THE UNIVERSITY OF CALGARY

CYCLING AND AVAILABILITY OF NITROGEN AND PHOSPHORUS IN FOUR ROCKY MOUNTAIN CONIFEROUS FORESTS

by

CINDY ELLEN PRESCOTT

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGY

CALGARY, ALBERTA

SEPTEMBER, 1988

ISBN 0-315-46648-0

THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled CYCLING AND AVAILABILITY OF NITROGEN AND PHOSPHORUS IN FOUR ROCKY MOUNTAIN CONIFEROUS FORESTS, submitted by CINDY ELLEN PRESCOTT in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

D. Parkinson, Supervisor
Kananaskis Centre for
Environmental Research

J. Culp
Department of Biological Sciences

E.A. Johnson
Department of Biological Sciences

G. Pritchard
Department of Biological Sciences

R. Revel
Faculty of Environmental Design

K. Van Cleve, External Examiner
University of Alaska

ABSTRACT

Internal cycling of nitrogen and phosphorus were compared among a 90-year-old lodgepole pine forest, a 120-year-old white spruce forest, a 350-year-old Engelmann spruce-subalpine fir forest, and a 13-year-old clearcut site in the Rocky Mountains of southwestern Alberta. Aboveground biomass of vegetation ranged from 109 - 203 t ha^{-1} while net primary productivity ranged from 4.4 - 5.3 t ha^{-1} yr^{-1} in the forests. Annual uptake of nutrients (production minus resorption) was between 1.8 and 2.2 g m^{-2} yr^{-1} for N and 0.2 - 0.4 g m^{-2} yr^{-1} for P. Efficiency of nutrient use by vegetation (mg new biomass produced per mg nutrient taken up in one year) ranged from 249 - 262 for N and 1604 - 2355 for P in the forests, and 72 and 642, respectively, in the clearcut stand.

Rates of input of aboveground litter in the forests ranged from 286 to 321 g m^{-2} yr^{-1}. The mass of litter accumulated on the forest floors ranged from 6.3 to 11.0 kg m^{-2}. Residence times of organic matter in the forest floor were 11 years in the pine stand, 16 years in the spruce-pine stand, and 23 years in the spruce-fir stand.

Addition of N, P, and S to each forest did not alter biomass or activity of forest floor microorganisms, but did increase rates of decomposition, N and P mineralization and nitrification in the forest floors. Fertilization enhanced productivity of young

lodgepole pine trees at the clearcut site and ground vegetation at all sites. Differences in nutrient content of vegetation in fertilized plots were particularly apparent for nitrogen in the pine and spruce-pine stands and for phosphorus in the spruce-fir forest.

Concentrations of N and P in vegetation, litterfall and forest floors, and rates of net mineralization were lower in the pine stand, than in the spruce stand. Concentrations and mineralization rates in the spruce-fir forest relative to the other forests were high for N and low for P. Results indicated N to be the nutrient most limiting to productivity of vegetation in the lower elevation pine and spruce forests, and P to be most limiting in the high elevation spruce-fir forest.

ACKNOWLEDGEMENTS

My research benefitted tremendously from the dedicated efforts of many people. My thanks are extended first to my supervisor, Dr. Dennis Parkinson for his assistance, guidance, encouragement, and confidence in me which allowed me to carry out the research to the best of my abilities. Thanks to John Corbin for assistance with the multitude of decisions and samples which became this thesis, and for thoughtful discussions which enabled us to maintain perspective (and consciousness) through the seemingly endless sampling and sorting stage.

The initial stage of "The Project" benefitted greatly from the intellectual and physical labours of Dan Durall and Bill Parsons. John Corbin and Kim McLean provided information on vegetation biomass and stand history, respectively. Assistance with field and laboratory work was provided by Holly Baradoy, Calvin Davies, Sharon Illerbrun, Stacey Grant, Jane Lancaster, Melody Michel, Brenda Mottle, Jan Podrasky, Aaron Roth, Sharon Theissen, and Trixi von Frenckell.

I would like to thank the members of my committee: Drs. Joe Culp, Ed Johnson, Gordon Pritchard, Richard Revel and Keith Van Cleve for their interest and advice. Fellow graduate students of D.P. provided valuable information and discussions; David Wardle also helped with statistics and proofread the thesis. My thanks to

the staff of the Kananaskis Centre for accommodating even my most unusual requests, and to Lynn Ewing and Della Patton for typing the thesis. Ed Johnson and Allan Legge provided equipment and interesting discussion. Unpublished or hard-to-find data were graciously provided by Keith Van Cleve, Hamish Kimmins and Suzanne Visser. Additional thanks to Suzanne Visser for sharing her expertise with me during my extended sojourn in the lab, and to Joyce Nelligan for help with photographic emergencies. Financial support during my doctoral program was provided by the Province of Alberta, The Alberta Heritage Scholarship Fund and the Killam Trust.

Finally, thanks once again to Kim McLean, Wendy Dean and my parents, Lois and Murray Prescott, for their continued support and encouragement. We did it!

TABLE OF CONTENTS

TABLE OF CONTENTS (Concluded)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF TABLES (Concluded)

LIST OF FIGURES

CHAPTER 1

1. GENERAL INTRODUCTION

The internal nutrient cycle of a forested ecosystem comprises the processes of primary production, litterfall, and decomposition. Linkages among these processes allow much of the nutrient capital of an ecosystem to be recycled within the system rather than being lost. The principle organisms involved in the cycle are primary producers (plants) and decomposers (soil microorganisms), although consumers may circumvent or alter the rate of some processes. The present study examines the internal cycling of two critical nutrients, nitrogen and phosphorus, between the vegetative and microbial components of four coniferous forests.

The major reservoir for nitrogen is in gaseous form in the atmosphere. Nitrogen enters a forest through fixation of N_2 by microorganisms and through wet and dry deposition of NH_3 and NO_2. Most N in soil is present in the organic form in the uppermost layer. Organic N is mineralized through enzymatic activity of decomposing microorganisms to NH_4^+, which may become fixed to clay minerals, bonded onto cation exchange sites, taken up by soil microorganisms or plants and incorporated into biomass, or taken up by nitrifying bacteria and converted into nitrite and nitrate. If converted to nitrate, nitrogen may be leached from the soil or immobilized by plants and microorganisms. Plants absorb nitrogen as NH_4^+ or NO_3^- through their roots and convert it to small organic compounds such as amides, amino acids and ureide compounds. These

compounds are transported through the plant and eventually converted into proteins and other large molecules or stored as glutamine and other amino acids. A portion of the immobilized N is remobilized and redistributed during leaf senescence and the remaining organic N is returned to the soil in litter. The nitrogen cycle is described in more detail elsewhere (Barber 1984; Haynes 1986; Stevenson 1986).

The primary source of phosphorus in a terrestrial ecosystem is phosphate derived from the primary mineral apatite of soil-forming rocks. Phosphorus is much less mobile in soil than is nitrogen as it forms complexes with aluminum and iron at low pH levels, and is more tightly bonded on cation exchange sites. Phosphorus occurs in solution primarily as $H_2PO_4^-$ in slightly or moderately acidic soils such as in coniferous forests. Absorption of $H_2PO_4^-$ by plants is usually aided by association with mycorrhizal fungi. Within plants P is transported as $H_2PO_4^-$ or in ester form through the plant before incorporation into biomass. Some of the P incorporated in biomass is remobilized and redistributed during senescence and the remaining organic P is returned to the soil in litter. More detailed information on the P cycle may be found elsewhere (Barber 1984; Marschner 1986; Stevenson 1986).

Both N and P are essential nutrients in all living organisms. Nitrogen is a component of proteins, nucleic acids and ATP; P occurs in nucleic acids, ATP and cell membranes (Waring and Schlesinger 1985). Insufficient levels of nitrogen retard growth of plants and causes nitrogen to be mobilized from mature leaves to

areas of new growth, leading to premature leaf senescence. Phosphorus deficiencies cause general reductions in the rates of many metabolic processes including cell division and expansion, respiration and photosynthesis (Marschner 1986). As a consequence of reductions in rates of growth and reproduction of plants, the productivity and biomass of forest vegetation may be reduced on soils deficient in nitrogen or phosphorus (Waring and Schlesinger 1985). Nitrogen and phosphorus are the two most abundant nutrients occurring in microorganisms (Stevenson 1986); therefore low availability of either of these nutrients in soil could also limit the productivity of the soil microbial biomass.

Nitrogen and phosphorus are the two most frequently limiting nutrients in terrestrial ecosystems (Swift et al 1979; Vitousek 1982, 1984). Nitrogen has often been found to limit productivity of temperate forests, especially in early stages of development. This reflects the lack of nitrogen capital present in recently disturbed ecosystems such that sufficient nitrogen must be brought into the system through fixation or deposition before enough is being internally recycled to meet the requirements of the vegetation. Phosphorus, by contrast, is most abundant in recently formed soils as it becomes complexed with aluminum and iron and thus unavailable over time. Therefore, phosphorus deficiencies occur most often in very old, highly-weathered soils such as the utisols and oxisols underlying many tropical forests (Vitousek and Sanford 1986). Nutrient deficiencies may also arise when climate conditions are not conducive to organic matter decomposition, as in arctic,

alpine and desert areas, where rates of mineralization from organic matter are sufficiently low to limit nutrient availability in soil (Swift et al 1979). The degree of nutrient deficiency may vary with the age of the forest.

The demand by vegetation for soil nutrients is greatest early in stand development when potential productivity is highest and internal recycling is not sufficiently developed to meet this demand. As a result, nutrient limitations to productivity of forest vegetation are most intense around the time of canopy closure (Vitousek and Reiners 1975).

Organisms in nutrient deficient environments have a number of characteristics which allow them to make more efficient use of the limiting nutrient(s). These nutrient conservation mechanisms may show up as alterations in the species composition or physiological changes in species already present. Characteristics of plants growing on soils of low nutrient availability include lower productivity and nutrient content, longer retention of foliage (hence predominantly evergreen), and greater resorption capacity for nutrients during leaf senescence. Litter produced by these plants tends to have low nutrient content and high polyphenol content, which make it of poor nutritional quality for decomposer organisms. Under these conditions, soil microorganisms absorb a greater proportion of the nutrient into their biomass during mineralization activities. Upon death and decomposition of microorganisms, these nutrients are rapidly sequestered by other microorganisms, such that most of the nutrients remain within the soil microbial pool and very little is

made available to plant roots. Ultimate consequences of this more efficient use of limiting nutrients within individual plants and within the soil microbial community is a very "tight" internal cycle for the ecosystem with very small rates of leaching losses of the nutrient(s), and the exacerbation of the already low levels of available nutrient(s) in the soil (Gosz 1984).

Since shortages of nutrients are capable of limiting the productivity of ecosystems, it is necessary to be able to assess the degree of nutrient limitation, such that ameliorative measures may be taken if desired. The degree to which a nutrient limits the productivity of an organism is a function of the degree to which the "demand" or potential rate of use exceeds the "supply" or amount of nutrient available. The availability of a nutrient may be measured in a number of ways. The total amount of the nutrient present in the soil provides an estimate of the nutrient "capital" of the ecosystem, but will not indicate how much of this is present in a form available to organisms. The amount of available (extractable) nutrients present in soil is a better estimate of the supply of the nutrient, but this measure is extremely variable (Stevenson 1986) and provides no indication of the rate at which nutrients are becoming available. Measurements of nutrient mineralization rates determined as the net increase in extractable nutrients during incubation are more useful but are difficult to carry out under field conditions or extrapolate from laboratory measurements (Keeney 1980).

The demand (i.e. potential rate of uptake) of vegetation for a nutrient can be estimated from the amount and nutrient content of new biomass produced annually. However, the proportion of incorporated nutrients derived from internal (within-plant) redistribution must be determined and subtracted from the total. For this reason, the amount of nutrient lost annually in litterfall can be used as an estimate of demand, assuming this to be the amount of nutrient which the plant must acquire in order to continue its current rate of biomass production (Vitousek 1982). The concentration of the nutrient in plant tissue provides an indication of the amount of nutrient available to the plant (van den Driessche 1974), and allows for comparison of nutrient status of vegetation in different species and sites (Vitousek and Sanford 1986). Nutrient content may also be expressed as the amount of biomass produced per unit nutrient taken up (nutrient use efficiency - Vitousek 1982).

An indication of the degree to which nutrients are limiting to soil microorganisms can be obtained by determining the rates of net immobilization or mineralization of nutrients in litter during decomposition (Gosz 1984). Nutrients whose concentrations increase in litter relative to carbon during decomposition are being selectively immobilized in microbial biomass and thus must occur in the litter in quantities smaller than required by microbes. Net immobilization generally occurs in litter with a C:N ratio greater than 30 or a C:P greater than 300 (Stevenson 1986). Net mineralization of NH_3 and PO_4 generally occur in litter with C:N less than 20 and C:P less than 200 (Stevenson 1986). Rates of net mineralization of

nutrients from organic and mineral soil are also indicative of the demand by microbes relative to the supply of the nutrient in the soil.

While all these parameters provide indications of possible nutrient limitation, the best way to test for nutrient limitations is to measure the changes in any or all of these parameters following experimental addition of nutrients to the forest. This may be done for individual parameters in controlled laboratory experiments or for the entire ecosystem in field fertilization trials. Increases in the productivity or nutrient content of organisms in fertilized forests are indicative of their potential to use additional nutrients when they are made available and thus are indicative of the degree of nutrient limitation present.

In the present investigation, an attempt was made to assess the degree to which nitrogen and phosphorus limit the productivity of vegetation and microbial components of several Rocky Mountain coniferous forest ecosystems. This was achieved by measuring the size of pools and rates of major fluxes of these nutrients in the forests to acquire an understanding of their cycling dynamics, and examining the forementioned parameters which might be considered as indicators of nutrient limitation. This information is examined along with results of experimental addition of nitrogen and phosphorus to each forest in order to determine the extent to which either of these nutrients limit the productivity of vegetation or soil microorganisms in these forests. Comparisons among the different forests will allow determination of the ubiquity of any

nutrient limitation, and speculation regarding factors contributing to nutrient limitations.

This information will be presented in the following format: after a brief description of the study area and sites in Chapter 2, information on the dynamics of nitrogen and phosphorus cycling in aboveground vegetation is presented in Chapter 3. Chapter 4 provides a description of litter dynamics and fluxes of N and P between vegetation and the forest floor. In Chapter 5, results of the field fertilization experiments are presented. Information on parameters which are indicative of nutrient limitation are extracted from this information and discussed along with additional indicator parameters in the final chapter to determine the degree of N and P limitation existing in each forest and the relative utility of each indicator parameter.

CHAPTER 2

2. STUDY AREA AND SITE DESCRIPTION

2.1 STUDY AREA

The forests chosen for study are in the front range of the Rocky Mountains in the Kananaskis Valley of southwestern Alberta, Canada (51°2'N, 115°3'W). Most of the study area is located within the Montane ecoregion of Alberta (Strong and Leggat 1981). This region is subject to both Prairie and Cordilleran climatic influences. Mean monthly temperatures at the Kananaskis Centre for Environmental Research located in the study area range from -10.2°C in January to 14.1°C in July. The frost-free period averages 58 days, from 24 June to 22 August. Mean annual precipitation is 657 mm, of which 292 mm occurs as snow. Peak precipitation occurs in June. Snow cover is discontinuous due to frequent warm chinook winds throughout the winter. Variations in this climatic regime occur at different aspects and elevations. South- and west-facing slopes are usually warmer and drier than north- and east-facing slopes (Karkanis 1972). Increasing elevation is associated with cooler temperatures and greater winter precipitation. Above 7000' (2135 m), the area is in the Subalpine ecoregion (Strong and Leggat 1981) which has a Cordilleran climate characterized by greater depth and duration of snow cover and fewer frost-free days.

Vegetation in the Kananaskis Valley occurs in two zones: a lower montane zone of lodgepole pine (Pinus contorta Loudon) and white spruce (Picea glauca [Moench] Voss) or white x Engelmann spruce hybrids, and an upper subalpine zone of Engelmann spruce (P. engelmannii Parry ex Engelm.) and/or white x Engelmann spruce hybrids and subalpine fir (Abies lasiocarpa [Hook.] Nutt.) (Peet 1988). Fire is the major type of disturbance influencing forests in the valley; stand-replacing fires occur on an average of every 100 years (Johnson 1987). Lodgepole pine regenerates most rapidly after a severe fire, often forming dense even-aged stands (Day 1972; Wheeler and Critchfield 1985). Spruce may also regenerate after fire given sufficient seed source and moisture (Alexander 1987). Trembling aspen (Populus tremuloides Michx.) regenerates rapidly via suckering after less severe fires (Parker and Parker 1983). After canopy closure, spruce and fir become dominant in the understory. Given a sufficient period of time between fires, as occurs at higher elevations, spruce and fir come to dominate the overstory. Different life history traits of spruce (long lifespan, low recruitment) and fir (short lifespan, high recruitment) allow both species to remain in old growth forests, (Veblen 1986; Aplet et al. 1988). Additional information on the physical environment is available in the Kananaskis Country Environmental Education Library, Government of Alberta, Edmonton. Nomenclature of plants follows Moss (1983).

2.2 SITE DESCRIPTION

Within this mosaic of forests in the Kananaskis Valley, four stands with distinctly different overstory tree composition

were selected for study. All stands are within 5 km of one another in the Lusk Creek watershed (51°02'N, 115°03'W). Soils in the watershed are mostly well-drained brunisols of sandy-loam texture derived from predominantly limestone parent material. Glacial reworking of parent material has led to intermixing of calcareous and noncalcareous rocks in the watershed (Crossley 1951). Study sites are named according to the dominant species of overstory tree in the stand: Pine, Spruce and Fir, as well as a Clearcut, and are described in Table 1.

The "Pine" site is located on a flat ground moraine of glacial till (Stalker 1973) at 1530 m elevation. The soil is an orthic eutric brunisol. Canopy trees are almost exclusively lodgepole pine approximately 70 - 90 years of age and 15 m in height. A few older (100—127 year old) fire-scarred trees are present. Density of canopy trees is 1716 stems per hectare; stand basal area is 30.5 m^2 per hectare. Extensive natural thinning has already occurred in this stand, with considerable numbers of standing dead and fallen pines all of DBH less than 10 cm. White (or white x Engelmann) spruce, poplar (Populus balsamifera L.) and aspen dominate the understory. The shrub layer is composed of buffaloberry (Shepherdia canadensis), big willow (Salix scouleriana) and juniper (Juniperus communis). Ground vegetation is dominated by forbs (Cornus canadensis, Hedysarum sulphurescens, Lathyrus ochroleucus, Aster conspicuus, Epilobium angustifolium) and grasses (Calamagrostis rubescens, Elymus innovatus). The forest floor is approximately 6 cm thick with substantial amounts of incorporated charred wood and large amounts of uncharred wood on the surface.

Table 1. Characteristics of the forests at the four study sites in the Rocky Mountains of southwestern Alberta.

Site	Elevation (m)	Slope	Aspect	Age[a] (yr)	Density[b] (stems ha^{-1})	Basal Area[b] (m^2 ha^{-1})	Forest Floor[c] Depth (cm)
Clearcut	1410	0	-	13	0	0	3.9 ± 0.8
Pine	1530	0	-	90	1716	30.52	6.4 ± 1.4
Spruce	1500	3°	NW	120	750	39.14	11.9 ± 3.9
Fir	1830	30°	WNW	350	1177	40.04	12.1 ± 4.2

[a] Apparent age since last fire, or time since cutting at the Clearcut site.

[b] Values for canopy trees only, >10 cm DBH for subalpine fir, spruce, aspen; >5 cm DBH for Douglas fir, pine, poplar

[c] Each value is the mean ± standard deviation of 40 values

The present stand probably originated after a severe fire destroyed a similar stand, most likely the fire determined by Johnson (1987) to have swept through the area in 1889.

The "Spruce" stand is located on a north-facing 3° slope at 1500 m elevation. The soil is an orthic dystric brunisol on an alluvial outwash fan overlying lake deposits (Stalker 1973). The overstory is composed of white (or white x Engelmann) spruce and lodgepole pine up to 120 years of age. Canopy trees average 20 m in height, and have a density of 750 stems per hectare and a basal area of 39 m^2 per hectare. Spruce is also predominant in the understory, along with Douglas fir (Pseudotsuga menziesii [Mirb.] Franco), aspen and balsam poplar (Populus balsamifera L.). This stand is considerably less dense than the pine stand with relatively few standing dead or fallen trees. Buffaloberry and green alder (Alnus crispa) are common shrubs. Ground vegetation is composed of mosses (Pleurozium schreberi, Hylocomnium splendens, twinflower (Linnaea borealis) and forbs (A. conspicuus, E. angustifolium, Arnica cordifolia, Mertensia paniculata). The forest floor is about 12 cm thick with many large partially charred boles incorporated. It appears that this stand originated from a similar stand after a fire in 1865 (Johnson 1987).

The "Fir" site is situated at 1830 m on a WNW-facing 30° slope. The soil is an orthic eutric brunisol on a layer of glacial till overlying bedrock (Stalker 1973). The overstory is composed of subalpine fir up to 200 years old and Engelmann (or Engelmann x white) spruce up to 350 years old. The height of canopy trees

ranges from 15 to 25 m. Density is 1177 stems per hectare; stand basal area is 40 m^2 per hectare. As in other Rocky Mountain spruce-fir forests (Day 1972; Veblen 1986), subalpine fir are more numerous in the understory while spruce make up the greatest proportion of the biomass of the overstory. Large numbers of dead and fallen trees of both species are present. The shrub layer is dominated by green alder while mosses (H. splendens, P. schreberi) dominate the ground vegetation. The forest floor is on the average 12 cm thick with much surface and incorporated wood, none of which is charred. It appears that this forest has not experienced a fire for at least 3 centuries.

The fourth site ("Clearcut") is a 1500 m^2 area cut from a lodgepole pine forest at 1410 m. The soil is an orthic eutric brunisol on glaciofluvial and fluvial deposits. Live trees were removed during cutting in 1972 while standing dead trees were felled and left on the surface. Understory trees were left intact, and no further site treatment occurred. The present stand is composed of lodgepole pine from 1 - 11 years of age, white (or white x Engelmann) spruce 3 - 19 years, willow, aspen, buffaloberry and alder. Ground vegetation is composed primarily of grasses (E. innovatus, C. rubescens), dwarf shrubs (Arctostaphylos uva-ursi, L. borealis) and forbs (A. conspicuus, E. angustifolium, L. ochroleucus, C. canadensis). The forest floor averages 4 cm deep with small amounts of incorporated charred wood. Analysis of the surrounding pine forest suggests that this forest is of similar origin as the "Pine" site.

CHAPTER 3

3. BIOMASS, PRODUCTIVITY AND NUTRIENT USE EFFICIENCY OF VEGETATION

3.1 INTRODUCTION

Quantification of the internal nutrient dynamics of vegetation is an essential component of studies of nutrient cycling in terrestrial ecosystems. In addition to providing information on nutrient immobilization in biomass and demand by annual production, analysis of nutrient dynamics of vegetation also provides an indication of nutrient availability in the ecosystem. Foliar nutrient levels have been shown to fluctuate to some extent according to levels of available nutrients in soil (Birk and Vitousek 1986). The extent of resorption of nutrients from foliage during senescence has also been shown to vary with nutrient availability (Stachurski and Zimka 1975; but see Chapin and Kedrowski 1983). This flexibility in nutrient levels and resorption capacity lead to differences in nutrient use efficiency (amount of biomass produced per unit nutrient taken up), which may also be used as an indicator of nutrient availability in soil. The purpose of this chapter is to characterize the aboveground vegetation in each forest according to composition, biomass and productivity, and to compare the efficiency with which these potentially limiting nutrients are used by the vegetation in each forest.

3.2 METHODS

The species and diameter at breast height (DBH) of all live and standing dead trees on two 20 x 30 m plots at each site were recorded in the summer of 1984. Published equations (Singh 1982) were used to convert DBH to aboveground live wood biomass for each species. Published values for the proportion of wood to "foliage" (current year's increment and all previous year's foliage plus current year twigs) for each species (Keays 1971) were used to calculate the biomass of "foliage" for each tree. The mass of current year foliage was estimated as the mass of foliage of each species in annual litterfall. Litterfall was harvested monthly from fifteen 0.25 m^2 littertraps randomly placed within one 20 x 30 m plot at each site (Chapter 4). Samples of branches of each species were then used to determine the proportions of current twigs, current needles or leaves and previous years needles for each tree. In February 1986 one mid-canopy branch was harvested from each of six healthy canopy trees of each dominant species at each site (pine at the Pine site, pine and spruce at the Spruce site, and spruce and fir at the Fir site). The proportion of the total "foliage" mass which occurred as needles or twigs of each branch was determined and averaged for each species at each site. Foliage production by deciduous trees was estimated using regression equations relating DBH to foliage mass for each species (Keays 1971).

Annual wood increment of trees was estimated by measuring the average width of annual growth rings over the last ten years. Two cores were taken from each 5 cm diameter class of each dominant

species at each site in July 1985. Using the DBH-wood mass regression equations, the mass of wood including and excluding average annual growth were calculated for each tree; the difference between the two masses was equal to the mass of the average annual wood increment for that tree.

Net primary production (NPP) of the aboveground portion of each tree was calculated as the sum of the biomasses of current year's needles, current year's twigs and annual wood increment. Total aboveground biomass was calculated as the sum of annual production plus previous year's needles and old live wood for each tree. Values for individual trees were summed for each species and for all trees on the plots to estimate NPP and biomass per unit area at each site.

Published equations relating DBH to wood mass were not reliable for trees of DBH less than 10 cm. This necessitated harvesting of understory trees of each species to develop regression equations for trees of DBH between 1 and 10 cm. The number of individuals of each species harvested ranged from 10 - 15 for common species and 4 - 10 for rare species. Individuals from across this range of diameters were harvested from areas outside the study plots in October 1985 and separated into biomass categories: current year needles or leaves, current year twigs, previous year needles, live wood and attached dead wood. The average width of annual rings over the last ten years was again used to determine the mass of new wood. Regression equations relating DBH to the mass of each biomass component were calculated for each species (Corbin, unpublished

data) and used to determine annual production and total biomass for each understory tree. Values for individual trees were summed for each species and for all trees on the two plots (1200 m^2) to estimate annual NPP and biomass of understory trees at each site. For rare species, the regression equations developed for understory trees were also applied to canopy trees of the same species. The mass of standing dead trees was estimated using the regressions for live trees minus the mass of foliage.

Aboveground NPP and biomass of shrubs was determined in a manner similar to that for understory trees. The basal diameter and species of each live stem on three 20 x 30 m plots at each site was recorded in July 1984. Four to fifteen individual stems of each species (depending on their abundance at the site) across the range of basal diameters present at each site were clipped at ground level and separated into biomass categories. Regression equations relating basal diameter to mass of each biomass component were developed for each species (Corbin, unpublished data) and used to convert DBH to mass of each component of each individual. The mass of appropriate components were summed to estimate NPP and biomass of each stem; these were summed for the sample area (1800 m^2) to determine the annual aboveground production and biomass of shrubs at each site.

Net primary production and biomass of ground vegetation (grass, forbs, small shrubs) was estimated by clipping aboveground portions in ten 0.25 m^2 quadrats within one 20 x 30 m plot in August 1985. Harvesting of quadrats at monthly intervals during summer in 1984, as well as previous studies in the area (Dennis 1970)

indicated late July to be the time of maximum biomass of all species of ground vegetation combined. For herbaceous species, the aboveground mass at peak growth served as the estimate of both NPP and biomass. For woody species, current year growth was separated from that of previous years to calculate annual NPP, and combined to determine total biomass. All live (green) moss was removed from forty 0.0625 m^2 samples of forest floor taken in August 1984 and separated into current and previous year's growth. Annual NPP and biomass of each type of ground vegetation (grass, forb, small shrub, moss) were determined separately.

All samples of vegetation used to estimate biomass of production were dried at 80°C to constant weight before final weight determination. Nitrogen and phosphorus content of each type of vegetation was also estimated from these samples. For common species of canopy trees, current year's needles and twigs harvested from one branch of six trees of each species at each site, and a bulk sample of needles of all age classes from a second branch of each tree were analyzed. The nitrogen and phosphorus content of wood of common canopy trees was estimated from two cores taken from healthy canopy individuals of each species. For less common species of canopy trees, and for all species of understory trees, the small trees harvested to produce biomass regression equations were used for nutrient analysis. Each component of 3 trees between 1 and 5 cm DBH, and 2 trees between 5 and 10 cm DBH of each species were analyzed. N and P content of shrubs was estimated from samples of each biomass component of 3 stems of each species across the range

of diameters present at each site. Samples of each type of ground vegetation (grasses, forbs, small shrubs) from 5 quadrats, and green portions of moss from 5 samples of the forest floor from each site were analyzed for N and P content.

Portions of each sample to be analyzed for N and P content were ground through a 20 μm sieve in a Wiley mill and dried at 80°C. 150 mg of each non-wood sample or 250 mg of each woody sample to be used for N and P analysis were digested at 360°C in sulphuric acid and hydrogen peroxide, filtered through Whatman #1 paper, and analyzed for total N and P content in mg per gram sample on a Technicon II autoanalyzer. The average N and P content of each biomass component was multiplied by the mass of that component for each species or type of vegetation. The total mass of N and P in annual NPP and biomass was then determined for each species or type of vegetation, and summed for each site to estimate the total mass of N and P in aboveground net primary production and biomass at each site.

Annual nutrient resorption was determined from differences in the green and senescent N and P contents of foliage. Concentrations of N and P were multiplied by the mass of foliage of each species or type of vegetation in annual litterfall (for trees and shrubs) or annual production (for ground vegetation) to determine the mass of N and P in each type of foliage at each time. The N and P contents of tree foliage harvested in February 1986 were used to estimate concentrations of nutrients in green needles, and needles of each species collected in littertraps in October 1985 were used to determine nutrient content of each species after senescence.

Shrub foliage was harvested from each species at maximum biomass in August 1986 and immediately after abscsision in October 1986 to determine green and senescent nutrient content, respectively. Current year production of ground vegetation harvested in September 1985 and October 1986 were used to determine nutrient content at maximum biomass and following senescence. Although nutrient withdrawal from ground vegetation may not have been complete by October, the difficulty of sampling and the potential for heightened rates of leaching of N and P from vegetation brought on by accumulation of snow precluded further postponement of harvesting. Green and yellow portions of moss from the forest floor samples were used to determine the nutrient content of live and senescent moss, respectively. The difference in total mass of each nutrient in live and senescent foliage was used as an estimate of the amount of each nutrient resorbed from foliage annually. This calculation assumes no mass loss or leaching during senescence, or resorption from non-foliar components.

Amounts of N and P resorbed from foliage annually were subtracted from the amounts in net primary production to estimate the amount of N and P taken up annually by vegetation to produce new aboveground biomass. This value was used as a relative estimate of annual uptake or nutrient demand of the vegetation at each site. The efficiency of nutrient use of vegetation at each site was estimated by dividing the amount of new aboveground biomass by the amount of N and P taken up in one year.

The significance of differences among sites were tested using one-way analysis of variance followed by Scheffé's tests, or t-tests. Data sets with non-homogeneous variances according to Bartlett's tests were analyzed by Kruskall-Wallis tests. All statistical analyses were carried out using SPSS^{X} (SPSS Inc. 1986).

3.3. RESULTS

The composition of vegetation in each forest is shown in Tables 2 and 3. The Spruce site supported the greatest biomass of trees (Table 2); this was due to their large size as density of canopy trees was lowest at this site. The canopy was composed primarily of white x Engelmann spruce, along with smaller amounts of lodgepole pine and a few standing dead trees which were mostly pine. Spruce was also the most abundant species in the understory. The Pine site had the greatest density of overstory trees, but the lowest biomass of the three forested sites. Canopy trees, both live and standing dead, were almost exclusively lodgepole pine (many of the trees under 10 cm DBH were essentially canopy trees). Balsam poplar, trembling aspen and white x Engelmann spruce were most abundant in the understory. Canopy trees at the Fir site were of intermediate density and biomass. White x Engelmann spruce dominated the canopy in terms of biomass, while subalpine fir was the most numerous species in all layers. A large mass of standing dead of both species was present. At the Clearcut site, all trees were of DBH less than 10 cm. Lodgepole pine and white x Engelmann spruce

Table 2. Density and biomass of trees at the four study sites in the Rocky Mountains of Alberta.

Site / Species	Density (stems ha^{-1}) Understory (<0.5 cm DBH)	Understory (0.5-10 cm DBH)	Canopy (>10 cm DBH)	Standing Dead (Total)	Biomass ($g\ m^{-2}$) Live Understory	Live Canopy	Dead Understory	Dead Canopy
Clearcut								
pine	217	100	0	0	27.66	0	0	0
spruce	150	133	0	0	65.53	0	0	0
Douglas fir	125	0	0	0	0.22	0	0	0
subalpine fir	25	0	0	2	0	0	1.05	0
aspen	34	33	0	0	16.08	0	0	0
Total	551	266	0	2	109.49	0	1.05	0
Pine								
pine	20	33	2467	1429	8.96	10676.03	48.88	1289.48
spruce	125	84	8	92	53.77	30.53	0.00	0
poplar	400	34	8	33	17.29	34.19	3.49	28.25
aspen	120	17	0	25	1.47	0	17.34	0
Total	665	168	2483	1579	81.49	10740.75	69.71	1317.73

continued...

Table 2. (Concluded.)

Site / Species	Density (stems ha^{-1}) Understory (<0.5 cm DBH)	Understory (0.5–10 cm DBH)	Canopy (>10 cm DBH)	Standing Dead (Total)	Biomass ($g\ m^{-2}$) Live Understory	Live Canopy	Dead Understory	Dead Canopy
Spruce								
pine	0	0	267	67	0	5509.01	0.95	670.01
spruce	5900	400	400	117	265.39	13241.07	48.99	262.07
Douglas fir	180	17	58	0	14.25	783.54	0.00	0
poplar	130	8	0	25	0.37	0	0	107.81
aspen	270	0	8	17	0.60	279.06	0	41.54
Total	6480	425	750	226	280.61	19812.68	49.94	1081.43
Fir								
subalpine fir	6400	1117	783	514	507.89	5377.78	123.12	633.77
spruce	450	423	394	257	174.51	9028.74	107.50	1394.73
Total	6850	1540	1177	771	682.40	14406.56	230.62	2038.50

Table 3. Aboveground biomass (g m^{-2}) of ground vegetation in four Rocky Mountain coniferous forests.

Site	Moss	Grass	Forb	Small Shrubs[a]	Total Ground Vegetation	Large Shrubs[b]
Clearcut	9.8 ± 4.0	39.1 ± 15.6	12.8 ± 8.9	55.3 ± 57.9	117.0	182.4
Pine	15.0 ± 17.8	15.8 ± 9.6	28.1 ± 9.3	24.6 ± 24.4	83.5	37.7
Spruce	64.5 ± 26.2	3.1 ± 2.0	10.7 ± 7.6	25.1 ± 19.8	103.4	118.7
Fir	46.8 ± 25.7	0.9 ± 1.1	3.3 ± 2.9	1.3 ± 3.0	52.3	92.9

NOTE: Each value is the mean ± standard deviation. For moss, n = 40, for grass, forbs and small shrubs, n = 10.

[a] Primarily woody, creeping species such as Linnaea borealis, Arctostaphylos uva-ursi, Vaccinium caespitosum

[b] Species greater than 1 m in height, primariliy Shepherdia canadensis and Alnus crispa.

were most abundant; Douglas fir and trembling aspen saplings were also present.

The greatest biomass of large shrubs occurred at the Clearcut site and the least amount occurred at the Pine site (Table 3). Ground vegetation was also most abundant at the Clearcut site, especially grass and small shrubs. The Spruce site had large amounts of ground vegetation, especially moss. Forbs were the most abundant type of ground vegetation at the Pine site. Ground vegetation was least abundant at the Fir site and dominated by moss.

The biomass of aboveground vegetation and the amount of N and P immobilized in biomass were highest at the Spruce site, followed by the Fir, Pine and Clearcut sites, reflecting the biomass of the canopy layer at each site. Net primary production and immobilization of N were highest at the Pine site, followed closely by the Spruce site which had slightly more P immobilized in new biomass. The shrub layer attained its greatest biomass and nutrient mass at the Fir site, but was most productive in terms of mass and nutrients at the Clearcut site (Table 4). Biomass and production of ground vegetation was greatest at the Clearcut site and lowest at the Fir site (Table 4). In summary, nutrient immobilization in biomass was in the order: Spruce > Fir > Pine > Clearcut. Nutrient immobilization in new growth was in the order: Pine > Spruce > Fir > Clearcut. The amount (%) of new growth produced annually per unit existing biomass was Pine 4.25 > Fir 2.66 > Spruce 2.18 for canopy trees, and Clearcut 21.17 > Pine 13.73 > Spruce 8.75 > Fir 4.34 for the shrub layer.

Table 4. Mass of N and P in annual net primary production and biomass of aboveground vegetation in four Rocky Mountain coniferous forests.

Site Layer	Net Primary Production			Biomass		
	Dry Mass	N	P	Dry Mass	N	P
Clearcut						
canopy	0	0	0	0	0	0
shrub	0.62	10.24	0.88	2.93	27.44	2.43
ground	0.74	10.17	1.56	1.17	18.00	2.37
Total	1.36	20.41	2.45	4.10	45.45	4.80
Pine						
canopy	4.57	18.96	2.65	107.41	131.03	16.11
shrub	0.16	2.09	0.22	1.20	8.47	0.92
ground	0.61	11.62	1.49	0.82	17.18	2.12
Total	5.34	32.68	4.36	109.43	156.58	19.14
Spruce						
canopy	4.32	17.87	2.97	198.13	263.27	29.59
shrub	0.35	3.70	0.56	4.02	24.40	3.99
ground	0.47	7.36	1.44	1.05	17.29	3.23
Total	5.15	28.93	4.97	203.20	304.97	36.81
Fir						
canopy	3.83	15.98	1.92	144.07	244.78	23.75
shrub	0.34	4.35	0.38	7.76	40.15	4.73
ground	0.21	3.06	0.31	0.53	6.32	0.80
Total	4.37	23.39	2.61	152.36	291.25	29.28

NOTE: Dry mass in t ha^{-1}, N and P content in kg ha^{-1}.

Foliar N and P concentrations for trees of the same species and ground vegetation of the same type at different sites are shown in Tables 5 and 6. Nitrogen concentrations were remarkably similar among sites for all vegetation types; phosphorus concentrations were consistently low at the Fir site. Both N and P concentrations tended to be highest in current year foliage and understory trees (Tables 5 and 6).

The mass and proportion of N and P resorbed from trees, shrubs and ground vegetation at each site is shown in Table 7. The mass of both nutrients resorbed depended largely on the mass of resorbing tissue present at the site. Proportional resorption of nutrients by surface vegetation was slightly lower at the Clearcut for both N and P (Table 7). Proportional resorption of nutrients by trees and shrubs was greatest at the Pine site for N and greatest at the Fir site for P. Trees and shrubs at the Clearcut site resorbed the lowest amount and proportion of both N and P.

The proportion of nutrients resorbed by a given species at different sites is shown in Table 8. Even where differences among sites occur in concentrations of a nutrient, the degree of resorption does not change appreciably for a given species.

Annual nutrient uptake was calculated as the difference between the amount of N and P in new production and the amount of N and P resorbed annually. The apparent uptake of both nutrients by trees and shrubs declined in the order Spruce > Fir > Pine > Clearcut (Table 9). Nutrient uptake by ground vegetation was greatest at the Clearcut site and lowest at the Fir site. Thus, total nutrient

Table 5. Average N and P content of major types of ground vegetation in four Rocky Mountain coniferous forests.

Vegetation Type†	Site	n	Surface Vegetation % N	Surface Vegetation % P
Moss	Clearcut	4	1.37 ± 0.16^{a}	0.24 ± 0.04^{a}
	Pine	5	1.49 ± 0.12^{a}	0.25 ± 0.02^{a}
	Spruce	5	1.18 ± 0.09^{a}	0.24 ± 0.01^{a}
	Fir	5	1.29 ± 0.32^{a}	0.15 ± 0.04^{b}
Grass	Clearcut	2	1.26 ± 0.10^{a}	0.21 ± 0.01^{bc}
	Pine	3	1.74 ± 0.03^{a}	0.29 ± 0.10^{ab}
	Spruce	3	1.99 ± 0.18^{a}	0.40 ± 0.03^{a}
	Fir	3	2.77 ± 0.96^{a}	0.16 ± 0.04^{c}
Forb	Clearcut	2	1.81 ± 0.07^{a}	0.20 ± 0.01^{b}
	Pine	3	2.19 ± 0.27^{a}	0.26 ± 0.05^{b}
	Spruce	3	1.94 ± 0.17^{a}	0.44 ± 0.05^{a}
	Fir	3	2.04 ± 0.37^{a}	0.16 ± 0.06^{b}
Small shrub*	Clearcut	2	1.02 ± 0.01^{b}	0.12 ± 0.001^{c}
	Pine	3	1.44 ± 0.17^{a}	0.16 ± 0.01^{b}
	Spruce	3	1.71 ± 0.10^{a}	0.28 ± 0.02^{a}
	Fir	3	1.79 ± 0.12^{a}	0.10 ± 0.01^{c}

NOTE: Each value is the mean ± standard deviation. Values in the same column for each vegetation type followed by the same letter are not significantly different ($p < 0.05$) based on one-way analysis of variance and Scheffé's tests.

† samples of all species within quadrat combined for each vegetation type

* foliage only

Table 6. Average N and P content of lodgepole pine and white x Engelmann spruce needles from trees in four Rocky Mountain coniferous forests.

Lodgepole Pine Needles					White X Engelmann Spruce Needles				
Type	Site	n	% N	% P	Type	Site	n	% N	% P
Understory current	Clearcut	4	1.26 ± 0.09[a]	0.13 ± 0.02[a]	Understory current	Clearcut	5	1.06 ± 0.15[a]	0.18 ± 0.03[a]
	Pine	2	1.17 ± 0.04[a]	0.13 ± 0.01[a]		Pine	5	1.14 ± 0.35[a]	0.21 ± 0.04[a]
						Spruce	5	1.28 ± 0.07[a]	0.24 ± 0.01[a]
						Fir	5	1.23 ± 0.12[a]	0.20 ± 0.03[a]
previous	Clearcut	4	1.10 ± 0.06[a]	0.10 ± 0.01[a]	previous	Clearcut	4	0.85 ± 0.09[b]	0.13 ± 0.03[a]
	Pine	3	1.02 ± 0.32[a]	0.09 ± 0.03[a]		Pine	4	0.86 ± 0.06[b]	0.12 ± 0.03[a]
						Spruce	5	1.06 ± 0.11[a]	0.15 ± 0.03[a]
						Fir	5	1.04 ± 0.09[ab]	0.11 ± 0.04[a]
Overstory current	Pine	6	0.93 ± 0.04[a]	0.13 ± 0.01[a]	Overstory current	Spruce	5	0.94 ± 0.029[a]	0.17 ± 0.02[a]
	Spruce	6	0.94 ± 0.08[a]	0.12 ± 0.01[a]		Fir	5	0.93 ± 0.05[a]	0.12 ± 0.02[b]
current plus previous	Pine	6	0.89 ± 0.05[b]	0.12 ± 0.02[a]	current plus previous	Spruce	5	0.86 ± 0.04[b]	0.12 ± 0.01[a]
	Spruce	6	1.01 ± 0.07[a]	0.09 ± 0.01[a]		Fir	5	0.99 ± 0.09[a]	0.09 ± 0.06[b]

NOTE: Each value is the mean ± standard deviation. Values within each column for each type of needle followed by the same letter are not significantly different ($p \leq 0.05$) based on t-tests for two-mean comparisons or one-way analysis of variance and Scheffé's tests for comparisons among four means.

Table 7. Mass of N and P resorbed by vegetation in four Rocky Mountain coniferous forests.

Site	Litterfall Mass ($g\ m^{-2}\ y^{-1}$)	Nutrient Mass ($mg\ m^{-2}$)[a] Green Tissue N	Green Tissue P	Litterfall N	Litterfall P	Resorption[b] N ($mg\ m^{-2}$)	N %	P ($mg\ m^{-2}$)	P %
Ground Vegetation									
Clearcut	70.44	973	148	704	118	269	28	30	20
Pine	55.61	1087	136	637	105	450	41	31	23
Spruce	25.88	482	93	317	67	165	34	26	28
Fir	4.96	105	8	71	5	34	32	3	38
Trees and Shrubs (foliage only)									
Clearcut	6.94	98	8	80	5	18	18	3	26
Pine	172.78	1575	201	798	44	777	49	157	78
Spruce	143.07	1373	169	839	82	534	39	87	51
Fir	119.15	1333	119	785	77	548	41	72	60

[a] Nutrient concentration x mass, determined separately for type of surface vegetation and each species of tree and shrub.

[b] Mass of nutrient in green tissue minus mass of nutrient in litterfall, and per cent of mass of nutrient in green tissue which is resorbed.

Table 8. Concentration and resorption of N and P from pine and spruce needles in trees from different sites in the Rocky Mountains of southwestern Alberta.

Needle Species	Site	mgN g^{-1}			mgP g^{-1}		
		Green	Litterfall	Resorption*	Green	Litterfall	Resorption*
pine	Pine	8.90 ± 0.50[b]	4.61 ± 0.32[a]	4.29 (48%)	1.16 ± 0.18[a]	0.26 ± 0.05[a]	0.90 (78%)
	Spruce	10.13 ± 0.74[a]	4.48 ± 0.06[a]	5.65 (56%)	0.90 ± 0.11[b]	0.24 ± 0.01[a]	0.66 (73%)
spruce	Spruce	10.56 ± 1.10[a]	5.15 ± 1.04[a]	5.41 (51%)	1.97 ± 0.24[a]	0.61 ± 0.09[a]	1.36 (69%)
	Fir	10.28 ± 0.66[a]	5.37 ± 0.48[a]	4.91 (48%)	1.30 ± 0.18[b]	0.35 ± 0.01[b]	0.95 (73%)

NOTE: Each value is the mean ± standard deviation. Values in different columns for each species followed by the same letter are not significantly ($p \leq 0.05$) different based on t-tests.

* Concentration of nutrient in green tissue minus concentration of nutrient in litterfall, (per cent of concentration in green tissue)

uptake by all aboveground vegetation was greatest at the Spruce site, followed by the Pine, Clearcut and Fir sites (Table 9).

Nutrient use efficiency was calculated as the amount of new biomass produced per unit N or P taken up annually (Table 9). For ground vegetation, nitrogen use efficiency was similar among the sites, while phosphorus was used most efficiently at the Fir site and least efficiently at the Spruce site. Efficiency of use of N and P by trees and shrubs was greatest at the Pine site and least at the Clearcut. The resulting order of P use efficiency was Fir > Pine > Spruce > Clearcut (Table 9).

3.4 DISCUSSION

Estimates of net primary production of the forests in the Lusk Creek watershed (437 - 534 g m^{-2} yr^{-1}) are slightly lower than average values for boreal forests (600 g m^{-2} yr^{-1}, Lieth 1975) or montane coniferous forests (600 g m^{-2} yr^{-1}, Olson 1975). Inclusion of estimates of belowground production and consumption losses would bring these estimates into the range of those in the literature.

Aboveground biomass at the pine site falls within the range reported for other lodgepole pine forests of similar age and density (Table 10). The nitrogen content of the pine stand is similar to that reported in Wyoming, but is higher than that reported in British Columbia (Table 11). The few data available for spruce-fir stands have similar biomass as that found at the Spruce site, but are higher than those at the Fir site (Table 10). Biomass productivity of the forest of the Spruce site are about 20% higher than

Table 9. Annual uptake and efficiency of N + P use by aboveground vegetation in four Rocky Mountain coniferous forests.

	N				P			
	Annual Production[a] ($mg\ m^{-2}yr^{-1}$)	Annual Resorption[b] ($mg\ m^{-2}yr^{-1}$)	Annual Uptake[c] ($mg\ m^{-2}yr^{-1}$)	Efficiency[d]	Annual Production[a] ($mg\ m^{-2}yr^{-1}$)	Annual Resorption[b] ($mg\ m^{-2}yr^{-1}$)	Annual Uptake[c] ($mg\ m^{-2}yr^{-1}$)	Efficiency[d]
Tree and Shrubs								
Clearcut	1024	18	1006	62	89	3	86	721
Pine	2106	777	1329	357	287	157	130	3646
Spruce	2157	534	1623	288	353	87	266	1756
Fir	2033	548	1485	281	230	72	158	2639
Ground Vegetation								
Clearcut	1017	269	748	99	156	30	126	587
Pine	1162	450	712	86	149	31	118	517
Spruce	736	165	571	82	144	26	118	398
Fir	306	34	272	77	31	3	28	750
Total								
Clearcut	2041	287	1890	72	244	33	212	642
Pine	3268	1227	2041	262	436	188	248	2157
Spruce	2893	699	2194	281	497	113	384	1604
Fir	2339	582	1757	249	261	75	186	2355

[a] From Table 4
[b] From Table 7
[c] Mass of nutrient in annual production minus mass of nutrient resorbed annually
[d] Milligrams of new biomass produced per mg N or P taken up in one year

Table 10. Aboveground biomass of some Rocky Mountain coniferous forests.

Dominant Trees	Stand Age (years)	Density (stems ha^{-1})	Biomass ($t\ ha^{-1}$)	Location	Reference
Lodgepole pine	75	1280	96.3	S.E. Wyoming	Pearson et al. 1984 (Rock Creek)
	110	1850	144.1	S.E. Wyoming	Pearson et al. 1984 (Nash Fork)
	71	1600	70.1	central Colorado	Moir 1972 (stand 4.3)
	200	--	101-104	northern Colorado	Reid et al. 1976
	125	--	194.5	central B.C.	Kimmins 1974 (Parsnip plot)
	100	1020	245.0	southern Alberta	Johnstone 1971 (stand 1)
	85	1716	107.4	southern Alberta	this study (Pine site)
White or Engelmann spruce - subalpine fir	250	--	197.0	Colorado	Landis and Mogren 1975 (average)
	350	--	213.1	central B.C.	Kimmins 1974 (McGregor plot)
	350	1177	144.1	southern Alberta	this study (Fir site)
	120	750	198.1	southern Alberta	this study (Spruce site)

those reported in a white spruce stand (plot 26) of similar age and density in interior Alaska (Yarie and Van Cleve 1983). Nitrogen content of the Spruce and Fir stands was similar to, and phosphorus content lower than those reported in British Columbia (Table 11).

Nitrogen and phosphorus content of overstory tree foliage was similar to that reported from other forests of lodgepole pine (Beaton et al. 1965; Kimmins 1974; DeByle 1980; Stark 1983) and white or Engelmann spruce (Beaton et al. 1965; Kimmins 1974; Stark 1983; Ballard and Carter 1985). Subalpine fir foliage in the Lusk Creek watershed had higher levels of N and lower levels of P than those found in British Columbia (Kimmins 1974) and Montana (Stark 1983). Levels of N and P in foliage of pine and spruce were less than most estimates of adequate levels for these species (Morrison 1974a; van den Driessche 1974; Ballard and Carter 1985). Similar data for subalpine fir are not available. Concentrations of N and P in live moss are lower than those reported elsewhere (Kimmins et al. 1985) for the same species. Proportional resorption of N from pine needles at these sites (50%) was similar to, and resorption of P (75%) was higher than that reported for other species of pine (Grizzard et al. 1976 in Chapin and Kedrowski 1983; Wells and Metz 1963 in van den Driessche 1984). Annual uptake of N and P in these forests (18 - 20 kg ha^{-1} yr^{-1}) is very close to that predicted by Miller (1984) for temperate forests with these rates of net primary production.

The Pine site might be expected to be the most productive of the forests in this study because it is younger and is composed

Table 11. Mass of N and P in aboveground biomass of some Rocky Mountain coniferous forests.

Dominant Trees	Biomass ($t\ ha^{-1}$)	N ($kg\ ha^{-1}$)	%	P ($kg\ ha^{-1}$)	%	Reference
Lodgepole pine	144.1	185	0.13	--	--	Fahey et al. 1985 (Nash Fork)
	142.2	169	0.12	--	--	Fahey et al. 1985 (Dry Park 1)
	194.5	155	0.08	19.8	0.010	Kimmins 1974 (Parsnip plot)
	107.4	131	0.12	16.1	0.015	this study (Pine site)
White or Engelmann spruce - subalpine fir	213.1	324	0.15	41.7	0.019	Kimmins 1974 (McGregor plot)
	144.1	245	0.17	23.7	0.016	this study (Fir site)
	198.1	263	0.13	29.6	0.015	this study (Spruce site)

primarily of fast-growing lodgepole pine (Wheeler and Critchfield 1985). The low levels of N and P in annual production, biomass and foliage, and the high degree of resorption are demonstrative of high efficiency of nutrient use by trees at this site. The intermediate levels of nutrient and resorption in ground vegetation and the similar degree of resorption of pines at both the Pine and Spruce sites suggest that this efficiency is a characteristic of pine trees, and not necessarily evidence of lower nutrient availability at this site. High efficiency of water and nutrient use has been demonstrated for other species of pines (Miller et al. 1979); thus the prevalence of this species is probably responsible for the efficient use of N and P by vegetation at the Pine site.

The Spruce site had the greatest biomass and productivity, but the lowest productivity per unit biomass of the forests. Resorption of N and P by the overstory was relatively small, resulting in the greatest rates of uptake and lowest efficiency of use of these nutrients at this site. Values for the amounts of N and P in tree biomass annual production (requirement), and the efficiency of use of both nutrients at the Spruce site are similar to average values for white spruce stands in interior Alaska (Van Cleve et al. 1983). This observation, as well as the similarity in levels of N and P in foliage and in the degree of resorption of N and P from pine and spruce foliage from this and other sites suggest that the efficiency of N and P use in this forest is also a consequence of the species composition of the stand, rather than a result of substantially greater nutrient availability at this site.

Although the Fir site ranked second in terms of total biomass, it was the least productive of the three forested sites. Nitrogen levels in vegetation were similar to those at the Spruce site and other spruce-fir forests (Kimmins 1974), as was the degree of N resorption and the efficiency of N use. Phosphorus levels, however, were lower in foliage from the Fir site than from other forests, and P was used much more efficiently by vegetation at this site. Comparison of data for levels of available nutrients in soils at these sites (Chapter 6) demonstrates consistently lower levels of P in soil at the Fir site. This may be partially responsible for the low primary productivity of vegetation at this site, but many other factors such as the greater age, prevalence of slow-growing subalpine fir (Alexander 1987), lower temperatures, and shorter growing season at this higher elevation site cannot be ruled out.

The low biomass and productivity of vegetation at the Clearcut site are obvious consequences of the lack of overstory (> 10 cm DBH) trees at this site. The resulting increase in shrubs and ground vegetation which have higher levels of nutrients in foliage, a greater foliage to wood ratio (Waring and Schlesinger 1985) and a more limited nutrient resorption capacity led to this site having rates of nutrient uptake similar to that at the forested sites. This finding supports similar reports of fast-growing early successional vegetation retaining nutrients within recently disturbed ecosytems (Marks and Bormann 1972; Vitousek and Reiners 1975).

In theory, vegetation may respond to reduced nutrient availability through difference in species composition towards

greater dominance by species more efficient in nutrient use or through change in the nutrient use efficiency of component species (Kost and Boerner 1985). These physiological changes may arise from plants simply producing less nutrient rich tissues, or by resorbing a greater amount of nutrients during senescence. Patterns of tree species composition in the forests in the present study are probably the result of factors other than nutrient availability, such as disturbance type and frequency and microclimate, and thus do not provide evidence for the first mechanism. Only in situations where differences in nutrient availability were much larger than differences in other factors could the species composition of forests be reliably related to levels of available nutrients. There was some evidence of greater efficiency of use of limiting nutrients by vegetation in the low levels of P in vegetation at the Fir site. The greater efficiency of P use at this site appeared to arise from production of more biomass per unit P taken up, rather than through greater resorption of P from senescing foliage.

With the exception of this apparent response of vegetation at the Fir site to low availability of phosphorus, the efficiency of nutrient use by vegetation in these forests appeared to be mostly related to the inherent nutrient use efficiencies of the tree species present. Since the species composition of these forests is most likely the result of factors other than nutrient availability, the nutrient use efficiency of each forest is also for the most part a consequence of factors other than nutrient availability.

Analysis of the nutrient content of foliage or litterfall has often been suggested as a simple and reliable means of assessing nutrient availability or deficiency in forests (van den Driessche 1974; Waring and Schlesinger 1985). The reliability of this technique requires demonstration that nutrient levels in foliage from sites with different nutrient availability are detectably different from one another. The limited data presented in this study suggest that these species of trees are, for the most part, remarkably consistent in levels of nutrients in foliage regardless of location. However, it appears that substantial differences in nutrient availability (as suggested for phosphorus at the Fir site) may be detected through analysis of the nutrient content of foliage or litterfall.

CHAPTER 4

4. INPUT, ACCUMULATION AND RESIDENCE TIME OF CARBON, NITROGEN AND PHOSPHORUS

4.1 INTRODUCTION

Comparison of litter dynamics among forested ecosystems provides information on a number of aspects of ecosystem functioning. The mass of litter produced on a yearly basis may be used as an index of primary productivity of the forest (Bray and Gorham 1964). Comparison of litter input rates with the amount accumulated on the forest floor may be used as an estimate of the residence time of litter in the forest floor, or reciprocally, the turnover rate of litter (Olson 1963). Together, rates of litter input and turnover provide an estimate of the rate at which matter is cycled within the ecosystem. Quantification of the nutrient content of litter inputs and accumulation allows estimates to be extended to rates of nutrient cycling within the ecosytem. Comparison of rates of cycling of different nutrients within one ecosystem, or of a single nutrient among different ecosystems provides an indication of the relative availability of different nutrients in different ecosystems.

Increasing recognition of the prevalence of disturbance in forested ecosystems (White 1979) has important implications for the calculation of litter turnover times. The assumption of steady state conditions in the detrital pool required by the turnover model

may not be achieved for several decades after a disturbance (Birk and Simpson 1980; Pearson et al. 1987). Means of reconciling this assumption in light of frequent disturbances must be addressed for estimates of litter turnover rates to be useful descriptors of ecosystem functioning.

In the present investigation, the mass and nitrogen and phosphorus content of annual litter input and litter accumulation were compared in four different coniferous forests in order to characterize and quantify the cycling of matter and nutrients in each forest and to compare the relative availability of these nutrients among these forests. Separation of litter input and accumulation into components allowed for comparison of decay rates of individual litter types among sites, and examination of means by which the turnover method could be used as a valid measurement of litter turnover rates in forests subjected to fire or logging disturbances.

4.2 METHODS

4.2.1 Litter Input

The mass of current year's production of ground vegetation (grass, forbs, shrubs <1 m high) was estimated by harvesting ten 0.25 m^2 quadrats from one 20 x 30 m plot at each site at time of maximum biomass in August 1985 (Chapter 3). The mass of litter input from grass and forbs was considered to be equal to the total mass while the mass of litter input from small shrubs was considered

to be equal to the mass of current year's production only. Ten additional quadrats were harvested in October 1986; all non-perennial portions of vegetation were analyzed to determine the nutrient (C,N,P) content of senescent ground vegetation as will be described later. The concentration of each nutrient was then multiplied by the mass of each type of ground vegetation at the time of maximum biomass to determine the mass of C, N and P in annual litter input from ground vegetation. This calculation assumes no loss of mass during senescence and thus may overestimate the mass and nutrient content of annual litter input from ground vegetation. Differences in total mass of harvested quadrats between the maximum biomass and senescence harvests were inconsistent, due to considerable spatial heterogeneity; therefore a reliable correction factor could not be determined. Annual input of moss litter was considered to be equal to the mass of one year's production of moss. Since moss has an average lifespan of three years in these forests (pers. observ.), moss litter input was estimated as 33% of total live moss biomass determined from forty 0.0625 m^2 samples of the forest floor (Chapter 3). The nutrient content of yellow portions from 5 of the 40 samples was used to estimate input of C, N, and P in moss litter.

Overstory (tree and shrub) litter was collected in fifteen 0.25 m^2 littertraps placed randomly in one 20 x 30 m plot at each site and weighed after drying at 80°C. During the first year of the study (August 1984 - July 1985), litterfall was collected monthly except during snowcover (December - May) and separated into components (needles, leaves, male cones, female cone bracts, buds,

seeds, other) before weighing. During the second and third year, litterfall was collected monthly and bimonthly, respectively, and weighed unseparated. At the Clearcut site, litter input collections were initiated in August 1985. The C, N, and P content of second year litterfall from 5 of the 15 traps at each site was used to estimate the mass of nutrients in annual overstory litter input.

Input of woody litter was estimated from annual harvesting of all bark, intact female cones, twigs (<1 cm diameter) and branches (1 - 4 cm diameter) on ten 3 x 3 m plots at each site. These plots had been cleared of all litter in August 1984 in order to measure litter accumulation, as will be described later. All new woody litter on each plot was collected in August 1985 through 1987, separated into components, dried to constant weight at 80°C and weighed. The C, N, and P content of woody litter on 5 of the 10 plots at each site from the second year's harvest was used to estimate nutrient input via woody litterfall.

Input of trees was estimated from 3 annual harvests of all newly fallen trees on three 20 x 30 m plots at each site. All fallen trees on the plots were marked with paint in August 1984 to aid in identification of new trees. Newly fallen trees were identified in August 1985 through 1987; the entire bole plus all attached branches of each tree were weighed in the field. Two disks were removed approximately 50 cm from each end of each bole, weighed, dried at 80°C and reweighed to determine the moisture content of each tree. The weight of moisture in each tree was subtracted from its field weight to determine its dry mass. Masses of individual

trees were summed for each of the three 20 x 30 m plots at each site, and the average annual input in grams per m^2 calculated for each site.

The bole samples from each newly fallen tree used for moisture content determination were also used to estimate concentrations of C, N and P in each tree for the first annual harvest in August 1985. In subsequent years, the species and decay class of each newly fallen tree were recorded and the average concentrations of C, N and P in boles of each species-decay class combination from the first treefall harvest or from representative samples were used. The number of samples of each species-decay class combination varied from 1 to 8, depending on their availability at the site. Decay classes were based on visual properties of the boles, ranging from wholly intact (class 1) boles through loss of bark and twigs (class 2), loss of branches and softening of wood (class 3) and fragmentation and incorporation into the forest floor (classes 4 and 5). Concentration of C, N and P in trees of each combination were multiplied by the mass of newly fallen trees of that combination and summed for each plot to determine the total mass of each nutrient in annual tree input in grams per m^2.

4.2.2 Litter Accumulation

The mass of the forest floor organic mat (LFH layers) was determined from forty 0.25 m^2 samples from each site. Four samples were taken from each of ten 3 x 3 m plots in August 1984 at Pine, Spruce and Fir sites and in August 1985 at the Clearcut site.

All green plants on the samples were clipped at ground surface and removed. The litter (L) layer of one quarter of each sample (0.0625 m^2) was separated into components (herbaceous material, reproductive structure, moss, needles). Moss was separated into live (green) and dead (yellow or brown) portions of each plant and the mass of each component was determined. Separation of litter layer material from underlying fermentation and humus (FH) layer material was based on the visual appearance of each litter type. Needles and herbaceous material were considered to be in the L layer if they were mostly unstained and firm. Litter layer moss was that portion of each plant which was yellow or brown but not stained or fragmented. As discolouration and softening of litter did not occur to a great extent until it entered the more compacted fermentation layer below, these visual characteristics related well to the degree of incorporation of the litter into the forest floor. Buried wood and large roots (> 1 mm diameter) were removed from the entire 0.25 m^2 sample and roots were separated into live and dead categories. Samples of all components were dried at 80°C and weighed separately. The composition of the forest floor was determined from the mass of each component separated from the 0.0625 m^2 samples; the total mass of the forest floor (g m^{-2}) was determined from the mass of the entire 0.25 m^2 samples. Concentrations of C, N and P in 5 subsamples of each of 5 randomly picked forest floor samples from each site were used to determine the average nutrient content of the forest floor at each site.

The mass of woody litter accumulated at each site was estimated by harvesting all such material on ten 3 x 3 m plots in August 1984 (August 1985 at the Clearcut site). Collections from each plot were separated into components (intact female cones, bark, twigs and branches), dried at 80°C and weighed. At the Clearcut site, where all standing trees had been felled in 1972 and left on the surface, there was sufficient mass of fallen trees (<4 cm diameter) to estimate the mass of this component on the 3 x 3 m plots. All such material was cleared from the ten plots, weighed in the field and subsampled for moisture content to determine total dry mass of fallen trees in grams per m^2.

At the Pine, Spruce and Fir sites, there was not a sufficient mass of fallen trees on the 3 x 3 m plots to obtain an accurate estimate of fallen tree mass. Consequently, the mass of such material on one of the 20 x 30 m plots was determined. Since harvesting all downed trees would have involved considerable disturbance of the plots, analysis of volume and density of fallen trees was performed instead. The species, decay class, length within plot, and upper and lower diameters of each fallen tree on the plots were first determined. Then samples of each species and decay class combination were harvested from areas outside the plots, as described earlier. One half of each sample was dried at 80°C, weighed, dipped in paraffin wax and analyzed for density (g cm^{-3}) as mass when immersed in water (American Society for Testing of Materials 1978). The volume of each fallen tree was calculated from length and diameter measurements using the formula for a truncated

cone and multiplied by the average density for that species-decay class combination to estimate the dry mass of each fallen tree. The other half of each species-decay class sample was used to determine the average C, N and P concentrations of fallen trees of each combination. The mass of each tree was multiplied by the average concentration of each nutrient for that combination to estimate the mass of each nutrient in each fallen tree. The total mass of fallen trees and nutrients therein on each plot was determined from the sum of the masses of individual trees and divided by the total area sampled (1800 m^2 at Pine and Spruce, 1650 m^2 at Fir) to estimate the mass in g m^{-2} at each site. The number of years for which dry matter, organic matter, N and P reside in the forest floor was estimated using the formula: $T = H/L$, where T is the residence time in years, H is the mass of the forest floor, and L is the mass of annual litter input (Vogt et al. 1986).

The calculation of residence times of litter assumes that the litter be in steady state with respect to inputs and losses. This means that each type of litter must have been entering the system at a constant rate for at least the period of time required for one year's input to be completely decomposed. Therefore, we can assume steady state conditions for a given litter type if samples of that type are found in all stages of decomposition, i.e. until no longer recognizable in the humus layer. This rationale, along with knowledge of the history of the sites, was used to determine which types of litter could be meaningfully analyzed for residence time in the forest floor at each site. In situations where a given

litter type is not in steady state in the entire forest floor, it may be possible to examine its residence time in the litter (L) layer alone, provided that inputs of litter have been coming in at a reasonably consistent rate for the shorter period of time required for one year's litter to pass completely through the L layer. This analysis of the validity of the steady state assumption for each litter type and forest floor layer allowed the determination of which litter type and layer could be used to compare residence times of litter among the sites.

At the Clearcut site, much of the fermentation and humus layers were probably remaining from the previous stand and thus could not be included in residence time calculations. The surface wood was composed mostly of small trees or standing dead trees which were cut and left on the site in 1972, and so could not be considered to be in steady state. Herbaceous litter, however, was found throughout the L and F layers; thus it was possible to determine the residence time for non-woody litter in the L layer at this site. This was also possible at the other three sites, where herbaceous litter was observed in all forest floor layers. Small woody litter (twigs, branches, bark and cones) was also observed throughout the forest floor at the Pine, Spruce and Fir sites; therefore the residence time of these materials in the L layer could be determined. Bole wood was also found throughout the organic layer at these sites, but at the Pine and Spruce sites it was usually charred and thus considered to be from a previous stand. Since bole wood could not be considered to be in steady state in these stands, it was

excluded from estimates of forest floor mass. By also excluding values for the rate of input of bole wood, it was possible to determine the residence time for all non-bole litter at the Pine, Spruce and Fir sites. At the Fir site, large boles were found in all stages of decay with no evidence of charring, thus a residence time for all litter including boles was calculated for this site, in addition to the estimate derived by excluding bole wood.

A portion of all samples to be analyzed for nutrient content was ground through a 20 μm sieve in a Wiley mill and dried at 80°C overnight. One 250 mg subsample of each sample of woody material, and 150 mg of each non-woody sample were digested at 360°C in sulphuric acid and hydrogen peroxide, filtered through Whatman #1 paper and analyzed for total N and P as NH_4 and PO_4 on a Technicon II autoanalyzer. Values were converted to NH_3-N and PO_4-P and finally %N and %P. Per cent carbon was determined from the average of three 150 mg subsamples of each milled sample combusted in a Leco carbon analyzer. The ash content of the forest floor samples was determined by combustion of approximately 3 g of each milled sample at 400°C for 24 hours in a muffle furnace.

The significance of differences between sites was tested for using one-way analysis of variance followed by Scheffé's test. Data sets with non-homogeneous variances were analyzed using the Kruskall-Wallis test. All statistical analyses were carried out using $SPSS^X$ (SPSS Inc. 1986).

4.3 RESULTS

4.3.1 Litter Input

The mass and composition of annual litter input at each site is shown in Figure 1. The Pine site had the greatest total litter input mass, followed by Spruce, Fir and Clearcut sites. Litterfall at the Clearcut site was mostly ground vegetation as well as small amounts of foliage from shrubs and small trees. At the three forested sites, overstory litter made up the greatest proportion of annual litter input, followed by treefall and ground vegetation. Non-woody overstory litterfall was composed of 90 - 95% needles, 1 - 3 % deciduous leaves, and 3 - 6% reproductive structures (seeds, male cones). Twigs were the predominant form of woody litter at the Fir and Spruce sites; female cones were also important at the Pine and Spruce sites where the heavier lodgepole pine cones were common. Bark and branches contributed relatively small amounts of litterfall.

The amount of annual variation in the rate of input of each type of litter is shown in Table 12. The mass of most litter types was fairly consistent over the three years examined; annual variability between years was usually smaller than spatial (between sample) variability. Exceptions to this trend are attributable to a very high rate of conefall (hence woody litter) at the Spruce site in Year 2, and an extremely high rate of treefall at the Fir site in Year 3.

Seasonal distribution of overstory litterfall demonstrated a prominent peak in autumn (Figure 2). This coincided with the

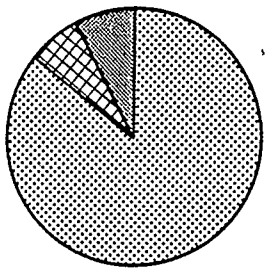
Table 12. Total mass of annual litter inputs in g m^{-2} yr^{-1} in four Rocky Mountain coniferous forests.

Site	Year	Ground Vegetation (n = 10)	Overstory (n=15)	Woody (n=10)	Tree (n=3)
Clearcut	1	70.44 ± 25.01	11.41±9.48†	0	0
Pine	1	55.61 ± 8.17	172.10 ± 18.93[a]	48.91 ± 15.89[a]	25.43 ± 11.78[a]
	2	--	188.12 ± 31.76[a]	48.25 ± 24.76[a]	67.91 ± 64.77[a]
	3	--	182.30 ± 71.53[a]	39.11 ± 11.06[a]	49.35 ± 18.84[a]
	$\bar{x}$ (n=3)	-	180.83 ± 8.11	45.42 ± 5.48	47.56 ± 21.30
Spruce	1	25.88 ± 11.12	184.86 ± 32.20[a]	45.39 ± 17.49[b]	9.69 ± 10.94[a]
	2	--	143.27 ± 40.76[b]	96.46 ± 42.48[a]	10.04 ± 17.39[a]
	3	--	135.10 ± 40.28[b]	58.81 ± 24.32[b]	5.03 ± 5.78[a]
	$\bar{x}$ (n=3)	-	154.41 ± 26.69	66.89 ± 26.48	8.25 ± 2.80
Fir	1	4.96 ± 4.62	139.42 ± 44.12[a]	47.70 ± 24.16[a]	1.90 ± 1.83[b]
	2	--	128.47 ± 30.78[ab]	54.59 ± 29.97[a]	3.98 ± 3.44[b]
	3	--	104.65 ± 28.28[b]	40.03 ± 16.09[a]	81.00 ± 64.81[a]
	$\bar{x}$ (n=3)	-	124.18 ± 17.78	47.44 ± 7.28	28.96 ± 45.08

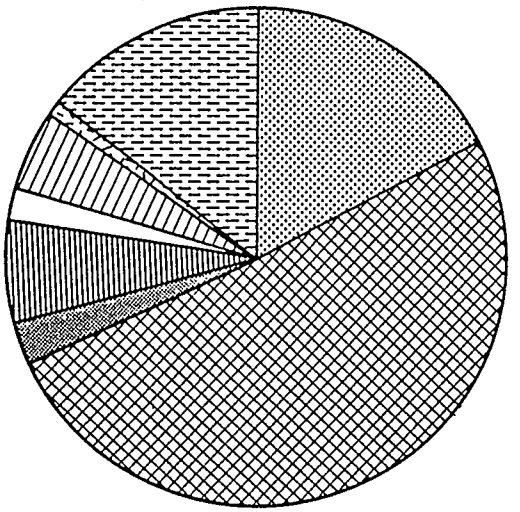
NOTE: Each value is the mean ± standard deviation. Values for each site in each column followed by the same letter are not significantly different at $p \leq 0.05$) based on one-way analysis of variance and Scheffé's test.

† Average of two years (August 1985 - August 1987).

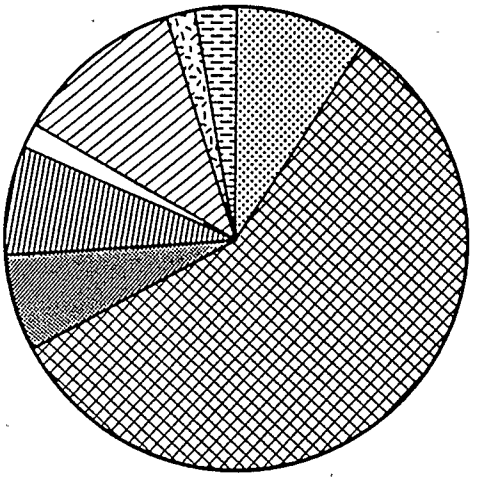
Figure 1. Composition of aboveground litter input in four Rocky Mountain coniferous forests.



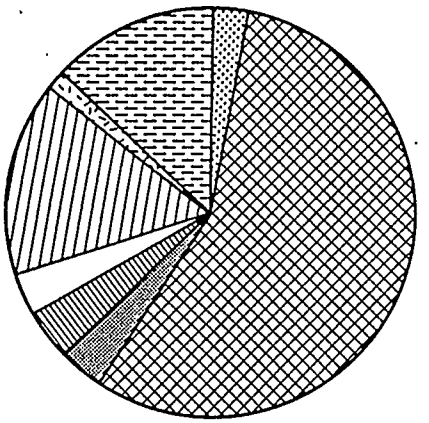
CLEARCUT
82 $g \cdot m^{-2} \cdot y^{-1}$



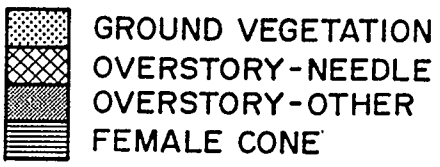
PINE
321 $g \cdot m^{-2} \cdot y^{-1}$



SPRUCE
286 $g \cdot m^{-2} \cdot y^{-1}$



FIR
222 $g \cdot m^{-2} \cdot y^{-1}$



distribution of needlefall, which peaked in autumn for all species. All species of conifers also displayed a peak in release of male cones in late spring.

4.3.2 Litter Accumulation

The total mass of accumulated litter was greatest at the Fir site, followed by the Spruce, Clearcut and Pine sites (Figure 3). The mass of the organic layer decreased in the order Fir > Spruce > Pine > Clearcut. The majority of the litter mass was incorporated in the organic (LFH) layers of the forest floor rather than on the surface at all sites (Figure 3). Only 1 - 3% of the total litter mass was in the L layer. Understory vegetation made up most of the mass of the L layer at the Clearcut site, while Pine needles were the most abundant litter type at the Pine site. Needles were also abundant in the L layers at the Spruce and Fir sites where dead moss made up an appreciable portion of the litter layer. Dead roots greater than 1 mm in diameter made up less than 1% and woody litter less than 10% of the forest floor mass at each site. The Clearcut and Pine sites both had a substantial mass of fallen trees on the surface, but very little buried wood. Buried wood was much more abundant at the Spruce and Fir sites, where its mass was greater than that of fallen trees on the surface of the forest floor.

The nutrient content of litter and forest floor material is presented in Table 13. Nitrogen and phosphorus content was highest in ground vegetation litter, followed by forest floor accumulation, overstory litter, woody litter, and tree litter. Nitrogen content

Figure 2. Rates of monthly litterfall in four Rocky Mountain coniferous forests. Each value is the mean and standard error of 15 samples. Values are for total tree and shrub litterfall and are corrected to equal 30 day sampling intervals. The width of the bar is proportional to the sampling interval.

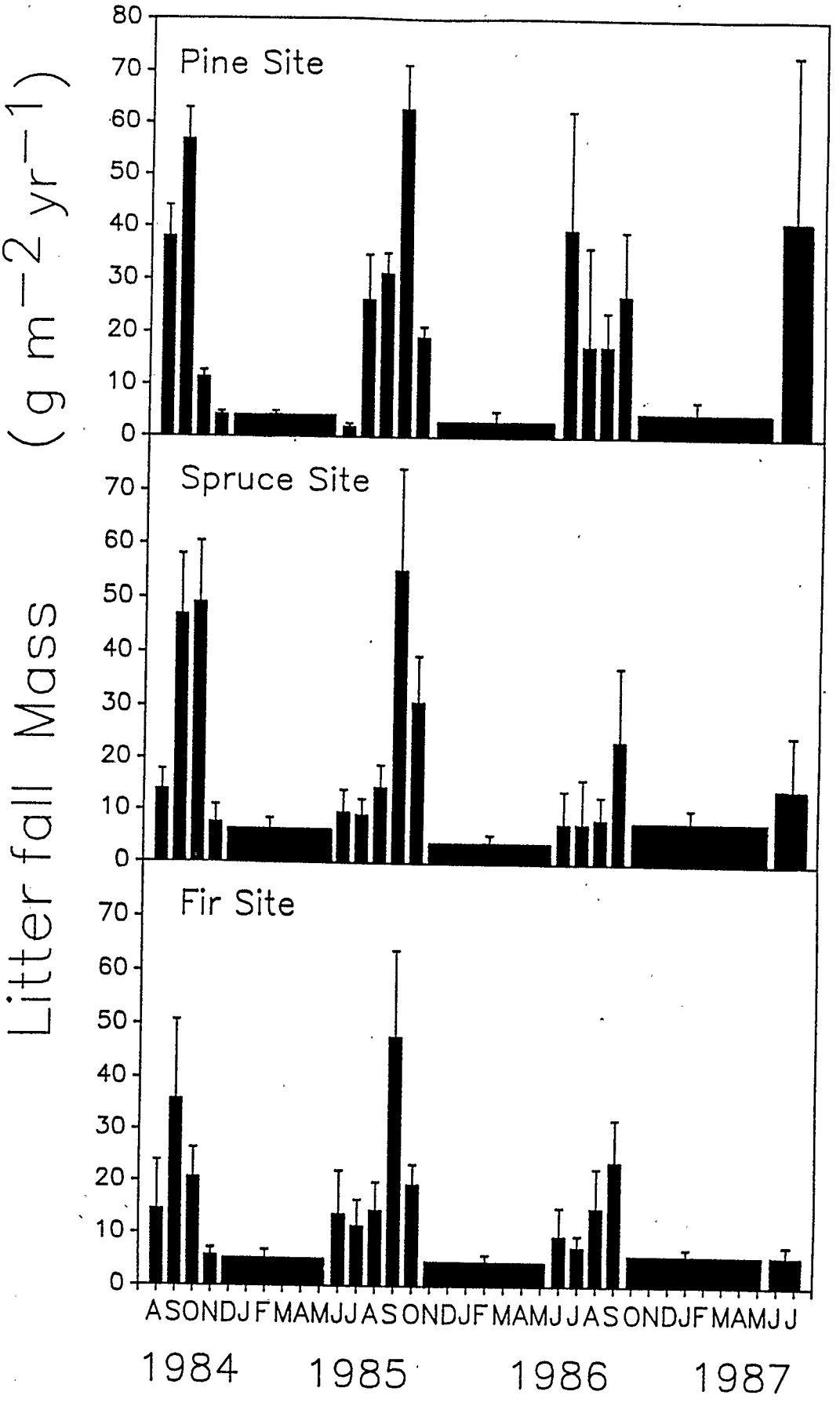
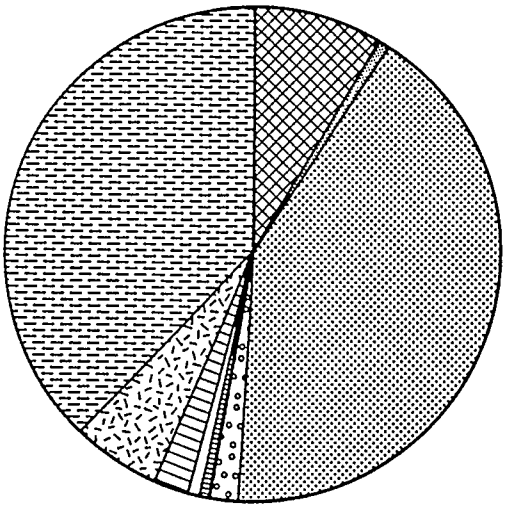
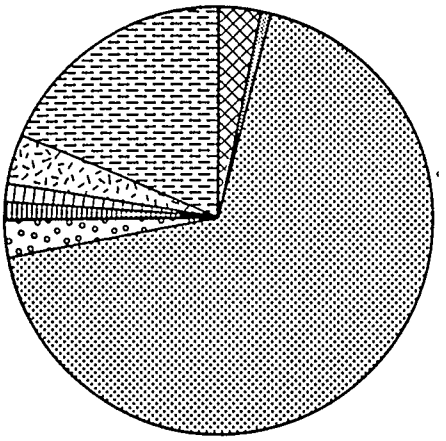

Litter fall Mass (g m⁻² yr⁻¹)
Pine Site
Spruce Site
Fir Site
0
10
20
30
40
50
60
70
80
ASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJ
1984
1985
1986
1987

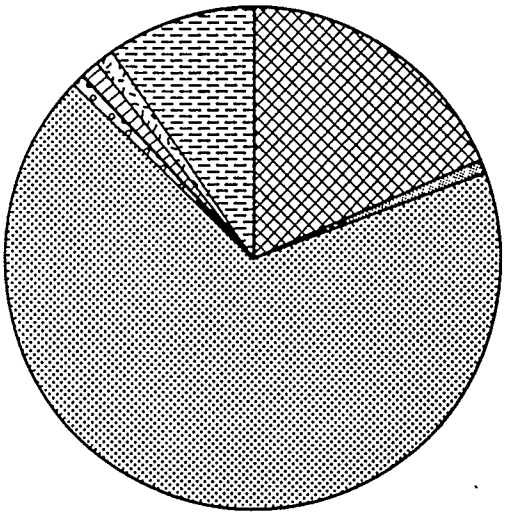
Figure 3. Composition of the forest floor of four Rocky Mountain coniferous forests.



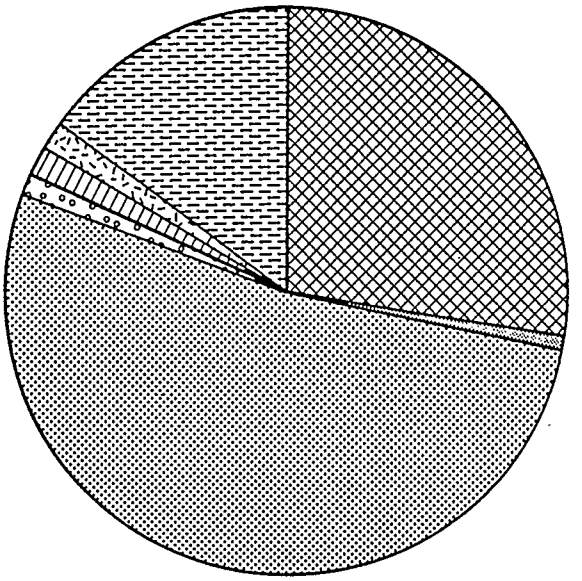
CLEARCUT
8.3 kg·m^{-2}



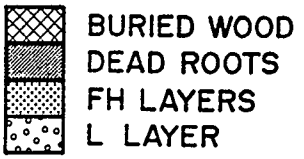
PINE
6.3 kg·m^{-2}

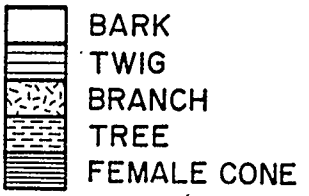


SPRUCE
8.3 kg·m^{-2}



FIR
11.0 kg·m^{-2}





of all litter types was greatest at the Fir site and lowest at the Pine and Clearcut sites; C:N followed the reverse trend. Phosphorus content was low at the Fir and Pine sites and highest at the Spruce site; C:P followed the reverse trend. N:P was highest at the Fir site and lowest at the Spruce site.

4.3.3 Litter Residence Times

The residence times of selected litter types in the forest floor litter (L) layer are shown in Table 14. Residence time of non-woody litter in the L layer was greatest at the Clearcut site. Since the samples used to determine the composition of the forest floor were harvested in August, just prior to peak litter input of non-woody litter, the proportion of annual litter input of each non-woody litter type remaining in the litter layer at this time should be reflective of the proportion of the annual input which has moved through the L layer in one year. Overall, 30% of the annual non-woody litter input had moved through the L layer in one year at the Pine, Spruce and Fir sites, while almost 2 years worth of litter was accumulated in the L layer at the Clearcut site. Needles and reproductive structures began leaving the L layer within one year, while surface vegetation and moss remained in the L layer for more than one year.

Woody litter remained in the L layer for 3 - 8 years (Table 14). The relative residence times of the various woody litter types was: branches > twigs > bark > cones, except at the Pine site where serotinous cones remained proportionately longer.

Table 13. Carbon, nitrogen, and phosphorus content of litter input and accumulation in four Rocky Mountain coniferous forests.

Site	% C.	% N.	% P.	C:N	C:P	N:P
Litter Input						
Ground Vegetation (n=10)						
Clearcut	46.12 ± 0.93^{a}	1.00 ± 0.25^{b}	0.17 ± 0.03^{b}	46.1	271.3	6.0
Pine	44.82 ± 0.89^{b}	1.14 ± 0.11^{b}	0.19 ± 0.02^{b}	39.3	243.5	6.1
Spruce	44.15 ± 0.62^{bc}	1.22 ± 0.25^{ab}	0.26 ± 0.05^{a}	36.2	169.8	4.7
Fir	43.68 ± 0.40^{c}	1.49 ± 0.10^{c}	0.11 ± 0.02^{c}	29.3	397.1	13.5
Overstory						
Pine	51.27 ± 0.03^{a}	0.58 ± 0.02^{b}	0.05 ± 0.00^{b}	88.9	1025.4	11.5
Spruce	49.14 ± 0.04^{a}	0.58 ± 0.03^{b}	0.08 ± 0.01^{a}	85.3	585.0	6.9
Fir	50.57 ± 0.06^{a}	0.82 ± 0.07^{a}	0.06 ± 0.01^{b}	61.7	919.5	14.9
Woody						
Pine	50.98 ± 0.41^{c}	0.26 ± 0.03^{c}	0.02 ± 0.00^{b}	199.9	2216.5	11.1
Spruce	51.67 ± 0.14^{b}	0.55 ± 0.02^{b}	0.05 ± 0.01^{a}	94.8	1099.4	11.6
Fir	52.82 ± 0.43^{a}	0.66 ± 0.06^{a}	0.05 ± 0.01^{a}	79.8	978.1	12.3
L Tree†						
Pine	47.75	0.03	0.003	1447.0	15916.6	11.0
Spruce	48.61	0.01	0.014	481.3	3472.1	7.2
Fir	49.90	0.02	0.012	326.1	4158.3	12.8
Litter Accumulation						
LFH Clearcut	30.44 ± 2.75^{a}	1.05 ± 0.1^{ab}	0.09 ± 0.01^{a}	29.0	334.5	11.6
Pine	36.41 ± 5.15^{ab}	0.97 ± 0.2^{b}	0.07 ± 0.02^{ab}	37.6	512.8	13.6
Spruce	31.82 ± 3.90^{b}	1.23 ± 0.1^{ab}	0.10 ± 0.01^{a}	26.0	331.51	12.8
Fir	41.37 ± 5.64^{a}	1.30 ± 0.1^{a}	0.07 ± 0.01^{b}	31.7	547.6	18.1

NOTE: Each value is the mean ± standard deviation. Values in the same column for each vegetation type followed by the same letter are not significantly different at the 0.05 level (one-way ANOVA and Scheffé's test).

Nutrient ratios are determined from the average values for each nutrient in each type of litter.

† Average C, N and P concentrations of newly fallen trees determined for each species-decay class combination, multiplied by the mass of trees of that combination, summed for all trees on 3 plots at each site, and divided by the total mass of annual treefall on the plots to estimate the average concentration of each nutrient in total annual treefall at each site.

Table 14. Residence time of various types of litter in the litter (L) layer of four Rocky Mountain coniferous forests.

Site	Litter Type	Annual Input ($g\ m^{-2}\ yr^{-1}$)	Accumulation ($g\ m^{-2}$)	Residence Time t (yr)*
Clearcut	moss	3.27	17.54	5.4
	grass	39.06	72.68	1.9
	other vegetation	31.38	48.52	1.6
	pine needle	4.99	10.00	2.0
	reproductive	0.79	0.41	0.5
	Total non-woody	79.49	149.15	1.9
Pine	moss	5.00	9.48	1.9
	grass	15.82	21.91	1.4
	other vegetation	39.78	23.11	0.6
	pine needle	162.40	111.77	0.7
	reproductive	5.33	2.39	0.5
	Total non-woody	228.33	168.66	0.7
	cone	21.3	73.0	3.4
	bark	6.1	7.9	1.3
	twig	16.4	77.8	4.7
	branch	2.6	229.4	88.2
	Total woody	46.4	338.1	8.4
Spruce	moss	21.49	56.15	2.6
	grass	3.08	10.92	3.6
	other vegetation	22.80	23.55	1.0
	pine needle	35.69	23.51	0.7
	spruce needle	120.95	39.65	0.3
	reproductive	8.20	1.07	0.1
	Total non-woody	212.21	154.85	0.7
	cone	23.5	5.4	0.2
	bark	4.2	5.1	1.2
	twig	34.4	103.5	3.0
	branch	5.8	83.8	14.4
	Total woody	67.9	197.8	2.9
Fir	moss	15.58	56.42	3.6
	grass	0.93	0.82	0.9
	other vegetation	4.03	2.45	0.6
	spruce needle	83.84	20.72	0.3

continued...

Table 14. (Concluded.)

Site	Litter Type	Annual Input (g m^{-2} yr^{-1})	Accumulation (g m^{-2})	Residence Time t (yr)*
Fir	fir needle	48.31	20.92	0.4
	reproductive	2.92	0.04	0.01
	Total non-woody	155.61	101.37	0.7
	cone	7.8	2.4	0.3
	bark	3.3	10.7	3.2
	twig	33.6	189.4	5.6
	branch	3.4	163.7	48.2
	Total woody	48.1	366.2	7.6
	boles only	28.96	1689.00	58.3

* residence time (t) = accumulation ÷ annual input

The residence time of cones at the Spruce and Fir sites may be underestimated as the input of cones was substantially larger during the two years after forest floor sampling than the year before. The large accumulation of branches at the Pine site is probably a consequence of the density of this stand and the resulting shedding of branches and thinning of trees and attached branches. As this process is probably decelerating now that the stand is 90 years old, present rates of branch input are probably lower than past rates; thus the residence time of branches at this site may be overestimated.

The residence time of all litter types combined (except bole wood) in the entire forest floor (LFH) was 14 years at the Pine site, 20 years at the Spruce site and 28 years at the Fir site (Table 15). Inclusion of bole wood at the Fir site which had a residence time of 149 years brings this estimate to 43 years. Residence times for organic matter were approximately 20% lower than those for dry mass. Residence times for carbon, nitrogen and phosphorus in the forest floor were also shortest at the Pine site, followed by the Spruce and Fir sites (Table 15). Nitrogen had the longest residence time at each site, and was retained for approximately twice as long as carbon, dry matter, and organic matter. Phosphorus also had a longer residence time than carbon and organic matter, especially at the Fir site.

Table 15. Residence times of mass, carbon, nitrogen and phosphorus in the forest floor at the Pine, Spruce and Fir sites.

	Dry Mass	Ash-Free Dry Mass	Carbon	Nitrogen	Phosphorus
Litter Input ($g\ m^{-2}\ yr^{-1}$)					
Pine	274.7	266.5	141.57	1.8	0.2
Spruce	280.1	271.7	121.9	1.5	0.2
Fir	203.7	197.6	90.2	1.4	0.1
Fir*	232.7	225.7	-	-	-
Litter Accumulation ($g\ m^{-2}$)					
Pine	3923.2	2953.0	1904.9	46.0	3.4
Spruce	5602.1	4376.9	2460.9	91.5	7.2
Fir	5692.7	4538.1	3911.4	118.6	6.5
Residence Time (t)					
Pine	14.3	11.1	13.5	25.6	14.6
Spruce	20.0	16.1	20.2	59.4	31.1
Fir	28.0	23.0	43.4	84.7	65.2
Fir*	43.1	35.4	-	-	-

NOTE: Trees (>4 cm diameter) are excluded from calculations except where otherwise signified with an asterisk.

4.4 DISCUSSION

Litterfall masses in these forests (286 - 321 g m^{-2} yr^{-1}) are lower than the average of 370 g m^{-2} yr^{-1} for evergreen trees in the northern hemisphere (Bray and Gorham 1964) and the average of 314 g m^{-2} yr^{-1} for cold temperate needle leaf evergreen forests (Vogt et al. 1986). Values are, however, very similar to average values for coniferous forests at this latitude (51°N) (Bray and Gorham 1964, Van Cleve et al. 1983, Vogt et al. 1986).

The mass and composition of overstory litter input in these forests is compared with that in other sites in the Rocky Mountains or boreal forests of North America in Table 16. Differences in litterfall mass among the forests were not related to stand basal area, suggesting that the stands are closed canopy and thus in steady state with respect to overstory litter input. Thus differences in litterfall mass should reflect differences in productivity among the forests (Bray and Gorham 1964). The Pine site in this study is among the most productive of the lodgepole and jack pine forests examined; productivity of the Spruce site is similar to white spruce forests in northern Alberta, and the Fir site is similar in productivity to white spruce sites in interior Alaska. The composition of overstory litterfall at the Pine, Spruce and Fir sites is similar to that of other forests of the same of similar species. Understory litter input at the Pine site (40 g m^{-2}) is similar to the 33 g m^{-2} reported by Foster (1974), but much less

Table 16. Mass of overstory litter input in Rocky Mountain and boreal forests of North America.

Predominant Species	Age (yr)	Stand Density (stems ha^{-1})	Stand Basal Area (m^2 ha^{-1})	Foliage		Male Cone		Wood[a]		Total		Location	Reference
				g m^{-2}	%	g m^{-2}	%	g m^{-2}	%	g m^{-2}	kg m^{-2} BA		
Pinus contorta	85	1716	30.5	164.9	75.4	5.1	2.3	46.7	21.3	218.5	71.6	south-west Alberta	This study (Pine site)
	105	1800	40.0	91.1	70.2	1.4	1.1	37.2	28.7	129.8	32.4	south-east Wyoming	Fahey (1983) (Dry Park I)
	105	1850	64.0	106.4	67.0	2.1	1.3	50.3	31.7	158.8	24.8	south-east Wyoming	(Nash Fork)
	71-77	-	-	260.0	70.6	6.0	2.0	110.0[b]	27.8	376.0	-	Colorado	Moir (1972) ($\bar{x}$ of 1.1., 2.2, 4.1., 4.3)
Pinus banksiana	85	1140	34.2	133.0	82.0	13.6	8.4	13.1	8.1	162.1	47.4	northern Alberta	Fyles et al. (1986) (HSL3)
	85	732	28.0	180.0	76.6	6.1	2.6	42.4	18.0	235.9	84.3	northern Alberta	(HSL12)
	75	1604	20.1	83.0	83.7	2.9	2.9	9.8	9.9	99.2	49.4	northern Alberta	(AOS10)
	75	1184	18.4	62.1	73.5	1.5	1.8	19.9	23.6	84.5	45.9	northern Alberta	(AOS4N)
	57	2440	24.8	150.0	76.1	0	0	40.0	21.1	197.0	79.4	New Brunswick	MacLean & Wein (1978)
	49	3480	17.8	140.0	92.1	0	0	15.0	9.7	152.0	87.1	New Brunswick	MacLean & Wein (1978)
P. contorta x *P. banksiana*	40	3962	21.0	102.5	95.0	2.9	2.7	2.5	2.3	107.9	51.4	west-central Alberta	Prescott & Parkinson (1985) (Site 3)
Picea glauca x *Picea engelmannii*	120	750	39.1	171.4	75.3	7.2	3.2	42.4	18.6	227.5	58.2	south-west Alberta	This study (Spruce site)
	350	1177	40.0	135.4	73.1	0.8	0.5	44.6	24.1	185.3	46.3	south-west Alberta	This study (Fir site)
Picea glauca	140	1217	38.5	136.0	61.0	7.7	3.4	53.7	24.1	222.9	57.9	northern Alberta	Fyles et al. (1986) (HSL4)
	80	2976	39.8	215.4	96.6	4.0	1.8	37.5	16.8	259.0	65.1	northern Alberta	Fyles et al. (1986) (HSL14)

[a] twigs, bark, female cones

[b] includes branches

than the 118 - 146 g m^{-2} reported by MacLean and Wein (1978) for jack pine forests in eastern Canada. Even inclusion of annual production of shrubs at the Pine site brings the estimate of understory litter input up to 76 g m^{-2} or just over half that reported by MacLean and Wein (1978).

Seasonal trends in overstory litter input are also similar to those reported in other pine forests, with a strong peak in needlefall in autumn (Fahey 1983; Fyles et al. 1986; but see Moir 1972) and high male cone drop in spring (Fyles et al. 1986). Spruce and fir trees in this study also demonstrated an autumnal peak in needlefall, which is not always found in trees of these genera (Bray and Gorham 1964; Fyles et al. 1986). Variation in annual input of needle litter seems to be relatively small in coniferous forests (Fahey 1983; but see Moir 1972), while large fluctuations in annual input of woody litter (especially trees) seem to be the norm (Christensen 1975; Boddy and Swift 1983; Harmon et al. 1986). Rates of treefall in these forests demonstrate the tendency for this process to "wax and wane" through the life of the stand (Lang 1985). Treefall rates are consistently high in a young stand undergoing thinning (Pine site), consistently low in a post-thinning stand (Spruce site), and high and variable in an old stand experiencing natural mortality of canopy trees (Fir site). The mass of coarse woody debris on the forest floor at these sites also changes through time as in other forests (Tritton 1980 in Harmon et al. 1986), being highest in very young and very old stands (Clearcut and Fir sites), and low in intermediate aged stands (Pine and Spruce sites).

Residence times of organic matter in the forest floor at these sites is compared with those reported in similar forests in Table 17. Residence time at the Pine site was intermediate to those reported in lodgepole pine stands in Colorado and Wyoming. Residence time at the Spruce and Fir sites was in the low range of values found in white spruce stands in Ontario. Residence time of dry matter, N and P at the Spruce site in Ontario are substantially lower than those found in white spruce stands (Nos. 12 and 26) of similar age and density in interior Alaska (K. Van Cleve, University of Alaska). Many of the difficulties involved in comparing residence times of different forests might be alleviated through separation of litterfall and forest floor components based on their proximity to steady-state conditions. Removal of those components not in steady-state from samples of both litter input and accumulation would allow for meaningful comparison of residence times of other components. For example, while bole wood is not included in most estimates of litter input, it is not usually mentioned whether or not such material was included in estimates of forest floor mass. Thus it cannot be ascertained whether or not estimates of residence time are at least valid for non-bole litter.

It has been suggested (Lang 1985) that estimates of turnover rates of bole wood are invalid. The temporal variability of input of trees both annually and throughout the lifespan of the stand means that reliable estimates of input rates take several years to obtain, and then are only reflective of rates occurring in that stand at its present stage. Calculation of turnover rates for

Table 17. Residence time of organic matter in Rocky Mountain and boreal forests of North America.

Predominant Species	Age (yrs)	Organic Matter Accumulation* t/ha	Residence Time (t) (yrs)	Location	Reference
Pinus contorta	85	29.5	11.1	south-west Alberta	This study (Pine site)
	105	23.9	18.8	south-east Wyoming	Fahey (1983) (Dry Park I)
	105	30.7	19.6	south-east Wyoming	Fahey (1983) (Nash Fork)
	77	38.6	7.4	Colorado	Moir and Grier (1969) (4.1)
	72	36.2	7.7	Colorado	Moir (1972), (LH2)
	72	31.6	7.5	Colorado	Moir and Grier (1969) (1.1)
	71	29.5	8.7	Colorado	Moir and Grier (1969) (2.2)
	71	28.5	7.7	Colorado	Moir and Grier (1969) (4.3)
Pinus banksiana	75	7.0	8.6	northern Alberta	Visser (unpublished) (site AOS4N in Fyles et al. (1986)
	65	40.7	10.2	eastern Ontario	Weber (1988) (stand No. 1)
	57	74.1	38.0	New Brunswick	MacLean and Wein (1978)
	49	129.6	43.2	New Brunswick	MacLean and Wein (1978)
P. contorta x P. banksiana	30	20.0	5.0	northern Ontario	Foster and Morrison (1976)
	40	10.4	9.3	west-central Alberta	Prescott and Parkinson (1985) (Site 3)
Picea glauca x Picea engelmannii	125	43.8	16.1	south-west Alberta	This study (Spruce site)
	350	45.4	23.0	south-west Alberta	This study (Fir site)
	350	79.9	35.4	south-west Alberta	This study (Fir site-boles included)
Picea glauca	105	68.5	19.0	northern Ontario	Gordon (1983) (Mixed wood, fresh till)
	100	110.7	33.0	northern Ontario	Gordon (1983) (Mixed wood, silt-sand)

* average ash-free mass of the organic (LFH) layer of the forest floor.

boles also requires one to ascertain that all wood in the forest floor is from the present stand. In young stands, much or all of the buried wood may be from previous stands, and thus cannot be included in estimates of forest floor mass used in calculating residence times. In fire-disturbed forests such as those in the present study, previous-stand wood is usually charred and thus easy to separate from present-stand (uncharred) wood. In other systems, carbon dating of incorporated wood could be applied (Harvey et al. 1981) providing that the year of the last major disturbance is known. Given the effort and risks of error involved in sorting incorporated wood, and the tendency for the mass of wood litter to vary through time, it would seem preferable to exclude bole wood from estimates of input and accumulation. However, ignoring input of bole litter could lead to overestimation of rates of forest floor residence times in old forests where much of the wood from the present stand is decayed to the point of incorporation into humus and thus cannot be separated from other forest floor material. In such a situation, the error imposed by ignoring bole inputs without subtracting their mass from the forest floor may be larger than errors resulting from the variable nature of this litter input.

Like bole wood, some or all of the forest floor mat may be left from a previous stand; inclusion of the entire forest floor in such situations could lead to considerable overestimation of forest floor residence times. This is probably not critical in older stands such as the spruce and fir stands compared in Table 16, where enough time has lapsed for such material to completely decompose.

However, it could be of considerable significance in younger stands, such as the lodgepole pine forests compared in Table 16. Forest floor material remaining from previous stands is probably responsible for much of the great mass of forest floor and resultant extensive residence times in the jack pine stands of New Brunswick, as discussed by the authors (MacLean and Wein 1978). Thus the origin of the forest floor should also be examined when calculating residence times.

It must also be decided whether roots are to be included in estimates of forest floor residence times. Inclusion of rates of input of dead roots can dramatically change estimates of forest floor residence times (Vogt et al. 1983), but involves considerable effort and methodological problems. Alternatively, roots could be excluded from estimates of forest floor mass, such that calculated residence times would be at least valid for all non-root litter. In the present study, the mass of large (> 1 mm diameter) dead roots was not included in estimates of total forest floor mass. However, the mass of small roots was probably sufficient to cause forest floor residence times to be overestimated.

When residence times of specific nutrients are to be calculated, rates of input of nutrient in throughfall and stemflow should be included. As this was not done in the present study, the estimates of residence times of these nutrients in these forests may be slightly overestimated. As considerable enhancement of nutrient content of precipitation may well occur as it passes through the more nutrient-rich and less-cuticularized understory vegetation,

means of estimating input via leaching from this layer would also enhance the validity of estimates of nutrient residence times.

The residence times of different litter types in the L layer provides a relative measure of rates of decomposition of different litter types in the initial stages of decay. Because it does not involve enclosure of the litter, the rates of decomposition measured with this technique should more accurately reflect actual patterns of decay than those obtained via the litterbag technique. For instance, grass litter was found to decompose more slowly relative to other litter types when measured via input and accumulation measurement than by the litterbag method (Prescott, unpublished data). This reflects the tendency for grass to remain standing for one year before entering the L layer per se, which is not accounted for with the litterbag technique. Relative decay rates of other substrates (needles, moss, twigs and cones) were similar when determined by litterbag or turnover methods. The subjectivity involved in separating L layer material, however, limits the utility of this method to comparisons undertaken by a single researcher. The timing of the forest floor harvest will also affect the calculated residence time of litter, and should be standardized within a study.

The longer residence times for litter in the L layer at the Clearcut site as compared with the other sites is difficult to reconcile with reports of higher rates of decomposition in recently clearcut areas (Vitousek 1981) or the faster rates of decay of several litter types at the Clearcut site as compared with the other sites (Prescott, unpublished data). One possibility is that the

openness of the Clearcut intensifies moisture stress in these forests, thereby reducing the rate of decomposition of litter on the surface (Oconnell 1987). The lack of substantial needle litter input and moss to shelter litter and keep it moist may add to this effect. This stress may have been reduced in the litterbags, which will retain moisture (Witkamp and Olson 1963) and which were placed below the standing dead material, where conditions are moister. It may also be that the smaller amounts of most litter types in the litter layer at this site were insufficient for use in determination of residence time of individual litter types.

Differences in microclimate are probably responsible for the differences in residence times of litter among the three forested sites (Pine, Spruce and Fir). Effects of microclimate could be manifested directly and also indirectly through its influence on understory vegetation. Cooler temperatures and shorter snow-free seasons at the high-elevation Fir site could result in the longer residence times for litter found at this site. The Spruce site is at a lower elevation than the Fir site, but it is more sheltered than the Pine site, and has intermediate litter residence times. The Pine site is more open than the Spruce and consequently warmer and snow-covered less frequently, which may explain the shorter residence times for litter in this forest. The mass of understory vegetation was greatest at the Pine site, followed by the Spruce and Fir sites, respectively (Chapter 3). As understory vegetation litter is richer in nutrients and decomposes more rapidly than overstory vegetation in these forests (Prescott, unpublished

data) it may reduce forest understory residence times either by making up a larger proportion of the litter or by stimulating decomposition of other types of litter. A similar relationship between turnover rates of litter and mass of understory vegetation has been reported in other forests (Tappeiner and Alm 1975; Fahey 1983), suggesting that the abundance of understory vegetation may be an important determinant of, or at least a useful indicator of turnover rates of litter in forests.

The mass of N (1.4 - 1.8 g m^{-2} yr^{-1}) and P (0.1 - 0.2 g m^{-2} yr^{-1}) in litterfall in these forests are less than the average of 2.6 and 0.3 g m^{-2} yr^{-1} respectively for cold temperature needle leaf evergreen forests (Vogt et al. 1986). Since the total mass of litterfall at these sites is also less than the average value, the rates of litter input, rather than the N and P concentrations of litter content are probably responsible for the low mass of N and P in annual litterfall in these forests. Concentrations of nitrogen and phosphorus in litterfall at the Pine and Spruce sites are similar to estimates from other lodgepole pine (Fahey 1983) or white spruce (Van Cleve et al. 1983) forests. Concentrations of N and P in the forest floor at the Pine and Spruce sites were also similar to those reported from other lodgepole pine and white spruce forests (Kimmins 1974; Fahey 1983; Van Cleve et al. 1983). At the Fir site levels of N and P in the forest floor were higher and lower respectively, than those found in a spruce-fir forest in British Columbia (Kimmins 1974). The N:P ratios of litterfall and forest floor material at the Fir site were also

broader than the average values for cold temperate needle leaf evergreen forests (Vogt et al. 1986,) while those at the other sites were similar to the average values. The mass of N and P in the forest floor at the Pine site is less than average values of 50.4 and 4.5 g m^{-2} (Vogt et al. 1986), as is the mass of organic matter. However, the Spruce and Fir sites have masses of organic matter similar to the average value (4457 g m^{-2}), and masses of N and P greater than the average values. Since the rate of litter input in these forests is similar to the average, this suggests that decomposition rates are also similar, while immobilization of N and P is greater in the forest floor at the Spruce and Fir sites as compared with most coniferous forests. The forest at the Pine site may simply be younger than many of the forests used to calculate the average values, and thus have had a shorter period of time during which to accumulate litter.

The mean residence times for organic matter (18 yr), N (33 yr), and P (22 yr) in cold temperate needle leaf evergreen forests (Vogt et al. 1986) fall within the ranges encountered in these forests, being longer than those at the Pine site and shorter than those at the Spruce and Fir sites. The pattern of relative mobility of these elements (C > P > N) in the forest floor of these forests is also suggestive of immobilization of N and P in the forest floor. However, this could also be in part a consequence of not including inputs of these nutrients via precipitation. Rates of decomposition and nutrient immobilization in these forests are currently being examined in an in situ decomposition experiment.

Differences in N and P content of litter and forest floor material among the forests in the present investigation parallel trends in nutrient use efficiency of vegetation in these forests (Chapter 3). Litter at the Pine site had broad C:N and C:P ratios which correlate with the high nutrient use efficiency of both nutrients by vegetation at this site. The Spruce site had low C:N and C:P ratios in the litter and the lowest nutrient use efficiency for both nutrients. Fir site litter had a low C:N but high N:P ratios; this corresponds with the low efficiency of N use and high efficiency of P use by vegetation at this site (Chapter 3).

Analysis of the nutrient content of green needles from trees of the same species at different sites (Chapter 3) led to the conclusion that the observed differences in nutrient use efficiency among the forests were related to both differences in species composition (prevalence of nutrient efficient pines) and differences in nutrient availability (low P availability at the Fir site). The occurrence of similar trends in litterfall and forest floor material demonstrate the ability of organisms to alter their environment (Reiners 1986); in this case vegetation appears to influence the availability of nutrients in the forest floor.

CHAPTER 5

5. EFFECTS OF ADDITION OF NITROGEN AND PHOSPHORUS ON VEGETATION AND FOREST FLOOR MICROORGANISMS

5.1 INTRODUCTION

A number of indices may be used to estimate the availability of nutrients in forests, including deficiency symptoms, bioassays, soil and foliage analyses (Morrison 1974a; Mead 1984; Ballard and Carter 1986), nutrient use efficiency of vegetation (Vitousek 1982), and mineralization rates in the forest floor (Powers 1980). However, none of these indices will necessarily provide an indication of nutrient limitation, that is, the availability of nutrients relative to the potential rates of uptake or demand of plants and microorganisms in the ecosytem (Chapin et al. 1986). The most direct method of addressing this matter is by adding nutrients to forest plots. Comparison of the rates of productivity of plants and microorganisms in fertilized plots with that in control plots provides a measure of the response of organisms to improved nutrient conditions, thus the degree to which nutrients limit the productivity of these organisms.

The response of a forested ecosystem to nutrient addition depends on a variety of factors including soil nutrient and pH status, stand composition, density and age, and the timing, rate and form of nutrient addition (Ballard 1984). Nevertheless, some trends are apparent in the extensive literature on the effects of

fertilization on temperate and coniferous forests. Improved growth of vegetation has consistently followed the addition of nitrogen to the forest floor of coniferous forests. Increased rates of biomass production of trees have been reported following the addition of nitrogen to forests of Scots pine (Aronsson and Elowson 1980), Corsican pine (Miller and Miller 1976a), loblolly pine (Baker et al. 1974), monterey pine (Neilson et al. 1984), jack pine (Weetman and Fournier 1984), ponderosa pine (Cochran et al. 1979), western white pine (Scanlin and Loewenstein 1979), lodgepole pine (Bella 1978; Cochran et al. 1979; McIntosh 1982; Yang 1985a,b), sitka spruce (Harris and Farr 1979), black spruce (Weetman 1968), Norway spruce (Tamm 1968), white spruce (Ballard 1984), grand fir (Scanlin and Loewenstein 1979) and Douglas fir (Turner 1977).

Addition of elements other than nitrogen has had less consistent effects on tree growth. Although Neilson et al. (1984) reported increased growth rates of Pinus radiata seedlings with application of phosphorus in addition to nitrogen, the application of phosphorus or potassium in addition to nitrogen to established stands did not affect the growth of jack pine (Morrow and Timmer 1981; Weetman and Fournier 1984), western white pine or grand fir (Scanlin and Loewenstein 1979). Possible beneficial effects of sulphur, especially in addition to nitrogen, have been reported on some soils for lodgepole pine (Cochrane et al. 1979; Yang 1985a,b), ponderosa pine, monterey pine (Will and Youngberg 1978), white spruce and Engelmann spruce (Ballard 1984). Addition of phosphorus and/or sulphur in addition to nitrogen may help to prevent secondary

deficiencies of these nutrients which may occur after fertilization with nitrogen (Tamm 1968; Turner et al. 1980; Mohren et al. 1986). Increased growth of understory vegetation may also follow fertilization of forests, depending on the age of the stand and the species present (Baker et al.1974; Cochran et al. 1979; Turner 1979; Aronsson and Elowson 1980; Ballard 1984).

Fertilization of forests may also lead to qualitative differences in vegetation. Fertilization usually increases the foliar concentration of the added nutrient(s) (usually N), and decreases that of other elements due to growth dilution (Baker et al. 1974; Miller and Miller 1976a; Turner 1977; Morrow and Timmer 1981; McIntosh 1982). The higher nutrient content of foliage may persist through senescence, resulting in litterfall of higher nutrient content in fertilized forests, as reported for nitrogen content following nitrogen fertilization of forests of Scots pine (Miller and Miller 1976b) and Douglas fir (Turner 1977). These studies also reported lower masses of litterfall in fertilized forests, caused by greater retention of needles.

Effects of fertilization on forest floor microbial activity (respiration, biomass production, decomposition and mineralization) have been more variable than effects on vegetation. Increased rates of biomass production, respiration and decomposition have been reported following the addition of urea to the forest floor (Turner 1977; Kelly and Henderson 1978; Mahendrappa 1978). However, this has been shown to be the result of the higher pH and greater availability of carbon resulting from the hydrolysis of urea, rather

than a direct effect of greater nitrogen availability (Fessenden et al. 1971; Foster et al. 1980). Application of ammonium salts to forest humus has consistently led to reduced rates of microbial respiration (Fessenden et al. 1971; Salonius 1972; Foster et al. 1980a; Söderström et al. 1983). Despite this apparently detrimental effect of nitrogen fertilization on microbial activity, increased rates of mineralization of nitrogen have frequently been observed following the addition of ammonia or nitrate to humus (Keeney 1980).

In light of the variety of possible responses of forest floor microbes to increased nutrient availability and their ensuing implications for forest productivity, the present study was designed to allow us to concurrently examine the effects of nutrient addition on both microbial and vegetative components of forests. The availability of potentially limiting nutrients was improved through the addition of nitrogen, phosphorus and sulphur to the forest floor of four Rocky Mountain coniferous forests. The relative magnitude of the resulting differences in productivity of microbial and vegetative compartments between fertilized and unfertilized plots was used as an indicator of the degree of nutrient limitation existing for each of these compartments in each forest and thus the extent to which the productivity of these organisms might be enhanced through the addition of nutrients.

5.2 METHODS

Six 10 x 10 m plots for the fertilization experiment were established in the vicinity of three main study plots (each 20 x 30 m) at each site (Chapters 3 and 4) in October 1985. These six plots were arranged in pairs, with one member of each pair serving as the "fertilized" plot and the other serving as the "control" plot. Each plot contained at least one healthy canopy tree of each dominant species (pine at the Pine site, pine and spruce at the Spruce site, and spruce and fir at the Fir site). Plots were separated by a buffer zone of at least 2 m, and all plots at each site were within 100 m of one another. At the Clearcut site, insufficient space was available adjacent to the main study plots, necessitating the use of another small Clearcut area nearby for the fertilization experiment. Only four 10 x 10 m plots fit into this area, thus only two pairs of plots were used at the site. At each site, one additional 10 x 10 m plot was established and instrumented with littertraps; data from these plots were compared with data from littertraps on control plots (Chapter 4).

Ten kg of granular ammonium phosphate sulphate was applied to each "fertilized" plot at each site using a hand-held spreader. This added the equivalent of 160 kg N ha^{-1}, 86 kg P ha^{-1} and 140 kg S ha^{-1}, which is within the guidelines suggested by Ballard (1984) for established plantations, and similar to levels found to achieve a growth response in lodgepole pine in Alberta (Yang 1985, a,b).

Fertilization took place soon after snowmelt, on 20 May 1986 at the Clearcut, Pine and Spruce sites, and on 3 June 1986 at

the Fir site. Rainfall during the night following fertilization ensured rapid dissolution of the fertilizer granules.

In order to ascertain the ensuing degree and duration of enhancement of nutrient levels, concentrations of NH_4, NO_3, and PO_4 in the forest floor on control and fertilized plots at each site were measured one month after fertilization (July 1986), at the start of the second growing season (May 1987), and during the second summer after fertilization (July 1987). In July 1986, 3 samples of the forest floor (F and H layers) were removed from each control plot and each fertilized plot. In May 1987, a total of 5 samples of the forest floor were removed from fertilized and control plots, as well as the upper 10 cm of mineral soil beneath each forest floor sample. In July 1987, 2 samples of the forest floor were removed from each control and each fertilized plot. After sieving and handmixing to homogenize each sample, 10 g (wet weight) subsamples of each sample were shaken in 100 ml 1N KCl for 1 hour, filtered through glass fibre filter paper, and analyzed for NH_4-N and NO_3-N on a Technicon II autoanalyzer (Technicon Instruments 1977, 1978; Page et al. 1982). An additional 10 g of each sample was shaken for 5 minutes in 50 mL modified medium Bray's solution, filtered through glass fibre filter paper, and analyzed for PO_4-P concentration on a Technicon II autoanalyzer (Technicon Instruments 1976; McKeague 1978). Another 15 g of each sample was weighed before and after drying to constant weight at 80°C to determine moisture content of each sample. An additional 3 g of each forest floor sample and 12 g of each mineral soil sample were weighed

before and after combustion at 400°C for 24 hours to determine the organic matter content of each sample. These data were used to express the mass of each nutrient in each sample in $\mu g\ g^{-1}$ dry matter or organic matter. The pH of each soil sample was determined using a glass electrode after soaking 5 g of soil in 40 mL deionized water for one hour.

The rates at which nitrogen and phosphorus were becoming available in the forest floor was compared among fertilized and control plots by measuring rates of mineralization of NH_4 and PO_4, and rates of nitrification (production of NO_3) in samples of FH material buried in the forest floor in control and fertilized plots at each site (Eno 1960). One 100 g subsample of each sieved sample used for determining the availability of each nutrient in July 1986 and July 1987 were placed in polyethylene bags and incubated in the forest floor in the plot from which the soil was removed. After one month, the buried bags were retrieved and analyzed for moisture content, organic matter content, and concentrations of NH_4, NO_3 and PO_4, as described earlier. Differences in concentrations of each element in each sample prior to and following the one month incubation were used as estimates of rates of net mineralization and nitrification (if positive) or net immobilization (if negative) in each forest floor. Average rates of each process were determined for control and fertilized plots at each site during July 1986 and July 1987.

Three parameters were used to measure productivity of microorganisms in the forest floor: the rate of respiration, total microbial biomass, and the net rate of biomass production over a

one-month period. Respiration rates of unamended organic soil samples at field moisture content were measured using infra-red gas analysis and used as indicators of microbial activity on control and fertilized plots. Microbial biomass of each soil sample was determined using the substrate induced respiration technique (Anderson and Domsch 1978). 0.32 g of powdered glucose was added to plastic bags containing 10 g (dry weight) of FH material at field moisture content and rates of CO_2 production in each sample were measured by infra-red gas analysis and converted to mg biomass C using the relationship provided by Anderson and Domsch (1978). Differences in biomass C in soil samples before and after the one month in situ incubation were used to estimate the net change in microbial biomass on control and fertilized plots during that time, which was used to estimate microbial biomass production. Microbial biomass was also determined for mineral soil and FH material collected from control and fertilized plots in May 1987. For FH material, glucose amendation was as described above; for mineral soil, 0.024 g of glucose was added to 30 g dry weight of soil.

The response of ground vegetation to nutrient addition was estimated by comparing the mass and nutrient content of grasses, forbs, and small shrubs (<1 m high) on control and fertilized plots. Aboveground portions of all ground vegetation on three 0.25 m^2 quadrats on each control and each fertilized plot at each site were harvested in late August 1986. This has been found to be the time of maximum aboveground biomass for all species of ground vegetation combined (Chapter 2). The vegetation from each

quadrat was separated into grasses, forbs and shrubs, the latter of which was further separated into new (current year's) growth and old (previous years') growth. All samples were then dried to constant weight at 80°C and weighed, and the mass of current year's production and total biomass of ground vegetation was determined for each treatment at each site. Vegetation from the three quadrats from each plot were combined for each vegetation type and ground to <2 mm in a hammer mill and to <20 μm in a Wiley mill. 150 mg of each sample was digested in 5 mL sulphuric acid and hydrogen peroxide at 360°C, diluted to 75 mL with deionized water, filtered through Whatman #1 paper, and analyzed for NH_3 and PO_4 content on a Technicon II autoanalyzer (Technicon Instruments 1976, 1977; Lowther 1980). Three 150 mg portions of each sample were analyzed for % carbon by combustion at 1500°C in a Leco furnace. The average nutrient content of each vegetation type was multiplied by its mass on each plot to estimate the mass of carbon, nitrogen and phosphorus in ground vegetation on control and fertilized plots.

Differences in annual net primary production of trees due to nutrient addition were estimated by comparing the mass of needles, twigs and stemwood produced annually by trees on control and fertilized plots prior to and for the first two years following fertilization. One healthy canopy tree of each dominant species (pine at the Pine site, pine and spruce at the Spruce site, spruce and fir at the Fir site) on each control and each fertilized plot was selected prior to fertilization and sampled each year. Branches were harvested using clippers on extension poles in February or

March of each year when needles were dormant. Branches containing new growth were selected from the upper mid-canopy of each tree in order to approximate an average value for the entire crown (Ballard and Carter 1985).

After harvesting, branches were kept at -15°C until analyzed. Needles and twigs from each branch were separated into age classes (1983 through 1987 production), dried at 80°C to constant weight and weighed. One hundred needles of each age class from each tree were also weighed to determine the average needle weight. Weight of needles and twigs for each year after fertilization (1986 and 1987 growth) was divided by the average needle weight for that tree during 5 years prior to fertilization, thus standardizing growth response for each tree. A core of stem wood was also taken from each tree approximately 30 cm above the base in March 1988. The width of the rings for 1986 and 1987 was divided by the average ring width for that tree for 9 years prior to fertilization. For the small pine trees at the Clearcut site, cores were not taken, and needle and twig weights were divided by the value for the year prior to fertilization (1985) only.

The effect of fertilization on the nutrient quality of tree foliage was examined by comparing the concentrations of nitrogen and phosphorus in foliage of trees from fertilized and control plots. The assumption that trees on all plots at each site were of similar nutrient quality prior to fertilization was tested by determining the nitrogen and phosphorus content of current year's needles from one branch of each sample tree harvested in February 1986 (prior to

fertilization). In February 1987, a second branch was harvested from each tree, and the nitrogen and phosphorus content of new needles produced during the first year after fertilization was determined. Samples of all needles produced between 1983 and 1987 from branches collected from each sample tree in March 1988 were analyzed for nitrogen and phosphorus content, in order to determine the effect of fertilization on both new and old needles.

The effects of fertilization-induced changes in mass or nutrient content of vegetation on rates and quality of litter input were examined by comparing the mass and nutrient content of senescent ground vegetation and tree needles produced annually on control and fertilized plots. Aboveground portions of all grass and forbs were harvested from three 0.25 m^2 quadrats on each control and fertilized plot in October 1986, separated, dried at 80°C, weighed, and analyzed for carbon, nitrogen and phosphorus content as described earlier. Overstory litterfall was collected in six 0.25 m^2 traps lined with 1 mm mesh fibreglass screens on one 10 x 10 m fertilized plot at each site. The mass of litterfall collected annually in these traps was compared with that collected in 15 traps on one 20 x 30 m unfertilized plot at each site (Chapter 3). Additionally, the average weight and carbon, nitrogen and phosphorus content of needles of each species which fell during September 1986 and 1987 were compared between the 6 traps on the fertilized plots and 6 randomly selected traps on the unfertilized plot.

Changes in rates of decomposition resulting from fertilization of the forests were investigated by measuring the rate of decomposition of litter collected from fertilized and control plots placed on both fertilized and control pots. Senescent leaves of Epilobium angustifolium were collected from the instrumented fertilized plot and the surrounding unfertilized area at the Pine site in October 1986. Leaves were air-dried, and 0.5 g of one type (from fertilized or control plots) was placed into each of ten 10 x 10 cm litterbags made of 1 mm fibreglass screening. One bag of each type was pinned on the ground surface adjacent to one bag of the opposing type. Three pairs of bags were placed on each control and each fertilized plot at the Pine site in October 1986. All bags were harvested in October 1987, the contents were weighed, and the amount of weight lost over the one year incubation was determined for each bag.

Most of the data consisted of replicate samples from each plot and therefore the significance of differences between control and fertilized plots was tested for by a Model I two-way analysis of variance. This allowed determination of the significance of between-plot differences and treatment-plot interactions as well as treatment effects. Data which were derived from a single sample from each plot (trees and litterfall) were tested using one-way analysis of variance. The accepted level of significance was 5%, however, because of substantial variability in some of the measurements, differences with probabilities between 5 and 10% were also noted. All statistical analyses were carried out using SPSSx (SPSS Inc. 1986).

5.3 RESULTS

Concentrations of available NH_4-N and PO_4-P in the forest floor at each site one month after fertilization (July 1986), and the following spring (May 1987) and summer (July 1987), are shown in Figure 4. Concentrations of both nutrients were significantly higher in fertilized plots at all sites one month after fertilization. The following year, NH_4 levels were significantly higher in fertilized plots at the Clearcut and Fir site only, while PO_4 remained significantly more abundant in fertilized plots at the Clearcut, Pine and Fir sites. The Spruce site had higher levels of PO_4 in control plots than did the other sites, thus differences between these and fertilized plots were significant only at the 10% level. Similar trends in nitrogen and phosphorus availability occurred in mineral soil samples one year after fertilization (Table 18).

Concentrations of NH_4 in control plots were similar among sites and among sample times while concentrations of PO_4 were usually lowest at the Fir site and highest at the Spruce site (Figure 4). By the start of the second growing season after fertilization (May 1987), differences in concentrations of NH_4 on fertilized plots were very much diminished, while PO_4 levels in fertilized plots were at their highest levels.

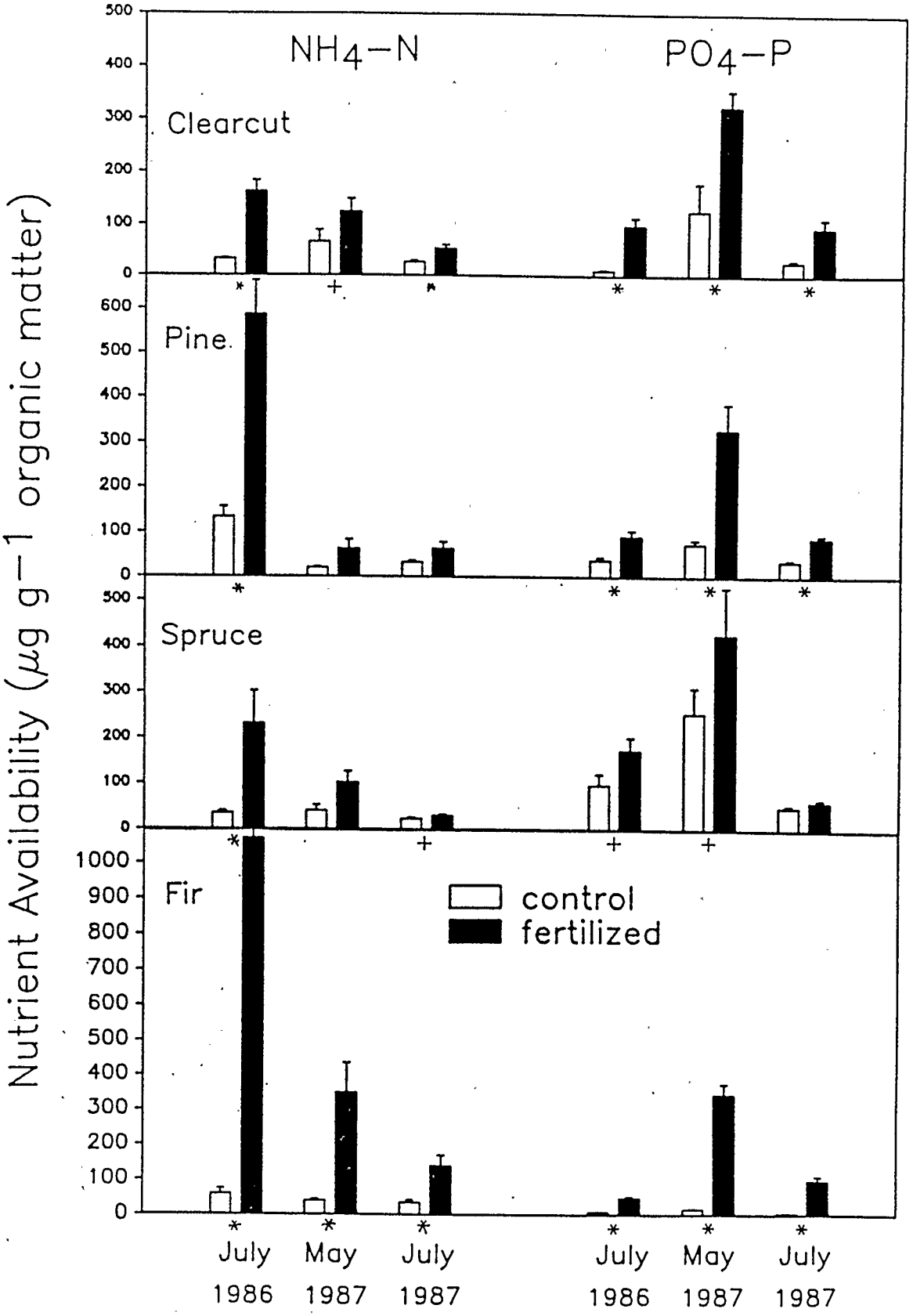
Nitrate was available in very small amounts (<10 $\mu g\ g^{-1}$ organic matter) in the forest floor at all sites, and was significantly more abundant in fertilized plots only on one occasion (July 1987 at the Fir site [unpublished data]). The pH of soil on control and fertilized plots were similar at all sites during the first summer and the following spring after fertilization (Table 19).

Figure 4. Levels of available N and P in the forest floor in control and fertilized plots in four Rocky Mountain coniferous forests. Fertilization occurred in May 1986. Each histogram represents the mean ± standard error of 9 (July 1986) or 5 (May and July 1987) samples. Histograms for fertilized plots with an asterisk beneath are significantly different from control plots based on two-way analysis of variance (*$p < 0.05$, + $p < 0.10$).

Table 18. Levels of extractable nutrients in mineral soil from control (c) and fertilized (f) plots one year after fertilization (July 1987).

		$\mu g\ g^{-1}$ dry weight of soil		
		NH_4	NO_3-N	PO_4
Clearcut	c	1.4 ± 1.7	0.0 ± 0.0	70.7 ± 22.0
	f	2.7 ± 2.1	0.0 ± 0.0	161.9 ± 16.3*
Pine	c	0.2 ± 0.3	0.0 ± 0.0	15.0 ± 5.5
	f	1.6 ± 1.8	0.0 ± 0.0	148.4 ± 56.3
Spruce	c	3.7 ± 1.2	0.0 ± 0.0	199.3 ± 69.6
	f	32.5 ± 62.0	28.7 ± 64.1	338.1 ± 157.2
Fir	c	4.8 ± 1.6	0.3 ± 0.3	13.0 ± 2.6
	f	40.9 ± 36.8*	0.4 ± 0.4	148.8 ± 45.4*

Note: Values represent the mean ± standard deviation of 5 samples. Values for fertilized followed by an asterisk are significantly different from values for control plots based on two-way analysis of variance ($p \leq 0.05$).


NH4–N
PO4–P
Clearcut
Pine
Spruce
Fir
control
fertilized
Nutrient Availability (μg g–1 organic matter)
July 1986
May 1987
July 1987
July 1986
May 1987
July 1987

Rates of mineralization of NH_4 and PO_4 during the first summer after fertilization (1986) were significantly higher on fertilized plots at all sites (Figure 5). During the second summer after fertilization (1987), differences in mineralization rates between control and fertilized plots were much diminished, although significantly higher rates of PO_4 mineralization were still found on fertilized plots at all sites. Rates of NH_4 mineralization were still significantly greater on fertilized plots only at the Pine site during the second summer after fertilization. Nitrification was detected during the first summer only at the Clearcut site, where its rate was highly variable and therefore not significantly different on fertilized plots. Nitrification rates were higher on fertilized plots at all sites during the second summer, although the considerable variability masked this trend at the Clearcut and Fir sites.

Rates of mineralization of NH_4 and PO_4 on control plots was usually lower at the Pine site than at the other sites (significant in 1986 for NH_4 and in 1987 for PO_4). Rates of nitrification in control plots were higher at the Clearcut site than at the other sites (this was significant in 1986 only).

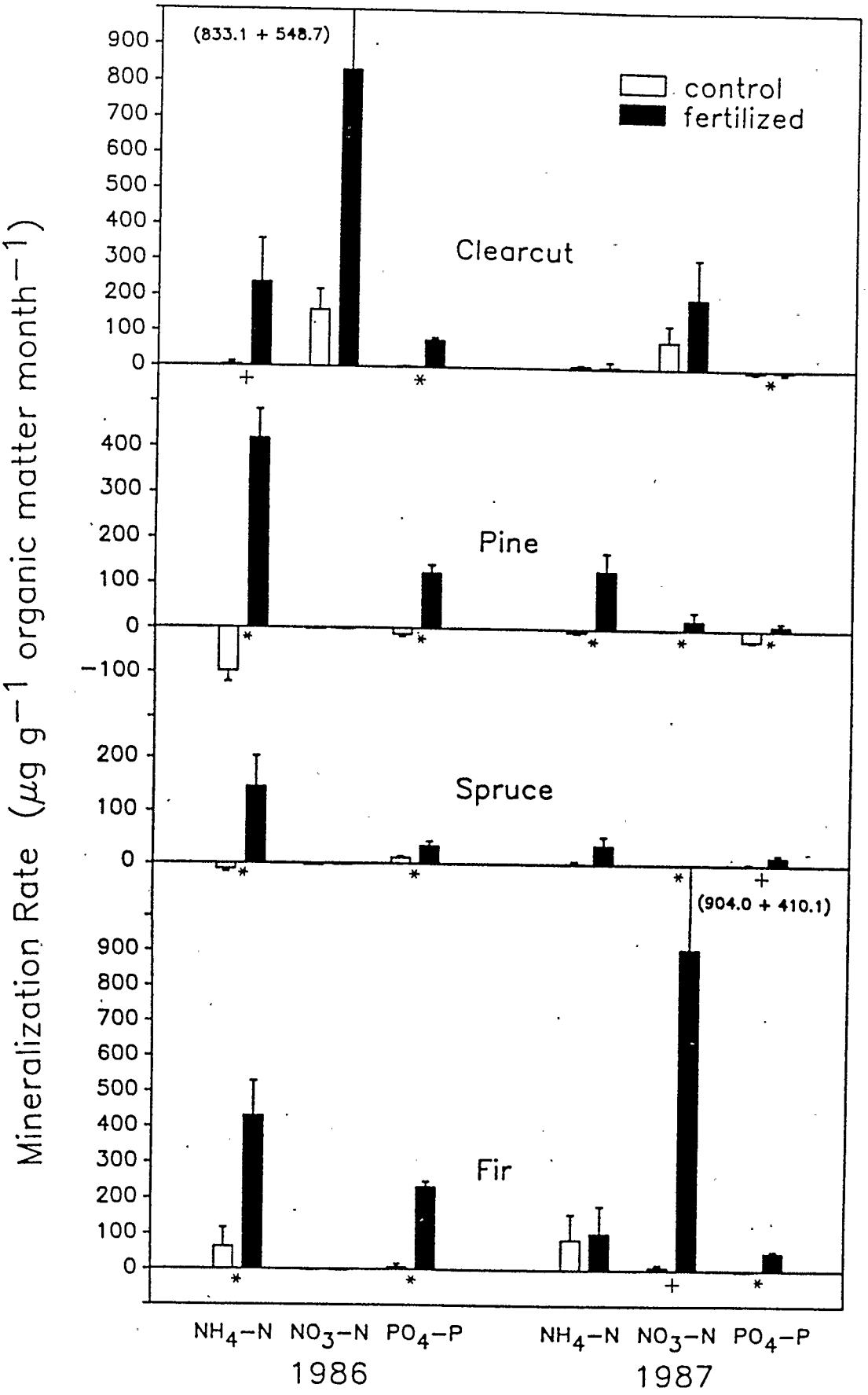
Microbial activity and biomass in the forest floor F and H layers was not significantly different in control and fertilized plots at any site two months after fertilization (Figure 6). The net change in microbial biomass over the one month in situ incubation was also similar on control and fertilized plots at all sites (Figure 6). Measurements of microbial respiration and biomass taken

Table 19. pH of forest floor (FH layers) and mineral soil in control (c) and fertilized plots (f) in four Rocky Mountain coniferous forests.

		Forest Floor				Mineral Soil	
Site	Treatment	n	August 1986	n	May 1987	n	May 1987
Clearcut	c	6	5.9 ± 0.2	5	5.8 ± 0.3	5	6.0 ± 0.2
	f	6	5.5 ± 0.2	5	5.8 ± 0.3	5	5.9 ± 0.2
Pine	c	9	5.2 ± 0.0	5	5.6 ± 0.4	5	5.8 ± 0.2
	f	9	4.9 ± 0.3	5	5.3 ± 0.4	5	5.9 ± 0.3
Spruce	c	9	5.5 ± 0.2	5	5.6 ± 0.3	5	6.1 ± 0.2
	f	9	5.4 ± 0.2	5	5.7 ± 0.3	5	6.0 ± 0.2
Fir	c	9	4.8 ± 0.2	5	5.5 ± 0.2	5	5.9 ± 0.1
	f	9	5.0 ± 0.3	5	5.3 ± 0.1	5	5.8 ± 0.2

Note: Fertilizer was applied in May 1986. Values represent the mean ± standard deviation. There were no significant differences between control and fertilized plots based on two-way analysis of variance ($p \leq 0.05$).

Figure 5. Rates of N and P mineralization and nitrification in the forest floor on control and fertilized plots at each site during the first (1986) and second (1987) growing seasons after fertilization. Each histogram represents the mean ± standard error of 9 (1986) or 6 (1987) samples. Histograms from fertilized plots with an asterisk beneath are significantly different from control plots based on two-way analysis of variance (*$p < 0.05$, + $p < 0.10$).


(833.1 + 548.7)
control
fertilized
Clearcut
Pine
Spruce
Fir
(904.0 + 410.1)
Mineralization Rate (μg g⁻¹ organic matter month⁻¹)
NH4–N NO3–N PO4–P
NH4–N NO3–N PO4–P
1986
1987

one year after fertilization (May 1987) also showed no differences between control and fertilized plots (Precott, unpublished data).

Fertilization of the forest floor resulted in higher levels of nitrogen and phosphorus in ground vegetation, as evidenced in the C:N and C:P ratios of tissues produced in the first growing season after fertilization (Table 20). C:N ratios were reduced by about 30% on fertilized plots at all sites as compared with control plots. C:P ratios were also reduced by about 30% on fertilized plots at the Clearcut and Pine sites. At the Spruce site, where phosphorus levels in control plots were the highest of the four sites, the C:P ratio was reduced by only 10%. Vegetation at the Fir site, which had the lowest phosphorus levels in control plots among the sites showed a 60% reduction in C:P ratios in fertilized plots. The mass of current year's production of ground vegetation was significantly increased on fertilized plots at the Clearcut, Pine and Spruce sites, as was the mass of nitrogen and phosphorus immobilized in annual production. The increases occurred primarily in grasses at the Clearcut and Pine sites and in forbs at the Spruce site. The small amount of ground vegetation at the Fir site was not significantly increased by fertilization, but the mass of phosphorus immobilized was greater in fertilized plots. Similar increases in the mass of ground vegetation were observed during the second growing season after fertilization (personal observation).

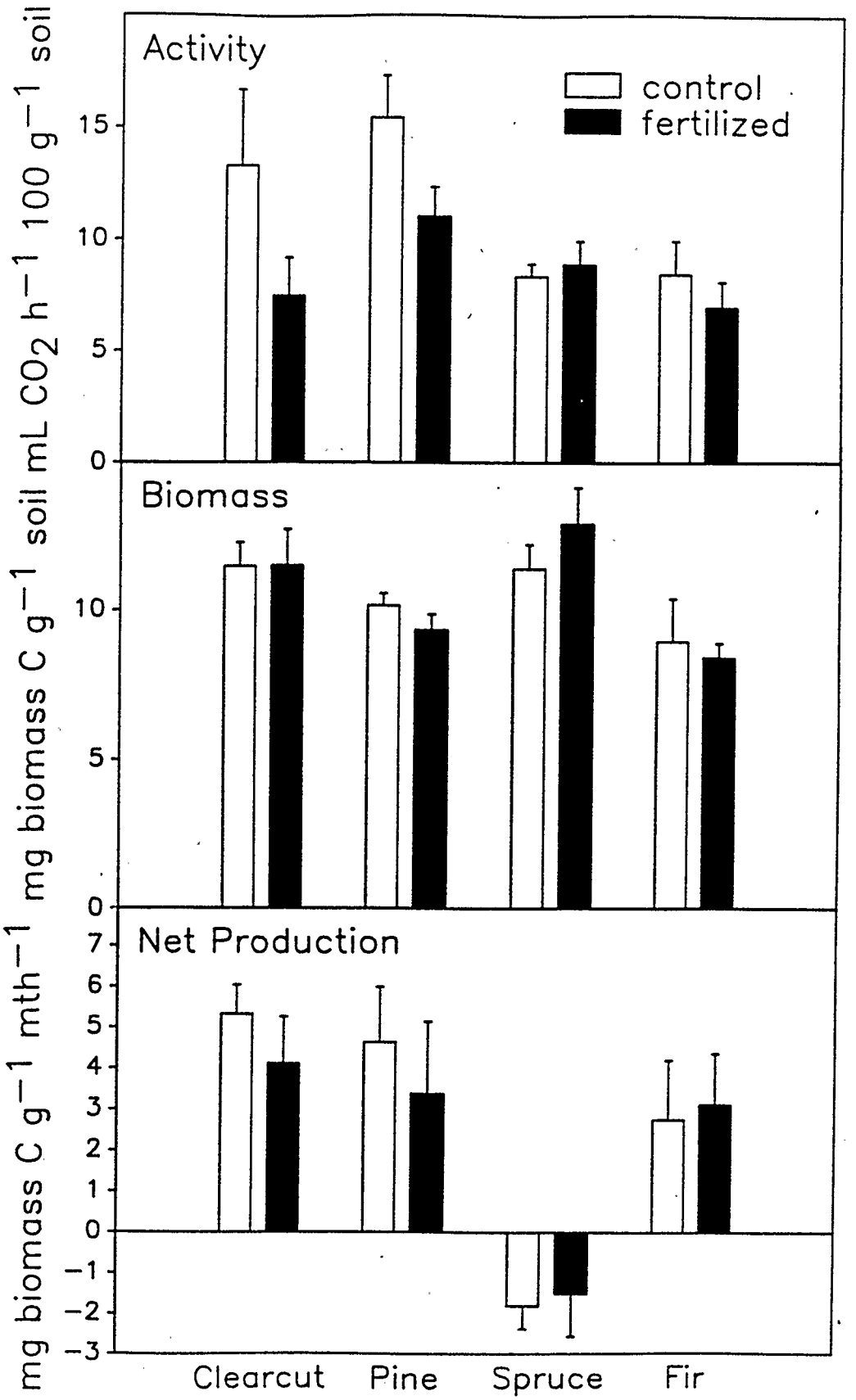
The same responses to fertilization were evident after the ground vegetation had senesced (October 1986 harvest). The mass of senescent ground vegetation was significantly greater on fertilized

Table 20. Mass and nutrient content of ground vegetation on control (c) and fertilized (f) plots at each site during the first growing season after fertilization.

		g m^{-2}	g N m^{-2}	g P m^{-2}	C:N	C:P	N:P
Green Tissue							
Clearcut	c	200.1 ± 59.5	2.34 ± 0.62	0.30 ± 0.07	40	313	8
	f	433.4 ± 77.3*	7.96 ± 1.43*	1.21 ± 0.24*	25	162	7
Pine	c	73.2 ± 20.9	1.32 ± 0.42	0.17 ± 0.05	25	193	8
	f	100.6 ± 21.6*	2.62 ± 0.58*	0.33 ± 0.07*	17	131	8
Spruce	c	42.7 ± 17.4	0.82 ± 0.33	0.18 ± 0.07	22	102	5
	f	87.9 ± 39.4*	2.41 ± 1.10*	0.43 ± 0.20*	16	88	7
Fir	c	7.2 ± 5.1	0.15 ± 0.11	0.01 ± 0.01	21	352	15
	f	10.8 ± 7.4	0.34 ± 0.31	0.04 ± 0.03*	14	128	9
Senescent Tissue							
Clearcut	c	80.1 ± 37.6	0.49 ± 0.22	0.07 ± 0.04	72	480	7
	f	233.0 ± 73.6*	3.04 ± 0.98*	0.31 ± 0.10*	35	339	10
Pine	c	32.2 ± 9.7	0.37 ± 0.13	0.05 ± 0.01	36	295	7
	f	53.9 ± 16.1*	0.90 ± 0.28*	0.13 ± 0.04*	26	188	7
Spruce	c	16.2 ± 8.7	0.21 ± 0.11	0.04 ± 0.02	32	177	5
	f	46.8 ± 18.5*	0.88 ± 0.38*	0.14 ± 0.05*	22	139	6
Fir	c	6.3 ± 6.2	0.08 ± 0.10	0.01 ± 0.01	31	373	8
	f	9.9 ± 6.9	0.21 ± 0.16*	0.02 ± 0.02*	18	166	10

Note: Values represent the mean ± standard deviation of 9 samples (6 samples at the Clearcut site) of current year's production. Values for fertilized plots followed by an asterisk are significantly different from values for control plots based on two-way analysis of variance ($p \leq 0.05$).

Figure 6. Biomass and rates of respiration and biomass production of forest floor microorganisms on control and fertilized plots at each site two months after fertilization. Each histogram represents the mean ± standard error of 9 samples (6 at Clearcut site). Values for fertilized plots were not significantly different from control plots on any occasion based on two-way analysis of variance ($p < 0.05$).


Activity
control
fertilized
Biomass
Net Production
mg biomass C g⁻¹ mth⁻¹ mg biomass C g⁻¹ soil mL CO2 h⁻¹ 100 g⁻¹ soil
Clearcut
Pine
Spruce
Fir

plots at all sites except the Fir site, while the mass of nitrogen and phosphorus in such tissue was significantly greater in fertilized plots at all sites (Table 20). C:N and C:P ratios in senescent tissues were narrower on fertilized plots than on control plots, and were broader than those found in green tissue.

The response of overstory trees to fertilization was less apparent than that of ground vegetation. The average diameter increment of stemwood, and average weights of needles and twigs for each of the two years preceeding fertilization, expressed as a function of the average value for each tree prior to fertilization, are shown in Table 21. At the Clearcut site, the young lodgepole pine trees on the fertilized plots had significantly larger needles than trees on control plots. The absence of any difference in twig weight suggests that the difference in total needle weight was caused by trees producing larger needles, rather than by increasing the number of needles produced, which would have necessitated a greater mass of twigs. There is evidence of a growth response in lodgepole pine trees at the Pine site, although differences in some parameters were not significant. No significant differences between trees on control and fertilized plots were found in any of the parameters of tree growth at the Spruce site. At the Fir site, fir trees had significantly wider growth rings both years after fertilization than found prior to fertilization, and weights of needles and twigs were considerably larger in the second year after fertilization than in preceding years. No significant differences were detected in spruce trees at the Fir site.

Table 21. Indices of biomass production by trees on control (c) and fertilized (f) plots during the 2 years following fertilization.

Site (Species)	Treatment	Annual Wood Increment Year 1	Annual Wood Increment Year 2	Weight of 100 Needles Year 1	Weight of 100 Needles Year 2	Total Weight of Needles Year 1	Total Weight of Needles Year 2	Total Weight of Twigs Year 1	Total Weight of Twigs Year 2
Clearcut (pine)	c	--	--	1.19 ± 0.29	0.99 ± 0.31	1.71 ± 0.48	2.08 ± 0.61	0.74 ± 0.17	0.75 ± 0.28
	f	--	--	2.28 ± 0.50*	1.79 ± 0.48*	2.94 ± 0.66*	4.77 ± 1.69*	0.61 ± 0.13	0.98 ± 0.14
Pine (pine)	c	0.88 ± 0.27	1.17 ± 0.38	1.01 ± 0.21	0.95 ± 0.10	1.08 ± 0.26*	1.08 ± 0.29	0.70 ± 0.12	1.17 ± 0.24
	f	0.80 ± 0.20	1.41 ± 0.55	1.33 ± 0.19	1.46 ± 0.37†	1.80 ± 0.10	1.68 ± 0.50	0.86 ± 0.11	2.19 ± 0.43*
Spruce (pine)	c	0.46 ± 0.36	0.52 ± 0.43	0.89 ± 0.13	1.03 ± 0.18	1.01 ± 0.26	1.10 ± 0.39	0.72 ± 0.04	0.98 ± 0.11
	f	0.67 ± 0.31	0.89 ± 0.19	0.91 ± 0.09	1.29 ± 0.07†	0.85 ± 0.44	1.22 ± 0.39	0.72 ± 0.17	1.16 ± 0.12
Spruce (spruce)	c	0.94 ± 0.22	0.75 ± 0.17	0.94 ± 0.04	0.96 ± 0.08	1.00 ± 0.11	2.05 ± 0.55	0.90 ± 0.06	1.38 ± 0.29
	f	0.99 ± 0.24	1.21 ± 0.63	0.89 ± 0.01	0.94 ± 0.01	0.79 ± 0.04	1.99 ± 0.59	0.79 ± 0.08	1.53 ± 0.40
Fir (spruce)	c	0.87 ± 0.06	0.97 ± 0.23	0.81 ± 0.07	0.91 ± 0.06	1.03 ± 0.27	1.71 ± 0.38	0.98 ± 0.20	1.39 ± 0.09
	f	0.84 ± 0.06	0.94 ± 0.49	0.86 ± 0.03	1.21 ± 0.02†	0.75 ± 0.28	2.50 ± 1.12	0.94 ± 0.36	2.44 ± 1.01
Fir (fir)	c	0.73 ± 0.01	0.81 ± 0.15	0.86 ± 0.12	0.79 ± 0.14	1.15 ± 0.09	0.86 ± 0.02	0.80 ± 0.06	0.55 ± 0.11
	f	1.32 ± 0.32*	1.51 ± 0.12*	1.16 ± 0.69	1.06 ± 0.05†	0.91 ± 0.52	1.41 ± 1.34	0.69 ± 0.38	1.30 ± 0.75

Note Each value represents the increment or mass of that year's growth divided by the average value for that tree prior to fertilization. Each value is the mean of 3 trees (4 at the Clearcut site) ± standard deviation. Values for fertilized plots followed by an asterisk are significantly different from control values at $p \leq 0.05$ based on a one-way analysis of variance; values followed by † are significantly different at $p \leq 0.10$.

The nitrogen and phosphorus content of needles of all species examined were similar on control and fertilized plots prior to fertilization (Table 22). Needles produced during the first growing season after fertilization (1986) had significantly higher levels of nitrogen in fertilized plots than in control plots (Table 22). The only exception to this trend was in subalpine fir needles which had lower nitrogen contents in fertilized plots. Levels of phosphorus in needles from trees in fertilized plots were significantly higher than those in control plots only at the Fir site. Needles produced during the second growing season after fertilization (1987) were significantly higher in nitrogen or phosphorus content in fertilized trees only in two instances (nitrogen in pine needles at the Spruce site [Figure 7], and phosphorus in fir needles at the Fir sites [Figure 8]). Needles from these branches which were produced during the first season after fertilization (1986) were significantly different in fertilized trees only in one instance (nitrogen in spruce needles at the Spruce site [Figure 7]). Where significant differences in nitrogen or phosphorus content of needles occurred in needles produced after fertilization, the same trend was also apparent in needles produced prior to fertilization (Figures 7 and 8). There was a general trend of slightly higher nitrogen and/or phosphorus levels in trees from fertilized plots in all needles, including those produced prior to fertilization (except for N in spruce trees at the Fir site which were lower in fertilized trees [Figure 7]). This increase was most noticeable for nitrogen at the Clearcut, Pine and Spruce sites and for phosphorus at the Fir site.

Table 22. Concentrations of N and P in current year's foliage of trees prior to and following fertilization (1985 and 1986 production, respectively).

Site		mg N g^{-1}		mg P g^{-1}	
Species		1985	1986	1985	1986
Clearcut					
pine	c	-	14.22 ± 1.27	-	1.53 ± 0.08
	f	-	16.73 ± 1.71*	-	1.59 ± 0.14
Pine					
pine	c	9.34 ± 0.36	9.99 ± 0.67	1.22 ± 0.16	1.27 ± 0.10
	f	9.32 ± 0.45	14.42 ± 0.73*	1.30 ± 0.30	1.68 ± 0.12
Spruce					
pine	c	9.34 ± 1.20	10.01 ± 0.80	1.19 ± 0.14	1.36 ± 0.22
	f	9.37 ± 0.44	11.35 ± 0.10*	1.25 ± 0.11	1.34 ± 0.50
spruce	c	9.20 ± 0.06	10.56 ± 1.10	1.54 ± 0.01	1.97 ± 0.24
	f	9.45 ± 0.24	11.69 ± 0.30*	1.81 ± 0.19	1.77 ± 0.57
Fir					
spruce	c	9.83 ± 0.11	10.28 ± 0.66	1.33 ± 0.04	1.30 ± 0.18
	f	8.95 ± 0.24*	12.82 ± 1.05*	1.11 ± 0.21	1.94 ± 0.12*
fir	c	12.73 ± 1.06	15.01 ± 1.09	1.40 ± 0.20	1.69 ± 0.17
	f	11.65 ± 2.28	9.90 ± 0.88*	1.34 ± 0.14	2.05 ± 0.08*

Note: Each value is the mean ± standard deviation of average values from 3 trees per treatment (2 trees at the Clearcut site). Values for the fertilized plots followed by an asterisk are significantly different from those for control plots based on a one-way analysis of variance ($p \leq 0.05$).

Figure 7. Nitrogen content of needles produced during the 3 years prior to (1983-1985), and 2 years following (1986-1987) fertilization upon harvest in 1988. Histograms represent the mean ± standard deviation of needles from 3 trees per treatment. Histograms for fertilized plots with an asterisk beneath are significantly different from control plots based on one-way analysis of variance (*$p < 0.05$, + $p < 0.10$).*

A: lodgepole pine needles from Clearcut site
B: lodgepole pine needles from Pine site
C: lodgepole pine needes from Spruce site
D: white x Engelmann spruce needles from Spruce site
E: white x Engelmann spruce needles from Fir site
F: subalpine fir needles from Fir site

* Arrow signifies time of fertilizer application

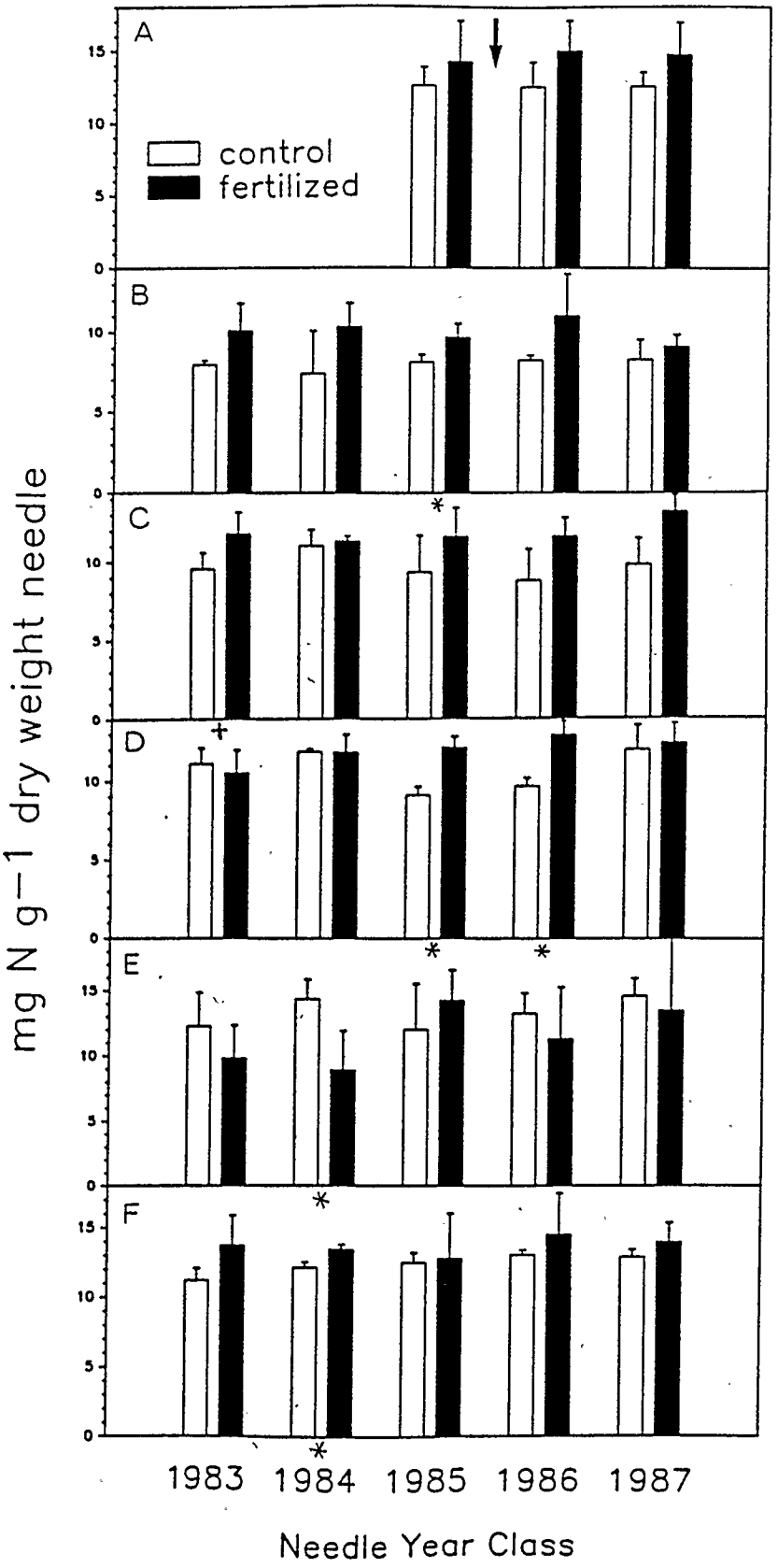
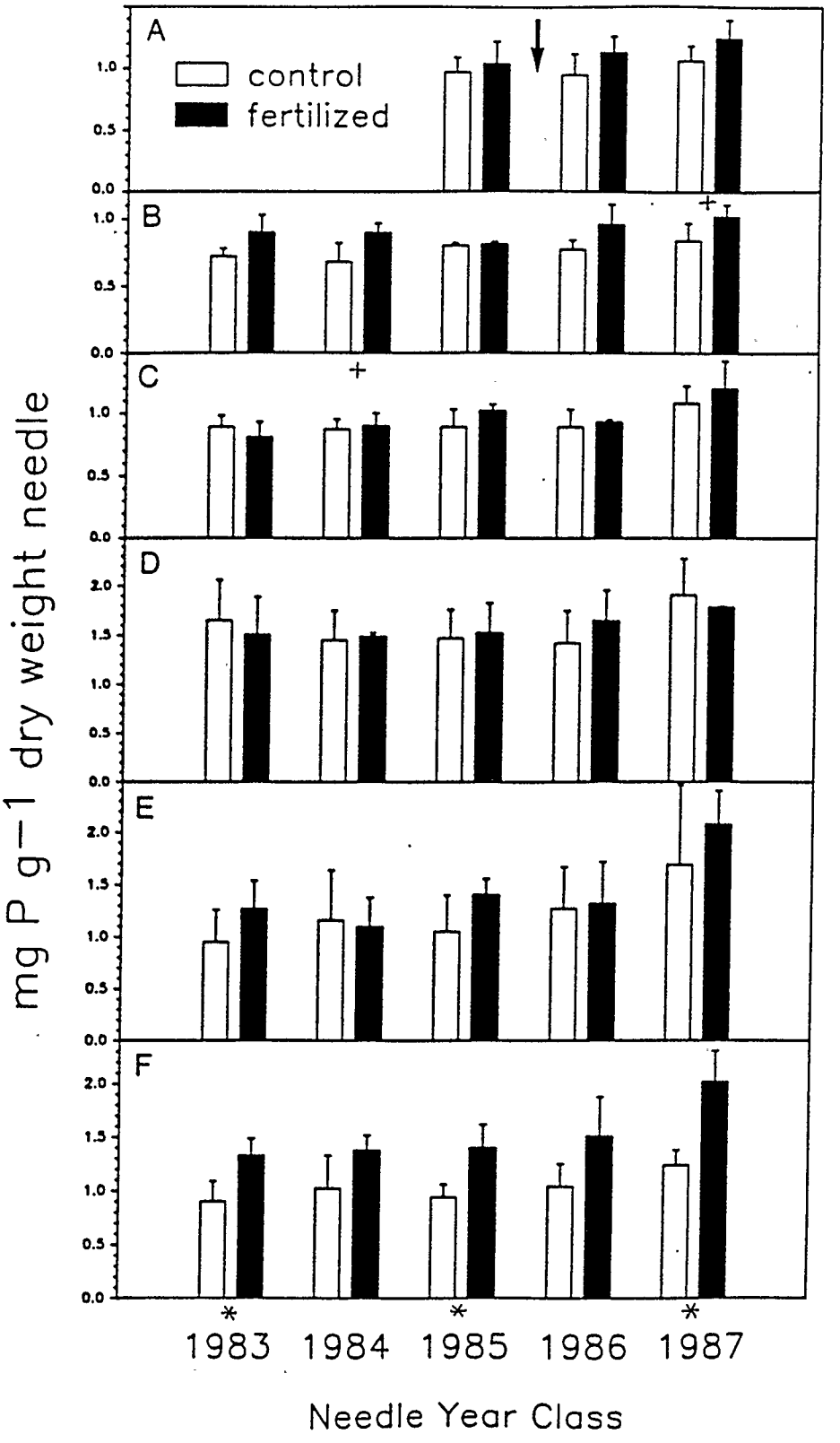

A
B
C
D
E
F
control
fertilized
mg N g−1 dry weight needle
1983
1984
1985
1986
1987
Needle Year Class

Figure 8. Phosphorus content of needles produced during the 3 years prior to (1983-1986), and 2 years following (1986-1987) fertilization upon harvest in 1988. Histograms represent the mean ± standard deviation of needles from 3 trees per treatment. Histograms for fertilized plots with an asterisk beneath are significantly different from control plots based on one-way analysis of variance (*$p < 0.05$, + $p < 0.10$).*

A: lodgepole pine needles from Clearcut site
B: lodgepole pine needles from Pine site
C: lodgepole pine needes from Spruce site
D: white x Engelmann spruce needles from Spruce site
E: white x Engelmann spruce needles from Fir site
F: subalpine fir needles from Fir site

* Arrow signifies time of fertilizer application


A
control
fertilized
B
C
D
E
F
mg P g−1 dry weight needle
1983
1984
1985
1986
1987
Needle Year Class

The implication that needles produced prior to fertilization were gaining nitrogen and/or phosphorus in trees from fertilized plots was pursued by comparing the nitrogen and phosphorus content of needles produced in 1985 upon harvest in February 1986 and March 1988 (i.e. at one and three years of age) for each sample tree on control and fertilized plots. The average change in nitrogen and phosphorus contents of needles during the three years is shown in Table 23. Needles from trees on control plots tended to decrease their nitrogen and phosphorus contents during aging, as is typical for these species (Prescott, unpublished data). Needles from trees on fertilized plots, on the contrary, tended to have higher nitrogen contents after three years of age than during their first year, especially at the Pine and Spruce sites. Differences in phosphorus contents of one and three-year-old needles from trees on fertilized plots were similar to those on control plots at the Pine and Spruce sites, but were significantly greater than those of control trees at the Fir site.

The mass of overstory litterfall during the first year following fertilization (1 August 1986 - 31 July 1987) was similar in control and fertilized plots at the Spruce and Fir sites, but was significantly lower in the fertilized plot at the Pine site. However, the mass of litterfall collected in fertilized plots at the Pine site prior to or very shortly after fertilization (1 September 1985 - 31 July 1986) was also about 50% lower than that in control plots. Thus this difference cannot be attributed to the fertilization treatment. Nitrogen and phosphorus contents of needles of the

Table 23. Differences in the N and P contents of tree foliage produced in 1985 at one and three years of age.

Site Species	Treatment	Change in N (mg g^{-1})	Change in P (mg g^{-1})
Pine			
pine	c	-1.22 ± 0.82	-0.42 ± 0.15
	f	0.35 ± 0.90	-0.50 ± 0.20
		(0.09)	(0.42)
Spruce			
pine	c	0.01 ± 1.59	-0.30 ± 0.07
	f	2.22 ± 1.85	-0.23 ± 0.12
		(0.19)	(0.41)
spruce	c	-0.08 ± 0.81	0.05 ± 0.28
	f	2.80 ± 0.71	-0.28 ± 0.12
		(0.02)	(0.15)
Fir			
spruce	c	2.49 ± 3.06	-0.23 ± 0.33
	f	5.32 ± 2.56	0.29 ± 0.08
		(0.29)	(0.05)
fir	c	-0.23 ± 1.34	-0.46 ± 0.14
	f	1.17 ± 1.28	0.06 ± 0.24
		(0.26)	(0.03)

Note: Fertilization occurred in May 1986; harvests took place in February 1986 and March 1988. Values represent the mean ± standard deviation of the net change in N and P concentrations in needles from 3 trees per plot between the two harvests. The level of significance of these changes based on one-way analysis of variance are provided in brackets.

dominant tree species collected in litterfall traps during the month of peak litter input (October 1986) were similar among control and fertilized plots (Table 24), with the exception of higher phosphorus levels in pine needles at the Pine site after fertilization. Any other differences, such as the lower N and P concentrations in spruce trees at the Spruce site and fir trees at the Fir site, were also evident in pre-fertilization litterfall (October 1985) and thus cannot be attributed to the fertilization treatment.

Senescent E. angustifolium leaves collected from the fertilized plot at the Pine site had average nitrogen and phosphorus concentrations of 19.5 and 3.2 mg g^{-1}, while those collected from the surrounding unfertilized area had nitrogen and phosphorus concentrations of 7.5 and 1.3 mg g^{-1}. Leaves grown in, or decomposed on fertilized plots (or both) lost a significantly greater amount of mass during one year of decomposition, as compared with leaves from unfertilized areas incubated on control plots (Table 25).

5.4 DISCUSSION

Results of this in situ fertilization experiment suggest that while the productivity of soil microorganisms is not affected by greater availability of nitrogen and phosphorus in these forests, the rate at which they release nutrients through decomposition, mineralization and nitrification is much increased. Under normal (control) conditions, very little nitrogen or phosphorus is released from the microbial pool and thus little is available to plant roots. When nitrogen and phosphorus are added, microbial activity

Table 24. Nutrient content of annual overstory litterfall on control (c) and fertilized (f) plots at each site during the first year prior to and after fertilization.

Site	Species	Treatment	mg N g^{-1}		mg P g^{-1}	
			Before	After	Before	After
Pine	pine	c	4.09 ± 0.27	4.61 ± 0.32	0.24 ± 0.00	0.26 ± 0.05
		f	4.23 ± 0.39	5.10 ± 0.51	0.24 ± 0.03	0.42 ± 0.07*
Spruce	spruce	c	4.28 ± 0.35	5.15 ± 1.04	0.61 ± 0.08	0.61 ± 0.09
		f	4.09 ± 0.17	4.39 ± 0.25	0.56 ± 0.03	0.50 ± 0.05*
Fir	spruce	c	4.17 ± 0.44	5.37 ± 0.45	0.24 ± 0.01	0.36 ± 0.01
		f	3.76 ± 0.17	5.76 ± 0.88	0.24 ± 0.00	0.36 ± 0.10
Fir	fir	c	7.48 ± 1.18	9.24 ± 0.78	0.47 ± 0.07	0.54 ± 0.07
		f	6.07 ± 0.43*	7.72 ± 0.85*	0.38 ± 0.05*	0.35 ± 0.00*

Note: Each value represents the mean ± standard deviation of 6 samples. Values for fertilized plots followed by an asterisk are significantly ($p \leq 0.05$) different from values for control plots based on one-way analysis of variance.

Table 25. Per cent of original dry mass of Epilobium angustifolium leaves remaining after one year incubation on control and fertilized plots at the Pine site.

Treatment	Plot	% Remaining
Control	Control	41.93 ± 5.93a
Control	Fertilized	35.31 ± 2.44b
Fertilized	Control	35.31 ± 2.69b
Fertilized	Fertilized	34.25 ± 1.90b

Note: Values represent means ± standard deviations of 9 samples. Values followed by different letters are significantly ($p \leq 0.05$) different based on a one-way analysis of variance and Scheffé test.

does not change, but more nutrient is released during this activity. This "priming effect" has frequently been observed following addition of nitrogen to forest soils (Broadbent 1965; Overrein 1967; Westerman and Kurtz 1973). Although Westerman and Tucker (1977) attributed it to increased microbial activity, there was no evidence of this in the present study. It may have been caused by initial adsorption of much of the added nitrogen and phosphorus onto organic matter such that normal rates of decomposition by microbes released these additional nutrients, leading to higher apparent rates of mineralization. Handling of the soil (sieving and shaking) may have added to this effect by aerating the soil and breaking up aggregates (Powers 1984), thus enhancing apparent differences in mineralization rates between control and fertilized soil.

The lack of response of soil microorganisms to addition of nitrogen as ammonium phosphate sulphate supports the contention that the significant responses observed after application of nitrogen as urea are due to higher pH and increased carbohydrate availability (Foster et al. 1980b). The similar biomass and activity levels of soil microbes on control and fertilized plots indicate that these organisms are limited by factors other than nutrient availability, such as available carbon, moisture or temperature. Changes in microbial biomass despite constant moisture conditions within the buried bags suggest that factors other than moisture influence microbial biomass production in these soils. The observed increase in microbial activity following addition of glucose to FH material from all sites indicates that readily available carbon limits

microbial activity. A similar response of microbial activity to carbon but not N or P was found in taiga forest floors (Flanagan and Van Cleve 1983).

Differences in the duration of enhanced nitrogen and phosphorus availability are consistent with those reported in other fertilization experiments (Ballard 1984), and reflect differences in retention mechanisms of the two elements (Miller 1984). Nitrogen is more mobile in soil and is more rapidly incorporated into microbial or vegetation biomass. Phosphorus, by contrast, is more tightly adsorbed onto organic particles of soil, and remains in the soil for a longer time after fertilization. This difference in soil retention capacity is also evident in the difference in the seasonal patterns of availability of the two elements. Phosphorus availability is highest in the spring at both control and fertilized plots, suggesting that much of the requirement of plants for this nutrient may be met by soil reserves which are supplemented during the winter months when plant and microbial immobilization rates are low. Levels of available nitrogen, conversely, were uniformly low at all sample times, suggesting that much of the requirement of the vegetation for nitrogen during the growing season is met through internal (within plant) redistribution of N.

The detection of nitrification under control conditions at the Clearcut site only is consistent with nitrification occurring at very low rates in temperate coniferous forests, except following disturbances (Keeney 1980). The immediate increase in the rate of nitrification in fertilized plots at the Clearcut site can be attributed to an increase in the level of ammonium available to an

already established population of nitrifying organisms. The small but significant increases in nitrification rates in fertilized plots at the Pine and Spruce sites during the second summer after fertilization suggest that higher levels of ammonium over a longer period of time were necessary to activate the small population of nitrifiers at these sites. The small increases at these sites may be indicative of N-limitation to nitrifiers, as N availability was increased to a lesser extent than P availability relative to annual nutrient uptake and total nutrient content of the forest floor by fertiliazation. The dramatic increase in nitrification activity at the Fir site during the second summer may indicate a relative shortage of phosphorus and relative abundance of ammonium at this site. The large addition of phosphate may have alleviated P limitations for nitrifiers (Purchase 1974), allowing nitrifiers to use relatively high levels of ammonium at the Fir site. Again, the absence of any significant mineralization at the Fir site during the first summer suggests that a priming period of higher nutrient levels is required to activate nitrifiers in this forest. A lag period prior to the onset of higher rates of mineralization following the onset of more favourable conditions for nitrifiers has been observed in other studies (Otchere-Boateng and Ballard 1978; Vitousek et al. 1979).

The higher rates of decomposition of E. angustifolium leaves in the presence of additional nitrogen and phosphorus suggest that while these nutrients may not be limiting to soil microorganisms (other than nitrifiers) in the FH layers of the forest

floor, a reduction in the C:N and C:P ratios of fresh (L layer) litter may increase the activity of L layer organisms. All types of litter in these forests had C:N ratios greater than 30 (Chapter 4) which usually leads to net immobilization (Stevenson 1986), while the FH layers at all sites had C:N less than 30 (Chapter 6). C:P ratios did not decline in a similar manner, and therefore it appears that microbial response to fertilization was related primarily to availability of N in their immediate environment.

The dramatic growth response of ground vegetation to fertilization indicates that some or all of the added nutrients are limiting productivity of this type of vegetation in these forests. This is especially noticeable at the Clearcut, Pine and Spruce sites where ground vegetation is most abundant. The greater response of ground vegetation relative to that of soil microorganisms to increased nutrient levels in soil is probably a consequence of the more limited accessibility of plant roots to soil nutrients (Haynes 1986). It may also reflect the ability of plants to fix carbon, such that energy is not more limiting as may occur with microbes. It is also apparent from the reductions in C:N and C:P ratios of ground vegetation that these plants could incorporate considerably more nitrogen and phosphorus than occurs under natural conditions. This supports the conclusion of McLaughlin and co-workers (1985) that ground vegetation may be an important means by which added nutrients are kept in the ecosystem to be recycled later rather than being lost via leaching from the soil.

The relative magnitude of the changes in C:N and C:P ratios at each site suggest that the ground vegetation at the Clearcut site has the greatest demand for additional nitrogen and phosphorus while that at the Spruce site has the lowest demand. Ground vegetation at the Pine site responded moderately to both nutrients, while that at the Fir site responded markedly to phosphorus. These findings agree with other information (in Chapter 3) suggesting that concentrations of nitrogen and phosphorus under natural conditions are most adequate at the Spruce site, less so at the Clearcut and Pine sites, and inadequate for phosphorus at the Fir site. Addition of nitrogen and phosphorus ameliorated these differences by allowing vegetation to absorb proportionately more of the nutrient which was the least plentiful at each site.

Reductions in C:N and C:P ratios continued through senescence of ground vegetation, such that this type of litter was more nutrient-rich in fertilized plots. Results of the decomposition experiment suggests that such litter would decompose more rapidly, perhaps leading to higher rates of microbial activity in the forest floor as found by Van Cleve and Moore (1978) when ground vegetation of greater mass and nutrient content entered the forest floor in fertilized forests. This in turn could increase the rate at which nutrients are released to the soil in fertilized forests, thereby prolonging the fertilization effect.

The limited response of overstory trees to fertilization may be due in part to the limited sample size, since much tree-to-tree variation in response is to be expected. The data do however

demonstrate that young trees such as the lodgepole pines at the Clearcut site are most responsive to fertilization. This is consistent with Miller's (1981) contention that tree growth in young (Stage 1) forests is very dependent on soil nutrient reserves (hence responsive to fertilization) while trees in older, closed-canopy (Stage 2) forests obtain most of their lower nutrient requirement from internal redistribution or foliar absorption.

The differences in nutrient content of first year needles shed some light on which nutrient is most limiting to tree growth at each site. Nitrogen was taken up by trees in considerably greater quantities when it was made more available at the Clearcut, Pine and Spruce sites, whereas phosphorus was taken up proportionately more by trees at the Fir site. This indicates lower levels of available phosphorus at the Fir site than at the other sites which agrees with the lower levels of phosphorus found in vegetation, litter and forest floor material at this site (Chapters 3 and 4).

The substantial differences in nutrient content of needles from fertilized and control plots during the year immediately following fertilization did not show up in needles of that year class one year later. This observation, as well as the slight but consistent increases in nutrient levels in needles produced prior to fertilization are suggestive of internal recycling of the extra nutrients acquired immediately after fertilization. This in turn suggests that much of the additional nitrogen and or phosphorus taken up was not immobilized immediately into biomass but rather stored in mobile compounds. Greatly increased levels of mobile

forms of nitrogen have been detected in needles following fertilization of forests (van den Driessche and Webber 1977); as has extensive remobilization of excess nitrogen into new tissues (Mead and Pritchett 1975; McIntosh 1982; Nambiar and Bowen 1986). This remobilization of excess nutrients has been used to explain enhanced growth of trees in the years following cessation of fertilizer application (Miller 1984); thus we might expect small increases in growth of trees in fertilized plots in these forests to continue.

The only evidence for growth dilution of foliar nutrient levels in this study is the significantly lower levels of nitrogen in subalpine fir trees on fertilized plots at the Fir site. This observation, as well as the fact that these trees have substantially higher foliar nitrogen levels than other species under control conditions, suggest that there is a relative abundance of nitrogen available to these trees. When both nitrogen and phosphorus were made more available, these trees took up substantially more phosphorus and produced a greater mass of foliage which had a lower nitrogen content. Spruce trees at this site also took up more phosphorus when it became more available, but also took up more nitrogen. Since they also had lower nitrogen levels in foliage than did fir trees under control conditions, spruce trees may have a greater capacity to use nitrogen or to take up phosphorus than do fir trees. These data demonstrate that both species at this site take up additional phosphorus when it is made more available. At the other three sites, there was no difference in phosphorus levels in foliage on control and fertilized plots, indicating that neither luxury

consumption nor growth dilution occurred as a result of fertilization. Although this stasis in phosphorus concentration might be interpreted as evidence that phosphorus is the limiting nutrient for trees in these forests (Morrison 1974a), it is more likely a reflection of differences in the physiological capacity of trees to store excess amounts of these two nutrients. While nitrogen may be transformed into a variety of compounds thus allowing continued uptake, phosphorus is stored almost exclusively as phosphate (Mengel and Kirkby 1982). Thus phosphorus levels will not increase as dramatically as nitrogen levels when availability increases. Thus differences in storage capacity of trees for different elements should also be considered when foliar nutrient levels are being used to estimate nutrient availability in forests.

The equilibration of nitrogen and phosphorus levels in foliage throughout several age classes indicates that changes in the nutritional quality of litterfall needles will be smaller than would be expected if internal redistribution did not occur, and may occur prior to senescence of the needles produced after fertilizer application. Given this and the fact that levels of available nitrogen in soil had returned to pre-fertilization levels by the end of the second growing season after fertilization, it is unlikely that any additional nitrogen will remain in tree foliage after senescence. Therefore, an enhancement of nitrogen levels in needle litter in fertilized plots is not expected. Phosphorus levels in foliage were different in fertilized trees only at the Fir site, where they too had equilibrated after one year. Thus, it is unlikely that

phosphorus levels in litterfall will be enhanced in fertilized plots at any site. The major differences in litter mass or quality will likely result from the more substantial changes in production and nutrient content of ground vegetation. The magnitude and timing of these potential changes in litter input and their effect on rates of decomposition and mineralization of nitrogen and phosphorus in the forest floor will be monitored to determine long-term effects of nitrogen and phosphorus addition in these forests.

CHAPTER 6

6. AVAILABILITY OF NITROGEN AND PHOSPHORUS

6.1 INTRODUCTION

In the preceding chapters, several aspects of nitrogen and phosphorus cycling in four Rocky Mountain forests have been described. In this chapter, some of these findings along with additional information will be examined to address questions regarding availability of N and P in these forests. Several parameters which are indicative of various aspects of nutrient availability will be examined at each site under natural conditions and following nutrient addition to determine the relative supply, demand, availability (supply relative to demand) of N and P and the degree to which these nutrients limit productivity of organisms in each of these forests. The parameters to be examined are:

1. leaching losses of N and P from the forest floor
2. mass and concentration of N and P in the forest floor
3. levels of extractable N and P in the forest floor
4. rates of net mineralization of N and P from FH layers of the forest floor
5. rates of immobilization and mineralization of N and P in fresh litter
6. biomass and activity of forest floor microorganisms
7. biomass and productivity of vegetation
8. resorption and uptake of N and P by vegetation

9. N and P content of vegetation

10. N and P content of litterfall.

6.2 METHODS AND RESULTS

6.2.1. Leaching Losses of N and P from the Forest Floor

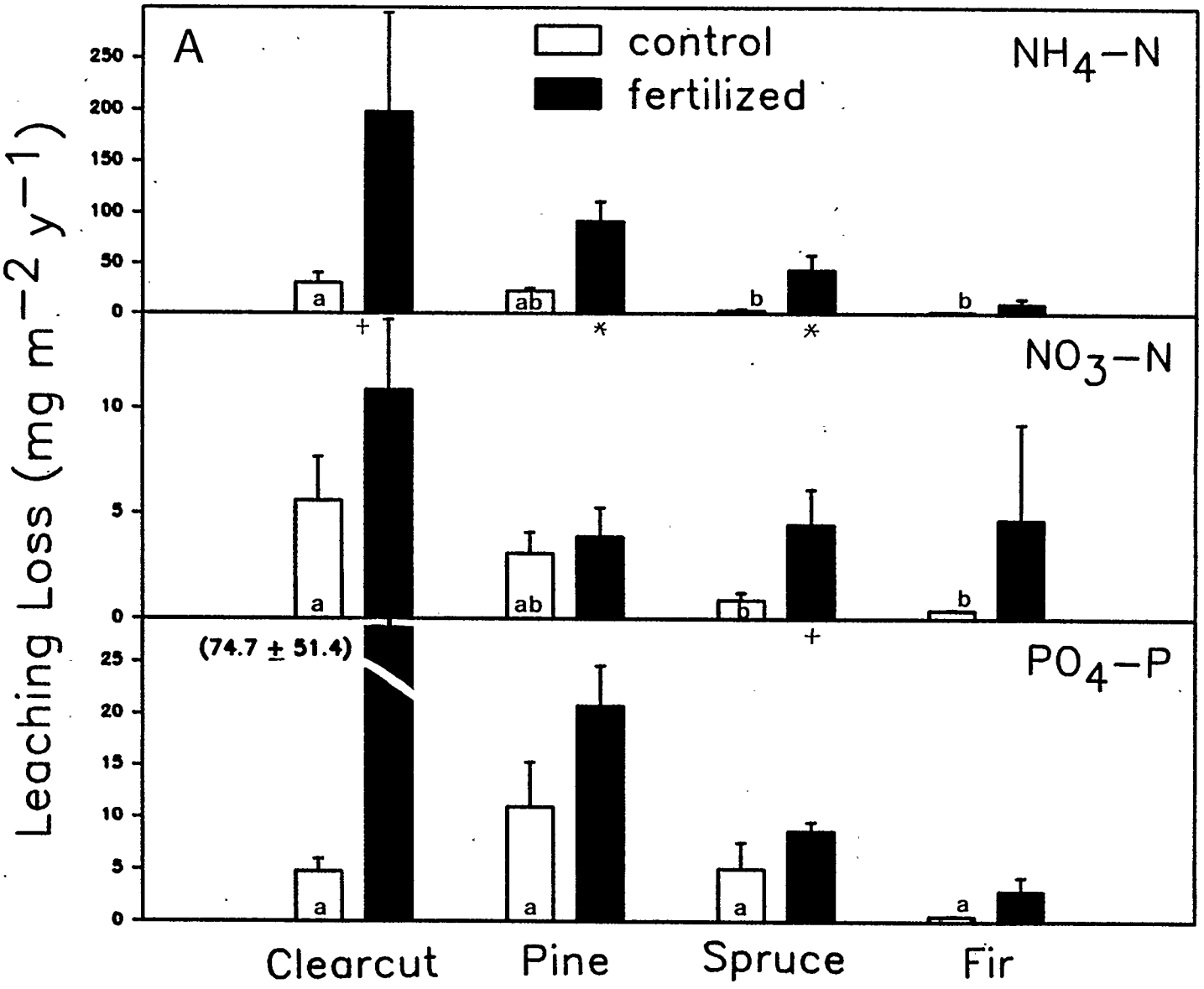
The amount of a nutrient transported from the forest floor in the soil solution is indicative of the availability of the nutrient, i.e. its supply relative to demand by plant roots and microorganisms. Leaching losses also vary according to the amount of precipitation, the composition of the forest floor, the soil type, and the form in which the nutrient occurs (e.g. NH_4 or NO_3), which limits the comparability of this parameter between ecosystems. The forests in the present study are of similar type (coniferous) and in close proximity to one another and therefore of similar climate. As a result, differences in leaching losses of N and P among sites should reflect differences in availability of these nutrients.

Leaching losses of N and P in the four forests in the present study were measured using zero tension lysimeters. At each site, four lysimeters were installed at each of two depths: immediately beneath the forest floor, and 10 cm into the mineral soil. Lysimeters were constructed from one 8 x 30 cm tray of polyvinylchloride tubing covered by a layer of glass wool and filled with acid-washed sand. A section of the forest floor or forest floor plus mineral soil was removed intact, trays were placed on the exposed surface at a slight angle to ensure drainage, and the soil

was replaced over the lysimeter. A 1 L bottle containing a small amount of phenyl mercuric acetate was attached via tubing to the tray to collect the leachate. Lysimeters were installed in September 1984 at all sites except the Clearcut which was instrumented in September 1985. An additional 6 lysimeters (3 at each depth) were installed in one 10 x 10 m "fertilized" plot at each site in September 1985. Bottles were collected whenever most contained sufficient liquid for analysis, beginning in the spring of 1986. After each collection, the volume and NH_4-N, NO_3-N and PO_4-N content of each leachate sample was determined with a Technicon II autoanalyzer (Technicon Instruments 1976, 1977, 1978). The total mass of each nutrient in each sample was divided by the surface area of the lysimeter (240 cm^2) to convert values to mg m^{-2}.

The amount of NH_4-N, NO_3-N and PO_4-P collected beneath the forest floor during the first year after fertilization and over the following winter are shown in Figure 9. Amounts of N and P leaching from the forest floor were usually greatest at the Clearcut site and lowest at the Spruce and Fir sites. Leaching losses on fertilized plots were greater than those on control plots, especially at the Clearcut and Spruce sites. In mineral soil (Figure 10), there was a similar pattern for leaching of NH_4-N and PO_4-P (Clearcut > Pine > Spruce > Fir) in the overwinter period, although no differences among sites were recorded during the first year. Differences in leaching from the mineral soil between control and fertilized plots were also not as consistent as recorded beneath the forest floor, and were most apparent at the Clearcut site. At the Spruce site,

Figure 9. Leaching losses of N and P beneath the forest floor during the first year after fertilization (A) and the following winter (B). Each histogram represents the mean ± standard error of 4 samples from each control plot and 3 samples from each fertilized plot. Histograms for fertilized plots with an asterisk below are significantly different from control plots based on one-way analysis of variance and Scheffé tests (*$p < 0.05$, + $0.05 < p < 0.10$). Histograms for control plots at different sites containing the same letter are not significantly different ($p > 0.05$) based on one-way analysis of variance and Scheffé tests.


A
control
fertilized
NH4–N
NO3–N
PO4–P
Leaching Loss (mg m−2 y−1)
250
200
150
100
50
0
10
5
0
25
20
15
10
5
0
a
ab
b
b
a
ab
b
b
a
a
a
a
+
*
*
+
(74.7 ± 51.4)
Clearcut
Pine
Spruce
Fir

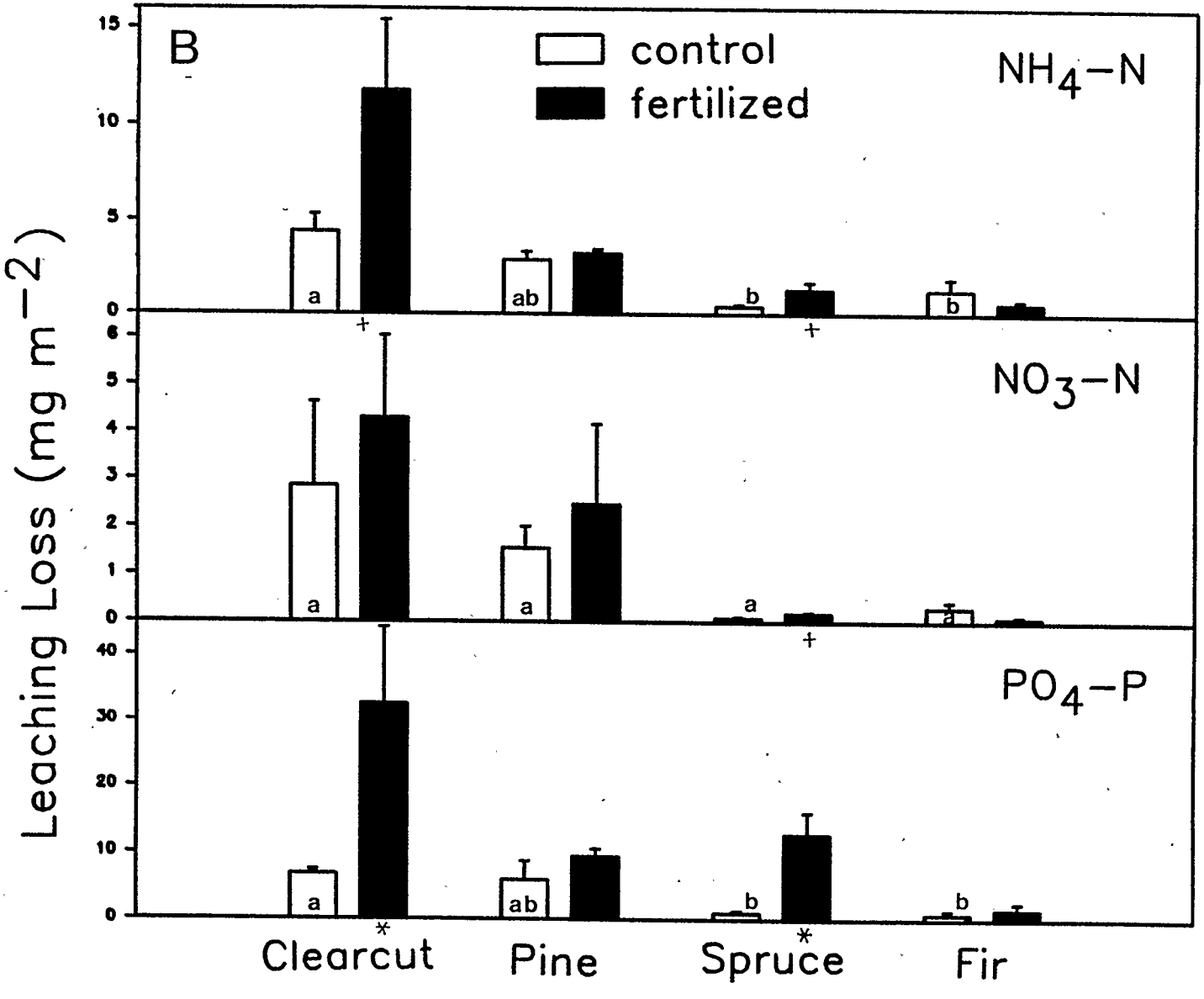
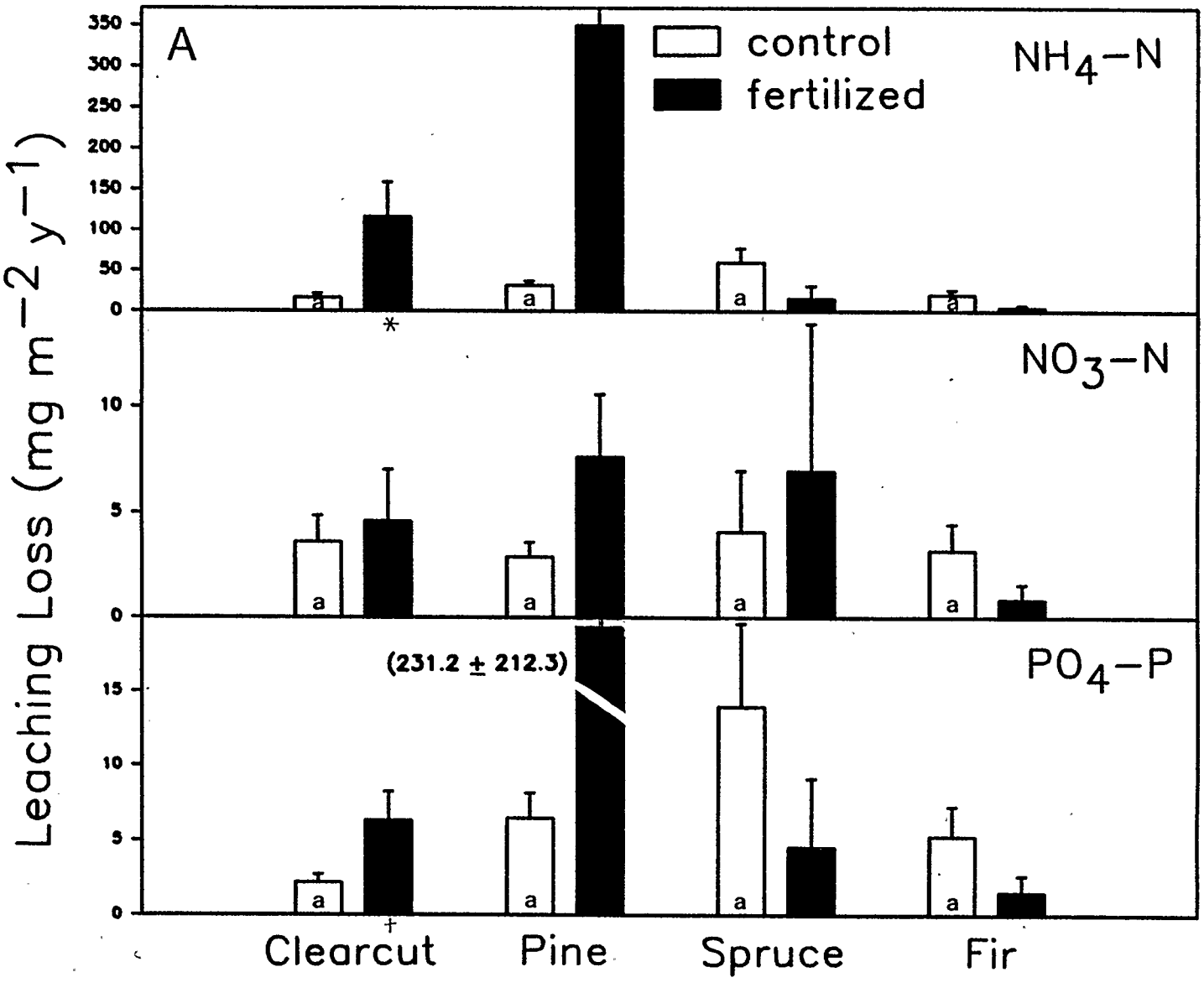
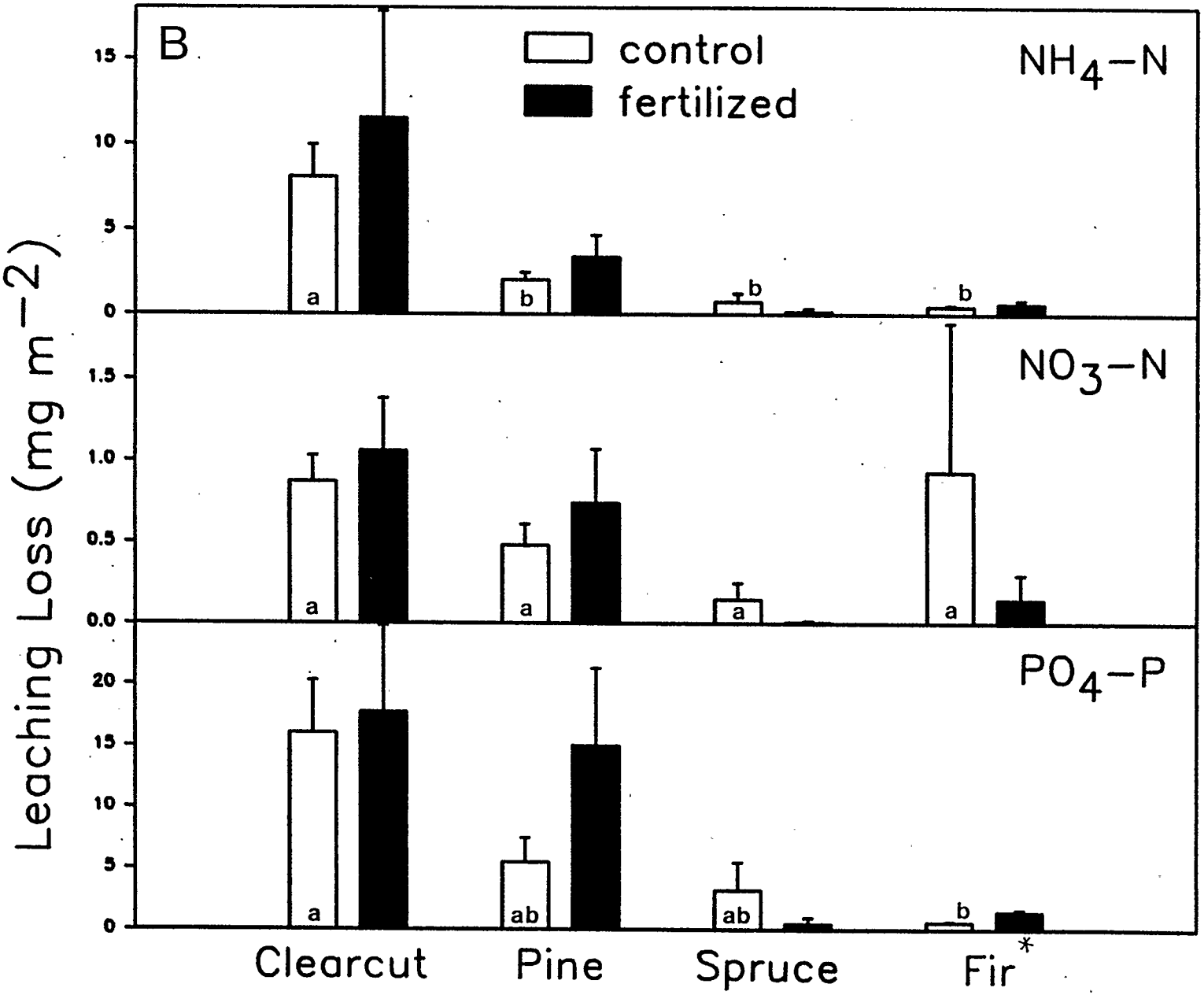

B
control
fertilized
NH_4–N
NO_3–N
PO_4–P
Leaching Loss (mg m^{-2})
Clearcut
Pine
Spruce
Fir
a
ab
b
+
*

Figure 10. Leaching losses of N and P 10 cm beneath the forest floor during the first year after fertilization (A) and the following winter (B). Each histogram represents the mean ± standard error of 4 samples from control plots and 3 samples from fertilized plots at each site. Histograms for fertilized plots with asterisk beneath are significantly different from control plots based on one-way analysis of variance and Scheffé tests (*$p < 0.05$, + $0.05 < p < 0.10$). Histograms for control plots at different sites containing the same letter are not significantly different based on one-way analysis of variance and Scheffé tests ($p > 0.05$).


A
control
fertilized
NH_4–N
NO_3–N
PO_4–P
Leaching Loss (mg m^{-2} y^{-1})
350
300
250
200
150
100
50
0
10
5
0
15
10
5
0
a
*
†
(231.2 ± 212.3)
Clearcut
Pine
Spruce
Fir


B
control
fertilized
NH_4–N
NO_3–N
PO_4–P
Leaching Loss (mg m^{-2})
15
10
5
0
1.5
1.0
0.5
0.0
20
15
10
5
0
a
b
b
b
a
a
a
a
a
ab
ab
b
Clearcut
Pine
Spruce
Fir*

the considerable leaching losses of N and P from the forest floor in fertilized plots was not observed in lysimeters in the mineral soil, suggesting that much of the excess nutrients leaving the organic layer were immobilized in the upper layer of mineral soil or in plant roots therein.

The major conclusion to be drawn from these observations is that the amount of N and P leaching from upper soil layers, and the extent to which this is enhanced by nutrient addition, is greater at the Clearcut site than at the other sites. The precision of this technique is seriously compromised by the inherent spatial and temporal variability of leaching rates. A minimum of ten lysimeters per treatment would allow more precise determination of differences among sites and between treatments. Examination of amounts of N and P occurring in small organic compounds in leachate would also ensure more accurate estimation of total leaching losses of these nutrients.

6.2.2. N and P Content of the Forest Floor

The total mass of a nutrient in the forest floor is indicative of the potential supply, as most of it must undergo mineralization before becoming available to plants or microorganisms. The concentration of nutrients in the forest floor provides an integrated measure of the concentrations of nutrients in all types of litter at all stages of decay.

Methods used to determine the mass and nutrient content of the forest floor at each site were described in Chapter 4. Data on

Table 26. Total mass and concentrations of C, N and P in the forest floor (LFH) of four Rocky Mountain coniferous forests.

Site Content	Nutrient Mass ($g\ m^{-2}$)			Nutrient		
	C	N	P	C:N	C:P	N:P
Clearcut	3283.6	50.8	4.3	29	335	12
Pine	1904.9	46.0	3.4	38	513	14
Spruce	2460.9	91.5	7.2	26	332	13
Fir	3911.4	118.6	6.5	32	548	18

the mass and nutrient content of the entire forest floor (LFH layers) are presented in Table 26. The total mass of N and P in the forest floor is greatest at the Spruce and Fir sites (N at Fir, P at Spruce). The low mass of N and P despite a large amount of C at the Clearcut site reflects the large amount of fallen wood on the forest floor at this site. The forest floor at the Pine and Fir sites had the highest C:N and C:P ratios; the Fir site had a particularly high N:P ratio.

The nutrient content of the FH layer may be more indicative of nutrient supply as this is the site of net mineralization of N and P. The C,N and P content of FH material from fertilized and control plots at each site in July 1986 is shown in Table 27. N content of the FH layers was high at the Clearcut site, while P content was low at the Fir site. Fertilization increased the total P content of FH material but did not significantly alter N content.

The only consistent finding among these data is the low P content of the forest floor at the Fir site relative to the other sites. Comparison of total N and P contents of the forest floor on fertilized and control site suggests that this measurement may be useful for detecting differences in PO_4 content but not NH_4 or NO_3, probably because of the overwhelming amount of organic N in the forest floor. Therefore, while total N and P content is indicative of potential availability, it is not useful for estimating actual availability, especially of N.

6.2.3. Concentrations of Extractable N and P in the Forest Floor

The amount of nutrients present in the soil solution or on exchange sites on forest floor material provides a good index of availability to plants and microorganisms as these nutrients are in a form and location in which they may be taken up by these organisms. Concentrations are determined by extraction with solutions which exchange ions for those in question, such that the extractant contains the nutrients already in solution or readily exchanged. Extractants used in this study were KCl for NH_4 and NO_3 and NH_4Fl for PO_4, as described in Chapter 5.

N and P were extracted from FH material at each site on 3 occasions following fertilization (Table 28). NH_4-N concentrations tended to be highest at the Pine and Fir sites; NO_3-N was highest at the Clearcut and Fir sites; and PO_4-P was highest at the Spruce site and lowest at the Fir site. Changes in nutrient availability

Table 27. Carbon, nitrogen and phosphorus content of the forest floor (FH) on control (c) and fertilized (f) plots in four Rocky Mountain coniferous forests.

	% Carbon	% Nitrogen	% Phosphorus	C:N	C:P	N:P
Clearcut						
c	40.49 ± 3.10	1.94 ± 0.17	0.11 ± 0.01	21	368	18
f	40.83 ± 2.17	1.85 ± 0.16	0.14 ± 0.01*	22	292	13
Pine						
c	42.07 ± 2.03	1.61 ± 0.12	0.11 ± 0.01	26	382	15
f	44.07 ± 2.98*	1.66 ± 0.10	0.14 ± 0.01*	27	314	12
Spruce						
c	29.87 ± 6.07	1.07 ± 0.13	0.09 ± 0.01	28	331	12
f	32.24 ± 6.23	1.23 ± 0.24	0.12 ± 0.02	26	269	10
Fir						
c	43.55 ± 8.27	1.61 ± 0.24	0.08 ± 0.01	27	544	20
f	42.19 ± 5.23	1.73 ± 0.23	0.13 ± 0.02*	25	325	13

NOTE: Values represent the mean ± standard deviation of 9 samples from each site (6 at Clearcut, taken 2 months after fertilizer application. Values for fertilized plots followed by an asterisk are significantly ($p > 0.05$) different from control plots based on one-way analysis of variance and Scheffé tests.

Table 28. Availability (mg m^{-2} y^{-1}) of N and P in the forest floor of four Rocky Mountain coniferous forests.

	August/1986 (n = 9)	October/1986 (n = 5)	May/1987 (n = 5)	$\bar{x}$ (n = 3)
NH_3-N				
Clearcut	72.1 ± 8.01^{b}	39.2 ± 13.7^{b}	43.2 ± 12.0^{b}	51.5 ± 18.0
Pine	411.0 ± 212.9^{a}	123.4 ± 17.0^{a}	93.2 ± 27.8^{ab}	209.5 ± 175.9
Spruce	103.6 ± 43.9^{b}	95.4 ± 40.3^{ab}	77.3 ± 25.4^{ab}	92.1 ± 13.5
Fir	243.8 ± 200.4^{ab}	110.3 ± 49.4^{a}	133.1 ± 76.6^{a}	162.4 ± 71.4
NO_3-N				
Clearcut	16.4 ± 76^{a}	0.6 ± 0.4^{b}	3.6 ± 3.9^{a}	6.9 ± 8.4
Pine	6.7 ± 2.5^{b}	0.5 ± 0.6^{b}	0.2 ± 0.3^{ab}	2.5 ± 3.7
Spruce	7.7 ± 3.3^{b}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	2.6 ± 4.4
Fir	19.2 ± 5.0^{a}	1.7 ± 0.1^{a}	0.2 ± 0.4^{b}	7.0 ± 10.6
PO_4-P				
Clearcut	24.9 ± 8.6^{b}	24.7 ± 19.6^{b}	45.3 ± 15.5^{c}	31.6 ± 11.8
Pine	119.7 ± 62.6^{b}	49.3 ± 18.7^{b}	101.8 ± 21.7^{b}	90.3 ± 36.6
Spruce	283.7 ± 211.1^{a}	149.1 ± 60.4^{a}	164.4 ± 35.4^{a}	199.1 ± 73.7
Fir	35.9 ± 8.6^{b}	19.5 ± 2.4^{b}	16.2 ± 5.8^{c}	23.9 ± 10.6

NOTE: Values represent the mean ± standard deviation values for different sites at each sample time followed by the same letter are not significantly different ($p > 0.05$) based on one-way analysis of variance and Scheffé tests.

following fertilization were presented in Figure 4 (p. 93). Concentrations of NH_4-N on fertilized plots were most increased at the Fir site, while PO_4-P concentrations were significantly higher on fertilized plots at all sites except the Spruce site which already had relatively high PO_4-P concentrations.

These data suggest that N is relatively available while P is not at the Fir site, while the opposite is true at the Spruce site. The Pine and Clearcut site showed intermediate availability of both nutrients. Measurement of concentrations of extractable nutrients in soil also suffers from considerable spatial and temporal heterogeneity (Mahendrappa et al. 1986), and provides information only on conditions at the exact time of sampling, and therefore requires a large number of replicates and sample times. However, because nutrient concentrations are determined by demand for nutrients as well as nutrient supply, it provides a good index of availability, i.e. supply relative to demand.

6.2.4. Rates of Net Mineralization of N and P in the Forest Floor

The rate at which nutrients become available for uptake by plants and microorganisms provides an estimate of the supply of nutrients. The rate of net mineralization of nutrients from FH layers of the forest floor can be determined from changes in nutrient concentrations in samples incubated *in situ* in buried bags. This method was used as described in Chapter 5 to estimate rates of net mineralization of N and P at each site over a one year period (Table 29). Annual N mineralization was highest at the

Table 29. Rates of net mineralization of N and P (g m^{-2} y^{-1}) in the forest floor of four Rocky Mountain coniferous forests.

	3 August/86 -10 Sept/86	29 Sept/86 -25 May/87	17 June/87 -26 July/87	Annual Total[1]
NH_4-N				
Clearcut	359.4 ± 320.1[a]	1642.1 ± 1295.5[a]	138.5 ± 177.3[a]	2140.0
Pine	-308.7 ± 224.9[b]	179.5 ± 123.5[b]	-16.4 ± 23.8[a]	-141.2
Spruce	-39.3 ± 45.3[ab]	33.0 ± 82.9[b]	4.7 ± 39.6[a]	5.1
Fir	257.5 ± 632.9[a]	612.3 ± 404.0[ab]	360.8 ± 656.4[a]	1230.6
NO_3-N				
Clearcut	349.7 ± 312.4[a]	1544.0 ± 1364.0[a]	125.8 ± 183.8[a]	2019.5
Pine	-4.1 ± 4.6[b]	-0.2 ± 0.9[a]	-0.2 ± 0.3[a]	-4.5
Spruce	-7.7 ± 3.3[b]	1.1 ± 2.5[b]	0.0 ± 0.0[a]	-6.6
Fir	-7.7 ± 7.6[b]	-0.7 ± 1.5[b]	31.6 ± 71.7[a]	23.2
PO_4-P				
Clearcut	3.7 ± 10.9[a]	34.5 ± 26.3[ab]	-10.0 ± 11.2[a]	28.2
Pine	-42.1 ± 55.2[a]	14.0 ± 20.3[ab]	-66.4 ± 16.6[b]	-94.5
Spruce	35.1 ± 24.6[a]	45.9 ± 35.6[a]	0.3 ± 23.7[a]	81.3
Fir	27.8 ± 124.1[a]	-5.3 ± 2.0[b]	-8.3 ± 5.0[a]	14.2

NOTE: Values represent the mean ± standard deviation. Values for different sites at each sample time followed by the same letter are not significantly different ($p > 0.05$) based on one-way analysis of variance and Scheffé tests.

[1]$\sum$ (3 Aug. 1986 - 26 July 1987 x 1.08)

Clearcut and Fir sites; at the Clearcut site most of the NH_4 mineralized was subsequently converted to NO_3. Very little nitrification occurred at the other sites. Net immobilization of PO_4 was recorded over one period at the Pine site; this may have been in part due to disturbance of the soil during sieving and homogenizing, as discussed in Chapter 5. Among the other sites, PO_4 mineralization was highest at the Spruce site and lowest at the Fir site. Fertilization increased rates of N and P mineralization and nitrification at all sites (Figure 5, p. 97).

Rates of mineralization of N and P at the four sites indicate that N supply is greatest at the Clearcut and Fir sites, and P supply is low at the Pine and Fir sites. Disturbance of soil samples during processing is the major complication in this method, as it may lead to inflated estimates of mineralization (the "priming effect" or "added nutrient interactions" [Jenkinson et al 1985]). This problem may be overcome by using intact cores, however this necessitates the use of paired samples and the associated assumption that nutrient levels in adjacent samples are similar. Considerable spatial and temporal heterogeneity in rates of mineralization necessitates frequent intense sampling (Powers 1984). Finally, estimates are indicative of the rate at which nutrients are made available to plants only, as microbial uptake continues in the bags.

6.2.5. N and P Concentrations in Decomposing Litter

Nutrients which occur in litter in small quantities relative to the requirement of decomposer microorganisms tend to be retained within the microbial biomass while other more available nutrients and mass are lost from litter. Therefore, comparison of the changes in concentrations of nutrients during decomposition provides evidence of selective immobilization and the relative availability of different nutrients to microorganisms.

Changes in concentrations of N and P in three different types of litter were determined over a 2 year period at each of the four sites. Senescent lodgepole pine needles were collected from one tree at the Pine site in September 1984; senescent grass (Elymus innovatus) and forb (Epilobium angustifolium) leaves were collected in September 1984 at the Pine, Spruce and Fir sites and in September 1985 at the Clearcut site. Litter was dried at 35°C to constant weight and 1.0 g needles, 0.5 g grass or 0.5 g of forb leaves from each site were placed in each of 20 10 x 10 cm bags of 1mm fibreglass mesh. 20 bags of each litter type were placed on the forest floor at each site in October 1984 (1985 at the Clearcut site). 10 bags of each type were harvested from each site in October 1985 and 1986 (1986 and 1987 at the Clearcut site), dried at 35°C and weighed. 5 samples of each type were randomly selected and analyzed along with 3 samples of the original (undecomposed) material for total N and P content as described in Chapter 4.

Changes in N and P concentrations in each type of litter at each site are shown in Figure 11 A - C. N concentrations increased

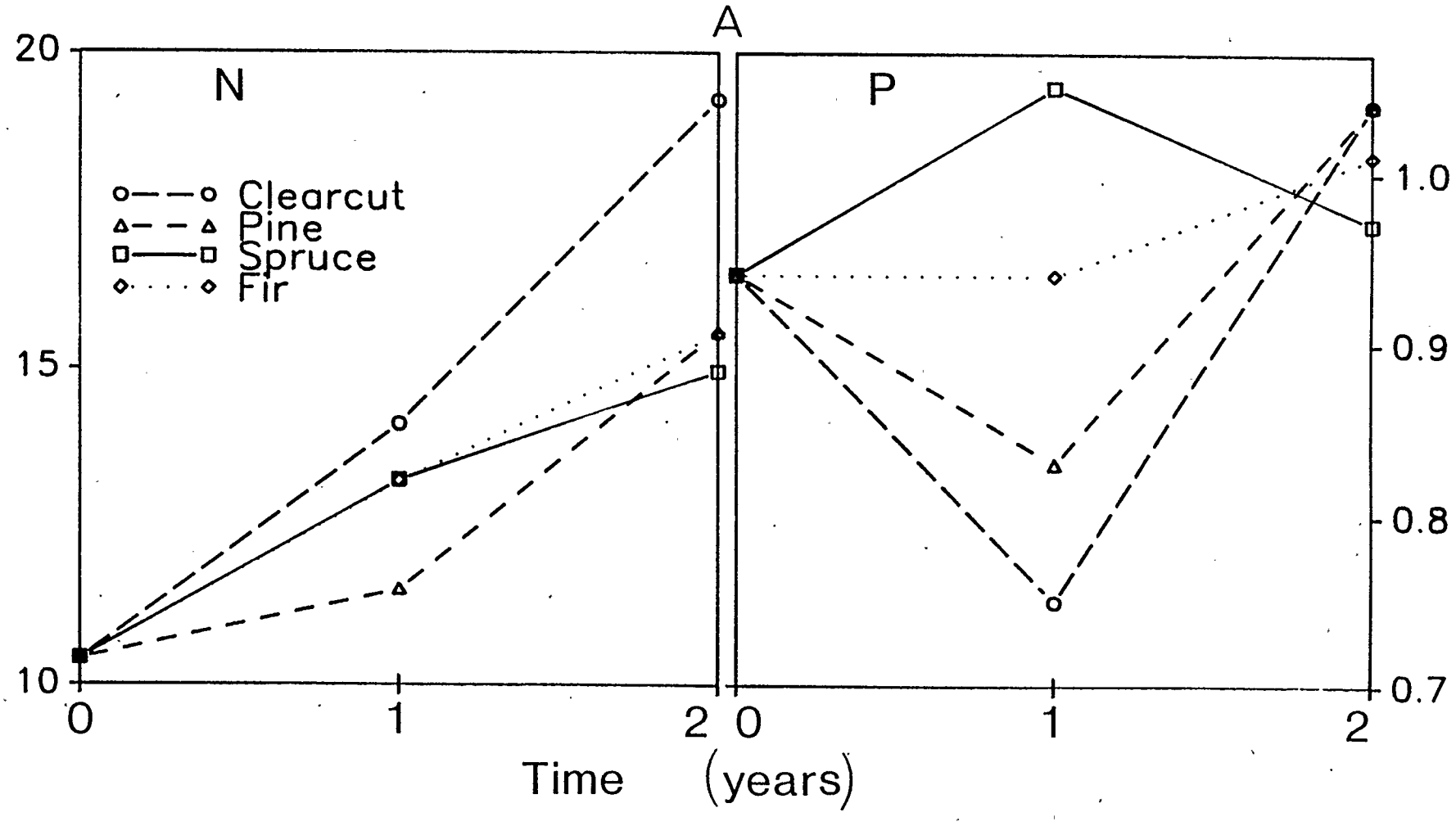
Figure 11. Concentrations of N and P (mg g^{-1}) in three types of litter during the first two years of decomposition in four Rocky Mountain coniferous forests.

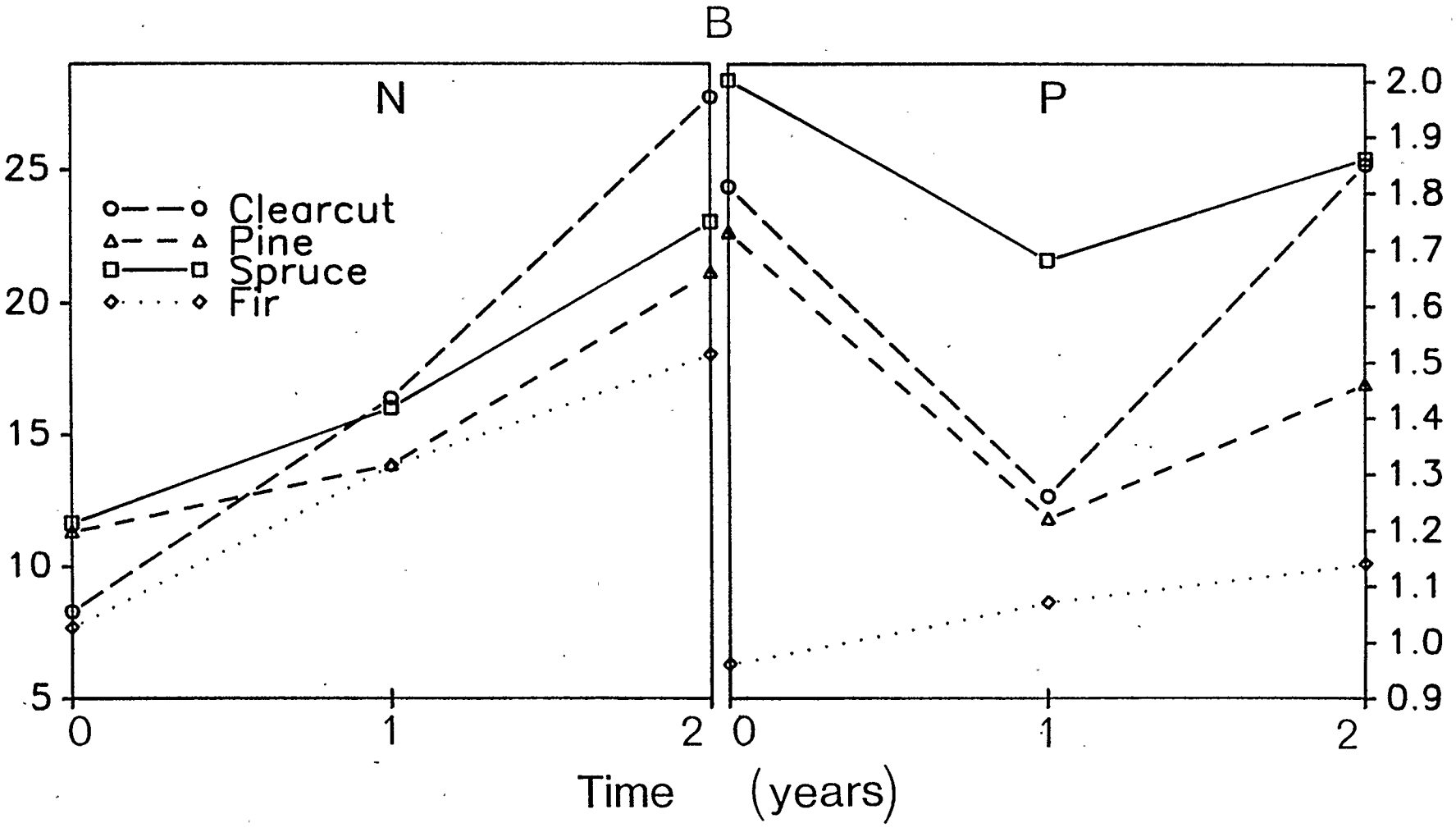
(A) pine (Pinus contorta) needles

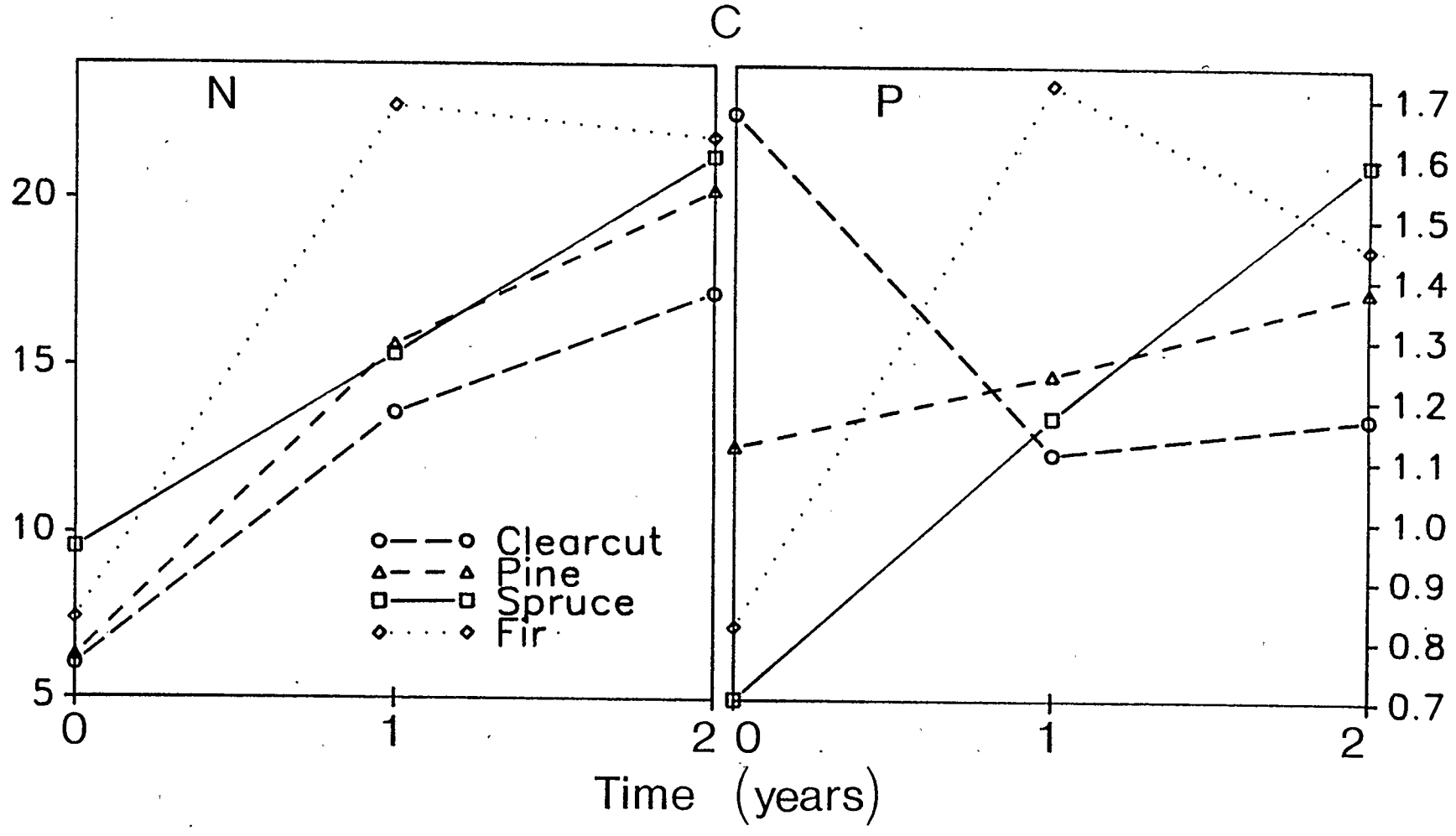
(B) grass (Elymus innovatus)

(C) forb (Epilobium angustifolium) leaves

(Values represent the mean of 5 samples at each harvest (n=3 at Time 0).


A
N
P
Clearcut
Pine
Spruce
Fir
20
15
10
1.0
0.9
0.8
0.7
0
1
2
0
1
2
Time (years)


B
N
P
Clearcut
Pine
Spruce
Fir
25
20
15
10
5
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0
1
2
0
1
2
Time (years)


C
N
P
20
15
10
5
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
Clearcut
Pine
Spruce
Fir
0
1
2
0
1
2
Time (years)

during the 2 years in all types of litter at all sites. Changes in P concentrations were less consistent; although concentrations after 2 years were fairly similar to initial concentrations, changes during the first year varied from net gain to net loss, depending on the initial P concentration of the litter (litter with relatively high P levels tended to lose P during the first year while litter with relatively low P levels gained P. As litter collected from the Fir site (grass and forb leaves) had a low initial P content, it gained P over the 2 year period. No consistent differences among sites could be discerned for N immobilization patterns.

The effects of greater availability of N and P on rates of nutrient immobilization during decomposition were determined from changes in the N and P content of Epilobium angustifolium leaves from fertilized and control plots before and after decomposing for one year on control and fertilized plots at the Pine site. Methods used in determining rates of mass loss and nutrient concentrations in the leaves were described in Chapter 5. Initial concentrations of N in leaves from control and fertilized plots were 7.5 and 19.5 mg g^{-1} respectively, while concentrations of P were 1.3 and 3.2 mg g^{-1} respectively. After one year, concentrations of N and P in leaves from fertilized plots were still higher than those from control plots (Table 30). Leaves from control plots which were decomposed on fertilized plots did not differ in N or P content from leaves incubated on control plots after one year. Leaves from control plots increased in N content by an average of 350% while leaves from fertilized plots doubled their N content during one year of

Table 30. Concentrations of N and P in Epilobium augustifolium leaves after one year incubation on control and fertilized plots at the Pine site.

Treatment	Plot	mg N g^{-1}	mg P g^{-1}
Control	Control	25.44 ± 3.96^{c}	2.34 ± 0.48^{ab}
Control	Fertilized	26.21 ± 4.20^{c}	2.02 ± 0.34^{b}
Fertilized	Control	41.00 ± 3.49^{a}	2.74 ± 0.37^{a}
Fertilized	Fertilized	35.45 ± 3.31^{b}	2.66 ± 0.28^{a}

NOTE: Values represent the mean ± standard deviation of 9 samples. Values in the same column followed by different letters are significantly different ($p > 0.05$) based on one-way analysis of variance and Scheffé's tests.

decomposition. The actual gain in N over the one year was similar in leaves from control and fertilized plots (18.3 and 18.8 mg g^{-1}). P content of leaves from control plots increased during decomposition regardless of site or placement, while P content of leaves from fertilized plots decreased regardless of site of placement.

Patterns of selective immobilization of N and P in decomposing litter indicate N to be of limited availability to microorganisms at all four sites. Increasing the N content of senescent litter by a factor of 250% did not alter the rate at which this nutrient is immobilized during the initial stages of decomposition, suggesting that N levels in fresh litter are very much less than those required by decomposer microorganisms. P levels in fresh litter appear to be adequate for microorganisms. Determination of net changes in the amount of N or P present or in C:N and C:P contents would eliminate some of the variability caused by different rates of decomposition among litter types and sites.

6.2.6. Biomass and Activity of Forest Floor Microorganisms

The biomass and activity rates of forest floor microbes, the agents of decomposition and nutrient mineralization, should be indicative of rates of gross mineralization of nutrients in the forest floor. Since much of the nutrients mineralized will be retained in microbial biomass, it is a better index of potential supply than net mineralization rate. Furthermore, changes in microbial biomass and activity in response to nutrient addition will provide an indication of the degree to which nutrients limit productivity of microorganisms.

Microbial biomass and activity in the F and H layers of the forest floor at each site were measured as described in Chapter 5 on 3 occasions (Table 31). Microbial biomass in the forest floor was roughly related to forest floor mass as it generally declined in the order Fir > Spruce > Pine > Clearcut. No consistent differences in microbial activity among the sites was apparent. Neither microbial activity or biomass were significantly different on fertilized plots at any site (Figure 6, p. 101). This similarity among sites is probably a consequence of the relatively similar climatic conditions and litter composition in these forests.

The similar biomass and activity of forest floor microbes at all sites, as well as the lack of response of microbial productivity to greater availability of N and P suggest that factors other than N and P availability, such as climate and availability of carbon, are more limiting to microbial growth. Therefore, this parameter is not a reliable indicator of nutrient availability in these forests.

6.2.7. Biomass and Productivity of Vegetation

The amount of nutrients immobilized in vegetation biomass can be used to make inferences regarding nutrient supply as these nutrients have been removed from the available pool. The rate of production of new biomass is reflective of nutrient demand, although the proportion of demand met from internal recycling should be taken into account. Low rates of biomass production in a forest relative to similar forests elsewhere may be indicative of nutrient

Table 31. Activity and biomass of microorganisms in the forest floor (FH) of four Rocky Mountain coniferous forests.

	August 1986 (n = 9)[1]	September 1986 (n = 5)	May 1987 (n = 5)
Microbial Activity (mL CO_2 m^{-2} h^{-1})			
Clearcut	289.0 ± 183.8^{ab}	186.6 ± 24.9^{b}	146.2 ± 112.7^{a}
Pine	474.3 ± 160.8^{a}	516.4 ± 160.8^{a}	223.1 ± 27.4^{a}
Spruce	243.4 ± 49.2^{b}	594.9 ± 207.6^{a}	269.5 ± 75.3^{a}
Fir	350.2 ± 184.6^{ab}	460.5 ± 97.1^{ab}	275.6 ± 92.7^{a}
Microbial Biomass (g biomass C m^{-2})			
Clearcut	25.0 ± 3.9^{a}	31.2 ± 3.8^{b}	24.7 ± 14.6^{a}
Pine	31.4 ± 3.5^{a}	42.0 ± 5.1^{ab}	40.4 ± 15.2^{a}
Spruce	33.4 ± 7.1^{a}	39.3 ± 8.6^{b}	46.7 ± 11.9^{a}
Fir	37.3 ± 17.9^{a}	59.0 ± 13.5^{a}	40.4 ± 13.4^{a}

NOTE: Values represent the mean ± standard deviation. Values for different sites at each sample time followed by the same letter are not significantly different ($p > 0.05$) based on one-way analysis of variance and Scheffé tests.

[1] n = 6 at Clearcut

limitation to productivity, although other potentially limiting factors such as climate must be excluded before this conclusion can be drawn. The best way to determine if nutrients are indeed limiting productivity of a forest is to measure changes in productivity in response to addition of nutrients.

Methods used in the present study to determine the biomass and productivity of aboveground vegetation were described in Chapter 3. As shown in Table 4 (p. 27), the mass of N and P in aboveground vegetation declined in the order Spruce > Fir > Pine > Clearcut while the amount immobilized in annual production was of the order Pine > Spruce > Fir > Clearcut. As shown in Table 20 (p. 100), ground vegetation responded to fertilization through increased biomass production at all sites. Productivity responses of trees were greatest at the Clearcut site; higher growth rates for some parameters also occurred at the Pine and First sites, while little change in productivity of trees was recorded on fertilized plots at the Spruce site (Table 21, p. 104). The response at the Clearcut site can be attributed to the younger age of these trees, rather than lower nutrient availability at this site. The lower response of trees at the Spruce site compared with trees of similar age and species at other sites, may however indicate that N and P are less limiting to productivity of trees at the Spruce site than at other sites.

Responses of vegetation to addition of N and P suggest that one or both of these nutrients limits productivity of ground vegetation at all sites, and limits productivity of trees most at the

Clearcut site and least at the Spruce site. A greater number of branches per tree and many more trees per site would be necessary to accurately measure the productivity response to fertilization. However, comparison of needles from the same branch following and prior to fertilization excludes some of the variability among trees, and allows determination of changes in productivity. Also, as discussed in Chapter 6, differences in storage capacity for different nutrients makes it difficult to determine the nutrient which is most limiting for vegetation; factorial experiments measuring productivity after addition of different nutrients and combinations are necessary for this purpose.

6.2.8. Resorption and Uptake of N and P by Vegetation

The mass of a nutrient resorbed by a plant during senescence of tissues (usually foliage) has been found to vary according to the availability of the nutrient, and could be used as an indicator of availability of nutrients in the soil. Determination of the amount resorbed and internally recycled also allows for the calculation of the amount of nutrients taken up from the soil annually by vegetation to produce new biomass.

Methods used to determine resorption and uptake of N and P in these forests were described in Chapter 3. From Table 8 (p. 32), it appears that the mass of N and P resorbed by vegetation in the forests depended primarily on the mass of tissue present from which nutrients could be resorbed. The proportion of nutrients in tissue which were resorbed was mostly a function of species. It will not

be possible to determine the effects of fertilization on nutrient resorption by trees until foliage of enhanced nutrient content senesces. Resorption of N and P from ground vegetation is probably not a good indicator as these plants are probably much more prone to leaching losses during senescence and estimates are probably more so a function of species composition rather than nutrient availability.

Annual uptake of N by vegetation was quite similar at all sites, while P uptake was highest at the Spruce site and low at the Clearcut and Fir sites (Table 9, p. 34). Estimates of rates of production of trees after fertilization are not sufficiently precise to determine changes in nutrient uptake after fertilization. However indications are that both biomass production and N and P content of foliage tended to be higher in fertilized trees, suggesting that more N and P were taken up when they were made more available.

6.2.9. N and P Content of Vegetation

The nutrient content of vegetation, especially foliage, is indicative of nutrient availability in the soil, as a result of the ability of plants to store nutrients when supply is high and to continue producing carbohydrates and other compounds not containing the nutrient when supply is low.

The N and P content of ground vegetation and tree foliage at each site was determined as described in Chapter 3. As shown in Tables 5 and 6 (p. 29, 30), vegetation at the Fir site had consistently high N and low P content, while vegetation at the Spruce site had high levels of both N and P. On fertilized plots, ground

vegetation had higher N levels, especially at the Clearcut and Pine sites, and higher P levels, especially at the Fir site (Table 20, p. 100).

Nutrient content of vegetation at each of the sites suggest that N availability is relatively low at the Clearcut, Pine and Spruce sites, while P availability is low at the Fir site. These data also demonstrated nutrient content of foliage to be characteristic of a species such that comparisons among different sites is limited to within-species comparisons. The difference in abilities of plants to store different nutrients complicates determination of the nutrient most limiting to production, as discussed in Chapter 5. Further advantages and disadvantages of foliage analysis have been discussed elsewhere (van den Driessche 1974, Powers 1984, Timmer and Morrow 1984)).

6.2.10 N and P Content of Litter

The nutrient content of senescent vegetation, particularly foliage, provides an estimate of annual requirement of vegetation, assuming that the amount lost in litter one year is equal to the amount which must be regained from the soil to produce new biomass in the following year. In addition, because it integrates both nutrient content of green tissue and the amount resorbed during senescence, it should also provide an indication of the availability of nutrients to vegetation.

Methods used to determine the N and P content of various types of litter in these forests were described in Chapter 4. As

shown in Table 13 (p. 62), the N content of ground vegetation declined in the order Fir > Spruce > Pine > Clearcut, while P content was in the order Spruce > Pine > Clearcut > Fir. N:P content of ground vegetation was highest at the Fir site and lowest at the Spruce site. Fertilization increased the N and P content of senescent ground vegetation at all sites, largely as a function of the N and P content of green tissue (Table 20, p. 100). Overstory litterfall had highest C:N and C:P ratios at the Pine site; while the Fir site had high C:P and N:P and the Spruce site had relatively low ratios of each nutrient (Table 13, p. 62). There was no change in N and P content of litterfall in fertilized plots during the first year after fertilization (Table 24, p. 114).

Nutrient contents of litterfall at the four sites suggest low availability of P relative to N at the Fir site and high availability of both N and P at the Spruce site. However, as nutrient content of green tissue and the proportion resorbed were both found to be primarily a function of species, regardless of site in these forests, the amount of N and P lost in litterfall may also reflect species composition more than nutrient availability in each forest.

6.3 DISCUSSION

From this examination of several indicators of nutrient availability, it is apparent that the most appropriate indicator to use depends on precisely which aspect of nutrient availability is to be measured.

Nutrient supply is best measured as rates of net mineralization in *in situ* buried bags. The total mass of nutrients in the forest floor is a measure of potential supply but rates of mineralization must be known for this to be of use. Levels of extractable nutrients in soil is a function of rates of uptake as well as supply and so is a better indicator of nutrient availability than supply *per se*.

Nutrient demand by vegetation can be measured as the amount of nutrients taken up annually, either by subtracting the amount internally recycled (resorbed) from the amount in new biomass, or by assuming annual uptake to be equal to the amount lost in litterfall annually. Nutrient demand by microbes requires estimation of nutrient content and rates of turnover of the biomass, both of which are exceedingly difficult to measure.

Nutrient availability (supply relative to demand) to vegetation can be inferred from the concentration of nutrients in the soil solution or on soil exchange sites (via extraction) or from the amount leached from the soil (via lysimetry). Availability of nutrients to microbes can be inferred from the degree of selective immobilization of nutrients in fresh litter.

Nutrient limitation (i.e. the extent to which productivity is limited by availability of nutrients) can only be determined from changes in productivity of plants and microbes following addition of nutrients.

Concurrent measurement of several indicators of nutrient availability is the most preferable means of gaining an

understanding of patterns of nutrient cycling, availability and limitation in ecosystems. Information on the ten indicator parameters measured in four Rocky Mountain coniferous forests in the present study allows patterns of N and P cycling to be compared among the sites in order to assess the relative availability of these nutrients in each forest.

Availability of N and P in the young pine-spruce stand at the Clearcut site appears to be greater than that in the older pine forest at the Pine site but less than that in the older spruce-pine stand at the Spruce site. This is evident in the higher rates of mineralization and leaching of N and P in the forest floor at the Clearcut site. The relatively low levels of exchangeable NH_4 in the forest floor at the Clearcut site are the consequence of higher rates of nitrification at this site, such that much of the NH_4 mineralized is converted to NO_3.

Higher rates of nitrification at the Clearcut site cannot be attributed to climate or pH levels as conditions were similar to those at the Pine site. It is more likely attributable to greater availability of NH_4 after clearcutting due to reduced plant uptake and the decomposition of residue and root systems. Higher availability of NH_4 would allow greater populations of nitrifying organisms and higher rates of nitrification in the clearcut area. Although these residues are now largely decomposed and root uptake of N and P is approaching rates measured in the older forests, large populations of nitrifiers may still remain in the forest floor, such that higher rates of nitrification are still found at this site.

Competition between nitrifiers (in addition to the regular microflora) and plant roots for available N and P may explain the dramatic growth of vegetation in response to N and P addition. Continued proliferation of tree roots and development of internal cycling as trees mature should allow trees to compete more successfully with nitrifiers for NH_4, which may eventually reduce populations of nitrifiers to low levels found in the older forests.

At the Pine site, availability of N and P are relatively low, as indicated by low rates of mineralization and leaching of N and P, and low levels of extractable N and P in the forest floor. Nitrification was detected only during the second year after fertilization, suggesting that in the unfertilized forest this process is limited by low availability of NH_4 in the forest floor. Productivity and nutrient uptake rates of vegetation are high and foliar nutrient levels are low in the unfertilized forest at the Pine site and enhanced on plots receiving additional nutrients. Lodgepole pine trees are efficient users of nutrients and are capable of rapid growth and hence have high nutrient demand, particularly when young. Therefore, the species composition and age of the stand may be sufficient to explain the tight cycling of N and P at this site.

The Spruce site appears to have the greatest availability of nutrients, especially P, of the four forests. This is evident in the relatively high N and P content of vegetation, litter and forest floor material and the high levels of extractable PO_4 and P mineralization. This forest had the greatest amount of N and P tied up in vegetation biomass, the highest rates of uptake and lowest

rates of resorption of N and P. Productivity of ground vegetation but not of trees was enhanced by nutrient addition. Nitrogen was not available in sufficient quantities to encourage leaching or nitrification losses, however, and nitrification was detected only after nutrient addition. The large amount of N and P at this site compared to the Pine site may be the result of a less severe stand-initiating fire at the Spruce site, such that a greater mass of forest floor nutrients remained from the previous stand.

The Fir site is characterized by relatively high availability of N and low availability of P relative to the other sites. High N availability is indicated in the high rates of N mineralization, high levels of extractable NH_4, and the low C:N ratio of litter and forest floor material. Low P availability is indicated in low rates of P mineralization, low levels of extractable PO_4, and high C:P and N:P ratios of litter and forest floor material. Ground vegetation and tree foliage had high N content and low P content relative to that at other sites and spruce trees at the Fir site had lower levels of foliar P than at the Spruce site. Fertilization did not change the N content of vegetation but did increase the P content, suggesting that vegetation in this forest already had access to sufficient N, but not sufficient P to meet its demands.

The apparent deficiency of P at this site, in contrast to the other sites, may be the result of either low availability of P or high availability of N such that P becomes most limiting. Low P availability in soil might occur if P is either weathered out or tightly bound in mineral complexes. Phosphorus may also be

immobilized in the large masses of forest floor organic matter, microbes, and moss at the Fir site, as found in black spruce forests in the Alaskan taiga (Flanagan 1986, Chapin et al. 1987). Lower activity of mycorrhizal fungi in this forest due to differences in species composition or climate might also lead to lower P uptake by vegetation and thus low levels in litter and forest floor. Higher N availability may be the result of the older age of the forest at the Fir site as it has had a much longer period of time to accumulate N than have the younger forests. High rates of N fixation have been measured in other Rocky Mountain subalpine fir forests, particularly in wood in advanced stages of decay (Jurgensen et al. 1987). The large amount of decaying wood buried in the forest floor at the Fir site may further enhance availability of N at this site. Analysis of P characteristics of the mineral soil, mycorrhizal and N-fixation activity, and rates of P mineralization under similar climatic conditions at each site is necessary to determine the cause of the apparent P deficiency at the Fir site.

Comparison of the characteristics of N and P cycling among the three mature forests (Pine, Spruce and Fir sites) provides some insight into the factors controlling nutrient use and availability in these forests. As discussed in Chapter 3, nutrient use efficiency (NUE) of trees in these forests is primarily related to the species composition, which is mostly related to climatic and disturbance factors. At the Pine and Spruce sites, NUE of trees is a function of the prevalence of nutrient efficient pines, and patterns of NUE are similar to those in other lodgepole pine and white spruce

forests. At the Fir site, however, N use is less efficient and P use more efficient than in other spruce-fir forests, suggesting that factors other than species composition are influencing NUE of trees at this site. Therefore, it appears that NUE of trees and shrubs in these forest is mostly a function of species composition, but may be altered (without changes in species composition) by low availability of one or more nutrients.

Possible consequences of these patterns of nutrient use by trees and shrubs in these forests are presented along with supporting data in Table 32. As discussed in Chapter 4, NUE of vegetation will determine the nutrient content of litterfall and the forest floor. As a result, the N and P contents of overstory litterfall and forest floor material are low at the Pine site, high at the Spruce site, and low for P but high for N at the Fir site. This should in turn influence the balance between mineralization and immobilization of N and P by forest floor microorganisms and hence the rate of net mineralization and N and P. As shown in Table 32, net immobilization of both N and P was recorded over a one-year period at the Pine site, where net mineralization occurred only during the winter (Table 29, p. 140). Annual net mineralization of N and P was greater at the Spruce site, while annual N mineralization was very high and P mineralization very low at the Fir site.

Rates of N and P mineralization in the forest floor should in turn affect vegetation, especially ground vegetation which root predominantly in or immediately below the organic mat. As shown in Table 32, NUE of ground vegetation reflected rates of net

Table 32. Consequences of N and P use by vegetation in three mature coniferous Rocky Mountain forests.

	Site	Tree Shrub NUE*	Overstory Litterfall C:N	Overstory Litterfall C:P	Forest Floor C:N	Forest Floor C:P	Net Mineralization mg m^{-2} y^{-1}	Ground Vegetation NUE*
	Pine	357	89		38		-141	86
N	Spruce	288	85		26		5	82
	Fir	281	62		32		1231	77
	Pine	3646	1025		513		-95	517
P	Spruce	1756	585		332		81	398
	Fir	2639	920		548		14	750

* Nutrient Use Efficiency = annual biomass production/annual nutrient uptake.

mineralization of N and P in the forest floor, being more efficient for N and P at the Pine site than at the Spruce site, and efficient for P but not N at the Fir site. Rates of N and P mineralization in the forest floor would also be expected to influence NUE of trees and shrubs, thereby creating a feedback loop in the nutrient cycle depicted in Table 32. In the forests at the Pine and Spruce sites, this probably only reinforces patterns of NUE by trees set by species composition. At the Fir site, this feedback loop may be allowing the low rates of P mineralization in the forest floor to alter normal patterns of N and P use by these species.

6.4 CONCLUSIONS

From the information presented in Chapters 3 through 6, the following conclusions can be made regarding cycling of N and P in the four Rocky Mountain coniferous forests in the present study:

1. Aboveground biomass and productivity of vegetation and rates of litter return are very close to those predicted for coniferous forests at this latitude and altitude.
2. Vegetation and litter are of low nutrient content; as a result N and P are selectively immobilized during decomposition.
3. Net mineralization occurs only in the F and H layers of the forest floor, and rates are normally low.

4. Nitrification occurs only after disturbance such as clearcutting or fertilization when availability of NH_4 is increased.
5. Leaching losses of N and P from the forest are usually low.
6. Vegetation in all forests is limited to some extent by availability of N or P, while forest floor microbes are limited by other factors, such as available carbon.
7. Nutrient use efficiency of vegetation in these forests is primarily a function of species composition of trees, with forests dominated by pine using N and P more efficiently than forests dominated by spruce or fir.
8. Nutrient use by vegetation determines nutrient quality of litter thereby influencing rates of net mineralization and availability of N and P in the forest floor.
9. Nitrogen is least available and used most efficiently by vegetation in the pine and spruce-pine forests; phosphorus is less available and used more efficiently in the older spruce-fir forest.
10. Site factors causing P to be immobilized in the forest floor in the spruce-fir forest have necessitated efficient use of P, thereby altering nutrient use efficiency of vegetation in this forest.

7. LITERATURE CITED

Alexander, R.R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service Agricultural Handbook No. 659.

American Society for Testing of Materials. 1978. Annual Book of ASTM Standards. Vol. 409: Wood. American Society for Testing of Materials, Philadelphia.

Anderson, J.P.E., and Domsch, K.H. 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10: 215-221.

Aplet, G.H., Laven, R.D., and Smith, F.W. 1988. Patterns of community dynamics in Colorado Engelmann spruce - subalpine fir forests. Ecology 69: 312-319.

Aronsson, A., and Elowson, S. 1980. Effects of irrigation and fertilization on mineral nutrients in Scots pine needles. Ecol. Bull. (Stockholm) 32: 219-228.

Baker, J.B., Switzer, G.L., and Nelson, L.E. 1974. Biomass production and nitrogen recovery after fertilization of young loblolly pines. Soil Sci. Soc. Amer. Proc. 38: 958-961.

Ballard, R. 1984. Fertilization of plantations. In Nutrition of Plantation Forests. Edited by G.D. Bowen and E.K.S. Nambiar. Academic Press, London. pp. 327-360.

Ballard, T.M. 1984. Nutrition of planted white spruce. Contract Research Report to B.C. Ministry of Forests, Victoria, B.C.

Ballard, T.M., and Carter, R.E. 1985. Evaluating forest stand nutrient status. British Columbia Ministry of Forestry. Land Management Report 20, Victoria, B.C.

Barber, S.A. 1984. Soil Nutrient Availability. A Mechanistic Approach. Wiley and Sons, Toronto.

Beaton, J.D., Moss, A., MacRae, I., Konkin, J.W., McGhee, W.P.T., and Kosick, R. 1965. Observations on foliage nutrient content of several coniferous tree species in British Columbia. For. Chron. 41: 222-236.

Bella, I.E. 1978. Fertilizing after thinning 70-year-old lodgepole pine (Pinus contorta Dougl. var latifolia Engelm.) in Alberta. Can. For. Serv., Ottawa. Bi-mon Res. Notes 34: 22-23.

Birk, E.M., and Simpson, R.W. 1980. Steady state and the continuous input model of litter accumulation and decomposition in Australian eucalypt forests. Ecology 61: 481-485.

Birk, E.M., and Vitousek, P.M. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. Ecology 67 69-79.

Boddy, L., and Swift, M.J. 1983. Wood decomposition in an abandoned beech and oak coppiced woodland in S.E. England. 1. Patterns of wood-litterfall. Holarctic Ecol. 6: 320-332.

Bray, J.R., and Gorham, E. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2: 101-157.

Bringmark, L. 1980. Ion leaching through a podsol in a Scots pine stand. In Structure and Function of Northern Coniferous Forests. Edited by T. Persson. Ecol. Bull. (Stockholm) 32: 341-362

Broadbent, F.E. 1965. Effect of fertilizer nitrogen on the release of soil nitrogen. Soil Sci. Soc. Amer. Proc. 29: 692-696.

Chapin, F.S. III, and Kedrowski, R.A. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64: 376-391.

Chapin, F.S., Oechel, W.C., Van Cleve, K. and Lawrence, W. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. Oecologia 74: 310-315.

Chapin, F.S. III, Vitousek, P.M., and Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. Amer. Natur. 127: 48-58.

Christensen, O. 1975. Wood litterfall in relation to abscission, environmental factors, and the decomposition cycle in a Danish oak forest. Oikos 26: 187-195.

Cochran, P.H., Youngberg, C.T., Steinbrenner, E.C., and Webster,S.R. 1979. Response of ponderosa pine and lodgepole pine to fertilization. In Proc. Forest Fertilization Conference. Edited by S.P. Gessel, R.M. Kenady, and W.A. Atkinson. Univ. Washington, Institute of Forest Resources. Contribution No. 40. pp. 89-94.

Crossley, D.I. 1951. The soils on the Kananaskis Forest Experiment Station in the subalpine forest region in Alberta. Silviculture Research Note No. 100. Forestry Branch, Canada Department of Resources and Development, Ottawa. 32 pp.

Day, R. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. Ecology 53: 472-478.

DeByle, N.V. 1980. Harvesting and site treatment influences on the nutrient status of lodgepole pine forests in western Wyoming. In Environmental consequences of timber harvesting. USDA Forest Service Gen. Tech. Rep. INT-80, Ogden, Utah.

Dennis, J.G. 1970. Aboveground accretion of vegetation and reproductive structures in an aspen understory vegetation in southwestern Alberta. Abstr. Bull. Ecol. Soc. Amer. 51: 31.

Eno, C.F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci. Soc. Amer. Proc. 24: 277-299.

Fahey, T.J. 1983. Nutrient dynamics of above-ground detritus in lodgepole pine (Pinus contorta ssp. latifolia) ecosytems, southeastern Wyoming. Ecol. Monogr. 53: 51-72.

Fahey, T.J., Yavitt, J.B., Pearson, J.A., and Knight, D.H. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. Biogeochemistry 1: 257-276.

Fessenden, R.J., Calvert, R.F., and Armson, K.A. 1971. Effect of some fertilizers and simazine on the activity of the micro-organisms in jack pine humus. For. Chron. 47: 227-228.

Flanagan, P.W. 1986. Substrate quality influences on microbial activity and nutrient availability in the taiga forest floors. In Forest Ecosystems in the Alaskan Taiga. Edited by K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck and C.T. Dyrness. Ecological Studies 57. Springer-Verlag, New York. pp. 138-151.

Flanagan, P.W. and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Can. J. For. Res. 13: 795-817.

Foster, N.W. 1974. Annual macroelement transfer from Pinus banksiana Lamb. forest to soil. Can. J. For. Res. 4: 470-476.

Foster, N.W., Beauchamp, E.G. and Corke, C.T. 1980a. Microbial activity in a Pinus banksiana Lamb. forest floor amended with nitrogen and carbon. Can. J. Soil Sci. 60: 199-209.

Foster, N.W., Beauchamp, E.G., and Corke, C.T. 1980b. The influence of soil moisture on urea hydrolysis and microbial respiration in jack pine humus. Can. J. Soil Sci. 60: 675-684.

Foster, N.W., Beauchamp, E.G. and Corke, C.T. 1985. Reactionsof ^{15}N-labelled urea with jack pine forest floor materials. Soil Biol. Biochem. 17: 699-704.

Foster, N.W., and Morrison, I.K. 1976. Distribution and cycling of nutrients in a natural Pinus banksiana ecosytem. Ecology 57: 110-120.

Fyles, J.W., La Roi, G.H. and Ellis, R.A. 1986. Litter production in Pinus banksiana dominated stands in northern Alberta. Can. J. For. Res. 16: 772-777.

Gardner, J.S., Smith, D.J., and Desloges, J.R. 1983. The Dynamic Geomorphology of the Mt. Rae Area: A high mountain region in southwestern Alberta. University of Waterloo, Department of Geography Publ. Series No. 19, Waterloo, Ontario

Gordon, A.G. 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. In Resources and Dynamics of the Boreal Zone. Edited by R.W. Wein, R.R. Riewe and I.R. Methven. Association of Canadian Universities for Northern Studies, Ottawa. pp. 97-118.

Gosz, J.R. 1984. Biological factors influencing nutrient supply in soil. In Nutrition of Plantation Forests. Edited by G.D. Bowen and N.K.S. Nambiar. Academic Press, London, pp. 119-146.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, Jr., K., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosytems. Adv. Ecol. Res. 15: 133-302.

Harris, A.S. and Farr, W.A. 1979. Response of western hemlock and sitka spruce to fertilization in southeastern Alaska. In Proc. Forest Fertilization Conference. Edited by S.P. Gessel, R.M. Kenady, and W.A. Atkinson. Univ. Washington Institute of Forest Resources. Contribution No. 40. pp. 78-81.

Harvey, A.E., Larsen, M.J., and Jurgensen, M.F. 1981. Rate of woody residue incorporation into northern Rocky Mountain forest soils. USDA Forest Service Research Paper INT-282.

Haynes, R.J. 1986. Mineral Nitrogen in the Plant-Soil System. Academic Press, Toronto.

Jenkinson, D.S., Fox, R.H., and Rayner, J.H. 1985. Interactions between fertilizer nitrogen and soil nitrogen - the so called "priming effect". J. Soil Sci. 36: 425-444.

Johnson, E.A. 1987. Fire Frequency in the Kananaskis River Watershed. Final Report to Alberta Environmental Research Trust, Calgary, Alberta.

Johnstone, W.D. 1971. Total standing crop and tree component distributions in three stands of 100-year-old lodgepole pine. In Forest Biomass Studies. Edited by I.U.F.R.O. Working Group for Forest Biomass Studies, Sec. 25, Growth and Yield. Life Sci. Agr. Exp. Sta., University of Maine, Orono. pp. 81-89.

Jurgensen, M.F., Larsen, M.J., Graham, R.J. and Harvey, A.E. 1987. Nitrogen fixation in woody residue of northern Rocky Mountain conifer forests. Can. J. For. Res. 17: 1283-1288.

Karkanis, P.G. 1972. Soils of the Kananaskis Valley. Kananaskis Centre for Environmental Research Res. Rep. No. 1. The University of Calgary, Calgary, Alberta.

Keays, J.L. 1971. Complete-Tree Utilization. An analysis of the literature. Part 2: Foliage. Inf. Rep. VP-X-70. Forintek Canada Corp. Vancouver, B.C.

Keeney, D.R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. Forest Sci. 26: 159-171.

Kelly, J.M. and Henderson, G.S. 1978. Nutrient flux in litter and surface soil after nitrogen and phosphorus fertilization. Soil Sci. Soc. Amer. J. 42: 963-966.

Kiilsgaard, C.W., Greene, S.E., and Stafford, S.G. 1987. Nutrient concentrations in litterfall from some western conifers with special reference to calcium. Plant Soil 102: 223-228.

Kimmins, J.P. 1974. Nutrient Removal Associated with Whole-Tree Logging on Two Different Sites in the Prince George Forest District. Final Report submitted to British Columbia Forest Service Producitivity Committee.

Kimmins, J.P., Binkley, D., Chatarpaul, L., and de Catanzaro, J. 1985. Biogeochemistry of Temperate Forest Ecosystems: Literature on inventories and dynamics of biomass and nutrients. Can. For. Serv. Inf. Rep. PI-X-473/F.

Kost, J.A., and Boerner, R.E.J. 1985. Foliar nutrient dynamics and nutrient use efficiency in Cornus florida. Oecologia 66: 602-606.

Landis, T.D., and Mogren, E.W. 1975. Tree strata biomass of subalpine spruce-fir stands in southwestern Colorado. For. Sci. 21: 9-12.

Lang, G.E. 1985. Forest turnover and the dynamics of bole wood litter in a subalpine balsam fir forest. Can. J. For. Res. 15: 262-268.

Lieth, H. 1975. Primary production of the major vegetation units of the world. In Primary Productivity of the Biosphere. Edited by H. Lieth and R.H. Whittaker. Springer-Verlag, New York. pp. 203-215.

Lowther, J.R. 1980. Use of a single sulphuric acid-hydrogen peroxide digest for the analysis of Pinus radiata needles. Commun. Soil Sci. Plant Anal. 11: 175-188.

MacLean, D.A., and Wein, R.W. 1978. Litter production in forest floor nutrient dynamics in pine and hardwood stands of New Brunswick, Canada. Holarctic Ecol. 1: 1-15.

Mahendrappa, M.K. 1978. Changes in the organic layers under a black spruce sand fertilized with urea and triple superphosphate. Can. J. For. Res. 8: 237-242.

Mahendrappa, M.K., Foster, N.W., Weetman, G.F., and Krause, H.H. 1986. Nutrient cycling and availability in forest soils. Can. J. Soil Sci. 66: 547-572.

Marks, P.L. and Bormann, F.H. 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176: 914-915.

Marschner, H. 1986. Mineral Nutrition of Higher Plants. Academic Press, Toronto.

McIntosh, R. 1982. Effect of different forms and rates of nitrogen fertilizer on the growth of lodgepole pine. Forestry 55: 61-68.

McKeague, J.A. (editor). 1978. Manual on Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Ottawa.

McLaughlin, R.A., Pope, P.E., and Hansen, E.A. 1985. Nitrogen fertilization and ground cover in a hybrid poplar plantation: effects on nitrate leaching. J. Environm. Qual. 14: 241-245.

Mead, D.J. 1984. Diagnosis of nutrient deficiencies in plantations. In Nutrition of Planation Forests. Edited by G.D. Bowen and E.K.S. Nambiar. Academic Press, London. pp. 259-291.

Mead, D.J. and Pritchett, W.L. 1975. Fertilizer movement in a slash pine ecosystem. II. N distribution after two growing seasons. I. Uptake of N and P and N movement in the soil. Plant and Soil 43: 567-578.

Mengel, K. and Kirkby, E.A. 1982. Principles of Plant Nutrition. 3rd Ed. International Potash Inst., Bern, Switzerland.

Miller, H.G. 1981. Forest fertilization: some guiding concepts. Forestry 54: 157-167.

Miller, H.G. 1984. Dynamics of nutrient cycling in plantation ecosytems. In Nutrition of Plantation Forests. Edited by G.D. Bowen, and E.K.S. Nambiar. Academic Press, London. pp. 53-78.

Miller, H.G., Cooper, J.M., Miller, J.D., and Pauline O.J.L. 1979. Nutrient cycles in pine and their adaptation to poor soils. Can. J. For. Res. 9: 19-26.

Miller, H.G. and Miller, J.D. 1976a. Effect of nitrogen supply on net primary production in Corsican pine. J. Appl. Ecol. 13: 249-256.

Miller, H.G. and Miller, J.D. 1976b. Analysis of needle fall as a means of assessing nitrogen status in pine. Forestry 49: 57-61.

Mohren, G.M.J., van den Burg, J., and Burger, F.W. 1986. Phosphorus deficiency induced by nitrogen input in Douglas fir in the Netherlands. Plant and Soil 95: 191-200.

Moir, W.H. 1972. Litter, foliage, branch and stem production in contrasting lodgepole pine habitats of the Colorado Front Range. In Research on Coniferous Forest Ecosystems Edited by J.F. Franklin, L.D Dempster and R.H. Waring. US Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. pp. 189-198.

Moir, W.H., and Grier, H. 1969. Weight and nitrogen phosphorus, potassium, and calcium content of forest floor humus of lodgepole pine stands in Colorado. Soil Sci. Soc. Amer. Proc. 33: 137-140.

Morrison, I.K. 1974a. Mineral nutrient of conifers with special reference to nutrient status interpretation: a review of literature. Canadian Forest Service Pub. No. 1343.

Morrison, I.K. 1974b. Dry-matter and element content of roots of several natural stands of Pinus banksiana Lamb. in northern Ontario. Can. J. For. Res. 4: 61-64.

Morrow, L.D. and Timmer. V.R. 1981. Intraseasonal growth and nutrient composition of jack pine needles following fertilization. Can. J. For. Res. 11: 696-702.

Moss, E.H. 1983. Flora of Alberta. Second Ed. Revised by J.G. Packer. Univ. Toronto Press, Toronto.

Nambiar, E.K.S., and Bowen, G.D. 1986. Uptake, distribution and retranslocation of nitrogen by Pinus radiata from ^{15}N labelled fertilizer applied to podzolized sandy soil. For. Ecol. Managem. 15: 269-284.

Neilson, W.A., Davis, G.R., McDavitt, J.F., and Pataczek, W. 1984. Growth and nutrient uptake of Pinus radiata seedlings over the first 3 years following treatment with nitrogen and phosphorus fertilizers. Austr. For. Res. 14: 1-10.

Oconnell, A.M. 1987. Litter decomposition, soil respiration and soil chemical and biochemical properties at three contrasting sites in Karri (Eucalyptus diversicolor Maell, F.) forests of south-western Australia. Austr. J. Ecol. 12: 31-40.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

Olson, J.S. 1975. Productivity of forest ecosytems. In Productivity of World Ecosystems. Edited by D.E. Reichle, J.F. Franklin and D.W. Goodall. National Academy of Sciences, Washington, D.C. pp. 33-43.

Otchere-Boateng, J., and Ballard, T.M. 1978. Urea fertilizer effects on dissolved nutrient concentrations in some forest soils. Soil Sci. Soc. Amer. J. 42: 41-54.

Overrein, L.N. 1967. Immobilization and mineralization of tracer nitrogen in forest raw humus. 1. Effect of temperature on the interchange of nitrogen after addition of urea-, ammonium-, and nitrate-N^{15}. Plant and Soil 27: 1-19.

Page, A.L., Miller, R.H., and Keeney, D.R. 1982. Methods of Soil Analysis. Part 2 - Chemical and Microbiological Properties. Agronomy No. 9, Second Ed., Soil Science Society of America Inc., Madison, Wisconsin.

Parker, A.J. and K.C. Parker. 1983. Comparative successional roles of trembling aspen and lodgepole pine in the southern Rocky Mountains. Great Basin Natur. 43: 447-455.

Pearson, J.A., Fahey, T.J., and Knight, D.H. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can. J. For. Res. 14: 259-265.

Pearson, J.A., Knight, D.H., and Fahey, T.J. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology 68: 1966-1973.

Peet, R.K. 1988. Forests of the Rocky Mountains. In: North American Terrestrial Vegetation. Edited by M.G. Barbour and W.D. Billings. Cambridge Univ. Press, New York. pp. 63-101.

Powers, R.F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. Soil Sci. Soc. Amer. J. 44: 1314-1320.

Powers, R.F. 1984. Estimating soil nitrogen availability through soil and foliar analysis. In Forest Soils and Treatment Impacts. Proc. 6th North American Soils Conference. Edited by E.L. Stone. Univ. Tennessee, Knoxville. pp. 353-379.

Prescott, C.E., and Parkinson, D. 1985. Effects of sulphur pollution on rates of litter decomposition in a pine forest. Can. J. Bot. 63: 1436-1443.

Purchase, B.S. 1974. The influence of phosphate deficiency on nitrification. Plant and Soil 41: 541-547.

Reid, C.P.P., Odegard, G.J., Hokenstrom, J.C., McConnell, W.J., and Frayer, W.E. 1976. Effects of clearcutting on nutrient cycling in lodgepole pine forests. Final Report on U.S. Forest Service Grants 16-256-GR and 16-324-6R. Rocky Mountain Forest and Range Experimental Station, Fort Collins, Colorado.

Reiners, W.A. 1986. Complementary models for ecosystems. Amer. Natur. 127: 59-73.

SPSS Inc. 1986. SPSS^{X} User's Guide. 2nd ed., McGraw-Hill, Toronto.

Salonius, P.O. 1972. Microbiological response to fertilizer treatments in organic forest soils. Soil Sci. 114: 12-19.

Scanlin, D.C. and H. Loewenstein. 1979. Response of inland Douglas fir and grand fir to thinning and nitrogen fertilization in northern Idaho. In: S.P. Gessel, R.M. Kenady and W.A. Atkinson (eds). Forest Fertilization Conference. University of Washington College of Forest Research, Seattle.

Singh, T. 1982. Biomass equations for ten major tree species of the prairie provinces. Can. For. Serv. Inf. Rep. NOR-X-242.

Söderström, B., Baath, E., and Lundgren, B. 1983. Decrease in soil microbial activity and biomasses owing to nitrogen amendments. Can. J. Microbiol. 29: 1500-1506.

Stachurski, A., and Zimka, J.R. 1975. Methods of studying forest ecosytems: leaf area, leaf production and withdrawal of nutrients from leaves of trees. Ekol. Polska 23: 637-648.

Stalker, A. MacS. 1973. Surficial Geology of the Kananaskis Research Forest and Marmot Creek Basin Region of Alberta. Geological Survey of Canada, Ottawa.

Stark, N. 1983. The nutrient content of Rocky Mountain conifers: A handbook for estimating nutrients lost through harvest and burning. Montana Forest and Conserv. Expt. Stn. Misc. Pub. No. 14.

Stevenson, F.J. 1986. Cycles of Soil. Carbon, nitrogen, phosphorus, sulfur, micronutrients. Wiley and Sons, Toronto.

Strong, W. and Leggat, K.R. 1981. Ecoregions of Alberta. Department of Energy Mines and Natural Resources, Ottawa.

Swift, M.J., Heal, O.W., and Anderson, J.M. 1979. Decomposition in Terrestrial Ecosystems. Univ. California Press, Los Angeles.

Tamm, C.O. 1968. An attempt to assess the optimum nitrogen level in Norway spruce under field conditions. Studia Forestalia Suecica Nr. 61.

Tappeiner, J.C., and Alm, A.A. 1975. Undergrowth vegetation effects on the nutrient content of litterfall on soils in red pine and birch stands in northern Minnesota. Ecology 56: 1193-1200.

Technicon Instruments. 1976. Ortho-phosphate in water and waste water. Industrial Method No. 94-70W/B. Technicon Industrial Systems, Tarrytown, New York.

Technicon Instruments. 1977. Ammonia in water and waste water. Industrial Method No. 98-70W/A. Technicon Industrial Systems, Tarrytown, New York.

Technicon Instruments. 1978. Nitrate and nitrite in water and wastewater. Industrial Method No. 100-70W/B. Technicon Industrial Systems, Tarrytown, New York.

Timmer, V.R. and Morrow, L.D. 1984. Predicting fertilizer growth response and nutrient status of jack pine by foliar diagnosis. In Forest Soils and Treatment Impacts. Proc. 6th North American Soils Conference. Edited by E.L. Stone. Univ. Tennessee, Knoxville. pp. 335-351.

Tritton, L.M. 1980. Dead wood in the northern hardwood forest ecosytem. Ph.D. dissertation, Yale University, New Haven, Connecticut.

Turner, J. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. For. Sci. 23: 307-316.

Turner, J. 1979. Effects of fertilization on understory vegetation. In Proc. Forest Fertilization Conference. Edited by S.P. Gessel, R.M. Kenady, and W.A. Atkinson. Univ. Washington, Inst. Forest Resources. Contribution No. 40.

Turner, J., Johnson, D.W., and Lambert, M. 1980. Sulphur cycling in a Douglas-fir forest and its modification by nitrogen applications. Acta Oecol. 1: 27-35.

Van Cleve, K. and Moore, T.A. 1978. Cumulative effects of nitrogen, phosphorus, and potassium fertilizer additions on soil respiration, pH, and organic matter content. Soil Sci. Soc. Amer. J. 42: 121-124.

Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosytems. Can. J. For. Res. 13: 747-766.

van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40: 347-394.

van den Driessche, R. 1984. Nutrient storage, retranslocation and relationship of stress to nutrition. In Nutrition of Plantation Forests. Edited by G.D. Bowen and E.K.S. Nambiar. Academic Press, London. pp. 181-209.

van den Driessche, R. and J.E. Webber. 1977. Variation in total and soluble nitrogen concentrations in response to fertilization of Douglas-fir. For. Sci. 23: 134-142.

Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. Ecology 67: 644-649.

Vitousek, P.M. 1981. Clear-cutting and the nitrogen cycle. In Terrestiral Nitrogen Cycles. Edited by F.E. Clark and T. Rosswall. Ecol. Bull. (Stockholm) 33: 631-642.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. Amer. Natur. 119: 553-572.

Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285-298.

Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M., Reiners, W.A., and Todd, R.L. 1979. Nitrate losses from disturbed ecosystems. Science 204: 469-474.

Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25: 376-381.

Vitousek, P.M. and Sanford, R.L., Jr. 1986. Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17: 137-167.

Vogt, K.A., Grier, C.C., Meier, C.E., and Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature Abies-Amabilis stands in western Washington, as affected by fine root input. Ecol. Monogr. 53: 139-158.

Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and below-ground detritus of world forests. Adv. Ecol. Res. 15: 303-377.

Waring, R.H., and W.H. Schlesinger. 1985. Forest Ecosytems: concepts and management. Academic Press, Toronto.

Weber, M.G. 1987. Decomposition, litterfall, and forest floor nutrient dynamics in relation to fire in eastern Ontario jack pine ecosystems. Can. J. For. Res. 17: 1496-1506.

Weetman, G.F. 1968. The nitrogen fertilization of three black spruce stands. Woodlands Paper No. 6, Pulp and Paper Res. Inst. Can.

Weetman, G.F., and R.M. Fournier. 1984. Ten year growth results of nitrogen source and interprovincial experiments on jack pine. Can. J. For. Res. 14: 424-430.

Wells, C.G., and Metz, L.J. 1963. Variation in nutrient content of loblolly pine needles with season, age, soil, and position on the crown. Soil Sci. Soc. Amer. Proc. 27: 90-93.

Westerman, R.L., and Kurtz, L.T. 1973. Priming effect of ^{15}N-labelled fertilizers on soil nitrogen in field experiments. Soil Sci. Soc. Amer. Proc. 37: 725-727.

Westerman, R.L., and Tucker, T.C. 1977. Effect of salts and salts plus nitrogen-15-labeled ammonium chloride on mineralization of soil nitrogen, nitrification, and immobilization. Soil Sci. Soc. Amer. Proc. 38: 602-605.

Wheeler, N.C., and Critchfield, W.B. 1985. The distribution and botanical characteristics of lodgepole pine: biogeographical and management implications. In Lodgepole Pine: the species and its management. Edited by D.M. Baumgartner, R.G. Krebill, J.T. Arnott and G.F. Weetman. Washington State University, Pullman, Washington.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45: 229-299.

Witkamp, M., and Olson, J.S. 1963. Breakdown of confined anc nonconfined oak litter. Oikos 14: 138-147.

Will, G.M., and Youngberg, C.T. 1978. Sulfur status of some central Oregon pumice soils. Soil Sci. Soc. Amer. J. 42): 132-134.

Yang, R.C. 1985a. Ten year growth response of 70-year-old lodgepole pine to fertilization in Alberta. Can. For. Serv. Info. Rep. NOR-X-266. Edmonton, Alberta.

Yang, R.C. 1985b. Effects of fertilization on growth of 30-year-old lodgepole pine in west-central Alberta. Can. For. Serv. Info. Rep. NOR-X-268. Edmonton, Alberta.

Yarie, J., and Van Cleve, K. 1983. Biomass and productivity of white spruce stands in interior Alaska. Can. J. For. Res. 13 767-772.