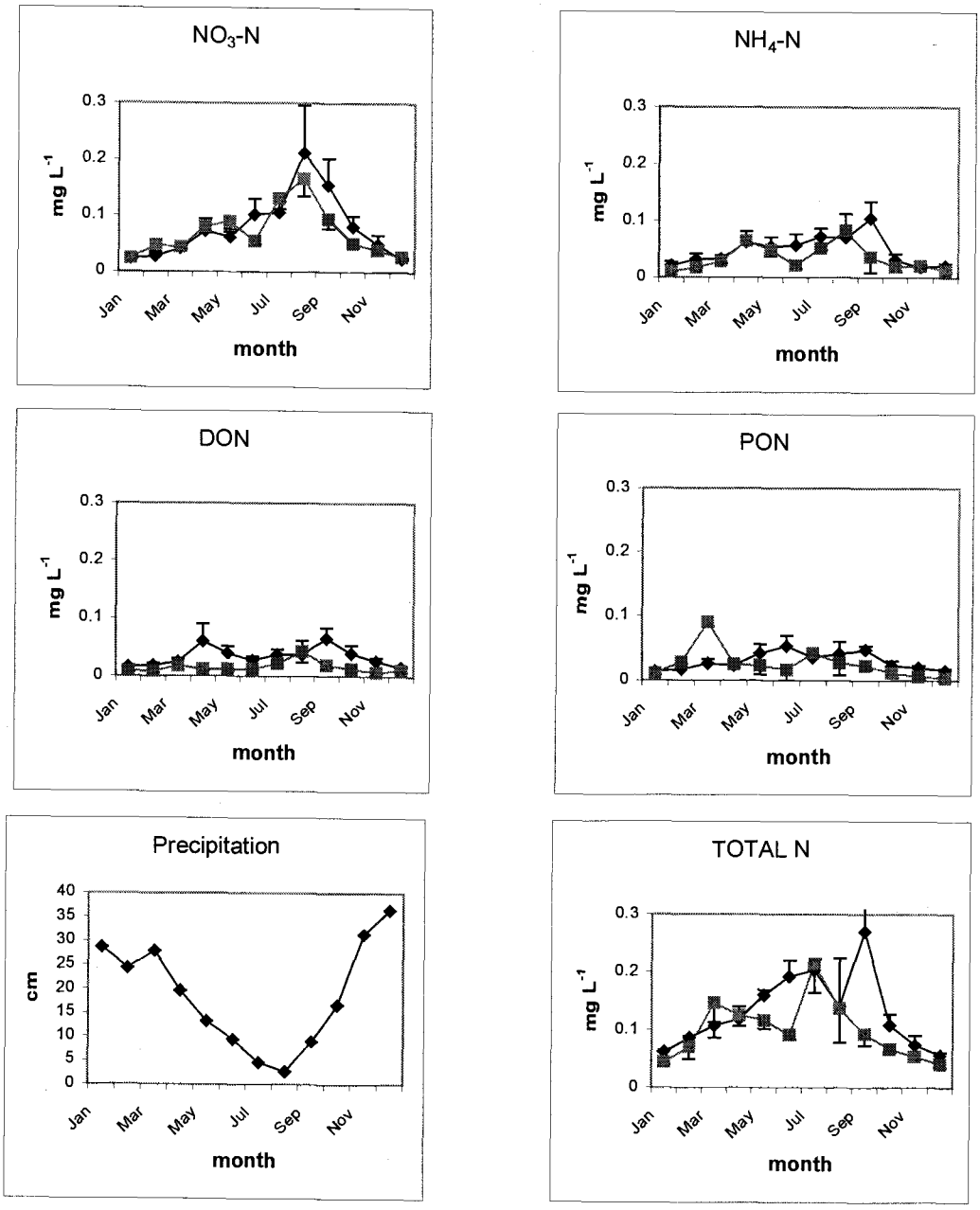

Figure 2-2 Mean monthly bulk deposition (diamonds) and wet-only deposition (squares) N concentrations (+1SE) and precipitation volume sampled at the high elevation precipitation collector. Water years included in averages for bulk deposition: NO_3-N: 1973-1988; NH_4-N: 1973, 1979-1998; DON: 1973, 1979-1988; PON: 1979-1988. Water years included in averages for wet-only deposition: 1989-1995 for all forms of N.

1.60 kg ha^{-1} yr^{-1}. DON was the largest proportion of N deposition at low elevation, followed by PON, NO_3-N, and NH_4-N (Table 2-4). At high elevation, NO_3-N was the largest proportion of N in bulk and wet-only deposition, followed by NH_4-N, DON, and PON.

At low elevation, mean annual input and mean annual concentrations of NH_4-N, DON, and PON in bulk deposition were not significantly related to total annual precipitation. Annual bulk NO_3-N concentration was significantly negatively related to total annual precipitation ($r^2 = 0.190$, $p = 0.0190$) at low elevation, but total annual NO_3-N input and total annual precipitation were unrelated. At high elevation, mean annual concentrations of NO_3-N, NH_4-N, DON, and PON in bulk and wet-only deposition are unrelated to total precipitation volume.

Mean annual input of DON and PON in bulk and wet-only deposition at high elevation is also unrelated to total annual precipitation volume. Total annual precipitation is, however, a significant predictor of total annual bulk NO_3-N deposition ($r^2 = 0.242$, $p = 0.0529$) and total annual wet-only NO_3-N deposition ($r^2 = 0.607$, $p = 0.0390$) at high elevation. Total annual precipitation was also a significant predictor of total annual bulk NH_4-N deposition ($r^2 = 0.420$, $p = 0.0380$) at the high elevation site.

Concentrations of NO_3-N and NH_4-N did not differ significantly between bulk and wet-only deposition at the high elevation collector. DON concentrations, however, were significantly greater in bulk precipitation than in wet-only precipitation ($p = 0.0002$). PON concentrations were also significantly greater in bulk deposition than in wet-only precipitation ($p = 0.0001$).

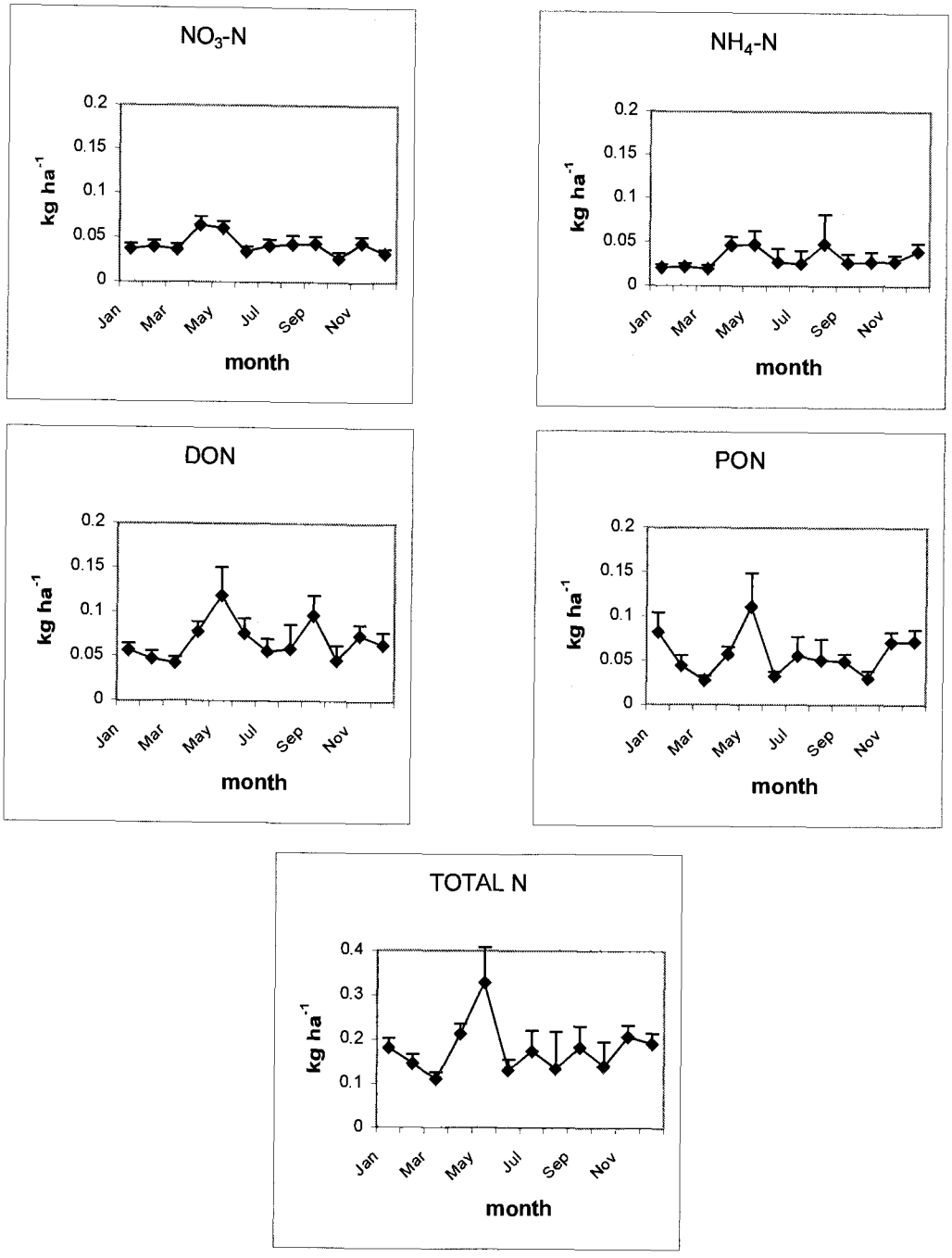

Figure 2-3 Mean monthly bulk input (kg ha^{-1}) of N (+1SE) sampled at the low elevation precipitation collector. Water years included in averages: NO_3-N: 1969-1995; NH_4-N: 1969-1973, 1979-1995; DON: 1969-1973; 1979-1995; PON: 1979-1995.

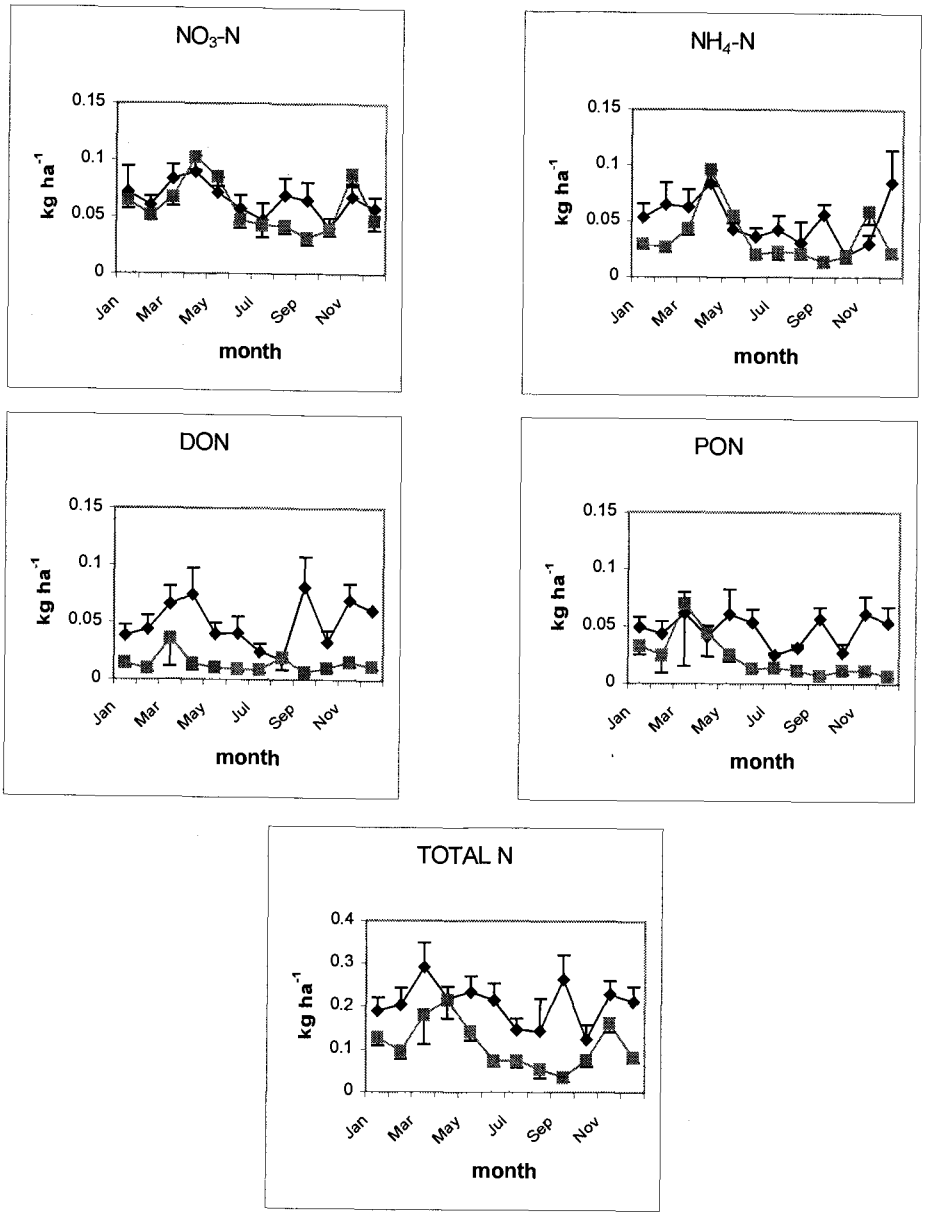

Figure 2-4 Mean monthly bulk input (kg ha^{-1}) of N (+1SE) (diamonds) and wet-only input of N (squares) sampled at the high elevation precipitation collector. Water years included in averages for bulk deposition: NO_3-N: 1973-1988; NH_4-N: 1973, 1979-1998; DON: 1973; 1979-1988; PON: 1979-1988. Water years included in averages for wet-only deposition: 1989-1995 for all forms of N.

Table 2-3. Annual mean concentration (mg L^{-1} yr^{-1}) of N in precipitation collected at the low elevation precipitation collector and the high elevation precipitation collector. Bulk deposition was collected at the low elevation site from 1969 to 1995. Bulk deposition was collected at the high elevation site from 1973 to 1988. Wet deposition was collected at the high elevation site from 1989 to 1995.

	Low Elevation Collector		High Elevation Collector			
	Bulk		Bulk		Wet	
	years	Mean Concentration (SE)	years	Mean Concentration (SE)	years	Mean Concentration (SE)
NO_3-N	27	0.021 (0.0021)	16	0.032 (0.0017)	7	0.034 (0.0014)
NH_4-N	21	0.016 (0.0024)	11	0.026 (0.0020)	7	0.020 (0.0023)
DON	21	0.03 (0.003)	11	0.02 (0.003)	7	0.01 (0.002)
PON	18	0.03 (0.006)	10	0.02 (0.006)	7	0.01 (0.004)

Table 2-4. Annual mean input (kg ha^{-1} yr^{-1}) of N in precipitation collected at the low elevation precipitation collector and the high elevation precipitation collector. Bulk deposition was collected at the low elevation site from 1969 to 1995. Bulk deposition was collected at the high elevation site from 1973 to 1988. Wet deposition was collected at the high elevation site from 1989 to 1995.

	Low Elevation Collector		High Elevation Collector			
	Bulk		Bulk		Wet	
	years	Mean Input (SE)	years	Mean Input (SE)	years	Mean Input (SE)
NO_3-N	27	0.458 (0.042)	16	0.678 (0.038)	7	0.685 (0.027)
NH_4-N	21	0.330 (0.060)	11	0.558 (0.055)	7	0.414 (0.044)
DON	21	0.638 (0.058)	11	0.467 (0.063)	7	0.161 (0.045)
PON	18	0.513 (0.064)	10	0.411 (0.116)	7	0.463 (0.082)
Total N	18	1.626 (0.124)	10	2.013 (0.282)	7	1.602 (0.143)

2.3.2 Long-Term Trends in N Deposition

Annual NO_3-N concentration in bulk precipitation collected at the low elevation site increased significantly from 1969 to 1991 ($r^2 = 0.601$, $p = 0.0001$), and has been decreasing since that time (Figure 2-5). Although annual NO_3-N concentration was significantly negatively related to annual NO_3-N concentration in bulk precipitation, the same decreasing temporal trend was still present once the effect of precipitation volume was removed from the data ($r^2 = 0.492$; $p = 0.0001$). Annual NO_3-N concentration in wet-only deposition from the NADP collector located in the same clearing as the Andrews low-elevation collector did not increase significantly during the interval 1980 to 1991 ($p = 0.1267$). No trends over time in annual PON, DON, NH_4-N and total N concentrations were observed at the low elevation site.

2.3.3 Composition of Annual N Export

On average, DON comprised the largest fraction of total annual N exported from both harvested and unharvested watersheds (Table 2-5 and Table 2-6). PON was the second largest fraction of total annual N exported, followed by NH_4-N and then NO_3-N in the three undisturbed watersheds. In watersheds that were harvested, more NO_3-N was exported in streamwater than NH_4-N on an average annual basis. Relative average annual concentrations reflected the annual trends in N export; that is, the order of concentration was DON > PON > NH_4-N > NO_3-N in the unharvested watersheds, and DON>PON>NO_3-N>NH_4-N in the harvested watersheds. Total annual N flux ranged from 0.376 kg ha^{-1} yr^{-1}in WS7 to 0.981 kg ha^{-1} yr^{-1} in WS10. Average annual percent of total N export that was organic N ranged from 28.1% in WS7 to 85.0% in WS9.

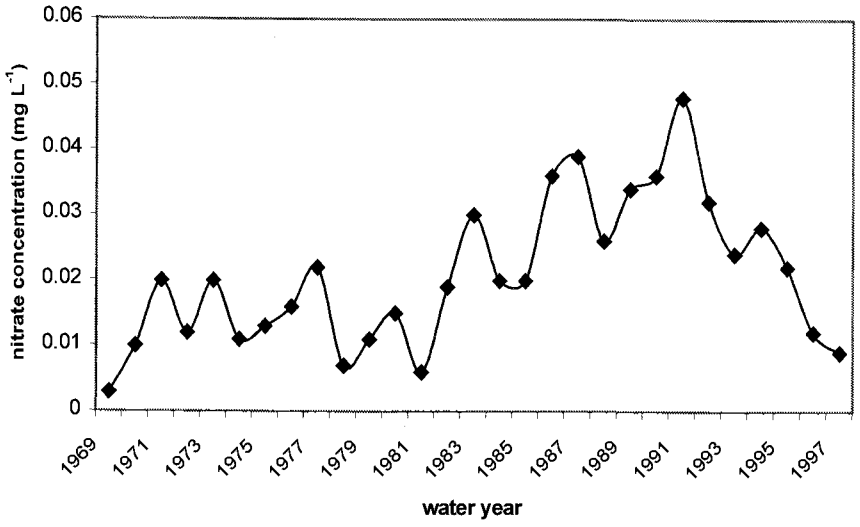

Figure 2-5 Mean annual NO_3-N concentration (mg L^{-1} yr^{-1}) in bulk deposition sampled at the low elevation precipitation collector.

2.3.4 Annual N Export Versus Annual Stream Discharge

The degree to which total annual N export is related to total annual stream discharge varied by watershed. Total annual NO_3-N export was related to total annual stream discharge only in WS2 (Figure 2-6). Total annual NH_4-N export was related to total annual stream discharge in three of the six watersheds (Figure 2-7), as was total annual PON export (Figure 2-8). Total annual discharge was a significant predictor of DON export in all watersheds (Figure 2-9).

2.3.5 Annual N Export Comparison Between Watersheds

Annual export of NO_3-N was correlated only between WS2 and WS9 (Table 2-7). NH_4-N export was uncorrelated between watersheds. DON export was correlated between all three watersheds. PON export was weakly correlated between WS8 and WS9.

2.3.6 Seasonal Variation in N Chemistry

No systematic seasonal trends were observed for NO_3-N (Figure 2-10) or PON concentrations. Elevated concentrations of NH_4-N in spring and early summer occurred in all three watersheds, although they are not synchronous. DON, however, increased in concentration in the fall in every watershed (Figure 2-11). The increase in concentration began in July or August, and peak DON concentrations occurred in November or December. DON concentrations then declined during the winter months.

Table 2-5 Average annual N outputs (kg $ha^{-1}yr^{-1}$), concentrations (mg $L^{-1}yr^{-1}$), and stream discharge for the undisturbed watersheds.

		WS2		WS9		WS8	
		n	Mean (SE)	n	Mean (SE)	n	Mean (SE)
Outputs (kg $ha^{-1}yr^{-1}$)	NO_3-N	14	0.015 (0.002)	27	0.030 (0.006)	22	0.042 (0.009)
	NH_4-N	14	0.086 (0.012)	21	0.078 (0.011)	18	0.085 (0.016)
	DON	14	0.209 (0.021)	21	0.435 (0.049)	18	0.246 (0.043)
	PON	7	0.186 (0.045)	17	0.256 (0.044)	16	0.143 (0.022)
	Total N Export	7	0.463 (0.065)	17	0.831 (0.070)	16	0.479 (0.048)
	% Organic N*	7	37.3 (5.2)	17	85.0 (1.7)	16	73.5 (2.2)
Concentration (mg $L^{-1}yr^{-1}$)	NO_3-N	14	0.001 (0.001)	27	0.003 (0.001)	22	0.004 (0.001)
	NH_4-N	14	0.007 (0.001)	21	0.008 (0.001)	18	0.009 (0.001)
	DON	14	0.02 (0.002)	21	0.04 (0.002)	18	0.02 (0.003)
	PON	7	0.02 (0.003)	18	0.02 (0.004)	16	0.01 (0.001)
Stream discharge (cm)		15	110.35 (10.75)	27	123.16 (7.92)	23	114.83 (8.72)

*% Organic N was calculated only for those years having complete PON and DON datasets.
% Organic N was calculated for each year, and then averaged across years.

Table 2-6 Average annual N outputs (kg ha-$^{-1}$yr^{-1}), concentrations (mg L^{-1} yr^{-1}), and stream discharge (cm) for the harvested watersheds.

			WS6		**WS7**		**WS10**
		n	Mean (SE)	n	Mean (SE)	n	Mean (SE)
Outputs (kg ha^{-1}yr^{-1})	NO_3-N	16	0.200 (0.056)	16	0.089 (0.039)	27	0.141 (0.040)
	NH_4-N	11	0.094 (0.017)	11	0.052 (0.011)	21	0.115 (0.017)
	DON	11	0.287 (0.061)	11	0.188 (0.032)	21	0.409 (0.043)
	PON	9	0.184 (0.035)	9	0.101 (0.011)	17	0.341 (0.036)
	Total N Export	9	0.721 (0.108)	9	0.376 (0.029)	17	0.981 (0.095)
	% Organic N*	9	48.4 (7.6)	9	74.7 (2.5)	17	79.4 (1.5)
Concentration (mg L^{-1} yr^{-1})	NO_3-N	16	0.013 (0.004)	16	0.008 (0.003)	27	0.009 (0.003)
	NH_4-N	11	0.007 (0.007)	11	0.005 (0.001)	21	0.009 (0.001)
	DON	11	0.02 (0.002)	11	0.02 (0.002)	21	0.03 (0.002)
	PON	10	0.01 (0.001)	10	0.01 (0.001)	18	0.02 (0.002)
Stream Discharge (cm)		16	171.21 (13.42)	16	113.03 (8.64)	27	152.08 (8.30)

*% Organic N was calculated only for those years having complete PON and DON datasets.
% organic N was calculated for each year, and then averaged across years.

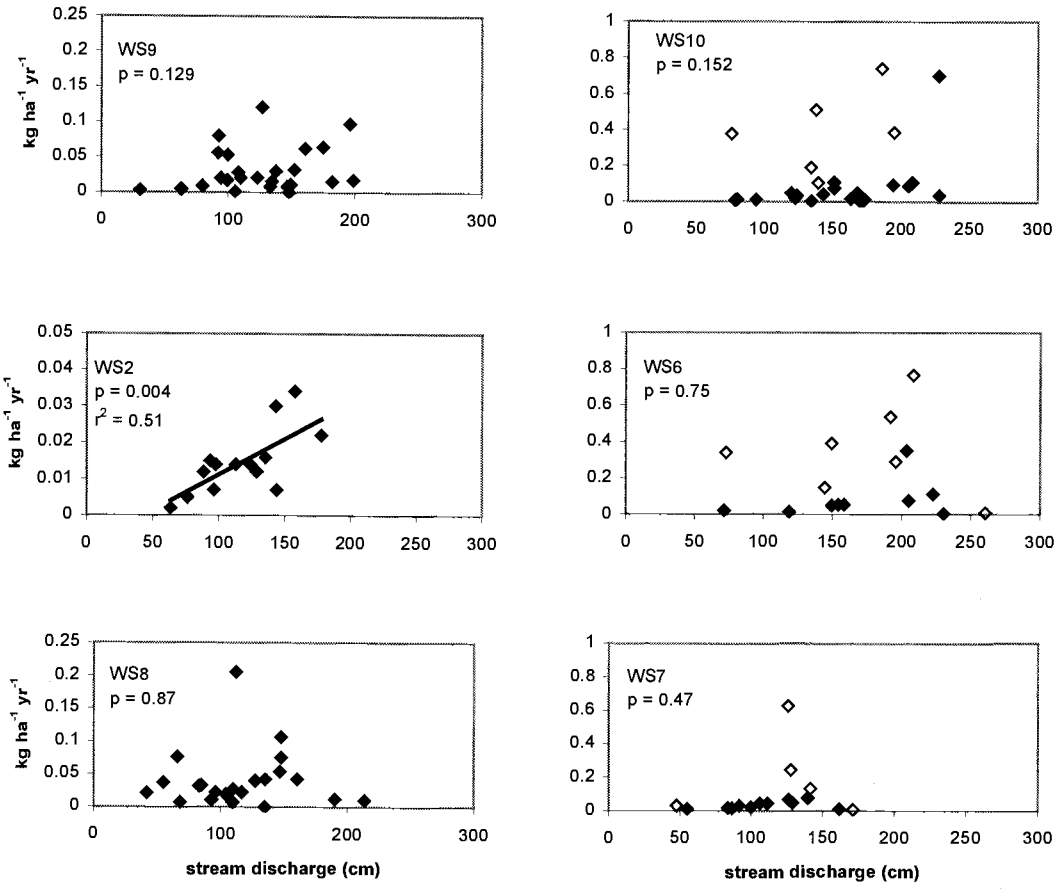

Figure 2-6 Annual NO_3-N export (kg ha^{-1} yr^{-1}) versus annual stream discharge. Open diamonds represent years following harvest in WS10, WS7, and WS6. Black diamonds represent pre- and post-harvest years (see text for definition of these intervals). Note difference in scale on y axis.

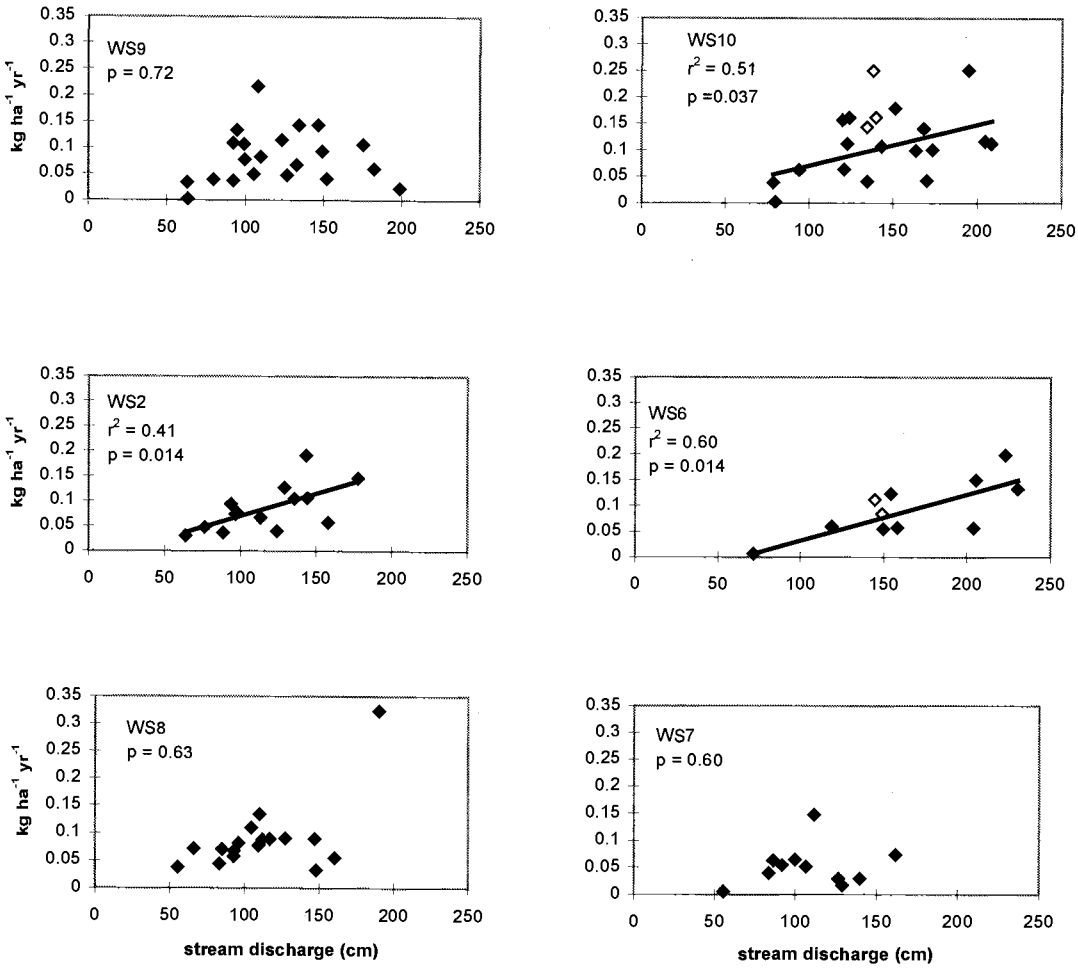

Figure 2-7 Annual NH_4-N export (kg ha^{-1} yr^{-1}) versus annual stream discharge (cm). Open diamonds represent years following harvest in WS10 and WS6. Black diamonds represent pre- and post-harvest years (see text for definition of these intervals).

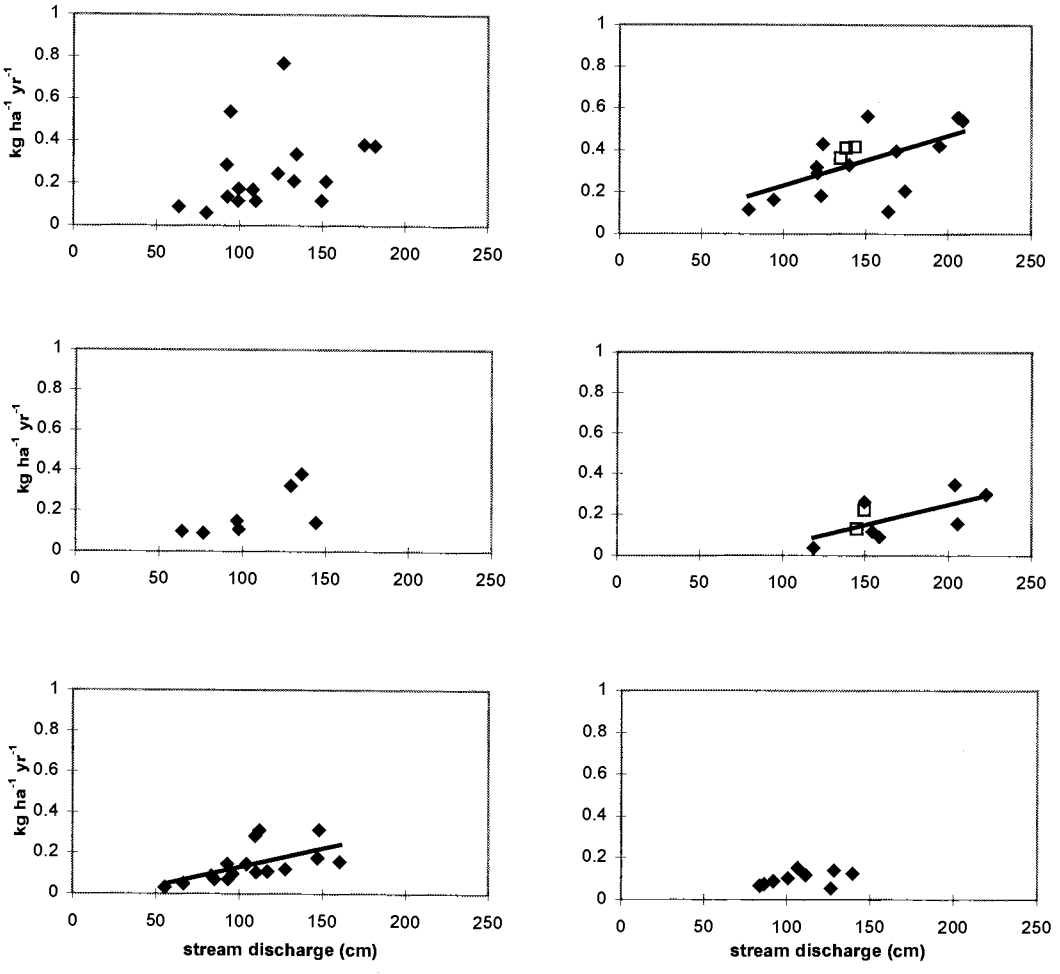

Figure 2-8 Annual PON export (kg ha^{-1} yr^{-1}) versus annual stream discharge (cm). Black diamonds refer to pre- and post-harvest years. Open diamonds represent years immediately following harvest (see text for definition of these intervals).

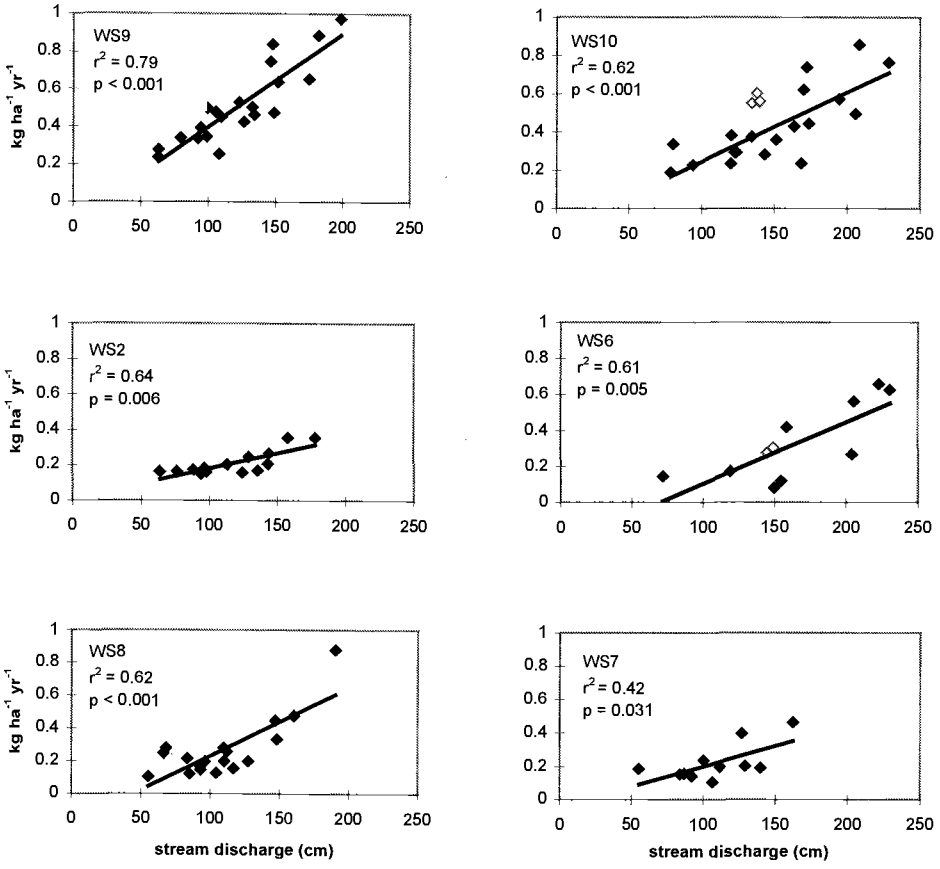

Figure 2-9 Annual DON export (kg ha^{-1} yr^{-1}) versus annual stream discharge (cm). Open diamonds in WS10 and WS6 refer to years following harvest. Black diamonds refer to pre- and post-harvest years (see text for definition of these intervals).

Table 2-7 Pearson correlations between N export in each water year from pairs of unharvested watersheds

		n	r	p	years
NO_3-N	2 vs. 9	14	0.31	0.286	1982-1995
	2 vs. 9	11	0.84	0.001	1982-1995 (1986-1988 deleted)†
	2 vs. 8	13	0.13	0.669	1982-1994
	8 vs. 9	22	0.16	0.470	1972-1994 (1986-1988 deleted)†
NH_4-N	2 vs. 9	14	0.06	0.836	1982-1995
	2 vs. 8	13	0.27	0.372	1982-1994
	8 vs. 9	16	0.42	0.102	1979-1994
DON	2 vs. 9	14	0.83	0.001	1979-1995
	2 vs. 8	13	0.71	0.007	1982-1994
	8 vs. 9	16	0.91	0.001	1982-1994
PON	2 vs. 9	7	0.27	0.560	1989-1994
	2 vs. 8	6	0.32	0.544	1989-1994
	8 vs. 9	16	0.62	0.010	1979-1994

† 1986-1988 were excluded from the regression because a flood in February 1986 may have resulted in elevated NO_3-N export for these three years.

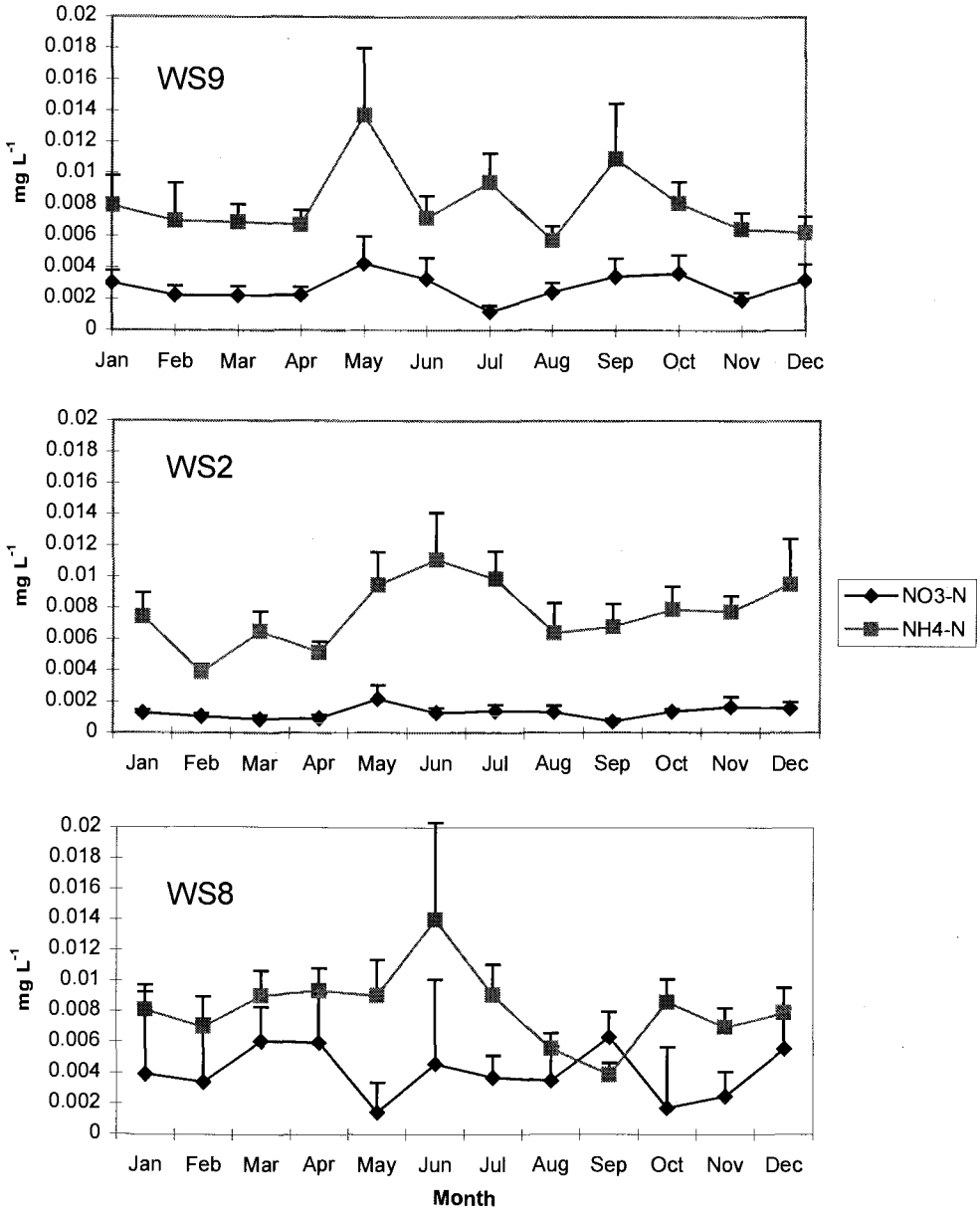

Figure 2-10 Mean monthly concentrations (mg L^{-1}) of NO_3-N and NH_4-N (+1SE) in three undisturbed watersheds at the Andrews Experimental Forest.

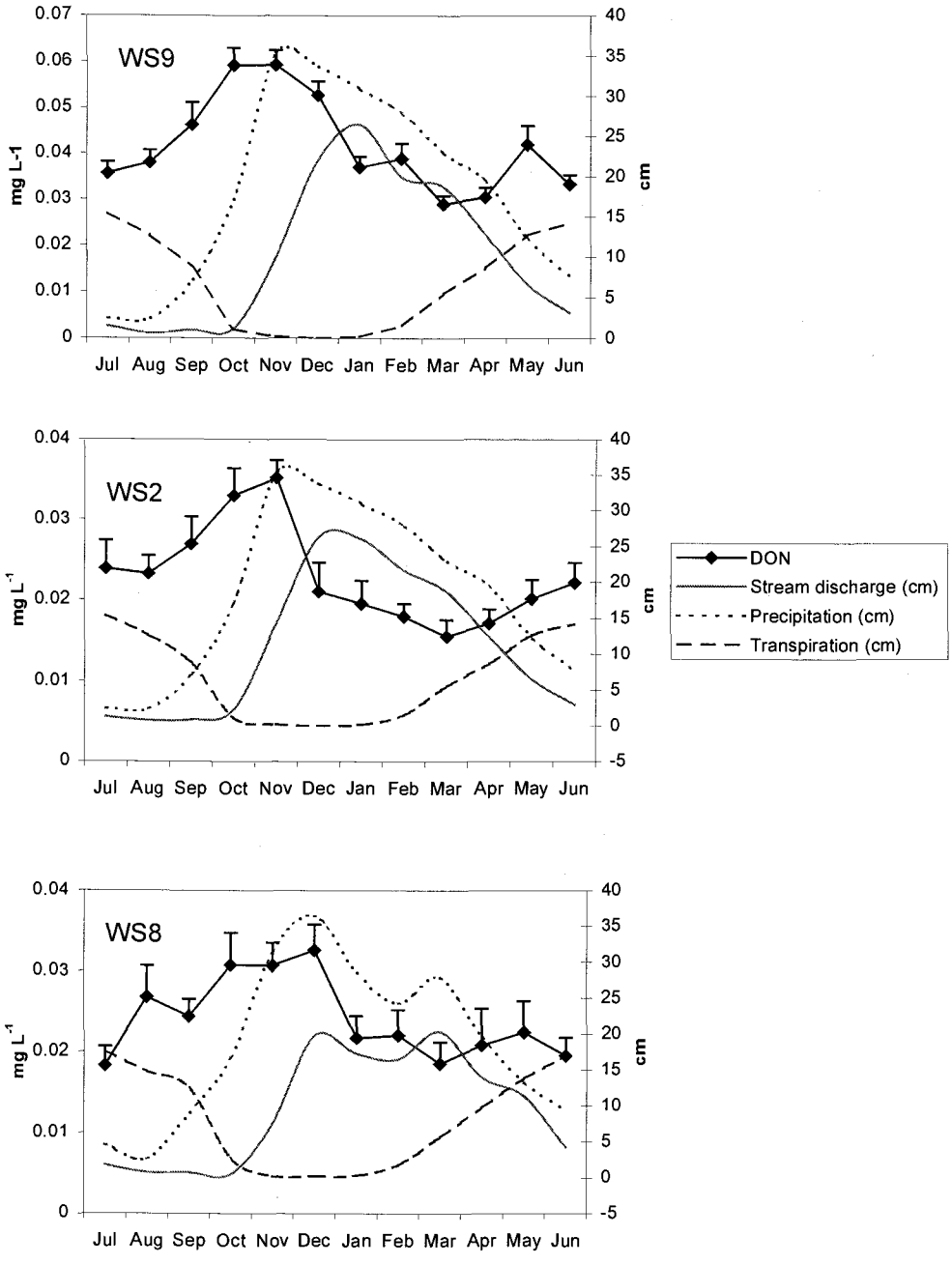

Figure 2-11 Mean monthly DON concentration (mg L^{-1}) in streamwater (+1SE) of three undisturbed watersheds at the Andrews Forest. Average monthly stream discharge (cm), average monthly precipitation (cm), and average monthly transpiration (cm) are also displayed.

2.3.7 Intra-annual Variation in N Concentration: Variables Related to N Concentration Based on Multiple Regression and Correlation Analyses

Correlation analysis revealed that as many as eight of the explanatory variables were correlated with each response variable (Table 2-8) within a single watershed. Selection of a particular variable within a season for all three watersheds was considered evidence that N concentrations in stream water may be mechanistically related to that variable at the three-week scale of observation. The selected variable may exert some control on N concentration, or both the variable and the concentration of N in streamwater may be affected by the same process. Instances where the same variable was correlated with stream concentration of N in the same season in all three watersheds are noted. Instances where multiple linear regression yielded identical equations for all three watersheds are also identified.

2.3.7.1 Nitrate

The probability of a non-zero NO_3-N concentration was not related to any variable in the Fall or Winter (Table 2-9). The odds of a non-zero NO_3-N concentration occurring increased significantly with increasing NH_4-N concentration in Spring/Summer. Stream discharge and NO_3-N flux were significantly positively correlated in all seasons (Table 2-10).

2.3.7.2 Ammonium

NH_4-N concentration was not significantly correlated with any variable in all three watersheds in any season. Stream discharge and NH_4-N flux were significantly positively correlated in all seasons.

Table 2-8 Pearson correlation coefficients for variables significantly correlated to N concentration by season and watershed.

FALL:

	WS2				WS8				WS9			
	Variable	r	p	n	Variable	r	p	n	Variable	r	p	n
NH_4-N	NH_4-N Load	0.317	0.063	35	Current Discharge	0.251	0.047	63	Current Precip.	-0.272	0.012	84
	DON Conc.	-0.408	0.002	55	PON Conc.	0.296	0.024	58	PON Load	-0.375	0.024	36
	Transpiration	-0.510	0.021	19	Soil Moisture	0.311	0.021	54	DON Load	-0.397	0.013	38
									Air Temp.	0.249	0.022	84
DON	Current Precip.	0.314	0.015	59	Current Precip.	0.491	0.000	69	Current Precip.	0.286	0.006	92
	Soil Temp	-0.336	0.013	54	Soil Temp.	-0.327	0.006	69	Soil Temp.	-0.243	0.019	92
					Air Temp.	-0.407	0.001	70	Air Temp.	-0.240	0.0194	92
					Current Discharge	0.254	0.034	70	PON Load	0.336	0.045	36
					Transpiration	-0.550	0.005	24	Transpiration	-0.560	0.0132	18
PON	Current Discharge	0.339	0.048	30	Soil Temp.	-0.295	0.025	57	--			
					Transpiration	-0.419	0.046	22				

Table 2-8 (cont.)

WINTER:

	WS2				WS8				WS9			
	Variable	r	p	n	Variable	r	p	n	Variable	r	p	n
NH_4-N	PON Load	-0.367	0.003	62	PON Conc.	0.274	0.012	83	DON Load	-0.219	0.048	82
	NH_4-N Load	0.259	0.019	81					Soil Moisture	-0.257	0.018	84
DON	Current Precip.	0.245	0.027	82	Current Precip.	0.289	0.004	100	Current Precip	0.282	0.003	107
	Soil Moisture	0.292	0.018	66	Soil Moisture	0.326	0.026	89	Soil Moisture	0.308	0.003	91
	Antecedent Discharge	-0.349	0.001	82					Antecedent Discharge	-0.287	0.003	106
									DON Load	0.337	0.001	88
									PON Load	0.326	0.004	76
									Air Temp	-0.348	0.000	107
PON	--				Current Discharge	0.298	0.005	88	Current Discharge	0.233	0.019	101
					PON Load	0.277	0.021	70	PON Load	0.251	0.030	75
					Soil Moisture	0.258	0.023	77	Soil Moisture	0.330	0.002	85
					Current Precip.	0.301	0.004	88	Antecedent Discharge	-0.288	0.003	101

Table 2-8 (cont.)

SPRING/SUMMER:

	WS2				WS8				WS9			
	Variable	r	p	n	Variable	r	p	n	Variable	r	p	n
NH_4-N	Current Precip.	0.228	0.012	104	PON Conc.	0.486	0.001	84	PON Conc.	0.212	0.031	104
	DON Conc.	-0.241	0.025	104								
DON	Antecedent Discharge	-0.328	0.001	107	DON Load	0.400	0.001	61	Antecedent Discharge	-0.197	0.019	142
	Antecedent Precip.	-0.262	0.007	107	NH_4-N Load	0.258	0.016	87	Antecedent Precip.	-0.175	0.037	142
	Current Discharge	-0.238	0.014	107								
PON	--				--				Current Discharge	-0.192	0.03	131
									Antecedent Discharge	-0.183	0.037	131
									Soil Temp.	0.319	0.000	129
									Air Temp.	0.278	0.001	131

Table 2-9 Results of single variable logistic regression relating NO_3-N presence/absence to environmental variables

	WS2				WS8				WS9			
	Variable	Odds ratio	p	n	Variable	Odds Ratio	p	n	Variable	Odds Ratio	p	n
FALL	--				--				NH_4-N Conc.	3.19	0.025	94
									DON Load	0.85	0.009	54
WINTER	--				DON Conc.	0.68	0.022	101	NO_3-N Load	1.3	0.028	141
					Current Discharge	0.89	0.031	136	NH_4-N Conc.	9.39	0.013	109
					Antecedent Discharge	0.89	0.025	136				
					Current Precip.	0.90	0.013	136				
SPRING/ SUMMER	NH_4-N Conc.	3.22	0.034	109	NH_4-N Conc.	2.53	0.019	125	NH_4-N Conc.	2.88	0.006	144
					Antecedent Discharge	0.86	0.034	163	Soil Moisture	3.22	0.038	162

Table 2-10 Pearson correlation coefficients for relationship between three-week fluxes of N (kg ha^{-1}) and current stream discharge (cm).

		WS2			WS8			WS9		
		r	p	n	r	p	n	r	p	n
FALL	NO_3-N	0.967	0.0001	47	0.875	0.0001	73	0.880	0.0001	103
	NH_4-N	0.926	0.0001	57	0.930	0.0001	63	0.855	0.0001	83
	DON	0.951	0.0001	43	0.874	0.0001	72	0.967	0.0001	75
	PON	0.869	0.0005	11	0.689	0.0001	71	0.792	0.0001	60
WINTER	NO_3-N	0.799	0.0001	70	0.667	0.0001	108	0.593	0.0001	99
	NH_4-N	0.710	0.0001	82	0.641	0.0001	93	0.723	0.0001	118
	DON	0.748	0.0001	82	0.671	0.0001	102	0.901	0.0001	106
	PON	0.730	0.0001	29	0.660	0.0001	96	0.782	0.0001	87
SPRING /SUMMER	NO_3-N	0.879	0.0001	82	0.775	0.0001	107	0.803	0.0001	123
	NH_4-N	0.837	0.0001	104	0.812	0.0001	111	0.927	0.0001	125
	DON	0.863	0.0001	102	0.671	0.0001	125	0.923	0.0001	141
	PON	0.907	0 0001	34	0.519	0.0001	118	0.691	0.0001	105

2.3.7.3 DON

Current precipitation was significantly positively correlated to DON concentration in all three watersheds in the fall. Soil temperature was significantly negatively correlated to DON concentration in all three watersheds in the fall. Stream discharge and DON flux were significantly positively correlated in all seasons.

Multiple linear regression analysis indicated that current precipitation is the single best predictor of DON concentration (WS9: $r^2 = 0.082$, $p=0.0062$; WS2: $r^2 = 0.284$, $p = 0.0001$; WS8: $r^2 = 0.341$, $p = 0.0001$). No other variables explained significantly more variation in DON concentration after current precipitation was in the model.

2.3.7.4 PON

PON concentration was not significantly correlated with any variable in all three watersheds in any season. Stream discharge and PON flux were significantly positively correlated in all seasons.

2.3.8 Litter Inputs Related to Stream Water Concentrations of N

Concentrations of NO_3-N and NH_4-N were not significantly related to litter N inputs as leaves, needles, woody, or miscellaneous N inputs. Filtered Kjeldahl N was significantly negatively related to needle inputs ($r = -0.550$, $p = 0.0004$), significantly positively related to woody inputs ($r = 0.379$, $p = 0.0204$), significantly positively related to miscellaneous (frass, flower parts, etc.) inputs ($r = 0.358$, $p = 0.0001$), and marginally negatively related to total N inputs in litterfall ($r = -0.287$, $p = 0.0848$).

2.4 Discussion

2.4.1 Seasonal N Concentration Patterns

In general, the patterns of intra-annual precipitation concentrations suggest dilution of N during periods of high rainfall at both elevations. The peaks for DON and PON in May at low elevation and for DON in April at high elevation may be due to pollen dispersal. Most pollen grains are less than 0.45 μm in diameter (Colinvaux 1973) but Douglas-fir and western hemlock pollen may be as large as 0.85 μm (Whitlock, pers. comm.) Pollen grains would therefore be found in both DON and PON fractions. Pollen may contribute substantial amounts of N to deposition. Pollen from 31 gymnosperm species, for example, averaged 2.44% N by dry weight, 63% of which was readily water soluble NH_4-N or DON (Greenfield 1999). Monthly DON concentrations in wet-only deposition were generally lower than or equal to DON concentrations in bulk precipitation at the high elevation site in the Andrews Forest, suggesting that DON concentrations in bulk deposition were influenced by dry deposition, which includes pollen. Annual DON inputs averaged 0.3 kg ha^{-1} yr^{-1} more in bulk deposition than in wet-only deposition at the high elevation site, also suggesting that N from dust or pollen was captured in bulk precipitation.

Curiously, mean annual DON concentrations in precipitation at the Andrews Forest (0.02-0.03 mg L^{-1}) are lower than DON concentrations found in precipitation at remote oceanic sites, which generally range from 0.084 to 0.224 mg L^{-1} (Cornell et al. 1995). N in pollen or other organic forms may be so refractory that the Kjeldahl analysis used at the Andrews Forest does not break it down into NH_4-N, while the ultraviolet photo-oxidation method used by Cornell et al. (1995) may more accurately measure DON.

High concentrations of N in deposition and substantial rainfall combine to produce highest N inputs in April and May at low elevation, and highest inputs in March at high elevation. These peak inputs may be asynchronous because of the

difference in organic N content in precipitation between elevations. DON is the major form of N input at low elevation, while NO_3-N dominates at high elevation. DON deposition may be linked to terrestrial processes (i.e. pollen dispersal), unlike NO_3-N which forms in the atmosphere.

2.4.2 Annual N Concentration Patterns

The temporal pattern of NO_3-N concentrations in bulk precipitation may be a function of increasing population in the Willamette Valley, changes in field burning practices in the Willamette Valley, construction at the Andrews Forest Headquarters site, or changes in forest management practices. There was no significantly increasing or decreasing trend in NO_3-N concentration in wet-only deposition collected by NADP at the same site as the low elevation HJA collector during the period from 1980 to 1991, suggesting that dry deposition may have been increasing during that period. Population within the Willamette Valley has increased during this time period, and NOx emissions in automobile exhaust have undoubtedly increased as well, which might explain the increasing trend. The decrease between approximately 1993 and 1998, however, is harder to explain but may be related effects of legislation that has limited burning of grass fields in the Willamette valley in recent years. The Willamette Valley is home to a $345 million grass seed industry. Growers have historically burned grass residues to control disease, but this practice has been dramatically scaled back in recent years because of concerns about air pollution. In 1984, 237,551 acres of fields were burned, and that number steadily decreased to 40,000 acres in 1998 (Gentiluomo, pers. comm.). This suggests that NO_3-N concentrations should have decreased starting in 1984, but this is not the case. Better burning techniques used in recent years, which are meant to use convection to punch through the inversion layer that is common in the Willamette Valley, may more successfully allow the smoke plume to reach the transport winds. Perhaps improved burning techniques

combined with the reduction in number of acres burned accounts for the decreasing NO_3-N in precipitation between 1991 and 1998.

The pattern in NO_3-N concentrations in precipitation may also be due to local forest management or construction activities. Several trailer homes were moved on to the Andrews Forest Headquarters site beginning in 1980. All trailers were in place by 1984, and the amount of activity at the headquarters site increased dramatically. Permanent apartment buildings at the Andrews Forest Headquarters site were constructed in 1990-1992, and an office/lab building was constructed in 1992-1994. The increased site usage and construction could account for the increased NO_3-N concentration between 1982 and 1994 relative to the 1969 –1981 period. The decrease in NO_3-N concentration between 1994 and 1997 may be due to the reduction in logging and slash burning that began in 1991 as a result of law-suits relating to the harvesting of old-growth forests used by the endangered Spotted Owl.

2.4.3 Annual N Deposition

Average annual DIN inputs in bulk precipitation at the Andrews Forest (0.79 kg ha^{-1} yr^{-1} at the low elevation site and 1.24 kg ha^{-1} yr^{-1} at the high elevation site) are a small fraction of values at sites in the eastern U.S. where deposition of atmospheric pollutants is much higher. Typical values of DIN inputs in bulk deposition for forested sites in the eastern U.S. are 8.7 kg ha^{-1} yr^{-1} at the Hubbard Brook Experimental Forest in New Hampshire (Likens and Bormann 1977) and 12.8 kg ha^{-1} yr^{-1} in eastern Tennessee (Boring 1988).

The average annual quantity of DON in bulk deposition at the Andrews Forest (0.47 kg ha^{-1} yr^{-1} at the high elevation collector, and 0.64 kg ha^{-1} yr^{-1} at the low elevation collector) is smaller than values reported elsewhere. Seely et al. (1998) found 1.9-2.3 kg ha^{-1} yr^{-1} DON in bulk precipitation on Cape Cod, and Campbell et al. (2000) found 1.3 to 2.4 kg ha^{-1} yr^{-1} DON in precipitation at forested watersheds in New Hampshire and Vermont. Total organic N deposition is lower

at the Andrews Forest (1.14 kg ha^{-1} yr^{-1} at the low elevation collector and 0.87 kg ha^{-1} yr^{-1} at the high elevation collector) than in the Sangre de Cristo Mountains of New Mexico, where Gosz (1980) reported organic N inputs of 1.9-3.3 kg ha^{-1} yr^{-1}, and in Walker Branch watershed, Tennessee, where Moore and Nuckols (1984) reported organic inputs of 1.6 kg ha^{-1} yr^{-1}. Storms at the Andrews Forest are from the west, off the Pacific Ocean, and may carry less DON than precipitation at the other sites where there may be more DON deposition that originates from terrestrial sources.

2.4.4 Annual N Outputs:

Outputs of N in stream water at the Andrews Forest are low compared to other locations, and much of the export is organic N. At Hubbard Brook Experimental Forest output of inorganic N alone averaged 3.91 kg ha^{-1} yr^{-1} (Bormann and Likens 1977), while total inorganic and organic outputs at Andrews Forest averaged 0.365 to 0.981 kg ha^{-1} yr^{-1}. Thirty-five to 85% of average annual N outputs from the Andrews watersheds was DON and PON. Other studies quantifying organic N losses in stream water also suggest that organic N may be the major form of N export in many ecosystems. Hedin et al. (1995) estimated that 95% of all N outputs from old-growth forests in southern Chile were in the form of DON. Eighty percent of total N exported from 20 small watersheds in Sweden and Finland was estimated to be organic (Arheimer et al. 1996). PON and DON account for 60-70% of the 4-9 kg ha^{-1} yr^{-1} N exported from Luquillo Experimental Forest in Puerto Rico (McDowell and Asbury 1994). DON comprised 59% of average dissolved N outputs in nine watersheds in Vermont and New Hampshire (Campbell et al. 2000). Fifty percent of exports from 25 tropical watersheds was DON, and 75% was organic N (Lewis et al. 1999).

In undisturbed watersheds at the Andrews Forest, NH_4-N output was roughly twice the NO_3-N output. Ratios of NH_4-N:NO_3-N output have been observed to exceed one for several other old growth forests in Chile and the United

States (Hedin et al. 1995). The low level of NO_3-N relative to NH_4-N in streams at the Andrews may be due to low populations of nitrifiers and/or to denitrification in the soil or stream. Denitrification potential and denitrification rates at upland sites in the Andrews are low, with the latter measuring less than 0.07 kg ha^{-1} $year^{-1}$ (Vermes and Myrold 1991). Denitrification in the stream or riparian zone has not been measured, so the in-stream influence of denitrification is unknown. Sollins (1980) reported, however, that soil solution samples collected in WS10 at depths of 30-200 cm had concentrations averaging between 0.013 and 0.020 mg L^{-1}, suggesting that the low concentrations of NO_3-N in streamwater are similar to those in soil solution and that denitrification is minimal.

2.4.5 Annual Export Related to Hydrology:

2.4.5.1 Nitrate:

The lack of correlation between total annual NO_3-N export and total annual stream discharge in five of the six watersheds may be a function of high biological demand for NO_3-N. Uptake length, a measure of how rapidly a nutrient is removed from stream water, has been measured at 42 m in WS2 during the summer (Munn and Meyer 1990), suggesting strong biotic control on NO_3-N concentration. N:P ratios of 0.74 (Triska et al. 1984) in WS10 and 1.8 in WS2 (Munn and Meyer 1990) have been measured, indicating that the streams are probably N limited, based on the Redfield ratio (Allan 1995). Terrestrial biotic demand for N is also high, and NO_3-N is probably efficiently sequestered by roots and microbes as it percolates through the soil. The pool of NO_3-N in the soil may be so small that stormflow flushes very little into the stream, and increasing stream discharge may not result in increasing NO_3-N export.

In contrast to the other five watersheds, annual NO_3-N export is related to total annual stream discharge in WS2. NO_3-N export is also higher in WS2 than in

the other two undisturbed watersheds. This watershed is at least three times as large as the other watersheds, suggesting that total watershed area may affect the relationship between stream discharge and NO_3-N export. Such an inference is made with caution, however, as hydrologic processes may differ between watersheds for many reasons. The presence of macropores in some watersheds could change the proportion of old water vs. new water delivered to the stream during storm events (Cirmo and McDonnell 1997). New water and old will likely have different NO_3-N signatures because old water will have longer contact time with soil and microorganisms, whereas new water will have a chemistry similar to precipitation. In addition, flushing of NO_3-N from soils in a catchment may be related to the catchment's potential to form variable source areas, and the rate of change of the expanding source area (Creed and Band 1998). A variable source area refers to the saturated soil areas contributing to stormflow that shrink and expand depending on antecedent conditions and storm rainfall. Creed and Band (1998) concluded that, within a given landscape, the dominant control on NO_3-N export may be the topographic complexity of individual catchments that controls variable source area dynamics.

2.4.5.2 Ammonium:

Annual NH_4-N export is significantly related to annual stream discharge in two of the low elevation watersheds and one of the high elevation watersheds. Soil depth in the high elevation watersheds is greater than in the low elevation watersheds, and slopes are not as steep. These differences may result in a longer transit time for water through the soil in the high elevation watersheds, providing greater opportunity for biotic uptake of NH_4-N and thereby lessening the relationship between NH_4-N and stream discharge that might have been detected as water flushed the soil of NH_4-N.

As postulated for NO_3-N, biological uptake in the terrestrial or aquatic ecosystem could obscure a relationship between NH_4-N flushing from the soil

profile and stream discharge. Munn and Meyer (1990) concluded that uptake of NH_4-N by biota in the stream sediment of WS2 was responsible for maintaining low concentrations of NH_4-N in the stream.

Watershed 9 is the outlier among the low elevation watersheds, exhibiting no relationship between annual discharge and annual NH_4-N export. Hillslope routing processes in WS9 deliver precipitation more efficiently to the stream in WS9 than WS2 (Perkins 1997). Water transit time in WS9 may also be less than in WS10, because WS10 has deeper soils than WS9. The variation in water transit times in the soil among the three watersheds could result in the different NH_4-N/discharge relationship observed. However, the most dramatic difference between WS9 and the other watersheds is that it is warmer and drier due to its SW aspect and location near the forest edge adjacent to Blue River reservoir. Higher temperatures may result in greater instream biological demand in WS9 compared to WS2 and WS10, obscuring the relationship between NH_4-N export and annual stream discharge.

2.4.5.3 DON

In contrast to annual NO_3-N and NH_4-N export, annual DON export is related to annual stream discharge in all watersheds. These results suggest that there may be less biological processing of DON in stream water compared to NO_3-N and NH_4-N. DON is thought to be recalcitrant by the time it reaches the stream (Hedin et al 1995; Northup 1995), and may be little modified by stream biota. Annual DON export and annual stream discharge have been shown to be strongly positively related in other sites. For example, fifty-five percent of the variation in annual DON export from 25 tropical watersheds was explained by annual stream discharge (Lewis et al. 1999). This study was a survey over many sites, whereas the results from the Andrews Forest underscore the consistency of the mechanism influencing DON export at a single site.

2.4.5.4 PON

Annual PON export is weakly related to annual stream discharge in four of the six watersheds. Greater discharge results in an increase in the wetted area of the streambank as the stream comes in contact with more detritus, potentially increasing PON concentration. Overland flow, although minor at the Andrews Forest, may also move organic matter into streams during intense storms. Other processes, including dry ravel, raindrop impact, needle ice, and animal movements (Swanson et al. 1982) introduce particles into the channel throughout the year. Even a light rain may wash particles from the forest canopy in throughfall into the stream, increasing PON concentration.

The lack of a relationship between annual PON export and annual stream discharge in WS7 may be due to the generally low discharge in that watershed. Particulate organic matter transport is influenced by physical stream characteristics such as stream bed roughness and woody debris dams, and by biological retention by filamentous algae, macrophytes, and invertebrates (Sedell et al. 1978). The stream in WS7 may not have enough power to entrain particles trapped in interstitial spaces or crevices in the stream bed. The lack of a relationship in WS9 appears to be the result of high PON export in a few years, implying that stochastic inputs of particles to the stream may weaken the discharge/PON export relationship.

2.4.6 Annual Export Comparison Between Unharvested Watersheds

In general, an increase in export of NO_3-N and NH_4-N in one watershed was not mirrored by an increase in export of the same nutrient from the other two unharvested watersheds. This suggests that the processes most strongly influencing NO_3-N export are not functioning at a regional scale; that is, climate variables are not the most significant drivers of NO_3-N and NH_4-N export in the Andrews Forest.

Within-watershed or within-stream processes may have a major impact on total annual NO_3-N and NH_4-N export.

The strong positive correlation between DON export in all three undisturbed watersheds implies that there may be processes operating at the regional scale that affect DON export. Increased precipitation, and therefore increased discharge, result in higher DON export. Within-watershed processes may have a lesser impact on DON export than export of NH_4-N and NO_3-N.

The lack of correlation between PON export in two of the three comparisons also suggests that there may not be a regionally unifying mechanism affecting PON export. Sample sizes for the two statistically non-significant comparisons, however, are small so the ability to detect statistically significant differences is low.

2.4.7 Seasonal Controls on N Concentrations:

Few variables were found to be related to a particular form of N in a given season across all watersheds. The general lack of common relationships found across all three watersheds underscores the value of using multiple watersheds from a single climate zone to make inferences about mechanisms that may control N export. Single watershed results may imply that a particular mechanism is important, but a lot of variation in the response across all watersheds and low correlation coefficients suggest that some of the correlations detected may be spurious. Interpretation of plots of nutrient concentrations and hypothesized mechanisms controlling seasonal N stream chemistry based on consistent statistical results across all three watersheds are discussed below.

2.4.7.1 Fall

The increase in DON concentration in fall as precipitation rises is probably a function of inputs from throughfall and increased decomposition after the dry

summer. Rain may wash the summer's accumulation of insect frass and dry deposition from the canopy to the forest floor and into the stream, resulting in increased stream DON concentration. Abee and Lavender's report (1972) that N in throughfall from six stands of old-growth Douglas-fir at the Andrews Forest had highest N concentrations in the fall support this hypothesis. In addition, decomposer activity increases in the fall as soils wet up, increasing the size of the DON pool and the amount of DON flushing into the stream.

DON stream concentrations also increase as soil temperature decreases. A decrease in DON concentration as a result of reduced decomposer activity due to declining temperatures could be posited. However, multiple linear regression analysis indicates that current precipitation is the single best predictor of DON concentration, and that no other variables explain significantly more variation after current precipitation is in the model. The dominant factor affecting DON concentration in streamwater in the fall is precipitation inputs to the watershed.

The literature suggests precipitation-related mechanisms for the increase in DON observed in the fall. Sollins and McCorrison (1981) observed an increase in DON at the 2.0 m depth in WS10 that began in August 1976 and peaked in November 1976. Decomposer activity may be stimulated as soils wet up in the fall, resulting in elevated Kjeldahl N in soil solution. Some of the fall increase in DON concentration in stream water may therefore be a function of elevated DON in groundwater seeping into the stream. Other evidence suggests that flushing from the upper soil horizons results in the increased concentration of DON in streamwater. DOC concentrations peak before spring stream discharge peaks in the Snake River (Hornberger et al. 1994) and in a small headwater catchment in Colorado (Boyer et al. 1996), in a pattern similar to that observed for DON in the Andrews Forest watersheds. These responses were hypothesized to be the result of increased flows through the upper soil horizon during snowmelt (analogous to rainfall at the Andrews Forest), which flushed DOC enriched interstitial water, built up during low flow periods, to the stream. Data taken during single storm events at the Andrews Forest also suggest that flushing may be occurring. DON

concentration in the stream during a storm in WS10 followed a typical hysteresis pattern (Fredriksen 1972), rising rapidly to peak concentration before the hydrograph peaked, and then declining.

It is unclear whether or not litter inputs into the stream may be related to the increase in DON concentrations in the fall, as needle inputs are negatively related to DON concentrations and woody and miscellaneous (frass, seeds, fruit) inputs are positively related to DON concentrations. Peak litter inputs coincide with rapidly increasing stream discharge, making it impossible to determine if litter inputs or soil flushing is the dominant source of DON in streamwater. Litter could potentially be a substantial source of dissolved organic matter in streams. In headwater streams at Coweeta and Hubbard Brook, for example, leaf litter in the stream can contribute as much as 30% to 40% of daily DOC export (McDowell and Fisher 1976; Meyer et al. 1998). Despite having such high potential to impact stream DON chemistry, however, litterfall has been reported to have no effect on stream N chemistry at the West Fork Walker Branch watershed in Tennessee (Nuckols and Moore 1982). Changes in N concentrations in stream water may not be observed because leaf litter leachate in the stream may be labile and stimulates decomposition, causing N leached from litter to be rapidly sequestered by decomposers. In Andrews Forest WS10, N concentrations of various litter substrates in the stream were lowest at abscission and increased as decomposition proceeded (Triska et al. 1984), suggesting uptake of N from the stream. Maximum absolute N content of Douglas-fir litter occurred at 30-40% loss of mass for leaf packs in the stream in WS10 (Triska and Buckley 1978), also implying net uptake of N in litter entering the stream.

2.4.7.2 Winter:

Positive correlations between current precipitation and soil moisture and DON concentration imply that DON concentration in stream water is related to the amount of water flushing through the soil. As soil moisture and precipitation

decline from December to April, DON concentration drops. Decomposition will be low during this season, and DON concentration in the stream may be a function of the level of the water table and the degree to which upper soil horizons are being flushed of nutrients. The pool of DON in the soil will have been depleted by the fall storms, and by April there may be little left to enter the stream.

2.4.7.3 Spring/Summer:

Biotic control on NO_3-N concentrations is implied during this period when elevated light and temperature stimulate biological activity in the stream. As NH_4-N concentration decreases, the chances of detection of a non-zero NO_3-N concentration decrease. NO_3-N concentration is positively related to NH_4-N concentration in stream water in all three unharvested watersheds, suggesting that NO_3-N concentration in stream water may be substrate limited, or that NO_3-N and NH_4-N concentrations are affected by similar processes. Biological demand by stream organisms may play a strong role in regulating stream chemistry during this season. Biological uptake in streams at the Andrews have been shown to be light-limited (Gregory 1980), and diel fluctuations in NO_3-N have been observed in a first-order stream in the Andrews Forest (Vanderbilt, unpublished data) with highest concentrations occurring during the night.

Statistically significant differences between DON or PON load and NH_4-N stream concentration were not detected in all watersheds. However, the small peaks in WS8 in June and in May in WS9, as well as the elevated levels of NH_4-N for the period May, June, and July may be related to pollen deposition. Gymnosperm pollen contains 1.9 to 3.68 % N of which 6.1 to 8.2 % is water soluble NH_4-N (Greenfield 1999). Pollen has been shown to be a significant source of N to soils in the spring-time. For example, a young *Pinus radiata* plantation in Canberra, Australia was estimated to produce 21 kg ha^{-1} N in pollen a year (Greenfield 1999). N deposition from pollen was 0.34-0.49 kg ha^{-1} in boreal forest sites in Manitoba (Lee et al. 1996). Pollen entering streams at the Andrews Forest

during the late spring and early summer may leach significant amounts of N rapidly. Interestingly, Sollins and McCorison (1981) noted a bi-modal peak in Kjeldahl N from lysimeters at four depths in WS10, one peak occurring in late spring just before saturated flow ceased. The peak seen in stream water may reflect increased concentrations of N soil water as well as the leaching of pollen falling directly into the stream.

2.4.8 Correlation Coefficients and the Scale of the Data

The amount of variation explained by any one variable in the seasonal analysis is quite small, with typical r values of 0.2 to 0.4. Much of the variation in streamwater N concentrations may be obscured by the coarse resolution of the data. The flow-weighted N concentration data reflect changes in concentration over a three-week period, during which concentration may have changed dramatically more than once. Processes affecting N concentrations may operate at scales too fine to be detected by three-week flow-weighted sampling. Concentrations of N, for example, have been observed to differ between rising and falling limbs of a storm hydrograph (Fredriksen 1972; Henderson et al. 1977; Bond 1979), and within a single day, probably due to instream biotic uptake (Vanderbilt, unpublished data). Bakke (1993) also reported low correlations when modeling NO_3-N concentrations using a long-term data set at another site in Oregon, and concluded that grab samples taken at two-week intervals also lacked the resolution to adequately capture fluctuations in NO_3-N concentrations.

2.4.9 Seasonal Patterns of Andrews Compared to Other Sites

Relatively few studies examine the relationship between seasonal variation in stream discharge and DON concentration (Table 2-11). A relationship between stream discharge and DOC has been more frequently reported, however, and DON and DOC response to discharge will probably be similar (Campbell et al. 2000).

Consistent with results of this study, most others report that DOC concentration increases with increasing discharge; in none of the studies I reviewed was there evidence of a dilution of DOC as stream discharge increased.

Few other studies report no seasonal patterns in NO_3-N concentration as were observed at the Andrews Forest (Williams and Melack 1997; Feller and Kimmins 1979; Stottlemyer and Troendle 1992). Bakke (1993) did note, however, that peaks in NO_3-N concentration occur during the fall, winter, and spring in other watersheds in Oregon, just as they do at the Andrews Forest. More commonly, NO_3-N pulses in stream water have been reported during snowmelt (Hubbard Brook, NH: Likens and Bormann 1995; Isle Royale National Park, MI: Stottlemyer et al. 1998; Stottlemyer and Toczydlowski 1999; Turkey Lakes, Ontario: Creed and Band 1998; Sierra Nevada, CA: Johnson et al. 1997).

This pattern is attributed to the flushing from the soil of NO_3-N built-up from decomposition during the winter (Rascher et al. 1987) and release of NO_3-N stored in the snowpack (Williams and Melack 1991). Similar pulses in NO_3-N concentration in streamwater have been observed when fall rains flush soils of decomposition products built up during a dry summer (Edmonds et al. 1998; Fenn and Poth 1999). Winter-time, or dormant season, increases in NO_3-N in these ecosystems are frequently followed by low growing season NO_3-N concentrations that are attributed to high NO_3-N uptake by soils and vegetation (Foster et al. 1989; Edmonds et al. 1995; Lajtha et al. 1995). Where vegetation demand for N is low, such as in mature deciduous forests, the summer-time low may not be observed (Vitousek and Reiners 1975; Martin 1979).

In contrast to the winter-maxima, summer-minima NO_3-N concentration pattern observed at many sites in the northeastern U.S. and Canada, streams at Coweeta Hydrologic Lab, NC (Swank and Vose 1997) and at Walker Branch, TN (Mulholland 1992) have the opposite seasonal NO_3-N pattern. Mulholland (1992) posited that in areas where streamwater temperatures remain above 0 ^{0}C

Table 2-11 Relationship detected between stream discharge and N or DOC concentrations at tropical and temperate forested sites. NA means data not reported.

	Bear Brook , NH (in Hubbard Brook Exp. Forest)*	Turkey Lakes, Ontario	Como Creek, CO*	Walker Branch, TN*	Coweeta Hydrologic Lab, NC	Northwest Costa Rica	New England (New Hampshire and Vermont)	Luquillo, Puerto Rico
WS size (ha)	130	2.3-62.7	664	38.4, 59.1	13, 61	37, 36, 55, 264, 311, 319	13-163 (9 watersheds)	16.2, 262, 326
Sampling interval		Two week interval	Weekly for three years	individual storms or weekly samples	weekly	monthly	Weekly or biweekly	weekly
Stream Order	2	1	2	1	2	NA	NA	NA
NO_3-N	+	0	-	-	0	+	+/0	0
NH_4-N	NA	NA	0	-	0	NA	0	0
DOC	+	NA	+	+	+	+	NA	+
DON	+	0	0	NA	NA	+	+/0	NA
POC	+	NA	NA	NA	+	NA	NA	+
PON	NA	NA	NA	+	NA	NA	NA	NA
TN	NA	NA	NA	+/-	NA	NA	NA	NA
Reference	Fisher and Likens 1973; McDowell and Likens 1988; Johnson et al. 1969	Nicolson 1988; Creed and Band 1998	Lewis and Grant 1979	Mulholland 1992; Elwood and Turner 1989; Henderson et al. 1977; Nuckols and Moore 1982	Meyer and Tate 1983; Swank and Vose 1997	Newbold et al. 1995	Campbell et al. 2000	McDowell and Asbury 1994

*adapted from Meyer et al. 1988

during the dormant season rates of N immobilization from autumn leaf litter by soil and streamwater organisms may be high. McDowell and Asbury (1994) found that leaf litter inputs were negatively correlated with stream NO_3-N concentrations in a tropical stream, also suggesting that litter inputs to streams may increase NO_3-N immobilization. At the Andrews Forest, peaks in NO_3-N concentration do occur sometimes when discharge is high, but not in any consistent temporal pattern. High biological demand in soils and streams, which remain unfrozen during the dormant season, may allow very little NO_3-N to leak from catchments at the Andrews Forest.

2.5 Conclusion

The long-term precipitation and streamwater N chemistry datasets at the Andrews Forest offer a valuable opportunity to examine temporal patterns of organic and inorganic N dynamics in forested watersheds in an area little affected by atmospheric pollution. Three of the six watersheds sampled for stream chemistry at the Andrews Forest have received no silvicultural treatments, making it possible to evaluate how patterns of N dynamics vary between undisturbed watersheds in a single region.

My analyses suggest that different factors control organic and inorganic N export. Annual DON export is closely tied to annual stream discharge, in contrast to annual DIN export. At the seasonal scale, DON concentrations in streamwater were positively related to precipitation inputs in the fall, suggesting flushing of DON into the stream. Variations in NO_3-N and NH_4-N concentrations at the seasonal scale were unrelated to precipitation or stream discharge in all watersheds, supporting the hypothesis that biotic processing significantly influences streamwater concentrations of DIN. Taken together, the results of this study imply that within-watershed biotic processing controls streamwater concentrations of DIN. Further, the significant relationships between annual DON export and stream discharge and seasonal DON export and precipitation imply that DON may be recalcitrant, and largely unavailable to streamwater organisms.

Research characterizing DON compounds in streamwater and tracing DON to its source as root exudates, leaf leachate, or decomposition products will help clarify what drives the seasonal DON patterns observed in this study.

3 Nitrogen Retention in Watersheds of the Andrews Forest

3.1 Introduction

Since the pioneering work of Likens et al. (1970) at Hubbard Brook, NH demonstrated how small watersheds can be used to quantify N losses from forest ecosystems following clear-cutting, many watershed studies have shown how variable N loss following forest harvest can be (Miller and Newton 1983; Martin et al. 1984; Feller and Kimmins 1984; Swank and Vose 1997). Presently, this variability in N export among harvested and unharvested watersheds is being re-examined with the new objective of learning what properties of forests can be used to predict the amount of atmospherically-deposited N a forest can retain.

Nitrogen deposition to temperate forest ecosystems has increased since pre-industrial times due to increased fossil fuel combustion, fertilizer use, and livestock production (Vitousek et al. 1997). Some forests are now receiving N inputs in excess of biological demand, a potentially deleterious condition termed N saturation (Agren and Bosatta 1988; Aber et al. 1989) that is characterized by increased nitrate leaching (Stoddard 1994). The question of how much atmospherically-deposited N a forest can retain before becoming N saturated is of great interest to forest managers, but the mechanisms controlling N retention are not yet well understood. Annual and intra-annual variability in N retention in long-term data sets may offer insights into the relative importance of factors affecting N retention. Pardo (1995), for example, used long-term data from four watersheds with different aged forests at Hubbard Brook, NH, to demonstrate the importance of land-use history on N retention.

Several fates are possible for N deposited in a forest. N may be immobilized by the soil microbial community, taken up by vegetation, volatilized as ammonia, non-biologically incorporated into humus or clay, denitrified, or leached from the soil. N transport and retention mechanisms are further influenced by catchment characteristics, including hydrologic regime, temperature, soil, and

vegetation. Studies in areas receiving elevated levels of N have shown the importance of soil texture (Lajtha et al. 1995), forest stand age (Emmett et al. 1993), and nitrogen status of the site (Gundersen et al. 1998a) to N retention.

Long-term stream-chemistry and atmospheric deposition data for three harvested and three unharvested watersheds at the Andrews Forest, OR, extend from 1969 to the present. These data represent a valuable resource for studying N retention for three reasons. First, the effect of vegetation age on N retention may be studied because watersheds contain either very young, mature, or old-growth forest. Second, while most other watershed studies have evaluated only dissolved inorganic nitrogen (DIN) outputs relative to DIN inputs (Dise and Wright 1995; Pardo 1995), both organic and inorganic fluxes have been monitored at the Andrews Forest, making it possible to explore how inclusion of DON affects retention estimates. Third, few studies of N retention have included inputs from N-fixing species, which are substantial at some sites in the Andrews Forest.

In this study, I report on seasonal and annual retention of N in the six small watersheds at the Andrews Forest. I predict that seasonal patterns of retention will show an imprint of vegetation uptake of N. I also predict that N retention will be lower in those watersheds receiving high inputs of biologically-fixed N, because elevated N inputs will lead to greater nitrate leaching. Finally, I expect that N demand by the young, regrowing forest in the years following harvest will be higher than the N demand by the old-growth forest that existed in the watershed prior to harvest, and that N retention in the watershed after the re-establishment of a young forest post-harvest will be greater than N retention pre-harvest.

3.2 Methods

3.2.1 Study Area

The six watersheds under study are located in the H.J. Andrews Experimental Forest in the west-central Cascade Mountains of Oregon (Table 3-1). This rugged, 6400-ha area is characterized by dense coniferous forests and steep slopes. Elevation ranges from 412 m to 1630 m. The Pacific Ocean lies 160 km to the west and strongly influences the climate of the Andrews Forest. Mean January and July temperatures are 2 and 18 degrees C, respectively. Annual precipitation averages between 208 cm at low elevations and 340 cm at high elevations (Daly 1995). About 80% of annual precipitation falls in the October-March period during storms of relatively long duration (12-72 hours) and low intensity. Precipitation is typically dominated by rain below 350 m, and snow above 1100 m. At elevations above 750 m, snowpack may persist for several months. Rain and snow events both occur between 400 and 1200 m elevation (Harr 1981).

3.2.2 Watershed Characteristics

Watersheds were classified into two categories: harvested watersheds (WS6, WS7, WS10) and unharvested watersheds (WS2, WS9, WS8). Vegetation within all the six watersheds before harvest was dominated by Douglas-fir (*Pseudotsuga mensiezii)*. Nitrogen-fixing *Ceanothus velutinus* dominated WS6 and WS7 for the first 15 years post-harvest, before being overtopped by Douglas-fir. Less common tree species occurring in the watersheds include *Tsuga heterophylla*, *Thuja plicata*, and, at high elevation, *Abies amabilis*. Understory shrub species included *Rhododendron macrophyllum*, *Acer circinatum*, and *Castanopsis chrysophylla*.

Almost all soils in the six watersheds are Inceptisols. Soils of high elevation WS6, WS7, and WS8 are frigid Andic Dystrudepts, with fine-loamy or

loamy-skeletal texture (D. Lammers, U.S. Forest Service, personal communication). Soil depth typically ranges from one to three meters to bedrock (Dyrness and Hawk 1972). Soils in WS2 are fine-loamy or loamy skeletal Typic Haplumbrepts, and fine-loamy Typic Dystrochrepts. WS10 soils are Typic Dystrochrepts with fine-loamy to loamy-skeletal texture, Umbric Dystrochrepts, and Typic Hamplumbrepts. Soils in WS9 are Typic Haplumbrepts with fine-loamy texture, Typic Dystrochrepts with coarse-loamy texture, and Ultic Hapludalfs of fine-silty texture. Soil depth to saprolite is less than 3 m in WS 9 (Fredriksen 1975), between one and two meters in WS2 (Rothacher, Dyrness, and Fredriksen 1967), and as much as six meters in WS10, although generally shallower (Fredriksen 1975).

3.2.3 Precipitation and Streamwater Sampling

One precipitation sampler used in this study is located in high elevation WS7, and the other is located in a clearing near low elevation WS9. Precipitation samples for chemical analysis were collected at three-week intervals prior to June 1988 and at one-week intervals thereafter. From the inception of the study until 1988, both precipitation collectors consisted of stainless steel funnels to catch bulk precipitation that was then fed through plastic tubing to an acid-washed polyethylene carboy within an insulated box for storage. In 1988, the high elevation funnel collector was replaced with an Aerochem collector that separates wet and dry deposition.

Table 3-1 Characteristics of the small gaged experimental watersheds at the Andrews Forest

Watershed	Area (ha)	Elevation (m)	Aspect	% Basal Area Logged (Year of Harvest)	Type of Harvest	Period of Record (WY)	Dominant Vegetation in 2000
WS2	60	530-1070	NW	0	Uncut	1982 – present	470-year-old Douglas-fir
WS9	8.5	425-700	SW	0	Uncut	1969 – present	470-year-old Douglas-fir
WS10	10.2	430-670	SW	100 (1975)	Clear-cut/ Not burned	1969 – present	25-year-old Douglas-fir
WS6	13.0	863-1013	S	100 (1974)	Clear-cut/ Broadcast burn	1972-1987	25-year-old Douglas-fir
WS7	15.4	908-1097	SSE	60 (1974) 40 (1984)	Shelterwood Cut/ Broadcast burn	1972-1987	25-year-old Douglas-fir
WS8	21.4	955-1190	SSE	0	Uncut	1972 - present	170-year-old Douglas-fir

Streamwater was sampled just above the weir at the outlet of each watershed. Sampling location has not changed since the inception of the study. Samples were collected by proportional water sampler (Fredriksen 1969), which samples a fixed volume of water at a frequency proportional to stream flow. Individual samples were composited in an acid-washed polyethylene carboy, stored in the dark, and collected at three-week intervals until June 1988. Since that time, carboys have been collected once a week, refrigerated, and combined at three-week intervals for chemical analysis. Comparisons of samples collected once a week and composited after three weeks vs. samples left in the gage house for three weeks have shown that concentrations of NO_3-N, NH_4-N, and DON do not change significantly when left in the gage house for three weeks (Vanderbilt and Lajtha, in review).

Stream discharge has been measured continuously with rectangular weirs at the high elevation watersheds (WS6, WS7, WS8) since 1963. Stream discharge has been measured continuously with trapezoidal weirs at the low elevation watersheds (WS2, W9, WS10) since 1953.

N flux at three-week intervals was calculated by multiplying N concentration by the volume of discharge for that interval.

3.2.4 Chemical analysis

Stream and precipitation samples were filtered in the laboratory prior to analysis. Glass-fiber GF/C filters (1.2 μm pore size) were used from the inception of the study until 1983, after which GF/F (0.7 μm pore size) filters were used (Martin and Harr 1989). Filters were pre-washed with deionized water and dried at 65 °C. NO_3-N was measured from 1968 to July 1978 manually using a cadmium reduction column and a Spec 20 spectrophotometer. Since July 1978, NO_3-N has been measured using the same chemistry on a Technicon Auto-Analyzer II. From 1966 to 1978, NH_4-N was analyzed on macro-Kjeldahl equipment by distillation and Nesslerization. Since 1978, NH_4-N has been measured using the phenate procedure on a Technicon Auto-Analyzer II. The

macro-Kjeldahl analysis was used to measure DON and PON. PON was calculated as the difference between Kjeldahl N content of filtered and unfiltered samples. DON concentration was calculated as the difference between Kjeldahl N and NH_4-N concentration in the filtered sampled.

3.2.5 Estimation of Missing Values in N Chemistry Data Sets

Missing values for NO_3-N and NH_4-N fluxes in the stream chemistry records were estimated using linear regression. Available flux data for each form of N were regressed against stream discharge data. Stream discharge data were then used to estimate NO_3-N or NH_4-N flux with the equation developed. Separate equations were derived for each watershed.

Six DON data points were missing from the stream chemistry record for the summer months of 1987 for WS6 and WS7. Regression of three-week values of DON fluxes against stream discharge was not significant. Regression of total annual export of DON against total annual stream discharge was also not significant. Therefore, to estimate DON for June through September of 1987, I summed DON fluxes from June to September for 1972 to 1986, averaged across years, and used this value to estimate summer DON export from WS6 and WS7 for summer 1987.

Summer N inputs were not recorded at the low elevation precipitation collector from 1969 to 1980. To estimate N inputs for these summers, I calculated summer N inputs (June through September) for years 1981 to 1997, and regressed summer N inputs against summer precipitation. Summer N inputs for 1969 to 1980 were then estimated using this equation and summer precipitation for these years.

Summer N inputs were not recorded at the high elevation precipitation collector from 1975 to 1981. To estimate N inputs for these summers, I calculated summer N inputs (June through September) for years 1972-73, and 1982 -1986, and regressed summer N inputs against summer precipitation. Summer N inputs

for 1975 to 1981 were then estimated using this equation and summer precipitation for these years.

A correction factor had to be applied to the high elevation precipitation data collected from water year 1988 to the present, because of the change from a bulk deposition collector to an Aerochem wet/dry deposition collector at this time. Precipitation sample collections were made for a short interval in both collector types (10/11/88 – 12/20/88), and these data indicate that NO_3-N and NH_4-N concentrations do not differ significantly between wet and bulk deposition (NO_3-N: n = 11, two-sided p = 0.522; NH_4-N: n = 11, two-sided p = 0.211). Only four data points were available to assess DON concentration difference in this interval, which was not considered sufficient. Mean annual concentration of DON in precipitation from 1970 to 1987 was 0.028 mg L^{-1}. Mean concentration of DON in precipitation from 1988 to 1998 was 0.010 mg L^{-1}. I corrected for this difference by adding (0.018 * precipitation volume) to each flux value in the high elevation precipitation N data set for 1988 to 1998.

3.2.6 Estimation of Total N Inputs

Wet deposition N inputs were based on chemical analysis of precipitation collected in bulk or wet/dry deposition collectors located at two elevations in the Andrews Forest, as described above. Dry deposition was estimated from measurements taken in a national survey of dry deposition in forest ecosystems. Estimates of biological fixation were based on values reported in the literature for the Andrews Forest.

Dry deposition N inputs were estimated using a regression analysis relating wet-only DIN input to total (wet+dry) total N inputs. This regression was developed using low-elevation watershed data from twelve Integrated Forest Study (IFS) sites across the continental United States, including two sites in the Pacific Northwest (r^2 = 0.91; Lovett and Lindbergh 1993). We used this regression because cloud water inputs of N from pollution sources are assumed to be minimal at our sites. The equation predicts that total DIN deposition is approximately 2.09

times wet-only DIN deposition. Although there is considerable disagreement in the literature over the relationship between wet and dry deposition (e.g. Ollinger et al. 1993), others have found that dry deposition is often about half, or slightly less, of total N inputs (Cappellato et al. 1995, Holland et al. 1999, Geigert et al. 1994). The contribution of dry N deposition to total deposition can vary annually (Geigert et al. 1994) as well as over small spatial scales, and thus I realize that this estimate of total deposition has a large error associated with it.

My estimates or total N inputs were made based on bulk deposition inputs, while the IFS regression equation applies to wet-only DIN. Although NO_3-N concentration in bulk deposition at the low elevation site did not differ significantly from NO_3-N concentration in an adjacent National Atmospheric Deposition Program (NADP) collector ($n = 252$, two-sided $p= 0.117$), NH_4-N concentration in bulk deposition was found to be significantly lower than in wet-only deposition ($n = 252$, two-sided $p = 0.021$). Total estimates of atmospheric inputs may therefore be slightly low at the low elevation precipitation collector. NO_3-N and NH_4-N did not differ between wet vs. bulk deposition at high elevation (as discussed above).

Inputs of biologically-fixed N were estimated from literature values from studies conducted in or near the Andrews Forest. In watersheds with old-growth vegetation, lichen inputs are considered to be constant each year at 2.8 kg ha^{-1} yr^{-1} (Sollins et al.1980). Ceanothus was the dominant species on WS6 and WS7 for the first 15 years post-harvest. N inputs from *Ceanothus* were calculated by assuming a fixation rate of 60 kg ha^{-1} yr^{-1}, an intermediate value in the range reported in the literature (Zavitkovski and Newton, 1968; Youngberg and Wollum, 1976; McNabb and Cromack 1983; Binkley et al. 1982) and multiplying it by the percent watershed cover of *Ceanothus*, estimated from vegetation data collected in 1979 and 1986 (Tucker, unpublished). The rate of increase of *Ceanothus* cover was estimated by subtracting cover of *Ceanothus* in 1979 from *Ceanothus* cover in 1986 and dividing by seven years. *Ceanothus* covered 7% of WS7 in 1979 and 47% in 1986, and thus its cover increase averaged 6% per year. *Ceanothus* covered 10% of WS6 in 1979 and 75% in 1986, thus averaging a 9%

increase per year. Inputs from free-living N-fixing bacteria in logs and soil were neglected, as they have been measured to be less than 1 kg ha^{-1} yr^{-1} (Heath et al. 1988; Jergensen et al. 1992).

3.2.7 Definition of Intervals Used for Retention Analysis

Three time intervals relating to watershed conditions were identified for each watershed that was treated. The pre-harvest interval extends from the beginning of the stream chemistry record to the year prior to harvest. The post-harvest interval begins the water-year of harvest and ends when annual NO_3-N concentrations had stabilized near pre-disturbance levels. The final period is termed early successional, and extends from the end of the post-disturbance interval until 1998, the last year used in this study.

3.2.8 Annual and Seasonal N Retention

Nitrogen flux for each three-week interval was calculated by multiplying the flow-weighted concentration with the volume of discharge or precipitation for that interval. Nitrogen inputs and outputs were summed over the water year (October 1 to September 30) to calculate annual fluxes. The amount of precipitation for each watershed was calculated by weighting the sampler precipitation volume at the relevant elevation by predicted annual values of precipitation for each watershed, based on an algorithm for spatially distributing estimates of precipitation data from thirteen sites in the Andrews Forest and vicinity (Daly 1995). Dry deposition and biologically-fixed N inputs were added to annual precipitation N fluxes to calculate total N input.

To explore the relationship between water storage and nitrogen storage in a watershed, I calculated annual water retention and annual N retention. This method was used by Jaworski et al. (1992), who used the concept of water yield and N yield (calculated as outputs/inputs of water or N) to evaluate how tightly

coupled N and water yield were in the Potomac River watershed near Washington, D.C.

Annual watershed N retention was calculated using the following formula:

% N Retention =[(N inputs - N outputs)/ N inputs] * 100 [1]

Separate calculations were done for (1) atmospheric DIN (NO_3-N and NH_4-N) inputs and stream DIN outputs, (2) atmospheric DIN + DON inputs and stream DIN + DON outputs, and (3) total N (atmospheric DIN + DON + biologically-fixed N) inputs and stream DIN + DON outputs. Annual water retention was calculated by substituting stream discharge and precipitation into the above equation. Monthly N retention and water retention estimates were also made using equation 1, except average monthly N and water inputs and outputs were used in place of annual N inputs and outputs.

Pearson correlation coefficients were used to compare annual N retention in WS8, WS9, WS2, and WS10. Watersheds 6 and 7 were not included in this analysis because the period of record is short. Pearson correlation coefficients were also used to see how closely N retention and water retention are related within WS8, WS9, WS2, and WS10. All statistical analyses were done using SAS (SAS Institute 1990).

3.2.9 Annual N Uptake Rates of Vegetation in WS10

3.2.9.1 Biomass Calculation:

In 1973, Hawk (1979) established thirty-six 10 X 15 m plots on WS10 in proportion to the area of the four habitat types in the watershed. The four habitat types consist of *Pseudotsuga-Castanopsis* (xeric, 39.2% of the watershed), *Pseudotsuga-Rhododendron-Gaultheria* (warm mesic, 31.2% of the watershed), *Pseudotsuga-Rhododendron-Berberis* (mesic, 17.5% of the watershed), and

Pseudotsuga-Acer-Polystichum (cool moist, 12.1% of the watershed). Variables necessary to calculate biomass of tree, herb, and shrub species were measured in 1973, 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1983, 1985, 1989, and 1993. A list of these variables and details of the study design are described by Gholz et al. (1985).

I obtained summaries of total aboveground tree, shrub, and herbaceous species biomass for 1980, 1983, and 1989 from Dr. Charles Halpern (University of Washington), who calculated them using BIOPAK (Means et al. 1994), software that uses a library of allometric equations developed in the Pacific Northwest to calculate biomass. Total aboveground biomass data were available for individual species. I divided total aboveground biomass into foliage and woody components (stems and branches), and estimated belowground biomass of roots in the following way:

3.2.9.1.1 Trees

Using allometric equations for foliage and stem biomass from BIOPAK (Means et al. 1994), I calculated on average how much of aboveground biomass of tree species is foliage and stems and then used these averages to make assumptions about biomass values. For *Cornus nuttallii*, 65% of aboveground biomass was assumed to be wood and 35% was assumed to be foliage; for *Castanopsis chrysophylla, Acer macrophyllum*, and species classified as 'other', wood was assumed to be 75% of aboveground biomass and foliage was assumed to be 25% of aboveground biomass. Eighty-five and 15% of aboveground biomass of conifers was assumed to be wood and foliage, respectively, based on an allometric equation for young Douglas-fir. Using allometric equations for total root biomass compared to total aboveground biomass, I estimated that total root system biomass (coarse and fine roots) is 21% of total aboveground biomass. Vogt et al. (1987) estimated that fine root (< 2 mm in diameter) biomass of conifers in western Washington was 13-27% of foliage biomass prior to canopy closure. Because canopy closure had not yet occurred on WS10 in 1989, I estimated fine root biomass at an intermediate value of 20% of foliage biomass for all years. Large

roots, defined here as roots > 2 mm in diameter, were calculated by taking the difference of total root biomass and fine root biomass.

3.2.9.1.2 Shrubs

Using allometric equations from BIOPAK for total aboveground biomass and total stem biomass for *Gaultheria shallon*, *Acer circinatum*, and *Holodiscus discolor*, I calculated that on average stems of these species are 57%, 55% and 69% of aboveground biomass, respectively. For all shrub species, I estimated stem biomass to be 60% of aboveground biomass. As for trees, I estimated that total root biomass is 21% of total aboveground biomass, and fine roots are 20% of foliage biomass.

3.2.9.1.3 Herbs

Using allometric equations from BIOPAK for total aboveground biomass of *Senecio sylvaticus*, I calculated that root biomass averages 31% of total aboveground biomass. I assumed this ratio for all herbaceous species, and that all roots of herbaceous species are fine roots.

3.2.9.2 Calculation of N content of Vegetation

3.2.9.2.1 Trees

Dry weight of wood, foliage, large roots, and fine roots of each species was multiplied by N concentration by dry weight of each component to calculate the total amount of N in tree biomass on WS10 in 1980, 1983, and 1989. The quantity of N in wood and foliage differs by species (Table 3-2). Coarse root N concentration was estimated as 0.09% of coarse root biomass (Sollins et al. 1980), and fine root N concentration was estimated as 0.622% of fine root biomass (Santantonio et al. 1977). The latter values were estimated from samples taken from Douglas-fir trees in the old-growth forest that occupied WS10 prior to

harvest. Because Gordon and Jackson (2000) did not find that angiosperm and conifer fine roots differ significantly in N concentration in a synthesis of data from 56 studies encompassing data from grasses, shrubs, and treees, I used these numbers to estimate N concentrations in roots of all species. Minimal N retranslocation was also assumed (Aerts 1992; Nambiar 1987; Gordon and Jackson 2000).

Table 3-2 N concentration (percent of dry weight) of wood and foliage of tree species.

Species	Wood	Foliage	Reference
Castanopsis chrysophylla	0.152	1.07	Gholz et al., unpublished Data from WS10
Cornus nuttallii	0.248	1.20	Gholz et al., unpublished Data from WS10
Pseudotsuga menziesii (also used to estimate *Tsuga heterophylla*)	0.133	1.30	Cole and Rapp 1981 Data from 22-year-old stand in Washington
Acer macrophyllum	0.225	2.00	Gholz et al., unpublished Data from WS10
Taxus brevifolia	0.150	1.30	Gholz et al., unpublished Data from WS10
Other species	0.100	1.00	Gholz et al., unpublished Data from WS10

3.2.9.2.2 Shrubs

Estimates of N concentration of foliage and stems of some shrubs sampled following harvest on WS10 were available from Gholz et al. (unpublished). *Acer circinatum* foliage N concentration was estimated as 1.8% of foliage biomass, and stem N concentration was estimated as 0.253% of stem biomass. Nitrogen concentrations of foliage and wood for other species were estimated as 1% and 0.25%, respectively, based on values reported by Gholz et al. (unpublished).

Large root N concentrations were assumed to be 0.09% of large root biomass, and fine roots were assumed to be 0.622% of fine root biomass, as for trees.

3.2.9.2.3 Herbs

N concentration of aboveground biomass was assumed to be 1.5%, the average N concentration of six herbaceous species samples on WS10 in 1976 (Gholz et al. unpublished). N concentration of fine roots was assumed to be 0.622%, the same as tree fine roots

3.2.9.3 Calculation of Annual N Uptake Rates

Total N in vegetation in WS10 was calculated for 1980, 1983, and 1989. N accumulation rates in perennial tissues (stems and coarse roots) for intervals 1980-1983 and 1983-1989 were calculated by taking the difference in N in these components between years, and dividing by number of years separating sampling dates. N uptake for 1983, for example, was then calculated as: N accumulation in perennial tissues + 100% of N in herbaceous species for 1983 + 30% of total N in fine roots of shrubs and trees + 50% of conifer foliage and 100% of deciduous tree and shrub foliage. Thirty percent of fine roots were assumed to turn over each year (Sollins et al. 1980), and young conifers were assumed to have a two year foliage turn over time (Overton et al. 1973).

3.2.10 Harvest Effects on N Dynamics

The effect of harvest on NO_3-N and DON + NH_4-N concentrations and fluxes was assessed using a paired t-tests for clear-cut watershed 10 compared to reference watershed 9. DON and NH_4-N could not be analyzed separately, because on Kjeldahl N data was collected during the post-harvest period.

3.3 Results

3.3.1 N Inputs

Total DIN inputs, including dry deposition, averaged 1.56 kg ha^{-1} yr^{-1} (SE = 0.13; range: 0.92 – 3.47 kg ha^{-1} yr^{-1}) at the low elevation collector and 2.42 kg ha^{-1} yr^{-1} (SE = 0.14; range: 1.89-3.71 kg ha^{-1} yr^{-1}) at the high elevation collector during the period of record. Total DIN + DON inputs at the low elevation collector, including dry deposition, averaged 2.54 kg ha^{-1} yr^{-1} (SE = 0.13; range: 1.44 – 4.39 kg ha^{-1} yr^{-1}) at the low elevation collector and 2.92 kg ha^{-1} yr^{-1} at the high elevation collector (SE = 0.15; range: 1.77 – 4.98 kg ha^{-1} yr^{-1}).

In WS2 and WS9, which receive N inputs from lichens, total N inputs ranged from 4.24 kg ha^{-1} yr^{-1} to 7.19 kg ha^{-1} yr^{-1} and from 4.57 to 7.72 kg ha^{-1} yr^{-1}, respectively (Table 3-3). In WS6 and WS7, which had N inputs from *Ceanothus*, total N inputs ranged from 1.77 to 48.02 kg ha^{-1} yr^{-1}, and 1.77 to 31.22 kg ha^{-1} yr^{-1}, respectively.

3.3.2 N Outputs

DIN outputs in the unharvested watersheds during the period of record averaged 0.118 kg $ha^{-1}yr^{-1}$ in WS9, 0.108 kg ha^{-1} yr^{-1} in WS2, and 0.153 kg $ha^{-1}yr^{-1}$ in WS8. DON outputs in unharvested watersheds during the period of record averaged 0.521 kg ha^{-1} yr^{-1} in WS9, 0.242 kg ha^{-1} yr^{-1} in WS2 and 0.293 kg $ha^{-1}yr^{-1}$ in WS8. Average annual DIN outputs and DON outputs were higher in the post-harvest period compared to the pre-harvest and successional periods (Table 3-3).

Table 3-3 Mean, SE, and range of N inputs and outputs (kg ha^{-1} yr^{-1}) in each watershed at the Andrews Forest. T refers to trace (inputs < 1 kg ha^{-1} yr^{-1})

Watershed	**Years**	**N Inputs** Mean (SE) Range		**N Outputs** Mean (SE) Range	
		Atmospheric	Biological Fixation	DIN	DON
2	1982-1998	2.51 (0.211) 1.44-4.39	2.8	0.108 (0.017) 0.032-0.238	0.242 (0.024) 0.155-0.477
6 (Pre-harvest)	1973-1974	2.36,3.02	T	0.090 (0.060) 0.029-0.137	0.311 (0.161) 0.145-0.466
(Post-harvest)	1975-1980	2.77 (0.265) 1.77-3.23	6-12	0.484 (0.084) 0.260-0.830	0.510 (0.098) 0.276-0.793
(Early Successional)	1981-1987	3.71 (0.300) 2.81-4.32	18-45	0.210 (0.047) 0.077-0.405	0.321 (0.080) 0.091-0.654
7 (Pre-harvest)	1973-1974	2.36, 3.02	T	0.045 (0.028) 0.017-0.073	0.552 (0.055) 0.183-0.292
(Post-harvest)	1975-1978	2.65 (0.392) 1.77-2.77	T	0.302 (0.136) 0.049-0.682	0.378 (0.100) 0.153-0.623
(Early Successional)	1979-1987	3.56 (0.253) 2.79-4.32	4.2-28.2	0.098 (0.013) 0.056-0.189	0.197 (0.081) 0.108-0.372
8	1973-1998	2.92 (0.146) 1.77-4.32	T	0.153 (0.018) 0.018-0.426	0.298 (0.036) 0.108-0.847
9	1969-1998	2.54 (0.128) 1.44-4.39	2.8	0.118 (0.012) 0.047-0.165	0.521 (0.037) 0.280-0.973
10 (Pre-harvest)	1969-1975	2.61 (0.192) 2.11-3.6	2.8	0.0.217 (0.105) 0.014-0.854	0.541 (0.114) 0.314-0.767
(Post-harvest)	1976-1981	2.54 (0.181) 1.80-2.98	T	0.468 (0.107) 0.219-0.834	0.692 (0.114) 0.434-1.214
(Early Successional)	1982-1998	2.51 (0.211) 1.44-4.39	T	0.202 (0.028) 0.045-0.439	0.383 (0.051) 0.190-0.858

3.3.3 Annual Nitrogen Retention

Within a given watershed, retention of N calculated by using only DIN inputs and outputs tends to be higher than retention of N calculated by using DIN and DON inputs and outputs (Figure 3-1 and Figure 3-2). The former retention calculation averaged 88-97% in the undisturbed watersheds during the pre-harvest and successional periods and in the harvested watersheds when NO_3-N export was not elevated. The latter calculation of retention averaged 80 to 94% during the same intervals. The retention estimate dropped regardless of whether only DIN or DIN and DON were used in the calculation for the years following harvesting in a watershed, due to increased outputs of NO_3-N. Retention of N as calculated by including DIN, DON and biologically-fixed N inputs is higher than when only DON and DIN inputs are included, but generally not as high as when retention is calculated using only DIN. DIN + DON + biologically-fixed N retention averaged 89 to 99%.

3.3.4 N Retention vs. Water Retention

Significant positive correlations were detected between annual water retention and annual N retention (Table 3-4). Annual DIN retention in each watershed was significantly positively correlated with DIN retention in the other watersheds, as was DON + DIN retention (Table 3-5 and Table 3-6).

3.3.5 Seasonal N Retention:

Seasonal patterns of N retention are similar in the three watersheds with mature or old-growth vegetation (Figure 3-3). Nitrogen retention is highest in September or October, when water retention is also highest. Nitrogen retention is lowest in December, January, and February, when water retention also

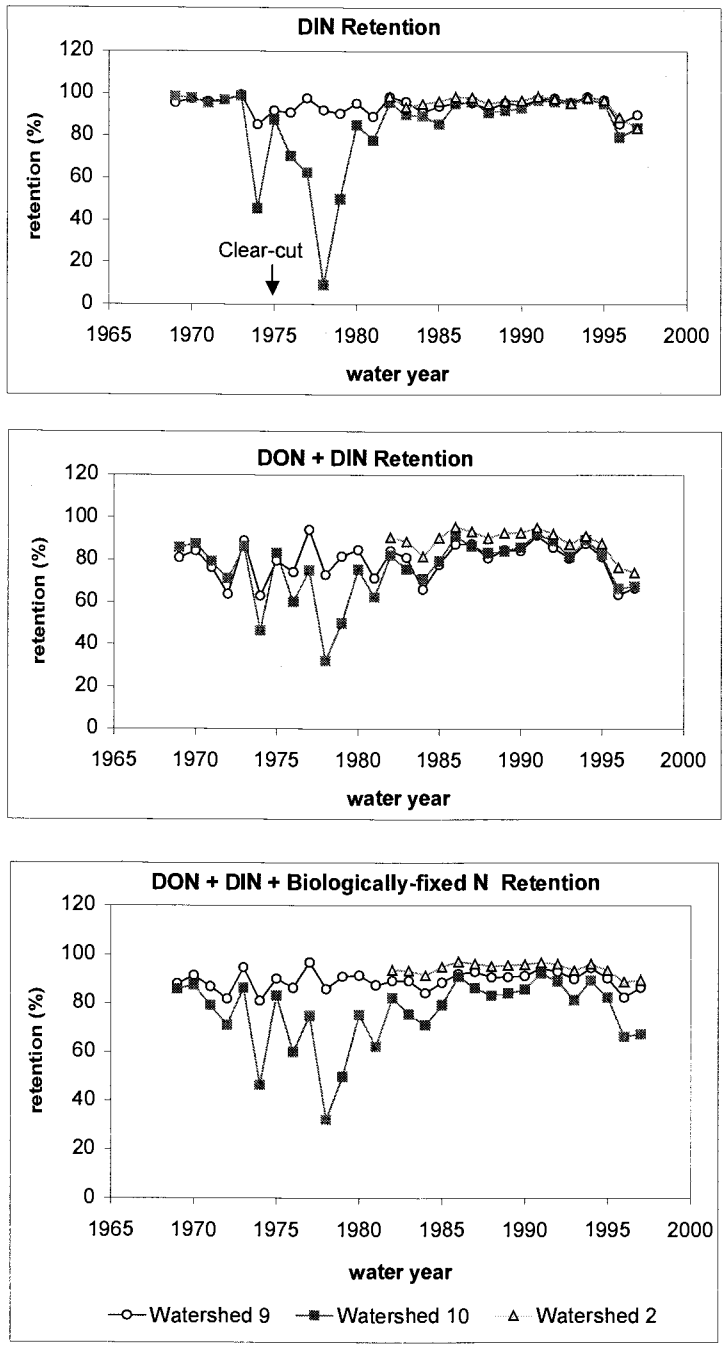

Figure 3-1 Annual N retention as calculated using DIN inputs and outputs, DIN + DON inputs and outputs, and DIN + DON + biologically-fixed N inputs and DIN+DON outputs in low elevation watersheds of the Andrews Forest. Watershed 10 was clear-cut in 1975. WS2 and WS9 are unharvested.

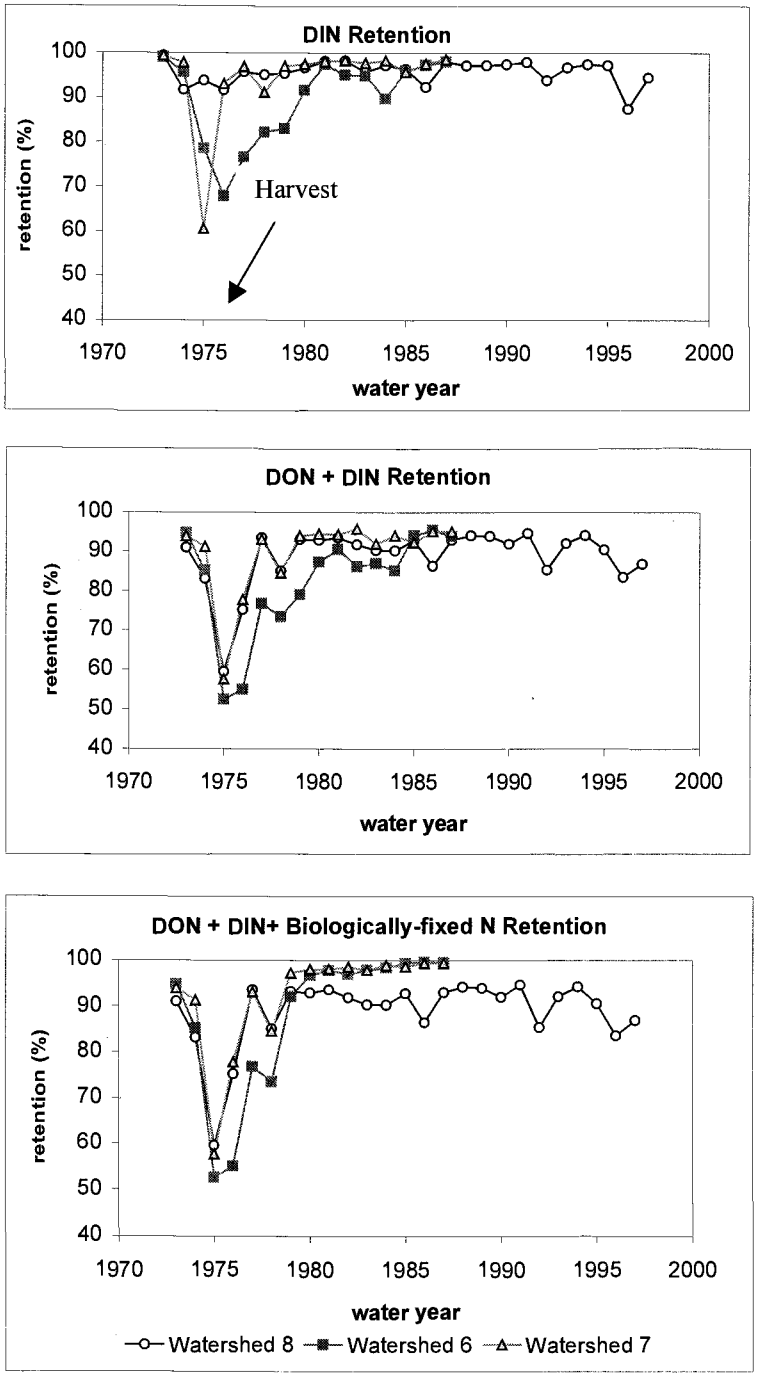

Figure 3-2 Annual N retention as calculated using DIN inputs and outputs, DIN + DON inputs and outputs, and DIN + DON + biologically-fixed N inputs and DIN + DON outputs in high elevation watersheds of the Andrews Forest. WS6 and WS7 were clear-cut and shelterwood cut, respectively, in 1976. WS8 is unharvested.

Table 3-4 Pearson correlation coefficients (p value) for DIN retention and DIN + DON retention vs. annual water retention

	WS2 (n = 16)	WS8 (n = 24)	WS9 (n = 28)	WS10 (n = 21)
DIN retention vs. water retention	0.554 (0.026)	0.388 (0.061)	0.340 (0.037)	0.522 (0.015)
DIN + DON retention vs. water retention	0.620 (0.011)	0.463 (0.023)	0.586 (0.001)	0.671 (0.002)

Table 3-5 Pearson correlation coefficients (n , p value) for annual DIN retention between watersheds.

	WS10	WS2	WS8
WS9	0.88 (21, 0.001)	0.77 (16, 0.001)	0.63 (25, 0.001)
WS10		0.81 (16, 0.001)	0.65 (21, 0.004)
WS2			0.52 (16, 0.042)

Table 3-6 Pearson correlation coefficients (n, p value) for annual DIN + DON retention between watersheds.

	WS10	WS2	WS8
WS9	0.89 (22, 0.001)	0.94 (16, 0.001)	0.53 (25, 0.007)*
WS10		0.93 (16, 0.001)	0.62 (18, 0.006)
WS2			0.53 (16, 0.036)

* Extreme outlier 1975 removed. The exceptionally high DON export in 1975 suggests analytical error or sample contamination.

tends to be lowest. In the spring, when water retention levels off (WS2 and WS8) or begins to rise (WS9), the ratio of N retained to water retained reaches its maximum in April (WS2, WS9), or May (WS8).

Seasonal N retention patterns are amplified during the period following harvest in the treated watersheds (Figure 3-4). Nitrogen retention becomes negative in WS10 in the months with lowest water retention during the post-harvest period. Seasonal retention patterns in WS6 and WS7 following harvest suggest greatly reduced N retention in the months with lowest water retention (January and December).

3.3.6 N Uptake by Vegetation

Total N in biomass in 1980, 1983, and 1989 was estimated to be 78, 101 and 110 kg ha^{-1}, respectively. Most N is in foliage, which includes the herbaceous layer (Table 3-7). N uptake rate in vegetation in 1983 was estimated to be 73.1 kg ha^{-1} yr^{-1}, while in the 1989 it was estimated to be 78.1 kg ha^{-1} yr^{-1}. Herbaceous vegetation accounts for over 30% of N demand in both years.

3.3.7 Effect of Harvesting on N Concentrations and N Output in WS9 and WS10

Annual NO_3-N concentrations (Table 3-8) were significantly elevated in clear-cut WS10 relative to NO_3-N concentrations in the reference watershed (WS9) during the six years following harvest (paired t-test, $p = 0.018$). Annual DON + NH_4-N concentrations did not differ significantly between the reference and clear-cut watersheds during the six years post-harvest (paired t-test, $p = 0.612$). Annual NO_3-N output was significantly higher in the clear-cut watershed in the six years following harvest compared to the reference watershed (paired t-test, $p = 0.015$), as was DON + NH_4-N output (paired t-test, $p = 0.010$). NO_3-N outputs did not differ between watersheds during either the pre-harvest period ($p = 0.281$), or during the early-successional period ($p = 0.283$). DON + NH_4-N output, however, was significantly lower in the harvested watershed pre-harvest ($p = 0.013$), although not during the early-successional period ($p = 0.066$).

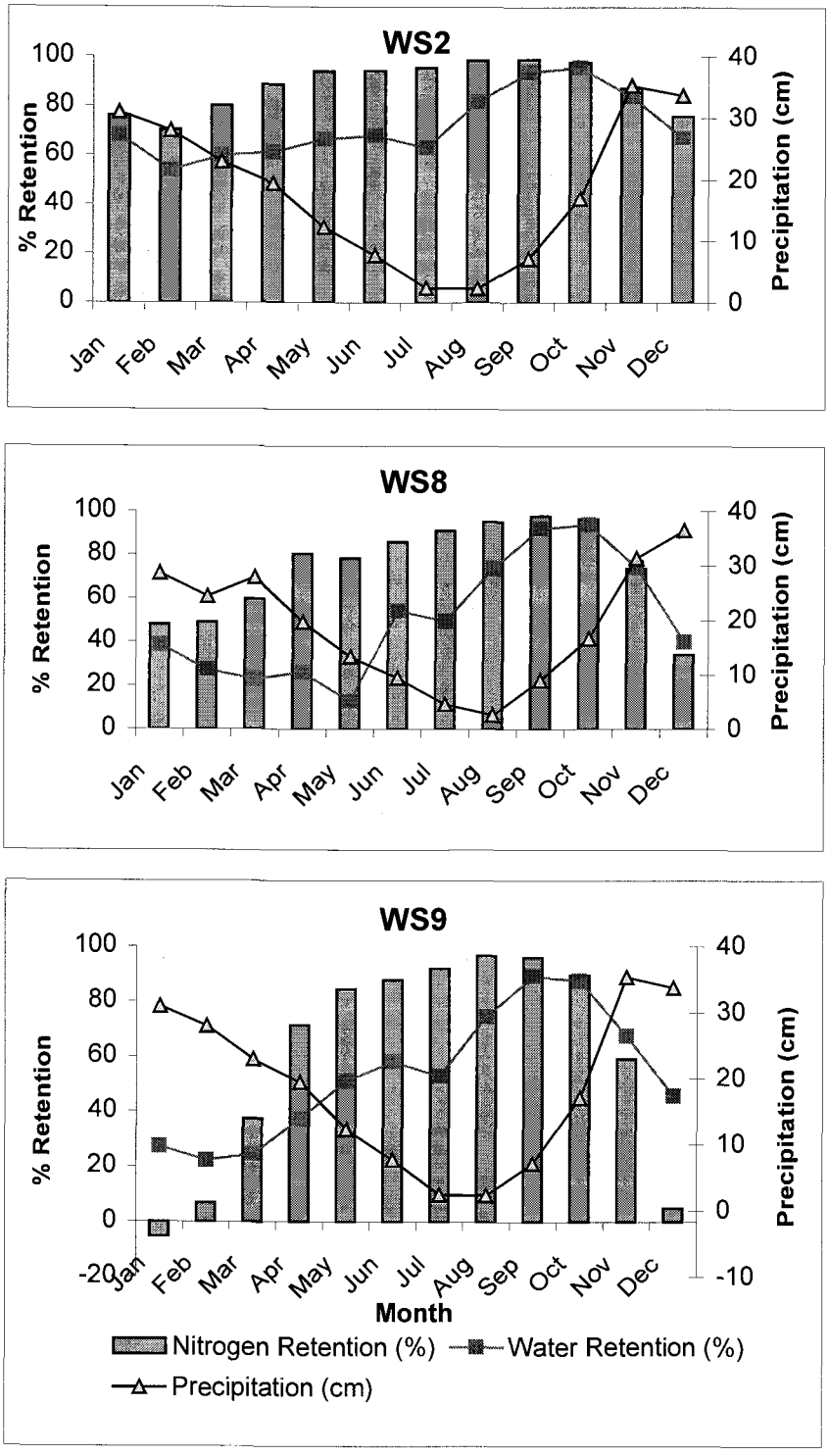

Figure 3-3 Monthly retention as calculated using DON and DIN inputs and outputs in the three unharvested watersheds at the Andrews Forest

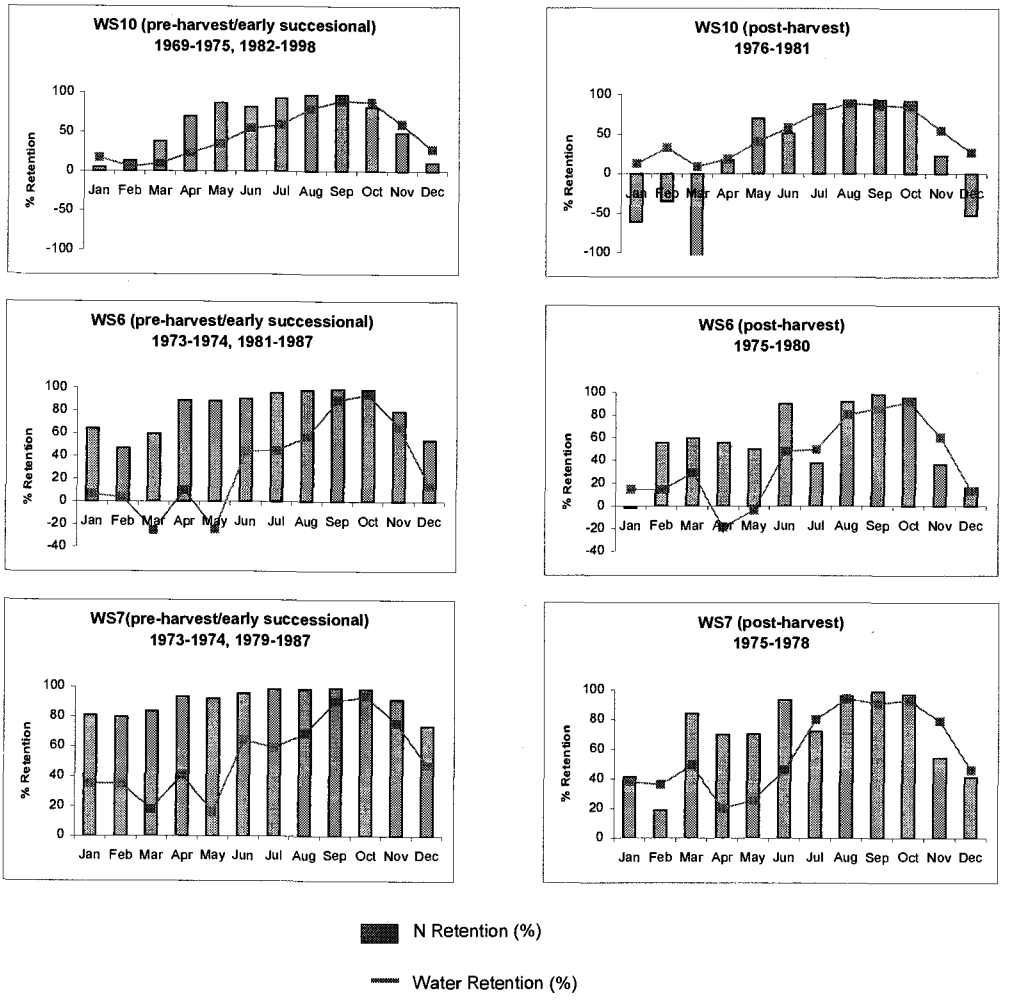

Figure 3-4 Monthly N retention as calculated using DIN + DON inputs and outputs during the pre-harvest/early-successional periods and post-harvest period in the three harvested watersheds at the Andrews Forest.

Table 3-7 Biomass and N (g m^{-2}) in vegetation in WS10 in 1980, 1983, and 1989. Values in parentheses are standard errors.

		Biomass				Nitrogen			
Year		Foliage	Roots	Fine Roots	Stems	Foliage	Coarse Roots	Fine Roots	Stems
1980	Herbs	286.9	--	57.4	--	3.2	--	0.4	--
		(32.68)		(6.54)		(0.36)		(0.04)	
	Shrubs	138.9	61.8	27.8	169.8	1.4	0.1	0.2	0.4
		(20.82)	(9.25)	(4.16)	(25.45)	(0.21	(0.01	(0.03)	(0.06)
	Trees	98.7	76.8	19.7	266.9	1.5	0.1	0.1	0.5
		(2.12)	(1.59)	(0.42)	(5.47)	(0.04)	(0.00)	(0.00)	(0.01)
	TOTAL	524.5	138.6	104.9	436.7	6.0	0.2	0.7	1.0
1983	Herbs	325.9	--	65.2	--	3.6	--	0.4	
		(35.27)		(7.05)		(0.04)		(0.04)	
	Shrubs	189.3	84.1	37.9	231.4	1.9	0.1	0.2	0.6
		(25.74)	(11.44)	(5.15)	(31.46)	(0.26)	(0.01)	(0.03)	(0.08)
	Trees	159.5	122.4	31.9	423.2	2.2	0.1	0.2	0.8
		(2.36)	(1.75)	(0.47)	(6.01)	(0.04)	(0.00)	(0.00)	(0.01)
	TOTAL	674.7	206.5	135.0	654.6	7.7	0.2	0.9	1.4
1989	Herbs	342.5	--	68.5	--	3.8	--	0.4	--
		(38.38)		(7.68)		(0.42)		(0.05)	
	Shrubs	175.3	77.9	35.1	214.2	1.8	0.1	0.2	0.5
		(22.56)	(10.03)	(4.51)	(27.57)	(0.23)	(0.01)	(0.03)	(0.07)
	Trees	235.3	228.4	47.1	852.5	2.4	0.21	0.3	1.4
		(3.01)	(3.01)	(0.60)	(11.59)	(0.03)	(0.00)	(0.00)	(0.02
	TOTAL	753.1	306.3	150.7	1066.7	7.9	0.3	0.9	1.9

Table 3-8 Mean concentrations and outputs (SE) of NO_3-N and DON + NH_4-N during the period prior to harvest, the six years following harvest, and the early-successional years when NO_3-N concentration had stabilized near pre-disturbance levels in WS9 and WS10. DON and NH_4-N are reported together because between 1974 and 1978 filtered samples were analyzed for Kjeldahl N (DON and NH_4-N), but not for NH_4-N alone. Pairs of values labeled with the same letter were not significantly different at the α=0.05 level.

Analysis Period (n = years)	Concentration (mg L^{-1})		Flux (kg ha^{-1} yr^{-1})	
	Reference (WS9)	Clear-cut (WS10)	Reference (WS9)	Clear-cut (WS10)
NO_3-N				
Pre-harvest (n = 7)	0.001 (0.0006)[a]	0.006 (0.0043)[a]	0.027 (0.012)c	0.127 (0.097)c
Post-harvest (n = 6)	0.003 (0.0008)[a]	0.028 (0.0038)[b]	0.033 (0.009)c	0.385 (0.094)d
Early Successional (n = 14)	0.003 (0.0008)[a]	0.003 (0.0005)[a]	0.036 (0.009)a	0.049 (0.009)a
DON + NH_4-N				
Pre-harvest (n = 7)	0.05 (0.003)[a]	0.04 (0.002)[b]	0.722 (0.106)[c]	0.597 (0.081)[d]
Post-harvest (n = 6)	0.06 (0.004)[a]	0.06 (0.004)[a]	0.557 (0.089)[c]	0.814 (0.114)[d]
Early Successional (n = 14)	0.05 (0.002)[a]	0.03 (0.001)[a]	0.552 (0.046)[c]	0.513 (0.053)[c]

3.4 Discussion

3.4.1 Seasonal Patterns of N retention

In the eastern U.S., where monthly precipitation is more constant throughout the year than it is in Oregon where precipitation is highly seasonal, researchers have related seasonal concentrations (Likens et al. 1977) and fluxes of N (Lajtha et al. 1995) to vegetation uptake. Here, we rely on seasonal patterns of DON + DIN retention to illustrate the influence of forest vegetation on N retention. The ratio of N retention to water retention can be interpreted as the amount of N retained by the ecosystem for each unit of water retained in the soil in the part of the year when precipitation and streamflow are both elevated, November through May. During the other months of the year, a higher proportion of streamflow is groundwater, and the N retention/water retention ratio is not interpretable as an index of vegetation influence on N retention. In the low elevation watersheds, the peak in N retention/water retention occurs in April, as vegetation is breaking dormancy and vegetation demand for N increases. The peak in this ratio occurs in May at high elevation watershed 8, which is delayed phenologically with respect to the low elevation watersheds because of snowpack and cooler temperatures.

Low N retention in the winter months demonstrates the influence of hydrology on N retention. N deposition is highest during these months (Vanderbilt and Lajtha, in review), but N retention is low because movement of large volumes of water through vegetation and soil flush N into the stream without the competing influence of vegetation uptake. The seasonal pattern of N retention in the disturbed watersheds (Figure 3-4) underscores the importance of hydrology on winter retention of N; in the absence of vegetation uptake, and when higher soil concentrations of nitrate exist due to disturbance, N retention may even be negative, as in WS10.

The magnitude of seasonal N retention in WS9 and WS10 (undisturbed conditions) is similar, while seasonal N retention in the other four watersheds

varies less. WS9 and WS10 have shallower soils than the other watersheds, and their hydrographs respond more quickly to storm events (Perkins 1997). More rapid flushing of the soil during the winter months may account for the reduced winter N retention in these watersheds. The high elevation watersheds also have a winter snowpack, and precipitation does not, therefore, immediately infiltrate the soil. In other sites in North America, a pulse of NO_3-N enters the stream at snowmelt (Johnson et al. 1997; Rascher et al. 1997; Foster et al. 1989), which is attributed to NO_3-N from the snow itself, or mineralization beneath the snowpack. No such pulse is observed at the Andrews, which may reflect higher uptake of NO_3-N in the spring at this very N-limited site compared to the others, or a lower input of N that is largely retained.

3.4.2 Annual Retention of Nitrogen

DIN retention, as calculated using only inputs and outputs of DIN, at the Andrews is higher than most estimates from the literature. DIN retention in the undisturbed watersheds at the Andrews averages around 95%, while at Hubbard Brook, except for very young stands (1-15 years old), retention of bulk deposition N ranges from 40 to 85% (Pardo et al. 1995). Mitchell et al. (1996) estimated 85% retention of wet and dry DIN deposition in a hardwood watershed in the Central Adirondacks, and Lovett et al. (2000) estimated that retention of dry and wet DIN deposition ranged from 69-90% in 39 small watersheds in the Catskills Mountains in southern New York. Higher estimates were reported by Stohlgren et al. (1991) in Sequoia National Park, CA, where nearly 100 % of DIN in bulk deposition was retained within the watershed.

The variation in the ability of forests to sequester atmospheric N may be affected by characteristics of the forest floor. Forest floor C/N ratio has been suggested as an important indicator of forest ability to retain DIN from the atmosphere. Gundersen et al. (1998a) examined a range of sites with DIN deposition ranging from 3-60 kg ha^{-1} yr^{-1} and found that sites with forest floor C/N

ratio below 25 leached NO_3-N, while leaching was negligible for sites having forest floor C/N ratio above 30. Nitrification rate increases significantly below C/N ratios of 24-27 in forested ecosystems (McNulty et al. 1991). Gundersen et al. (1998b) also found that N leaching is positively related to site "N status", an index based on a range of characteristics such as N mineralization and N fluxes in litterfall. Lovett et al. (2000) hypothesized that the variability in NO_3-N retention in Catskills watersheds is related to vegetation type; that is, watersheds with forests having low litter quality and therefore low rates of nitrification have higher N retention.

The difference in N status between the Andrews and Hubbard Brook may explain the difference in retention between these sites. Forest floor C:N ratio at the Andrews Forest is approximately 100 (Sollins et al. 1980), while at Hubbard Brook the C:N ratio of the soil in an uncut watershed was 23 (Johnson 1995). Although the total amount of N in both ecosystems is about the same, twice the amount of N at Hubbard Brook is stored in litter compared to the Andrews (Sollins et al. 1980). Coniferous vegetation typically has a higher C:N ratio than hardwood vegetation. These differences in C:N ratio, N distribution in the ecosystem, and litter quality may result in higher NO_3-N leaching at Hubbard Brook relative to the Andrews Forest. In addition, DIN inputs in bulk precipitation at Hubbard Brook are estimated to be 8.7 kg ha^{-1} yr^{-1} (Likens et al. 1977), approximately six times inputs of dry and wet deposition at the Andrews Forest. Many studies have reported that higher N deposition is associated with increased NO_3-N leaching from forested sites (Dise and Wright 1995; Tietema et al. 1998; Bredemeier et a. 1998).

Plant growth plays a major role in N retention. Johnson (1992) reported that in 19 of 24 cases he assessed, vegetation N increment could account for nearly all atmospheric N inputs. Vitousek and Reiners (1975) hypothesized that young, aggrading stands will retain more DIN than more slowly growing mature forests. Consistent with the Vitousek and Reiners (1975) hypothesis, elevated NO_3-N leaching in mature forests relative to young forests has been observed at locations in New England (Vitousek 1977; Pardo et al. 1995), Wales (Emmett et al. 1993), and Sweden (Wiklander et al. 1991). Results of our study, however, do little to

support this hypothesis. DIN retention is virtually identical between low elevation WS2 and WS9 (470-year-old forest) and WS10 (20-year-old forest). Similarly, DIN retention in high elevation WS8 (170-year-old forest), is almost the same as DIN retention in treated WS6 and WS7 fifteen years after harvest. The Andrews forests may be too N-limited, and N deposition too low, to express the stand age effect on DIN retention.

Inclusion of DON in retention estimates reduces percent N retention in all watersheds, but the pattern of DON + DIN retention is similar to that of DIN retention. In this case, the nutrient retention hypothesis of Vitousek and Reiners (1975) clearly is not supported, as old-growth forest in WS2 has consistently higher DIN + DON retention compared to 20-year-old forest in WS10. In the high elevation watersheds, DIN + DON retention is apparently equivalent in all watersheds, regardless of treatment. These results support Hedin et al. (1995) who concluded that biogeochemical theory regarding vegetation impact on N cycling may not apply when DON is included in retention estimates, because DON flux from a forest is more likely linked to watershed hydrology than vegetation parameters.

Inclusion of biologically-fixed N in the estimate of N retention suggests that biologically-fixed N inputs to this system are efficiently retained. High inputs of organic N (as much as 60 kg ha^{-1} yr^{-1}) by *Ceanothus velutinus* in the high elevation watersheds do not result in elevated nitrate leaching. This was contrary to expectations, as streams adjacent to red alder stands commonly have elevated NO_3-N concentrations (Van Miegroet and Cole 1984; Wigington et al. 1998). Further, sites receiving similar levels of N inputs from atmospheric DIN deposition frequently exhibit nitrate leaching in excess of historical levels (Dise and Wright 1995). *Ceanothus* litter may interact with soils in such a way as to preclude nitrate leaching. Binkley et al. (1982) determined that accretion rates of N in soil beneath *Ceanothus* in WS6 at the Andrews Forest were 42-48 kg ha^{-1} yr^{-1}. Soil C also increased 40-60% beneath *Ceanothus*. Binkley et al. (1982) also noted that a soil N availability index increased only slightly under *Ceanothus* compared to soils

under Douglas-fir. Similarly, Johnson (1995) found increased N and C accretion under *Ceanothus* compared to stands of Jeffrey Pine in the Sierras, but no increase in nitrate leaching. Johnson noted that the difference in C and N beneath the two stand types was probably not due to litter quantity, but rather the differential formation of humus by the condensation of phenols with amino acids in *Ceanothus* litter (Paul and Clark 1996).

There are a few interesting fluctuations in the retention estimates. In WS8, retention is reduced in 1986, the year a large flood occurred. Nitrate concentrations were elevated that year in WS8, presumably because of flood-related streamside disturbance. Also noteworthy is the decreased DON + DIN retention in WS8 in 1975 and 1976, which is unexpected and suspect. These low retention values are due to elevated DON concentrations in this period for which there is no explanation. The values of these concentrations are among the highest reported, and were sustained for six consecutive sampling periods, which is also a pattern that is not repeated in the rest of the data set. I believe that this result is due to laboratory error or sample contamination.

The lack of a decrease in retention in 1984 in WS7 indicates that the removal of the remaining 40% of forest in the shelterwood cut did not result in elevated NO_3-N leaching. The big reduction in N retention in WS10 in 1974 is either due to researcher activity in the watershed which disturbed near-stream areas or elevated NO_3-N leaching resulting from herbicide treatment on a small section of the watershed (Sollins et al. 1981).

Watershed hydrology undoubtedly has an impact on N retention in Andrews Forest watersheds. Annual DIN retention and annual DIN + DON retention are significantly (or nearly so, in the case of WS8 DIN retention) related to annual water retention, implying that more N is lost from the forest when more water flushes through the soil. Further, annual retention of DIN and DIN + DON is significantly correlated between watersheds, suggesting that regional-scale climatic processes influence N retention in Andrews Forest watersheds.

3.4.3 N Uptake by Regrowing Vegetation

The estimate of N uptake by regrowing vegetation in WS10 fourteen years after harvest (78.1 kg ha^{-1} yr^{-1}) is well above the estimate of N uptake in the third year following harvesting (13 kg ha^{-1} yr^{-1}; Gholz et al. 1985) and the estimate of N uptake by the old-growth forest (42 kg ha^{-1} yr^{-1}) that occupied WS10 before it was clear-cut (Sollins et al. 1980). Gholz et al. (1985) did not estimate N uptake by roots, but using biomass numbers from his paper and the N concentration data outlined above, I calculated that his annual N uptake rate in 1978 would be 15 kg ha^{-1} yr^{-1} if roots were included. These results suggest that N uptake on WS10 increases for at least the first 14 years after harvest but eventually decreases toward an old-growth steady state value.

Much of the N uptake in the early years on WS10 is attributable to herbaceous species, a successional pattern that may significantly impact N retention. Gholz et al. (1985) reported that *Senecio sylvaticus*, an exotic species, dominated the herbaceous vegetation during the first three years after clear-cutting on WS10, but was nearly absent in 1979. This is a typical successional pattern in Douglas-fir forests of the Cascades (Dryness 1973; Halpern 1989). The success of this species is due to its high production of wind-dispersed seed and annual life cycle, and its rapid revegetative ability may help prevent the loss of nutrients from a disturbed site. In the eastern United States, it has been posited that site revegetation by young, dense stands of pin cherry in response to increased nutrient availability significantly reduces the loss of nutrients following disturbance (Marks and Bormann 1972), but it is not clear that *Senecio sylvaticus* has the same magnitude of an effect in the Cascades. N uptake by 4-6 year old pin cherry stands is 50% greater than uptake in mature eastern deciduous forest, while N uptake during the peak year of *Senecio* growth was only 25% of N uptake by the old growth forest. NPP of 4-6 year old pin cherry was also higher than for a mature forest, while NPP of 3-year-old vegetation in WS10 was 20% of pre-disturbance NPP. The strength of *Senecio sylvaticus* as an N sink is smaller and shorter-lived than the pin cherry phenomenon of the eastern U.S. Further, the rapid decrease in

Senecio after three years may be related to a change in nutrient availability, but Halpern et al. (1997) showed that the limiting nutrient is probably not N.

A major source of error in the N uptake calculations are the assumptions made about fine root production. Sollins et al. (1980) assumed that 30% of a total pool of 11, 270 kg ha^{-1} of fine roots (as measured by Santantonio et al. 1977) turned over each year, which accounts for 21 kg ha^{-1} yr^{-1} N uptake alone. Their definition of fine roots was < 5 mm, as opposed to < 2 mm, which I used because of the relationship between stand age and fine root biomass of this size reported by Vogt et al. (1983) that I used as an assumption. Despite the difference in definition of fine roots, the discrepancy between the measured 11,270 kg ha^{-1} of fine roots in the old growth forest in WS10 (Santantonio et al. 1977) and my estimate of fine roots in 1989 of 1840 kg ha^{-1} seems large. Others (Raich and Nadelhoffer 1989) have suggested that fine root biomass and foliage biomass have a roughly 1:1 relationship. If I had used this estimate, I would have estimated fine root N turnover in 1989 as 29 kg ha^{-1} yr^{-1} instead of 8 kg ha^{-1} yr^{-1}, and total N uptake would have been estimated as 96.3 kg ha^{-1} yr^{-1}.

N uptake in WS10 three years following harvest was at least 6.5 times inputs of DIN from atmospheric deposition, based on the Gholz et al. (1985) estimate. Based on my estimates, N uptake in the 14-year-old Douglas-fir forest is 30-40 times DIN inputs from atmospheric deposition. The pre-harvest old-growth forest and the young forest in WS10 have almost identical DIN retention estimates, illustrating that in this N limited system vegetation demand for N may not have much of an imprint on N retention. However, it's worth noting that three years after harvesting, when vegetation N demand greatly exceeds deposition inputs, stream nitrate concentrations were still elevated. This may be because vegetation uptake and time of peak N availability in the soil are not synchronized; that is, vegetation will be taking up inorganic nitrogen in the spring and early summer, but shut down later in summer when soils dry. Soils wet up in the fall as vegetation senesces or becomes dormant, and DIN from litter and the many decomposing roots in the watershed following harvest will flush into the stream.

3.4.4 Disturbance Impacts on N Cycling in WS10

The magnitude of stream N chemistry response to clear-cutting may be related to the availability of N on the site prior to disturbance. At the Andrews Forest, the average annual increase in N export in the seven years following harvest relative to export in the control watershed was 0.51 kg ha^{-1} yr^{-1}, two-thirds of which is NO_3-N . Similar losses were observed in the high elevation clear-cut WS6 at Andrews Forest (Martin and Harr 1989). In contrast, during the ten years following harvest and herbicide application in a watershed at Hubbard Brook, approximately 50 kg ha^{-1} yr^{-1} of NO_3-N were lost in streamwater, compared to 4.3 kg ha^{-1} yr^{-1} lost from a control watershed (Likens et al. 1978). Vitousek et al. (1979, 1982) found that nitrate losses following disturbance were lower from N-poor forests than N-rich forests because litter in N-poor sites tends to have a greated immobilization capacity. Hubbard Brook is occupied by hardwood forests with higher litter quality than the conifers in the Andrews forest. Further, as noted by Sollins et al. (1980), the higher C/N ratio in soils at the Andrews will tend to favor N immobilization, while greater mineralization would be expected at Hubbard Brook with its lower C/N ratio.

Nitrate concentrations in streams draining clear-cut watersheds at Andrews Forest returned to reference watershed levels six or seven years following harvest (this study, Martin and Harr 1989). This recovery interval is similar to those reported for other studies in the Pacific Northwest for which long-term data are available (Scrivener 1982; Feller and Kimmins 1984; Adams and Stack 1989). The single exception is a watershed in the Bull Run area near Portland, OR, on which slash was left to decompose, as opposed to being burned or removed from the site as occurred elsewhere. Nitrate concentrations in the stream draining the Bull Run watershed were still significantly elevated relative to reference watersheds 10 years post-harvest (Harr and Fredriksen 1988).

The disposition of slash following harvest has been shown to influence N retention elsewhere. Rosen and Lundmark-Thelin (1987) found significantly elevated levels of DIN and DON in soil water collected beneath slash piles

compared to soil water between piles. Elevated DIN beneath piles was attributed to increased mineralization and lack of plant uptake. DIN concentration in precipitation decreased between the top and bottom of slash piles, indicating that slash piles are not themselves sources of DIN, an effect also observed in a study in Wales (Stevens and Hornung 1990). Emmett and Quarmby (1991) concluded that the presence of slash alters microclimatic conditions such that microbial immobilization of atmospheric DIN inputs is reduced.

3.4.5 Magnitude of N Loss Following Harvest

DIN and DON losses following harvesting were tiny compared to the amount of N removed from the watershed as boles and branches. N export from WS10 in the eight years following harvest exceeded N export from WS9, the control watershed, by 4.02 kg ha^{-1}. N removed during logging on WS10 was 576 kg ha^{-1} (Cromack et al. 1979).

3.5 Conclusion

Seasonal patterns of DIN retention in undisturbed watersheds at Andrews Forest exhibit an imprint of vegetation uptake in the spring and hydrology in the winter. Seasonal patterns of DIN + DON retention illustrate the major impact hydrology has on losses of N following disturbance, as losses of N sometimes exceed inputs of N during the rainy winter months in the first few years after forest harvest.

Patterns of annual DIN retention at the Andrews Forest do not support the hypothesis of Vitousek and Reiners (1975) that young, vigorously growing forests retain more N than older, more slowly growing forests. N demand by regrowing vegetation at WS10 is considerably higher than it was in the old-growth forest that existed pre-harvest, yet this has little effect on annual DIN retention. The lack of relationship between DIN retention and vegetation uptake at Andrews may be a

function of the lack of synchronicity between N inputs, which mostly occur in the winter, and vegetation growth.

Patterns of total dissolved N (DIN+DON) retention at the Andrews Forest also imply that that biogeochemical theory relating N retention to vegetation N demand does not apply when outputs of organic N are considered. The lack of nitrate leaching in Andrews watersheds with high inputs of biologically-fixed N suggests that organic N is very efficiently retained in this ecosystem.

The same processes that govern the magnitude of forest response to disturbances such as clear-cutting are relevant to explaining retention of atmospherically-deposited N. Very little N is lost from the soil following harvest at the Andrews compared to sites such as Hubbard Brook where the C/N ratio of the forest floor is lower and N capital is greater. This supports the hypothesis that N status of a site influences the amount of DIN that a site can retain, whether its source is increased mineralization following disturbance or elevated atmospheric deposition.

This ecosystem is highly retentive of N. Even a massive disturbance such as a clear-cut results in losses from the soil that are only about 0.05% of the total N in the watershed.

4 Conclusion

The purpose of this study was to determine how ecosystem properties affect N retention within small conifer-dominated watersheds at the H.J. Andrews Experimental Forest, OR. Because the Andrews Forest is one of the few extensively monitored sites in the world where the N cycle is unperturbed by inputs of N from human activities, these results provide valuable baseline information for predictive models of N saturation and for comparison with other forests characterized by elevated N inputs relative to historic levels. Andrews Forest stream chemistry records include DON, and hypotheses distinguishing between biotic and abiotic processes affecting organic vs. inorganic N in this ecosystem were examined.

The results presented in Chapter 2 support the hypothesis that factors that affect DON export from a watershed differ from factors controlling DIN export. At both annual and seasonal scales, DON export was related to watershed hydrology. DIN, in contrast, was rarely related to seasonal or annual hydrology, suggesting that intra-watershed biotic processing had a stronger effect on DIN export than did hydrology. Retention of DON is therefore likely to be a function of the quantity of water flushing through the soil, while retention of DIN, as expected, is strongly affected by biotic uptake by vegetation, soil organisms, and the stream community.

Results presented in Chapter 3 generally did not support hypotheses based on the biogeochemical theory of Vitousek and Reiners (1975), which related N retention to the strength of the vegetation sink. At the Andrews Forest, annual DIN retention varied little between watersheds at the Andrews Forest with vegetation differing by 450 years in age, and the younger, more vigorously growing forest did not display the expected higher DIN retention. Vitousek and Reiners' hypothesis was developed for deciduous forests in the eastern United States, which have historically higher N deposition and litter with lower C/N ratio and consequently a lower N immobilization potential. However, as noted by Vitousek (1977), net vegetation increment is only one factor that affects N retention. In this highly N

limited Pacific Northwest conifer ecosystem, so little N may escape soil and stream biotic demand that the effect of forest vegetation may not be detectable.

Inclusion of organic N in retention estimates supported the hypothesis that DON and DIN retention are affected by different processes (Chapter 3). Retention in WS2, dominated by 450-year-old forest, clearly exceeded retention in WS10, dominated by a young forest, when DON was included as part of the N balance. This observation is consistent with the point made by Hedin et al. (1995) that biogeochemical theory regarding N retention is more complex than that put forth by Vitousek and Reiners when DON is considered in addition to DIN. Further, results of the analysis in Chapter 3 did not the support the hypothesis that high inputs of biological fixation would lead to reduced N retention due to increased nitrate leaching. Elsewhere, elevated atmospheric N inputs have resulted in increased nitrate leaching, but biologically-fixed N is not equivalent to atmospherically-deposited DIN. Biologically-fixed N input is coupled to a carbon source, which likely promotes its immobilization so that biologically-fixed N is efficiently retained within the watershed.

The very low losses of N following major disturbance by clear-cutting underscore how retentive the Andrews Forest is of N. This may be a function of the high C:N ratio of the soil, a factor which has been negatively related to N leaching at numerous other sites where N saturation has been studied (Dise and Wright 1995; Gundersen et al. 1998a). The same processes that affect how much N a forest will leach following harvest are also relevant to the discussion about N saturation.

In summary, this study demonstrated that controls on organic and inorganic N retention in watersheds of the Andrews Forest differ. These data also illustrate the probable significance of the soil C:N ratio to N retention. These results are particularly useful in contributing to the understanding of processes influencing forest N retention because this study was conducted in a forest system little influenced by anthropogenic N inputs and far below N saturation levels.

Bibliography

Abee A & Lavender D (1972) Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands. In: Proceedings--Research on Coniferous Forest Ecosystems--A Symposium (pp 133-143). Bellingham, WA, March 23-24

Aber JD, Nadelhoffer KJ, Steudler P & Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. Bioscience 39:378-386

Adams PW & Stack WR (1989) Streamwater quality after logging in southwest Oregon. Project completion report (Supplement Number PNW 87-400) Pacific Northwest Research Station, Portland, OR

Aerts R, Bakker C & De Caluwe H (1992) Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. Biogeochemistry 15: 175-190

Agren GI & Bosatta E (1988) Nitrogen saturation of terrestrial ecosystems. Environ. Pollut. 54:185-197

Allan JD (1995) Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, New York

Andersson L & Lepisto A (1998) Links between runoff generation, climate and nitrate-N leaching from forested catchments. Water Air Soil Pollut. 105:227-237

Arheimer B, Andersson L & Lepisto A (1996) Variation of nitrogen concentration in forest streams--influences of flow, seasonality and catchment characteristics. J. Hydrol. 179:281-304

Bakke PD (1993) The spatial and temporal variability of nitrate in streams of the Bull Run Watershed, Oregon. MS Thesis, Oregon State University, Corvallis, Oregon. 230 pp

Binkley D, Cromack K Jr & Fredriksen RL (1982) Nitrogen accretion and availability in some snowbrush ecosystems. Forest Science 28:720-724

Bond HW (1979) Nutrient concentration patterns in a stream draining a montane ecosystem in Utah. Ecology 60:1184-1196

Boring LR, Swank WT, Waide JB & Henderson GS (1988) Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. Biogeochemistry 6:119-159

Boyer EW, Hornberger GM, Bencala KE & McKnight D (1996) Overview of a simple model describing variation of dissolved organic carbon in an upland catchment. Ecological Modelling 86:183-188

Bredemeier M, Blanck K, Xu Y-J, Tietema A, Boman AW, Emmett B, Moldan F, Gundersen P, Schleppi P & Wright RF (1998) Input-output budgets at the NITREX sites. Forest Ecol. Manage.101:57-64

Burns DA (1998) Retention of nitrate in an upland stream environment: a mass balance approach. Biogeochemistry 40:73-96

CADSWES (1993) Modular Modeling System User's Manual. University of Colorado, Boulder

Campbell JL, Hornbeck JW, McDowell WH, Buso DC, Shanley JB & Likens GE (2000) Dissolved organic nitrogen budgets for upland, forested ecosystems in New England. Biogeochemistry 49:123-142

Cappellato R & Peters NE (1995) Dry deposition and canopy leaching rates in deciduous and coniferous forests of the Georgia Piedmont: an assessment of a regression model. J. Hydrol. 169:131-150

Cirmo CP & McDonnell JJ (1997) Linking the hydrologic and biogeochemical controls of nitrogen transport in near-stream zones of temperate-forested catchments: a review. J. Hydrol. 199:88-120

Cole DW & Rapp M (1981) Elemental cycling in forest ecosystems. In: Reichle DE (Ed.) IBP Programme 23: Dynamic Properties of Forest Ecosystems (pp 341-409). Cambridge University Press, New York

Colinvaux P (1973) Introduction to Ecology. John Wiley and Sons, New York

Cornell S, Rendell A & Jickells T (1995) Atmospheric inputs of dissolved organic nitrogen to the oceans. Nature 376:243-246

Correll DL, Jordan TE & Weller DE (1999) Transport of nitrogen and phosphorus from Rhode River watersheds during storm events. Water Resour. Res. 35:2513-2521

Creed IF & Band LE (1998) Export of nitrogen from catchments within a temperate forest: Evidence for a unifying mechanism regulated by variable source area dynamics. Water Resour. Res. 34: 3105-3120

Creed IF & Band LE (1996) Regulation of nitrate-N release from temperate forests: a test of the N flushing hypothesis. Water Resour. Res. 32:3337-3354

Cromack K Jr, Swanson FJ, Grier CC & Youngberg CT (1979) Forest Soils and Land Use. In: Proceedings of the Fifth North American Forest Soils Conference (pp 449-476). USDA Forest Service

Daly C (1995) Modeled precipitation at the H.J. Andrews Experimental Forest: Output of the PRISM model. Oregon State University

Dise NB & Wright RF (1995) Nitrogen leaching from European forests in relation to nitrogen deposition. For. Ecol. Manage. 71:153-161

Dyrness CT (1973) Early stages of plant succession following logging and burning in the Western Cascades of Oregon. Ecology 54:57-69

Dyrness CT & Hawk G (1972) Vegetation and soils of the Hi-15 Watersheds, H.J. Andrews Experimental Forest. Coniferous Forest Biome, U. S. Analysis of Ecosystems International Biological Program. Internal Report 43. Seattle, WA, University of Washington.

Edmonds RL, Thomas TB & Blew RD (1995) Biogeochemistry of an old-growth forested watershed, Olympic National Park, Washington. Water Resour. Bull. 31:409-419

Elwood JW & Turner RR (1989) Streams: Water Chemistry and Ecology. In: Johnson DW & Van Hook RI (Eds). Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed (pp 301-350). Springer-Verlag, New York

Emmett BA & Quarmby C (1991) The effect of harvesting intensity on the fate of applied ^{15}N-ammonium to the organic horizons of a coniferous forest in North Wales. Biogeochemisty 15:47-63

Emmett BA, Reynolds B, Stevens PA, Norris DA, Hughes S, Gorres J & Lubrecht I (1993) Nitrate leaching from afforested Welsh catchments--interactions between stand age and nitrogen deposition. Ambio 22:386-394

Feller MC & Kimmins JP (1979) Chemical characteristics of small streams near Haney in Southwest British Columbia. Water Resour. Res. 15:247-258

Feller MC & Kimmins JP (1984) Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. Water Resour. Res. 20:29-40

Fenn ME & Poth MA (1999) Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, Southern California. J. Environ. Qual. 28:822-836

Fenn ME, Poth MA and Johnson DW (1996) Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. For. Ecol. Manage. 82:211-230

Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemley AD, McNulty SG, Ryan DF & Stottlemyer R (1998) Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecol. Appl. 8:706-733

Fisher SG & Likens GE (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43:421-439

Foster NW, Nicolson JA & Hazlett PW (1989) Temporal variation in nitrate and nutrient cations in drainage waters from a deciduous forest. J. Environ. Qual. 18: 238-244

Fredriksen RL (1969) A battery powered proportional water sampler. Water Resour. Res. 5:1410-1413

Fredriksen RL (1972) Nutrient budgets of a Douglas-fir forest on an experimental watershed in western Oregon. In: Proceedings--Research on Coniferous Forest Ecosystems--A Symposium (pp 115-131). Bellingham, WA, March 23-24

Fredriksen RL (1975) Nitrogen, phosphorus and particulate matter budgets of five coniferous forest ecosystems in the Western Cascades Range, Oregon. PhD Thesis, Oregon State University, Corvallis, Oregon. 127 pp

Geigert M, Nikolaidis N, Miller D & Heitert J (1994) Deposition rates for sulfur and nitrogen to a hardwood forest in Northern Connecticut, USA Atmospheric Environment 28:1689-97

Gholz HL, Hawk GM, Campbell A & Cromack K Jr (1985) Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15:400-409

Gordon WS & Jackson RB (2000) Nutrient concentrations in fine roots. Ecology 81: 275-280

Gosz J (1980) Nutrient budget studies for forests along an elevational gradient in New Mexico Ecology 61:515-521

Greenfield L G (1999) Weight loss and release of mineral nitrogen from decomposing pollen. Soil Biol. Biochem. 31:353-361

Gregory SV (1980) Effects of light, nutrients, and grazers on periphyton communities in streams. PhD Thesis, Oregon State University, Corvallis, Oregon. 151 pp

Gundersen P, Callesen I & de Vries W (1998a) Nitrate leaching in forest ecosystems is related to forest floor C/N ratios. Environ. Pollut. 102 (supple. 1):403-407

Gundersen P, Emmett BA, Kjonaas OJ, Koopmans CJ & Tietema A (1998b) Impact of nitrogen deposition on nitrogen cyling in forests: a synthesis of NITREX data. Forest Ecol. Manage.101:37-55

Halpern CB (1989) Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70:704-720

Halpern CB, Antos JA, Geyer MA & Olson AM (1997) Species replacement during early secondary succession: the abrupt decline of a winter annual. Ecology 78: 621-631

Harr RD (1977) Water flux in soil and subsoil on a steep forested slope. J. Hydrol. 33: 37-58

Harr RD (1981) Some characteristics and consequences of snowmelt during rainfall in western Oregon. J. Hydrol. 53:277-304

Harr RD & Fredriksen RL (1988) Water quality after logging small watersheds within the Bull Run watershed, Oregon. Water Resources Bulletin 24:1103-1111

Hawk GM (1979) Vegetation mapping and community description of a small Western Cascade watershed. Northwest Science 53:200-212

Heath B, Sollins P, Perry DA & Cromack K Jr (1987) Asymbiotic nitrogen fixation in litter from Pacific Northwest forests. Can. J. For. Res. 18:68-74

Holland EA, Dentener FJ, Braswell BH & Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. Biogeochemistry 46:7-43

Hedin LO, Armesto JJ & Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. Ecology 76:493-509

Henderson GS, Hunley A & Selvidge W (1977) Nutrient discharge from Walker Branch Watershed. In: Correll DL (Ed) Watershed Research in Eastern North America: A Workshop to Compare Results (pp 307-320). Chesapeake Bay Center for Environmental Studies, Smithsonian Institution, Edgewater, Maryland

Hill AR (1986) Stream nitrate-N loads in relation to variations in annual and seasonal runoff regimes. Water Resour. Bull. 22:829-839

Hornberger GM, Bencala KE & McKnight DM (1994) Hydrological controls on dissolved organic carbon during snowmelt in the Snake River near Montezuma, Colorado. Biogeochemistry 25:147-165

Jaworski NA, Groffman PM, Keller AA & Prager JC (1992) A watershed nitrogen and phosphorus balance: the upper Potomac river basin. Estuaries 15: 83-95

Johnson CE (1995) Soil nitrogen status 8 years after whole-tree clear-cutting. Can. J. For. Res. 25:1346-1355

Johnson DW (1992) Nitrogen retention in forest soils. J. Environ. Qual. 21:1-12

Johnson DW (1995) Soil properties beneath *Ceanothus* and pine stands in the Eastern Sierra Nevada. Soil Sci. Soc. Am. J. 59:918-924

Johnson DW, Susfalk RB & Dahlgren RA (1997) Nutrient fluxes in forests of the eastern Sierra Nevada mountains, United States of America. Global Biogeochem. Cycles 11:673-681

Johnson NM, Likens GE, Bormann FH, Fisher DW & Pierce RS (1969) A working model for the variation in stream chemistry at the Hubbard Brook Experimental Forest, New Hampshire. Water Resour. Res. 5:1353-1363

Jurgensen MF, Graham RT, Larsen MJ & Harvey AE (1992) Clear-cutting, woody residue removal, and nonsymbiotic nitrogen fixation in forest soils of the inland Pacific Northwest. Can. J. For. Res. 22:1172-1178

Lajtha K, Seely B & Valiela I (1995) Retention and leaching losses of atmospherically-derived nitrogen in the aggrading coastal watershed of Waquoit Bay, MA. Biogeochemistry 28:33-54

Landsberg JJ & Waring RH (1997) A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95:209-228

Lee EJ, Kenkel N & Booth T (1996) Atmospheric deposition of macronutrients by pollen in the boreal forest. Ecoscience 3:304-309

Lepisto A, Andersson L, Arheimer B & Sundblad K (1995) Influence of catchment characteristics, forestry, activities and deposition on nitrogen export from small forested catchments. Water Air Soil Pollut. 84:81-102

Lewis WM Jr & Grant MC (1979) Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Science 128: 353-363

Lewis WM Jr, Melack JM, McDowell WH, McClain M & Richey JE (1999) Nitrogen yields from undisturbed watersheds in the Americas. Biogeochemistry 46:149-162

Likens GE, Bormann FH, Johnson NM, Fisher DW & Pierce DW (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecological Monographs 40:23-47

Likens GE, Bormann FH, Pierce RS & Reiners WA (1978) Recovery of a deforested ecosystem. Science 199:492-496

Likens GE & Bormann FH (1995) Biogeochemistry of a Forested Ecosystem (second edition). Springer-Verlag, New York

Lovett GM & Lindberg SE (1993) Atmospheric deposition and canopy interactions of nitrogen in forests. Can. J. For. Res. 23:1603-1616

Marks PL & Bormann FH (1972) Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176:914-915

Martin CW (1979) Precipitation and streamwater chemistry in an undisturbed forested watershed in New Hampshire. Ecology 60:36-42

Martin CW & Harr RD (1988) Precipitation and streamwater chemistry from undisturbed watersheds in the Cascade Mountains of Oregon. Water Air Soil Pollut. 42:203-219

Martin CW & Harr RD (1989) Logging of mature Douglas-fir in western Oregon has little effect on nutrient output budgets. Can. J. For. Res. 19:35-43

Martin CW, Noel DS & Federer CA (1984) Effects of forest clearcutting in New England on stream chemistry. J. Environ. Qual. 13:204-210

McDowell WH & Fisher SG (1976) Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. Ecology 57:561-569

McDowell WH & Asbury CE (1994) Export of carbon, nitrogen and major ions from three tropical montane watersheds. Limnol. Oceanogr. 39:111-125

McDowell WH & Likens GE (1988) Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook Valley. Ecol. Monogr. 58:177-195

McNabb DH & Cromack, K Jr (1983) Dinitrogen fixation by a mature *Ceanothus velutinus* (Dougl.) stand in the Western Oregon Cascades. Canadian Journal of Microbiology 29:1014-1021

McNulty SG, Aber JD & Boone RD (1991) Spatial changes in forest floor and foliar chemistry of spruce-fir stands across New England. Biogeochemistry 14: 13-29.

Means JE, Hansen HA, Koerper GJ, Alaback PB & Klopsch MW (1994) Software for computing plant biomass—BIOPAK Users Guide. Gen. Tech. Rep. PNW-GTR-340. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 184 pp

Meyer JL & Tate CM (1983) The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. Ecology 64:33-44

Meyer JL, Wallace, JB & Eggert SL (1998) Leaf litter as a source of dissolved organic carbon in streams. Ecosystems 1:240-249

Miller JH & Newton M (1983) Nutrient loss from disturbed forest watersheds in Oregon's Coast Range. Agro-Ecosystems 8:153-167

Mitchell MJ, Driscoll CT, Kahl JS, Likens GE, Murdoch PS & Pardo LH (1996) Climatic control of nitrate loss from forested watersheds in the northeast United States. Environ. Sci. Technol. 30:2609-2612

Moore ID & Nuckols JR (1984) Relationship between atmospheric nitrogen deposition and the stream nitrogen profile. J. Hydrol. 74:81-103

Mulholland PJ (1992) Regulation of nutrient concentrations in a temperate forest stream: roles of upland, riparian, and instream processes. Limnol. Oceanogr. 37:1512-1526

Munn NL & Meyer JL (1990) Habitat-specific solute retention in two small streams: an intersite comparison. Ecology 71:2069-2082

Murdoch PS & Stoddard JL (1992) Role of nitrate in the acidification of streams in the Catskill Mountains of New York. Water Resourc. Res. 28:2707-2720

Nambiar EKS (1987) Do nutrients retranslocate from fine roots? Can. J. For. Res. 17: 913-918

National Atmospheric Deposition Program (NRSP-3)/National Trends Network (1999) NADP Program Office, Illinois State Water Survey, 2204 Griffith Drive, Champaign, IL 61820

Newbold JD, Sweeney BW, Jackson JK & Kaplan LA (1995) Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. J. N. Am. Bethol. Soc. 14: 21-37

Nicolson JA (1988) Water and chemical budgets for terrestrial basins at the Turkey Lakes Watershed. Can. J. Fish. Aquat. Sci. 45:88-95

Nihlgard B (1985) The ammonium hypothesis: an additional explanation to the forest dieback in Europe. Ambio 14:2-8

Northup RR, Yu Z, Dahlgren RA & Vogt KA (1995) Polyphenol control of nitrogen release from pine litter. Nature 377:227-229

Nuckols JR & Moore ID (1982) The influence of atmospheric nitrogen influx upon the stream nitrogen profile of a relatively undisturbed forested watershed. J. Hydrol. 57:113-135

Ollinger SV, Aber JD, Lovett GM, Millham SE, Lathrop RG & Ellis JM (1993) A spatial model of atmospheric deposition for the northeastern U.S. Ecological Applications 9:1330-1344

Overton WS, Lavender DP & Herman RK (1973) Estimation of biomass and nutrient capital in stands of old-growth Douglas-fir. In: IUFRO Biomass Studies (pp 91-103) University of Maine, Orono

Paul EA & Clark FE (1996) Soil Microbiology and Biochemistry. Academic Press, New York

Pardo LH, Driscoll CT & Likens GE (1995) Patterns of nitrate loss from a chronosequence of clear-cut watersheds. Water Air Soil Pollut. 85:1659-1664

Perkins RM (1997) Climatic and physiographic controls on peakflow generation in the Western Cascades, Oregon. PhD Thesis, Oregon State University, Corvallis, Oregon. 190 pp

Peterjohn WT, Adams MB & Correll DL (1996) Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. Biogeochemistry 35: 507-522

Raich JW & Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346-1354

Rascher CM, Driscoll CT & Peter NE (1987) Concentration and flux of solutes from snow and forest floor during snowmelt in the West-Central Adirondack Region of New York. Biogeochemistry 3:209-224

Rosen K & Lundmark-Thelin A (1987) Increased nitrate leaching under piles of slash—a consequence of modern forest harvesting techniques. Scand. J. For. Res. 2: 21-29

Rothacher J, Dyrness CT & Richardson RL (1967) Hydrologic and Related Characteristics of Three Small Watersheds in the Oregon Cascades. General Technical Report.67. U.S. Department of Agriculture, U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon. 54 pp

Santantonio D, Hermann RK, Overton WS (1977) Root biomass studies in forest ecosystems. Pedobiologia 17:1-31

SAS Institute, Inc. (1990). SAS/STAT Users Guide. Version 6 (4th edn). Volumes 1-2. SAS Institute, Inc., Cary, NC

Schnabel RR, Urban JB & Gburek WJ (1993). Hydrologic controls on nitrate, sulfate and chloride concentrations. J. Environ. Qual. 22:589-596

Scrivener JC (1982) Logging impacts on the concentration patterns of dissolved ions in Carnation Creek, British Columbia. In: Hartman GF (Ed.) Proceedings of the Carnation Creek Workshop: A Ten-Year Review (pp 64-79). Pacific Biological Station, Nanaimo, British Columbia

Sedell JR, Naiman RJ, Cummins KW, Minshall GW & Vannote RL (1978) Transport of particulate organic material in streams as a function of physical processes. Verh. Internat. Verein Limnol. 20:1366-1375

Seely B, Lajtha K & Salvucci GD (1998) Transformation and retention of nitrogen in a coastal forest ecosystem. Biogeochemistry 42: 325-343

Sollins P, Cromack K Jr, McCorison FM, Waring RH & Harr RD (1981) Changes in nitrogen cycling in an Old-Growth Douglas-fir site after disturbance. J. Environ. Qual. 10:37-42

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

Sollins P & McCorison FM (1981) Nitrogen and carbon solution chemistry of an old growth coniferous forest watershed before and after cutting. Water Resour. Res. 17:1409-1418

Stevens PA & M Hornung (1990) Effect of harvest intensity and ground flora establishment on inorganic-N leaching from a Sitka spruce plantation in north Wales, UK. Biogeochemistry 10:53-65

Stoddard JL (1994) Long-term changes in watershed retention of nitrogen. In: LA Baker (Ed) Environmental chemistry of lakes and reservoirs. Advances in chemistry series 237 (pp 223-284). Washington, DC: American Chemical Society

Stohlgren TJ, Melack JM, Esperanza AM & Parsons DJ (1991) Atmospheric deposition and solute export in giant sequoia-mix conifer watersheds in the Sierra Nevada. Biogeochemistry 12: 207-230

Stottlemyer R, Toczydlowski D & Herrmann R (1998) Biogeochemistry of a Mature Boreal Ecosystem: Isle Royale National Park, Michigan. Scientific Monograph NPS/NRUSGS/NRSM-98/01. United States Department of the Interior, National Park Service

Stottlemyer R & Toczydlowski D (1999) Seasonal relationships between soil precipitation, forest floor and streamwater nitrogen, Isle Royale, Michigan. Soil Sci. Soc. Am. J. 63:389-398

Stottlemyer R & Troendle CA (1992) Nutrient concentration patterns in streams draining alpine and subalpine catchments, Fraser Experimental Forest, Colorado. J. Hydrol. 140:179-208

Stottlemyer R & Troendle C (1987) Trends in streamwater chemistry and input-output balances, Fraser Experimental Forest, Colorado. USDA Research Report RM-275. 9 pp

Swank WT & Vose JM (1997) Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America. Global Biogeochem. Cycles 11:657-671

Swanson FJ, Fredriksen RL & McCorison FM (1982) Material transfer in a western Oregon forested watershed. In: Edmonds R L (Ed) Analysis of coniferous forest ecosystems in the western United States (pp 233-266). US/IBP Synthesis Series 14. Hutchinson Ross Publishing Company, Stroudsburg, PA

Tietema A, Emmett BA, Gundersen P, Kjonaas OJ & Koopmans CJ (1998) The fate of ^{15}N-labelled nitrogen deposition in coniferous forest ecosystems. For. Ecol.Manage. 101:19-27

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monogr. 57:189-214

Triska FJ, Sedell JR, Cromack K Jr, Gregory SV & McCorison MF (1984) Nitrogen budget for a small coniferous forest stream. Ecol. Monogr. 54: 119-140

Triska FJ and Buckley AM (1978) Patterns of nitrogen uptake and loss in relation to litter disappearance and associated invertebrate biomass in six streams of the Pacific Northwest, USA. Verh. Internat. Verein Limnol. 20: 324-332

Van Miegroet H & Cole DW (1984) The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J.Environ. Qual. 13:586-590

Vermes J-F & Myrold DD (1992) Denitrification in forest soils in Oregon. Can. J. For. Res. 22:504-512

Vitousek PM (1977) The regulation of element concentrations in mountain streams in the northeastern United States. Ecol. Monogr. 47:65-87

Vitousek PM, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH & Tilman DG (1997). Human alterations of the global nitrogen cycle: sources and consequences. Ecol. Appl. 7: 737-750

Vitousek PM & Melillo JM (1979) Nitrate losses from disturbed forests: patterns and mechanisms. Forest Science 25: 605-619

Vitousek PM & Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25:376-381

Vogt KA, Vogt DJ, Moore EE, Fatuga BA, Redlin MR & Edmonds RL (1987) Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. J. Ecol. 75:857-870

Wigington PJ Jr, Church MR, Strickland TC, Eshleman.KN & Van Sickle J (1998) Autumn chemistry of Oregon Coast Range streams. J. Am. Water Res. Assoc. 34:1035-1049

Wiklander G, Nordlander G & Andersson R (1991) Leaching of nitrogen from a catchment at Soderasen in southern Sweden. Water Air Soil Pollut. 55: 263-292

Williams MR and Melack JM (1997) Atmospheric deposition, mass balances, and processes regulating stormwater solute concentrations in mixed-conifer catchments of the Sierra Nevada, California. Biogeochemistry 37:111-144

Williams MW and Melack JM (1991) Solute chemistry of snowmelt and runoff in an alpine basin, Sierra Nevada. Water Resourc. Res. 27:1575-1588

Youngberg CT & Wollum AG II (1976) Nitrogen accretion in developing *Ceanothus velutinus* stands. Soil Sci. Soc. Am. J. 40:109-112

Zavitkovski J & Newton M (1968) Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. Ecology 49:1134-1145