FOREST NUTRIENT CYCLING IN A NORTH IDAHO CONIFER STAND

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DISSERTATION

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ABSTRACT

Overstory, understory, forest floor and soil elemental contents and litterfall flows of all macronutrients and most micronutrients and aluminum were measured during one growing season in a north Idaho conifer stand. These data were analyzed for differences which might explain past variation in fertilization response. The first phase of the study involved the examination of soil nutrient availability as measured by ion exchange resins. Goals were to detect possible causes of variation in past fertilization response, to develop an improved understanding of seasonal nutrient dynamics, and to examine changes in soil nutrient availability throughout the soil profile. Using ion-exchange resins, differences in elemental availability were detected by experimental block, as well as with soil depth and throughout the growing season. Results were discussed in light of findings by other researchers and used to help explain possible reasons for past variation in forest fertilization response. Soil nutrient availability was also compared to tree nutrient uptake throughout the growing season using graphical interpretation, and correlation analysis was performed between Douglas-fir foliar nutrient concentrations and ioin-exchange nutrient availabilitiy. Several interesting findings regarding interpretation of ion-exchange data in light of tree nutrient uptake were discussed. During the second phase of this study, differences in macronutrient, micronutrient and aluminum contents of various forest ecosystem components were analyzed and evaluated during one growing season. Block differences in overstory and litterfall contents that may help explain past fertilization response at this site are discussed. Needle attributes of overstory trees showed significant differences by species, crown class, crown position, foliar age class and sampling date. Foliar weight varied with the degree of foliage exposure to sunlight, and elemental foliar contents generally followed the same pattern. Understory vegetation showed significant nutrient content differences between growth forms and during the growing season for several elements. Litterfall dry weight and elemental contents showed seasonal variation, and forest floor content of most elements was within expected ranges. The final phase of this study entailed the compilation of overstory, understory, forest floor and soil elemental contents and litterfall flows into a systems analysis model, which was then projected over a three-year period. Model simulations were performed for three species composition scenarios, including pure grand fir, pure Douglas-fir and mixed conifer. For all species simulations, model components and flows were examined, and both seasonal and annual behavior were evaluated in biological and mechanistic terms. Significant differences in overstory elemental content and related flows were revealed through simulation of various species compositions. Overall, systems analysis was a useful tool for evaluating forest elemental cycling, and provided a better understanding of seasonal and short-term nutrient dynamics and component interactions of our experimental stand. Suggestions for future research are discussed in light of these findings.

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DEDICATION

In loving memory of my father, Edward William Garrison (March 8, 1928-May 28, 2003), for inspiring my love of the outdoors and my career in forestry. Thanks, Dad!

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INTRODUCTION

Forest ecosystem pools and flows of most nutrient elements and aluminum were monitored over the course of one growing season during this study of forest nutrient cycling in a north Idaho conifer stand. The site selected was part of a region-wide set of fertilization trials that were established in numerous Douglas-fir stands throughout the Inland Northwest during the early 1980's. Region-wide fertilization response was generally associated with parent material and vegetation series, however some unexplained variation occurred, though the precise mechanisms responsible for this variation were unclear. A detailed study of the nutrient dynamics of the forest ecosystem components of the Mallory Creek test site in north Idaho was carried out in an effort to detect possible causes of past variation in fertilization response, as well as to develop an improved understanding of seasonal nutrient dynamics. These data were then evaluated both seasonally and over a three-year period using a systems analysis model of forest ecosystem elemental cycling.

Soil elemental pools were the most difficult to measure, due in large part to the inadequacy of standard chemical analyses for forest soil nutrient evaluation. In Chapter I of this document, soil elemental availability over time is examined throughout the soil profile and between experimental blocks using ion-exchange resins. Other researchers have successfully detected spatial and temporal changes in forest soil nutrient availability using ion-exchange resins, and during this study this technology was evaluated for possible use in forest nutrient cycling modeling. Ion-exchange resins were evaluated for their use in detecting nutritional differences which might explain past variation in forest fertilization response, as well as for detection of seasonal variation in soil nutrient availability and changes with soil depth. In addition, comparative analyses of plant tissue chemistry and soil ion-exchange nutrient availability over time were performed, and provided a useful and innovative means of evaluating soil ion-exchange resins for assessment of vegetation nutrient status.

In Chapter II, overstory and understory vegetation, forest floor and litterfall nutrient contents are examined in detail. Tree foliage of the two major species on the site, Douglas-fir and grand fir, was evaluated for elemental content. This analysis provides useful insights into seasonal elemental retranslocation, and highlights the importance of sampling from the major species and crown classes present on a site, as well as sampling different foliage age classes at various points in the crown. Understory vegetation was a minor component of total nutrient pools at the experimental site, however seasonal measurements of different growth forms could be important when modeling nutrient cycling over the course of stand development or following forest stand manipulations.

While the first two chapters focus on the biological implications of seasonal elemental dynamics, Chapter III primarily focuses on the mechanistic implications of incorporating the collected data into a stand-level systems analysis model. A generalized model was developed and projected over a three-year period for each element measured at the experimental site. Model projections were performed for three different stand species composition scenarios, including the actual mixed conifer composition of the site, and simulated pure grand fir and pure Douglas-fir stands. Results of the various species composition scenarios were compared and evaluated for effects on overstory and related model components. The systems analysis approach worked well for describing elemental pools and flows, and the use of this model highlighted the strengths and weaknesses of field data collection procedures.

This study should provide a basis for future development of long-term forest elemental cycling models. Such models will be useful and necessary for understanding the interactions of various nutrient pools in response to overstory manipulations such as harvest or prescribed fire. Suggestions for model modifications to accommodate such predictions are also discussed.

Forest nutrient cycling in a north Idaho conifer stand I: Soil nutrient availability as measured by ion-exchange resins

Abstract. A detailed study of the nutrient dynamics of above- and below- ground components of a forest ecosystem in a north Idaho conifer stand was undertaken, including assessment by soil ion-exchange resins. The goals were to determine whether ion-exchange resins could be used to detect differences between experimental blocks which might explain past variation in forest fertilization response, as well as evaluate whether resins could be used *in situ* to detect seasonal nutrient availability changes or changes with soil depth. A graphical comparison of above-ground vegetation nutrient contents during the growing season with soil ion-exchange data was also performed, as well as a correlation analysis of tree foliage nutrient concentrations with soil ion-exchange data. Geochemical and petrographic analyses of rocks from two study blocks established during earlier fertilization trials did not reveal substantial differences which would explain past fertilization response. However, ion-exchange resin analysis indicated significantly lower NO_3^- in the upper horizons on the eastern block than on the western block, and a non-significant trend for greater S on the eastern block. Both factors could help explain that block's greater response to past N-fertilization. Soil ion-exchange resins were useful in detecting differences in soil nutrient availability by horizon for most elements. Nitrogen and K availability were greatest in the upper soil horizons, while Mg and B availability increased with depth. Phosphorus, Fe and Mn all showed greater availability in the Bw horizon than the other three horizons. Ion-exchange resins were also successful in detecting seasonal changes in soil nutrient availability. Nitrogen and the major cations generally decreased in availability throughout the growing season, while P, Fe and Mn availability remained constant early in the season, and then decreased later in the season. Soil S, B and Cu availability fluctuated throughout the season. Visual comparison of soil ion-exchange data with total above-ground nutrient quantities (kg ha^{-1}) revealed that while above-ground elemental contents always increased throughout the growing season, soil nutrient availability sometimes increased and sometimes decreased. Decreases in soil nutrient availability coincident with increasing vegetation nutrient contents during the growing season were likely indicative of nutrients under high demand and low supply. Thus N, K, Mg, Ca, S, Mn, Cu and B showed some potential as limiting nutrients during at least some portion of the growing season. Correlation analysis of Douglas-fir foliar chemical concentrations with soil ion-exchange data by horizon supported the contention that N and K were likely limiting nutrients throughout the growing season. Phosphorus, Mn and B were probably taken up by vegetation as they became soil-available, though not at rates which would deplete the short-term available soil pools of these elements. Correlations between soil ion-exchange availability and tree foliage chemical concentrations most often occurred in the Bw horizon, less often in the A and 2Bt horizons and rarely in the 2BC horizon. Other elements tested showed no correlation between soil and foliar chemistry, indicating that they were likely not in consistently limited supply throughout the growing season.

INTRODUCTION

Soils are an integral part of the forest nutritional environment. With the exception of nitrogen (N) and possibly sulfur (S) and boron (B), which are tied closely to organic matter cycling, most elements essential for plant growth are geologic in origin (Clayton, 1984;

Zabowski, 1990; Kolka et al., 1996). Nutrient availability to plants is tied to mineral weathering rates and is interrelated with physical and chemical properties of the soil. Evaluation of forest nutrient status requires some measure of this availability. However, most conventional soil tests were developed in conjunction with agricultural crops, and because they use various chemical reagents to mimic nutrient uptake for various soil types and crops, they often do not adequately portray forest soil nutrient availability (Powers, 1980; Peterson et al., 1984; Ballard and Carter, 1985). Several researchers have suggested that synthetic ion-exchange resins may provide a better test for plant-available nutrients in forest soils, compared to conventional soil tests (Olness and Rinke, 1994; Skogley and Dobermann, 1996a; van Raij, 1998).

The process of ion-exchange was first reported to occur in soils in the mid-1800's, and synthetic ion-exchange resins were first developed in 1935, and have been extensively developed and tested since that time (Amer et al., 1955; Arnold, 1958; Scott et al., 1960; Sibbesen, 1977; Smith, 1979; Binkley et al., 1986; Olness and Rinke, 1994; Skogley and Dobermann, 1996a; Huang and Schoenau, 1997; van Raij, 1998). Ion-exchange resins are typically comprised of a solid organic polymer with an electrostatic charge, which is neutralized by saturating the polymer with a weak ion of opposite charge prior to placement in soil (Skogley and Dobermann, 1996b; van Raij, 1998). Naturally-occurring ions in the soil then replace the weakly-held ions on the resin. Analysis of the ion-exchange resin typically involves extracting the adsorbed ions by placing the resin in either hydrochloric or nitric acid, and then analyzing the extract. Colorimetry is commonly used for ammonium (NH_4^+), nitrate (NO_3^-), potassium (K), phosphate and sulfate; acid molybdate blue for phosphate; and inductively-coupled plasma optical emission spectrometry (ICP) for phosphorus (P), K, S, calcium (Ca), magnesium (Mg), iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), B, cadmium (Cd) and lead (Pb).

In soil nutrition research, ion-exchange resins have predominantly been used for tests of soil P-availability (Amer et al., 1955; Smith, 1979; Huang and Schoenau, 1997; van Raij, 1998; Langlois et al., 2003). Nitrogen availability has also been widely tested using ion-exchange resins (Scott et al., 1960; Binkley et al., 1986; Lundell, 1989; Huang and Schoenau, 1997). Cation-exchange resins have sometimes been used to test for K release from clay minerals, as well as soil K-availability (Arnold, 1958; Schaff and Skogley, 1982; Rahmatullah and Mengel, 2000). Van Raij (1998) describes the various reactions governing resin-based ion-exchange for P, Mg, K and Ca, and hypothesizes that ion-exchange resins provide a good assessment of the labile form of various elements in the soil. Gibson (1986) also suggested that ion-exchange resins are suitable for field measurement of short-term nutrient availability. Langlois et al. (2003) utilized laboratory testing of various resin types to show that mixed-bed ion-exchange resins were better suited for tests of short-term P-availability than for short-term N-availability. Few studies have evaluated ion-exchange resins for detecting micronutrient availability, though one laboratory study tested the extraction of various macro- and micronutrients by both anion- and cation-exchange resins (Olness and Rinke, 1994).

Much of the ion-exchange research reported in the literature has been conducted under laboratory conditions (Dobermann et al., 1994 ; Schaff and Skogley, 1982; Skogley and Schaff, 1985; Yang et al., 1991; Olness and Rinke, 1994; Langlois et al., 2003). While laboratory testing is valuable for understanding the mechanisms of ion-exchange and comparison to conventional laboratory testing, it does not address the issue of on-site nutrient availability under field conditions. Various researchers have used ion-exchange resins *in situ* to demonstrate that field deployment of ion-exchange resins can provide a better assessment of site-specific nutrient availability than conventional soil tests (Smith, 1979; Hart and Binkley, 1985; Hart and Binkley, 1985; Binkley et al., 1986; Binkley et al., 1986; Krause and Ramial, 1987; Krause and Ramial, 1987; Lundell, 1989; Skogley and Dobermann, 1996b; Huang and Schoenau, 1997; van Raij, 1998). Most of these studies included only a few macronutrients, principally N, P, and K, and generally focused on changes in nutrient availability over time (Gibson, 1986; Krause and Ramial, 1987; Binkley et al., 1992; Huang and Schoenau, 1997). Few studies reported changes in nutrient availability with soil depth, and those typically focused only on the forest floor or upper 10 to 30 cm of soil (Binkley et al., 1986; Huang and Schoenau, 1996). Various researchers have successfully used ion-exchange resins *in situ* to detect experimental treatment effects on forested sites, including differences in species composition, fertilization treatments and harvesting regimes (Hart and Binkley, 1985; Gibson, 1986; Krause and Ramial, 1987; Binkley et al., 1992).

Soil ion-exchange resins may provide a valuable tool for evaluating forest sites for potential nutrient deficiencies because they can be used *in situ* on all soil types and plant cover types. Clarification of the relationship between soil ion-exchange measurements and plant nutritional status is an important component of this research. Several researchers have demonstrated correlations between ion-exchange data and plant foliar nutrient levels, while corresponding conventional soil test data often showed no such correlations (Smith, 1979; Binkley et al., 1986; Skogley and Dobermann, 1996b; Rahmatullah and Mengel, 2000). Very little research has been performed which compares temporal changes in soil nutrient availability with corresponding temporal changes in above-ground vegetation chemistry.

Such comparisons would provide valuable insight into the capability of ion-exchange resins to represent changes in short-term soil nutrient availability related to above-ground vegetation dynamics.

Previous studies have demonstrated the capability of ion-exchange resins to detect temporal and limited depth-related changes in soil availability of various macronutrients in agricultural, pastoral and some forested settings. Several studies provide evidence that ion-exchange resins can detect the effects of fertilization, harvesting, or vegetative composition on soil nutrient availability. Some studies provide evidence of correlations between soil ion-exchange data and plant foliar nutrient data, but few examine temporal changes in soil nutrient status with concurrent changes in vegetation nutrient content. Most ion-exchange resin studies examine only a few macronutrients, and rarely address micronutrients or non-nutritional elements. In this study, the following research questions were addressed for macro- and micronutrients, and Al on a mixed-conifer forested site in northern Idaho:

a) Can ion-exchange resins be used *in situ* to detect past forest fertilization treatment differences?

b) Can ion-exchange resins be used *in situ* to detect changes in nutrient availability throughout the soil profile?

c) Can ion-exchange resins be used *in situ* to detect seasonal changes in soil nutrient availability?

d) How do temporal changes in soil nutrient availability measured by *in situ* ion-exchange resins relate to temporal changes in above-ground vegetation chemical content?

e) Is there a correlation between ion-exchange resin data and above-ground plant tissue chemical concentration data?

MATERIALS AND METHODS

Site Selection

During the early 1980's, fertilization trials were established in numerous Douglas-fir stands throughout the Inland Northwest in order to determine which site characteristics might be associated with various levels of fertilization response (Moore et al., 1991; Mika and VanderPloeg, 1991; Shen et al., 2000). While response was found to be associated with parent material and vegetation series, the precise mechanisms responsible for the variation in response were unclear. The selected study site was known as Mallory Creek, and had showed high within-site variability during the Douglas-fir fertilization trials. During those trials, the stand was treated as a split-plot design with the stand partitioned into two blocks, where each block received three fertilization treatments consisting of an unfertilized control, 224 kg ha^{-1} nitrogen and 448 kg ha^{-1} nitrogen. The two blocks were separated by a stream, with one block occurring on the east side of the creek and the other occurring on the west. Six years following fertilization, the block on the eastern side showed the strongest response to nitrogen fertilization, with gross volume growth responses of 22% and 11% to the 224 kg and 448 kg N treatments, respectively (Mika and VanderPloeg, 1991; IFTNC, 1993). The western block showed 15% and 12% responses to the same treatments. These results indicated that the 224 kg treatment did address a nitrogen deficiency on both blocks, and that the deficiency was greater on the eastern block. Differences in soil nutrient status and/or parent materials were hypothesized as being responsible for the difference in fertilization response between the two blocks at the 224 kg ha^{-1} treatment level.

Site Characteristics

The Mallory Creek study site was located 14 miles northeast of Bovill, Idaho in the Inland Northwest of the United States, with latitude approximately 46° 50' and latitude 116° 16', Boise meridian. The elevation was approximately 1036 m. The study stand was approximately 50 ha in area, and located on generally southern-facing, slightly undulating hillslopes, with aspects ranging between 170 and 230°, and slopes ranging from 15 to 25%. Average annual precipitation between 1971 and 2000 was approximately 92 cm yr^{-1}, based on weather station data from nearby Elk River, Idaho (ISCS, 2003). Precipitation during 1999, the year of this study, measured slightly higher than normal at the Elk River weather station, with rainfall averaging 98 cm yr^{-1}. Weather station estimates of precipitation between June and September totaled about 13 cm, and on-site rain gauges at the Mallory Creek site also measured approximately 13 cm of precipitation during the study period. Air temperatures between 1971 and 2000 at Elk River ranged from –0.2 to 13.2° C, with a mean of 6.6°C (ISCS, 2003). During 1999, Elk River air temperatures averaged 6 °C , and ranged from a minimum of 0 °C to a maximum of 12 °C. From June through August of 1999, the mean air temperature at Elk River was 16 °C, with a minimum of 7 °C and a maximum of 24. Air temperatures measured at the Mallory Creek study site during the 1999 study period were normal, ranging from 3 °C to 28 °C, and averaging 16 °C.

The study stand was approximately 50 years old at the time of the current study, and no management activities had occurred on the site since the mid-1970's. Approximate quadratic mean diameter of the unfertilized portion of the stand in 1999 was 26 cm, site height was 20 m, and gross volume was approximately 357 m^3 ha^{-1} (IFTNC, 1993). Total basal area was estimated to be 44 m^2 ha^{-1}, consisting of 85% Douglas-fir (*Pseudotsuga menziesii*), 10% grand fir (*Abies grandis*), 2% western redcedar (*Thuja plicata*), 2% western white pine (*Pinus monticola*) and 1% western larch (*Larix occidentalis*). The understory consisted primarily of common snowberry (*Symphorocarpus albus*), western goldthread (*Coptis occidentalis*) and bunchberry dogwood (*Cornus canadensis*). The habitat type was identified as cedar-ginger (*Thuja plicata-Asarum caudatum*) (Cooper et al., 1991).

Sampling Procedures

The blocking scheme of the 1982 fertilization trials was observed during the current study. The two established blocks occurred on opposite sides of a tributary stream. Since streams often occur at geologic boundaries, geology was examined on either side of the stream to detect possible differences that might explain the variation in fertilization response. Rock samples were collected for geochemical and petrographic analyses. Due to the very deep weathering characteristics of the schist, fresh rock samples were not available, and only weathered schists taken from the 2C horizon of the soil pits were sampled. Samples of the quartz monzodiorite material were taken from soil pits and from outcrops. Whole-rock geochemical analysis was performed using X-ray fluorescence (Hooper et al., 1993). A polarizing light microscope was used to describe mineral composition of thin sections of both rock types (Nesse, 1991).

Soil pits were established at six locations across the site, with three pits located on each block. Pit locations were otherwise randomly selected, with the restriction that all pits occur on the same elevational contour, and that they were located at least 15 m away from old fertilization test plots. Each soil pit was described following standard procedures (Schoeneberger et al., 1998). Samples were collected from each horizon for bulk density measurement and composited for standard laboratory testing. Available P and K were tested using sodium acetate extraction, while NH_4^+ and NO_3^- were analyzed using 2M KCl extraction with analysis by colorimetry (Case and Thyssen, 1996a; Case and Thyssen, 1996d). Sulfate-sulfur was analyzed by calcium phosphate extraction and ion chromatography, and B was analyzed by calcium chloride extraction and spectrophotometric determination (Case, 1996; Case and Thyssen, 1996c). Extractable calcium (Ca), magnesium (Mg) and K were analyzed by 1N ammonium acetate extraction and inductively coupled plasma spectrometry (ICP), and micronutrients copper (Cu), zinc (Zn), manganese (Mn) and iron (Fe) by DTPA (Case and Thyssen, 1996b; Case and Thyssen, 2000).

Soil mineralogy was examined on samples from the Bw and 2BC horizons on each block. Particle-size differentiation was performed using a centrifuge technique to separate the clays, and sieve techniques to separate the silt and sand fractions. The clays were analyzed using X-ray diffraction (Whittig and Allardice, 1986), while grain mounts of the fine sands were examined under a polarizing light microscope to identify the mineralogy of the larger particles (Nesse, 1991). Selective dissolution procedures were performed on the same samples in order to quantify organic matter complexes and short-range order minerals.

Soil nutrient availability was estimated throughout the soil profile and over time using PRS™ ion-exchange resin probes. Each PRS™-probe consisted of an anion-exchange membrane (BDH product no. 55164) or a cation-exchange membrane (BDH product no. 55165) enclosed in a plastic frame measuring 15.2 x 2.8 x 0.5 cm, and tapered on one end for insertion into the soil (Huang and Schoenau, 1997). In this study, one ion-exchange resin unit consisted of two PRS™-probes, including one cation-exchange probe and one anion-exchange probe. Twelve pairs of membranes were placed in each soil pit, with three pairs each in the A, Bw, 2Bt and 2BC horizons. Every two weeks between June 12 and October 14, 1999, the membranes were removed and a new set placed in the same location, for a total of nine exchanges. The three pairs in each horizon were composited for analysis, and treated as a single observation. Due to excessive loss of soil from the slots following repeated replacements, the soil pit faces were cleaned and excavated back an additional 10 cm at the time of the fifth placement on August 5. The new set of membranes were placed in the same location from the top and sides of the pit as the previous set. The new slots were used through the conclusion of the study. At every replacement, soil temperature was measured with a thermometer. Soil volumetric water content was measured during the third through ninth periods using a hand-held time-domain reflectometry (TDR) device. Calibration of the TDR device was not performed and therefore the actual water content readings were suspect, however the general trends of increases and decreases in moisture were considered valid. During the entire study period, the open pits were lined with plastic and covered with plywood in order to slow temperature and moisture changes between sampling dates. After removal from the pits, the membranes were rinsed with triple-distilled water and sent to an outside laboratory, where the accumulated ions were extracted using weak (0.1M) hydrochloric acid. The extract was analyzed using colorimetry for ammonium and nitrate, and ICP for other ions. Results were calculated as total amount of ion extracted per resin membrane surface area, in units of $\mu g\ 10cm^{-2}$. Ions measured included N (as NO_3^- and NH_4^+), and various ionic forms of Ca, Mg, K, P, Fe, Mn, Cu, B, and S.

Comparison of above-ground nutrient contents with soil nutrient availability over the course of the growing season required periodic estimates of both vegetation and soil nutrient levels. Total above-ground nutrient content was estimated three times during the 1999 growing season, in kg ha^{-1}, using methods described in a companion paper (Garrison-Johnston, 2003). Only the tree portion of the above-ground vegetation was selected for comparison with soil values, because trees dominated the study site vegetation. Soil ion-exchange values were averaged across all six soil pits and four soil horizons for the same three time periods as foliar nutrient sampling occurred. Tree nutrient content was then visually compared to soil ion-exchange data across the growing season using line charts.

In addition to visual comparison of the nutrient content and soil ion-exchange data, a correlation analysis was performed between foliar nutrient concentrations and soil ion-exchange values. Douglas-fir was selected for correlation analysis because it was the dominant species in the study stand. Only trees from dominant/codominant crown classes were used for this analysis. The foliar nutrient concentrations of the last three age classes of needles from the upper crown were averaged for each block and collection date. Soil ion-exchange values were averaged by block, using the same three time periods as foliar nutrient sample collection. This resulted in six pairs of observations for each element tested, one from each of the three time periods and two experimental blocks. Soil ion-exchange values for the four soil horizons were retained separately in order to allow for correlation analysis by horizon.

DATA ANALYSIS

Geochemical and petrographic analyses of rock samples, and mineralogical and standard laboratory analyses of soils, were performed on composite samples from each study block. Because of the resultant small sample size, insufficient degrees of freedom were available to statistically test these data. Rather, the information was compiled and used to help explain soil ion-exchange results.

A split-plot design was selected for testing soil ion-exchange data for effects of time, horizon, and past treatment response (block). The soil ion-exchange data were analyzed following a split-plot factorial 2-4.8 design, with the three soil pits on each of the two blocks representing experimental units. The four horizons and eight time periods included in the analysis represented splits within each pit. Data from the fifth measurement period between August 5 and 19 were not included, as this time period was considered necessary to allow reestablishment of a diffusion zone around the resin membranes, following relocation of membranes within pits. Ions tested included NO_3^-, NH_4^+, and various ionic forms of Ca, Mg, K, P, Fe, Mn, Cu, B, and S. The data were analyzed multivariately using the following model equation:

$$Y_{ijkl} = \mu + \alpha_j + \pi_{i(j)} + \beta_k + (\alpha\beta)_{jk} + (\beta\pi)_{ki(j)} + \gamma_l + (\alpha\gamma)_{jl} + (\gamma\pi)_{li(j)} + (\beta\gamma)_{kl} + (\alpha\beta\gamma)_{jkl} + (\beta\gamma\pi)_{kli(j)} + \varepsilon_{ijkl} \quad (1)$$

Where: μ = population grand mean

α_j = effect of block (j=1..p and p=2 blocks)

$\pi_{i(j)}$ = effect of plot within block (i=1..n and n=3 plots within each block)

β_k = effect of time (k=1..q and q=8 time periods)

$(\alpha\beta)_{jk}$ = effect of block x time interaction

$(\beta\pi)_{ki(j)}$ = effect of time x plot(block) interaction

γ_l = effect of horizon (l=1..r and r=4 horizons)

$(\alpha\gamma)_{jl}$ = effect of block x horizon interaction

$(\gamma\pi)_{li(j)}$ = effect of horizon x plot(block) interaction

$(\beta\gamma)_{kl}$ = effect of time x horizon interaction

$(\alpha\beta\gamma)_{jkl}$ = effect of block x time x horizon interaction

$(\beta\gamma\pi)_{kli(j)}$ = effect of time x horizon x plot(block) interaction

ε_{ijkl} = residual error

All statistical analyses were performed using the Statistical Analysis System (SAS Institute Inc., 1990). Exploratory data analysis included testing for multivariate normality using a graphical test (Khattree and Naik, 1995). Homogeneity of variance was examined visually using side-by-side box plots, and then examined using the 'pool=test' option in SAS's Proc Discrim procedure. Initial tests indicated that the data were not normally distributed, therefore logarithmic transformations were applied to NO_3^-, NH_4^+, Ca, Mg, K, and Fe. This improved the graphical test for multivariate normality, however the data still did not show homogeneity of variance. Therefore, for univariate testing of time, horizon, and time by horizon effects the degrees of freedom were adjusted using the Greenhouse-Geisser epsilon produced during repeated measures analysis. Multivariate tests using Wilks' likelihood ratio test statistics indicated that all effects except for location by horizon were significant (p=0.10) during analysis of variance, and all effects were multivariately significant during analysis of covariance. To compensate for the lack of multivariate significance for the location by horizon effect in analysis of variance, a Bonferroni adjustment was applied such that a probability level of 0.009 was necessary to detect significance at p=0.10. Least squares means and t-tests for differences between means were produced using the Proc Mixed procedure in SAS. For reporting purposes, all means for variables that had been logarithmically transformed were reverted exponentially using an adjustment for bias (Baskerville, 1972).

Comparison of above-ground nutrient content with soil nutrient availability was carried out by compiling overstory nutrient content and soil ion-exchange data for each element. Both sets of data were charted on a single graph for each element, and visually compared for temporal patterns.

Correlation analysis was performed using the Correlation Procedure in SAS. Four correlation tests were examined for each foliar elemental concentration, one for each soil horizon. Pearson correlation coefficients were calculated for each comparison, and correlations were considered significant at p=0.10.

RESULTS

Geology

Current geologic mapping in the area showed that the bedrock was mica schist, probably part of the St. Regis Formation of the Belt Supergroup of Precambrian metasedimentary rocks, which was later metamorphosed (Lewis, 2001). Approximately 10% of the area also had pegmatite intrusions, indicating the possible presence of a deep granitic pluton in the area. Field examination revealed that the western block showed a slightly greater pegmatite influence than the eastern block, however the difference was very slight and would not be differentiated during standard geologic mapping procedures. Therefore, the geology of the two blocks was considered the same.

Thin section analysis indicated that the schist samples consisted of approximately 45% muscovite, 45% quartz, 5% biotite and 5% plagioclase, and exhibited deformed textures and clay alteration around the edges of the micas. The pegmatite composition was quartz monzodiorite, consisting of approximately 50% plagioclase (An20), 30% muscovite, 10% potassium feldspar and 10% quartz. Geochemical analyses of both rock types indicated that their chemical compositions were within expected ranges (Appendix A-1).

Soil Pits and Laboratory Tests

The six soil pits were examined and described morphologically (Appendix A-2). Data from the six soil pits were compiled to produce an average soil profile description for the site. Several morphological characteristics, average pH values and cation-exchange capacity (CEC) were compiled for the principal horizons (Table 1-1). Because of the strong volcanic ash influence, anion-exchange capacity (AEC) would have been a useful test, particularly for its value in explaining the behavior of elements such as S and P which are commonly present in anionic forms. However, this test is not commonly available, and was not performed during this study. The soil profile included a thin but well-developed A horizon, and a Bw horizon consisting of a mixture of volcanic ash, organic matter, and colluvial schist and quartz monzodiorite soils. Particle-size analysis indicated that the Bw horizon consisted of 27% sand, 60% silt and 13% clay. Mineralogy of the Bw fine sands in order of abundance included muscovite, biotite, quartz, volcanic glass (ash) and feldspars. The clay fraction included vermiculite, kaolinite, mica and quartz. Selective dissolution tests suggested the presence of allophane/ imogolite and iron oxides, as well as some metal-humus complexes and high concentrations of silicon in poorly-crystalline forms. The 2Bt, 2E, 2BC and 2C horizons were residual soils developed from mica schist. Particle-size analysis of the 2BC horizon showed 62% sand, 28% silt and 10% clay. Mineralogical examination indicated that muscovite dominated the fine sand fraction of the 2BC soils, followed by quartz and biotite in about equal proportions, and a few feldspars and garnets. Clay-sized materials identified in this horizon included vermiculite, kaolinite, mica, quartz and some montmorillinite. Vermiculite and mica were more strongly expressed in this horizon than in the Bw, and intergrades between vermiculite and kaolinite were noted. Selective dissolution showed that poorly-crystalline iron oxides were present in about equal proportions as in the Bw, but other short-range order minerals and metal-humus complexes were much less abundant. The 3BC and 3C horizons were sparse and intermittent horizons composed of decomposing quartz monzodiorite, sometimes underlain by additional mica schist. Soil mineralogy was not determined for the quartz monzodiorite horizons. Results of conventional laboratory chemical testing are provided in Appendix A-3. Soil temperature and moisture were measured during the 1999 study season (Figure 1-1).

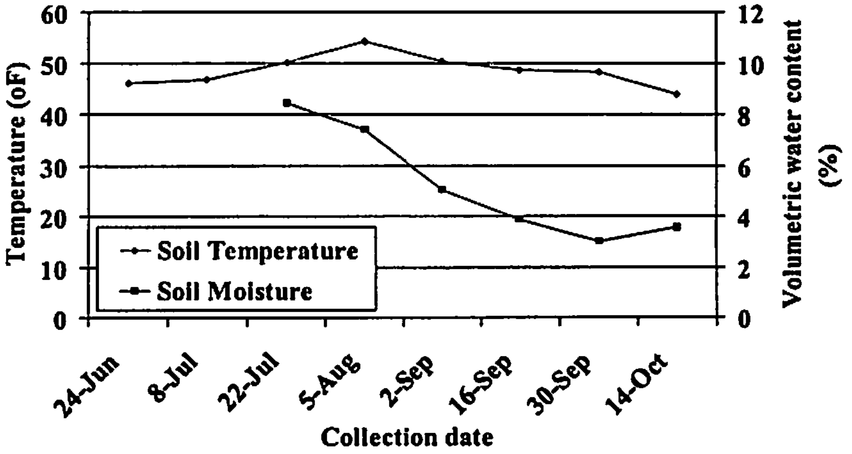
Table 1-1. Average soil profile description and selected soil characteristics in a north Idaho conifer stand.

Horizon	depth (cm)	Bulk Density (g/cm3)	Coarse Fraction (%)	Clay (%)	Mica (%)	pH	CEC	Textural Class	Roots
O	3.8	0.2	n/a	n/a	n/a	n/a	0	n/a	n/a
A**	0-11.9*	0.7	1.2	9.3	0.0	6.3	23.9	Silt loam	many, very fine through very coarse
Bw**	11.9-30.7	0.9	1.2	8.0	0.0	6.0	5.0	Silt loam	many, very fine through very coarse
2Bt and 2E (schist)**	30.7-70.1	1.8	8.1	14.4	21.6	5.2	4.5	Sandy loan to silt loam	few to common, very fine through very coarse
2BC and 2C (schist)**	70.1-90.6	1.6	9.3	10.2	68.2	5.0	4.3	Loamy sand to sandy loam	common fine to few coarse
3BC and 3C (quartz monzo-diorite)	90.6-95.8	1.5	15.0	5.0	20.0	5.8	0.6	Sand	common medium to few coarse

* The top of the A horizon was considered to be the mineral soil surface and was treated as 0 cm depth.

**Ion-exchange resins were placed in the A, Bw, 2Bt and 2BC horizons.

Figure 1-1. Soil temperature and moisture during the 1999 growing season in a north Idaho conifer stand. Values were averaged across four soil horizons.



Ion-exchange Resins

Block effects were examined in order to detect differences in soil nutrient status which might help explain past differences in tree response to fertilization. Main effects for block were not significant for any of the ions or elements tested during analysis of variance (AOV). However, significant block by time interactions were detected for NO_3^-, NH_4^+, P, Fe, Mn, B and S. Additionally, significant block by horizon interactions were detected for NO_3^-. This means that block effects were important for all of these variables, though somewhat obscured by time and horizon differences. Graphical representation of least squares means of the block by time effects showed especially interesting patterns for NO_3^- and Mn, in that both variables were almost always greater on the western block than the eastern block (Figures 1-2 and 1-3). The other elements showed more interactions and less obvious block effects. Nitrate and K were both greater in the upper horizons on the western block, and greater in the lower horizons on the eastern block (Figures 1-4 and 1-5). Overall, greater quantities of both NO_3^- and K were measured in the upper horizons than in the lower horizons, regardless of block.

Figure 1-2. Block by time interaction of soil nitrate estimates as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand. Values were averaged across four soil horizons.

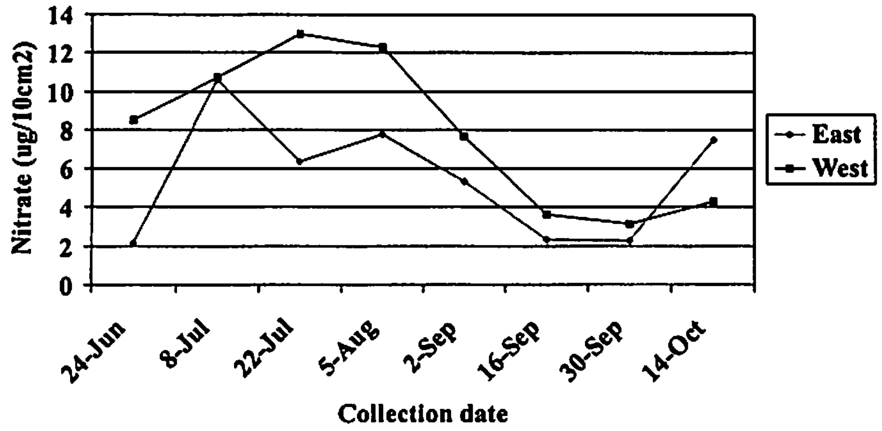


Figure 1-3. Block by time interaction of soil manganese estimates as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand. Values were averaged across four soil horizons.

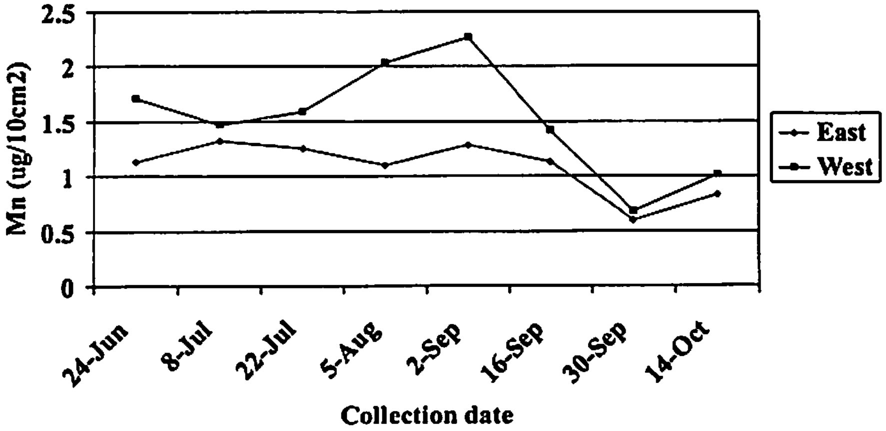
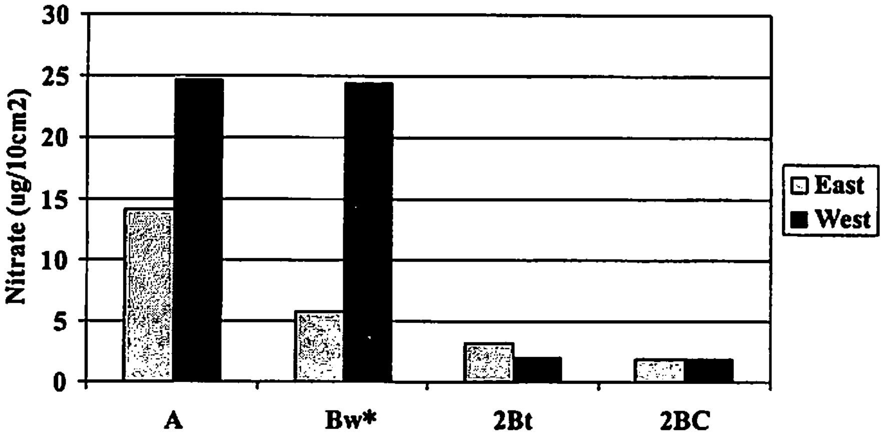


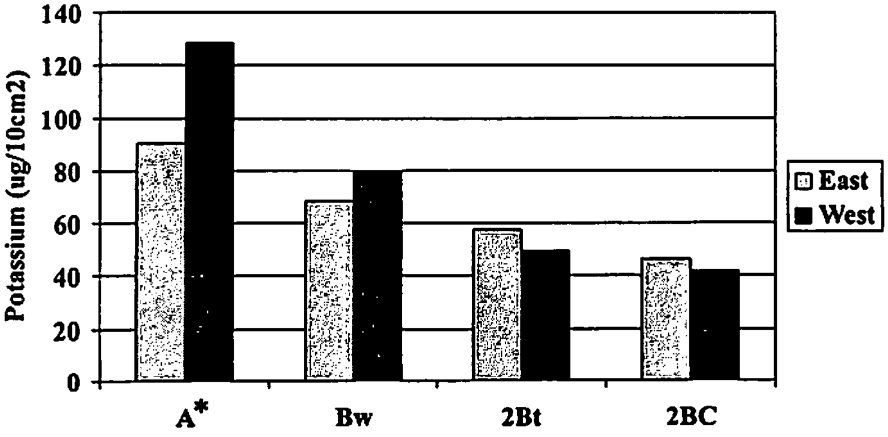
Figure 1-4. Block by horizon interaction of soil nitrate estimates as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand[1].



[1] Based on analysis of variance least squares means

* Asterisk signifies significant difference (a=.10) between blocks for that horizon

Figure 1-5. Block by horizon interaction of soil potassium estimates as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand[1].

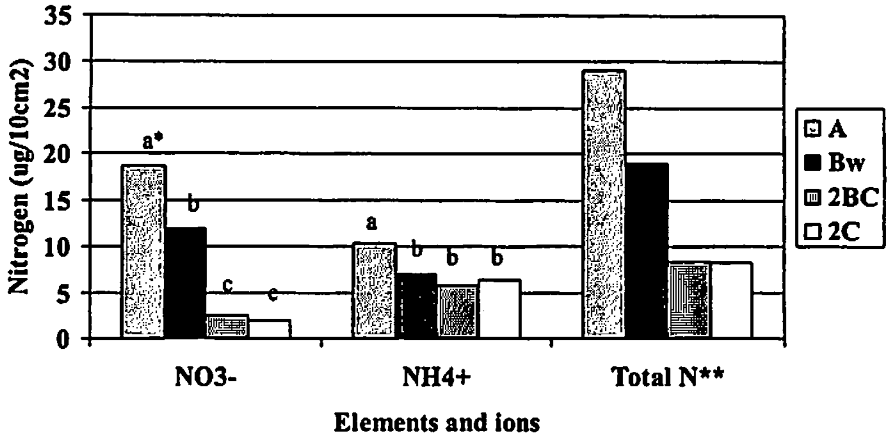


[1] Based on analysis of covariance least squares means

* Asterisk signifies significant difference (a=.10) between locations for that time period

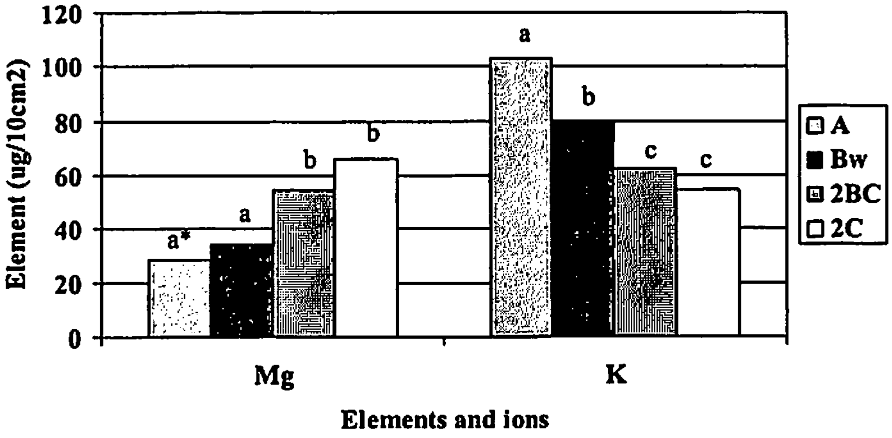
Changes in soil nutrient availability with depth were tested by analyzing soil ion-exchange data for horizon effects. Significant horizon effects were detected for NO_3^-, NH_4^+, Mg, K, P, Fe, Mn and B during AOV. Both NO_3^- and NH_4^+ decreased with depth through the soil profile (Figure 1-6). For NO_3^-, the A and Bw horizons were different from each other, and both were significantly greater than the 2Bt and 2BC horizons. For NH_4^+, the A horizon was significantly greater than the other three horizons, which did not differ from each other. The combined N values show that total N was greatest in the A horizon, followed by the Bw horizon, and then the 2Bt and 2BC horizons, which were about the same. Magnesium and K displayed opposite patterns from each other through the soil profile (Figure 1-7). Magnesium increased with depth in the soil profile, with the A and Bw values not significantly different from each other, but both were significantly lower than the 2Bt and 2BC values. Potassium decreased with depth, with the A, Bw and 2Bt horizons significantly different from each other, and the 2BC value not differing significantly from 2Bt. Phosphorus, Fe, Mn and B showed various patterns through the soil profile (Figure 1-8). For P, while the A and 2Bt measurements did not differ from each other, the Bw horizon showed a significantly higher value, and the 2BC horizon a significantly lower value. For Fe, the A horizon was significantly lower than the other three horizons, which did not differ from each other. The Mn measurements for A and Bw were significantly greater than the 2Bt and 2BC measurements.

Figure 1-6. Soil nitrogen estimates in four soil horizons as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand. Values were averaged across the entire growing season.



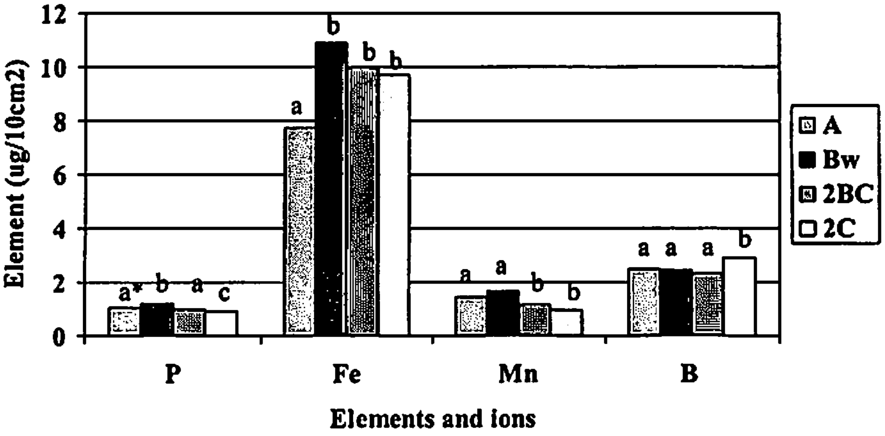
* Different letters signify significant differences (p=.10) between horizons
** Total N represents the sum of the nitrate (NO_3^-) and ammonium (NH_4^+) values

Figure 1-7. Soil magnesium and potassium estimates in four soil horizons as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand. Values were averaged across the entire growing season.



* Different letters signify significant differences (p=.10) between horizons

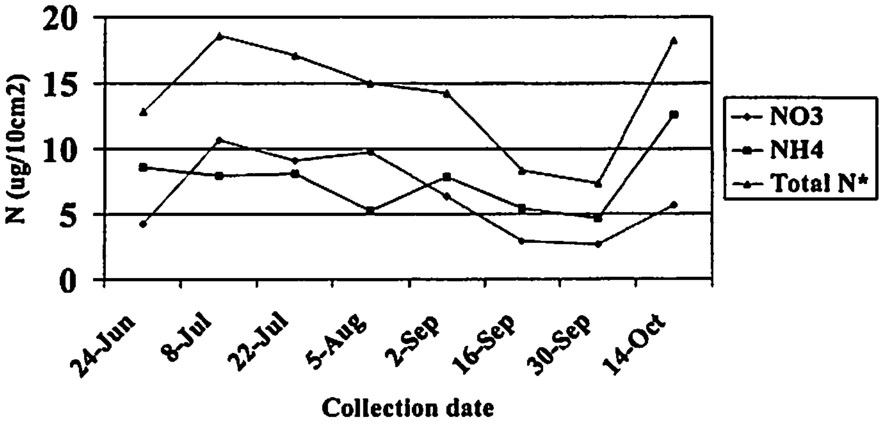
Figure 1-8. Soil phosphorus, iron, manganese and boron estimates in four soil horizons as measured by ion exchange resins during the 1999 growing season in a north Idaho conifer stand. Values were averaged across the entire growing season.



* Different letters signify significant differences (p=.10) between horizons

Seasonal differences in soil nutrient availability were tested by examining soil ion-exchange data for differences by time. Temporal effects were significant for all elements tested. Ammonium and NO_3^- showed somewhat erratic patterns of ion-exchange availability over the course of the growing season, however the overall tendency of combined NH_4^+-N and NO_3^--N was decreased availability over the course of the growing season (Figure 1-9). The NH_4^+ component dominated during the middle of the season, while the NO_3^- component dominated at other times. Values for Mg, Ca and K generally decreased over the course of the growing season (Figure 1-10). Calcium dominated among the major cations, showing values 2-3 times greater than Mg or K. Phosphorus, Fe and Mn remained fairly constant early in the season, then increased during mid-season and decreased towards the end (Figure 1-11). Sulfur showed an erratic pattern, increasing and decreasing sporadically throughout the season (Figure 1-12). Boron displayed a smoother pattern, increasing and decreasing twice during the growing season. Copper values increased early in the season, and then decreased towards the end (Figure 1-13). Almost all elements showed an increase during the final measurement period, probably due to a combination of increased soil moisture and the cessation of plant uptake as dormancy occurred.

Figure 1-9. Soil nitrogen estimates during the 1999 growing season as measured by ion exchange resins in a north Idaho conifer stand. Values were averaged across four soil horizons.



* Total N represents the sum of nitrate-N and ammonium-N

Figure 1-10. Soil calcium, magnesium and potassium estimates during the 1999 growing season as measured by ion exchange resins in a north Idaho conifer stand. Values were averaged across four soil horizons.

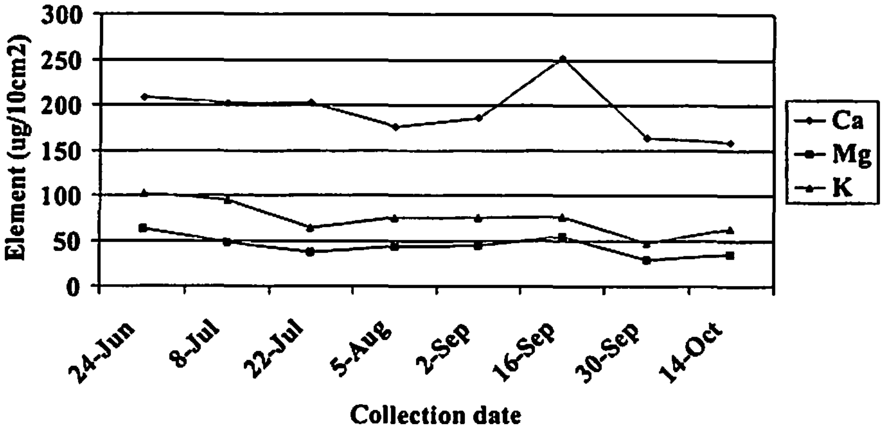


Figure 1-11. Soil phosphorus, iron and manganese estimates during the 1999 growing season as measured by ion exchange resins in a north Idaho conifer stand. Values were averaged across four soil horizons.

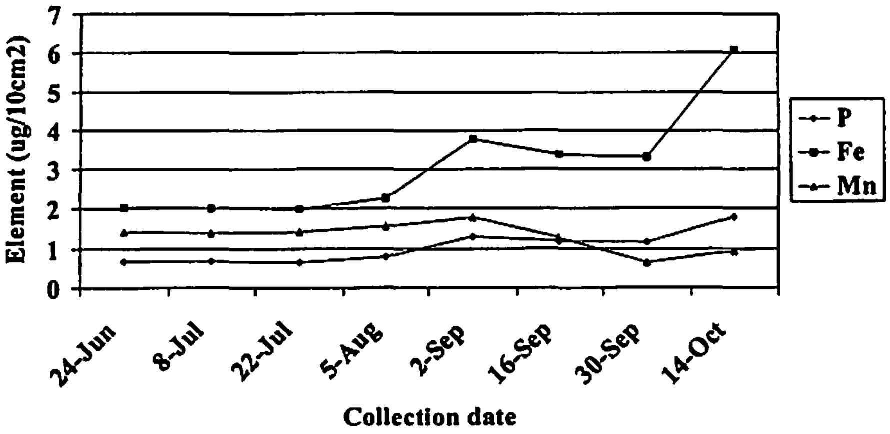


Figure 1-12. Soil boron and sulfur estimates during the 1999 growing season as measured by ion exchange resins in a north Idaho conifer stand. Values were averaged across four soil horizons.

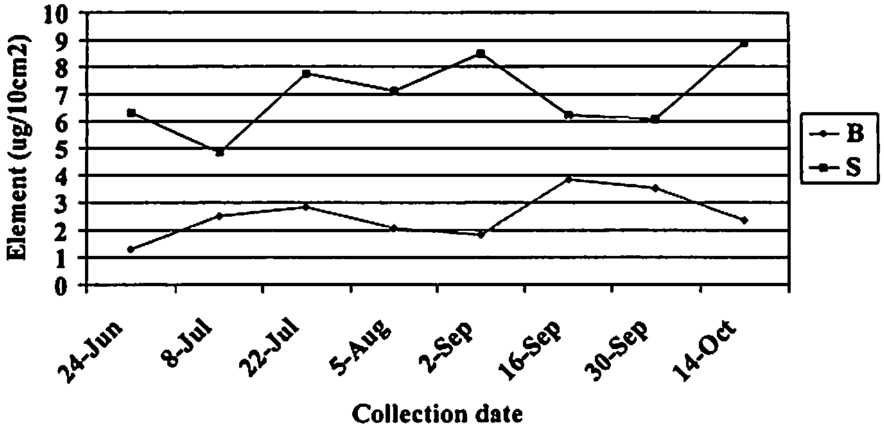
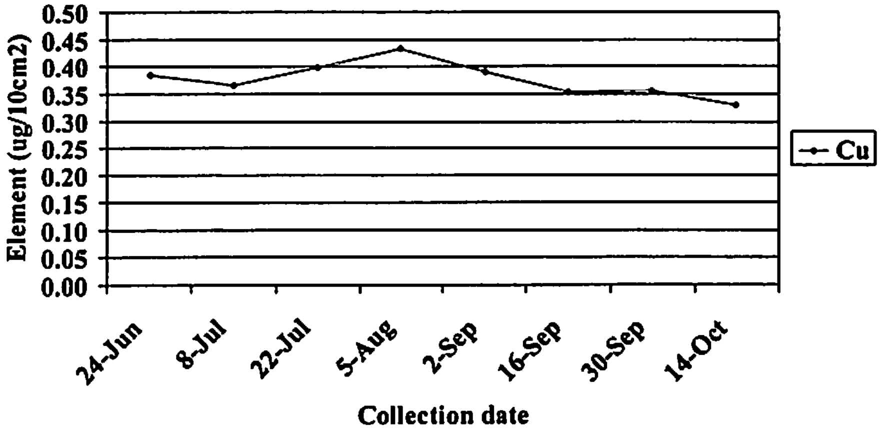


Figure 1-13. Soil boron estimates during the 1999 growing season as measured by ion exchange resins in a north Idaho conifer stand. Values were averaged across four soil horizons.



Comparison of Ion-Exchange Data with Tree Chemistry

Comparison of soil to overstory N, Mg and K showed opposite patterns across the growing season, with soil ion-exchange measurements decreasing as overstory nutrient content increased (Figure 1-14). Soil-available P and Fe and overstory P and Fe contents both increased during the growing season (Figure 1-15). The remaining elements showed a combination of these two patterns, with Ca and B showing opposite patterns early in the season and similar patterns later in the season (Figure 1-16), while Mn, Cu and S showed a reverse pattern (Figure 1-17).

Figure 1-14. Comparison of soil nitrogen availability as measured by ion exchange resins with overstory nitrogen content during the course of the growing season in a north Idaho conifer stand. Similar patterns were displayed for magnesium and potassium.

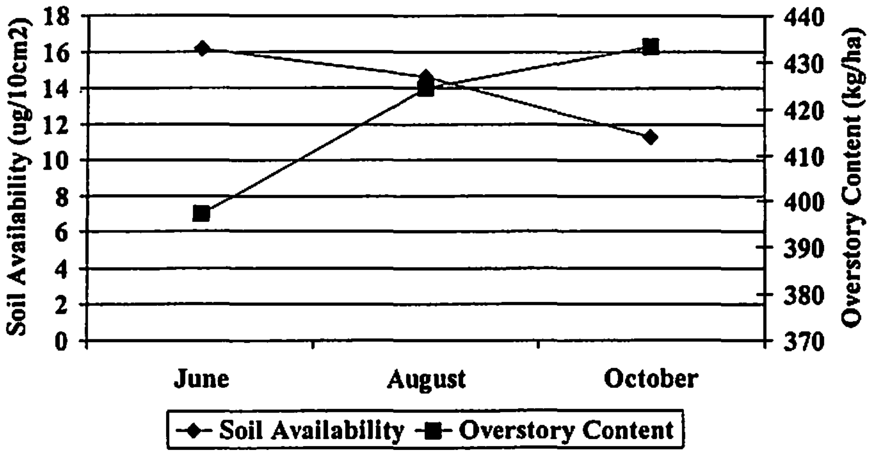


Figure 1-15. Comparison of soil phosphorus availability as measured by ion exchange resins with overstory phosphorus content during the course of the growing season in a north Idaho conifer stand. Iron displayed a similar pattern.

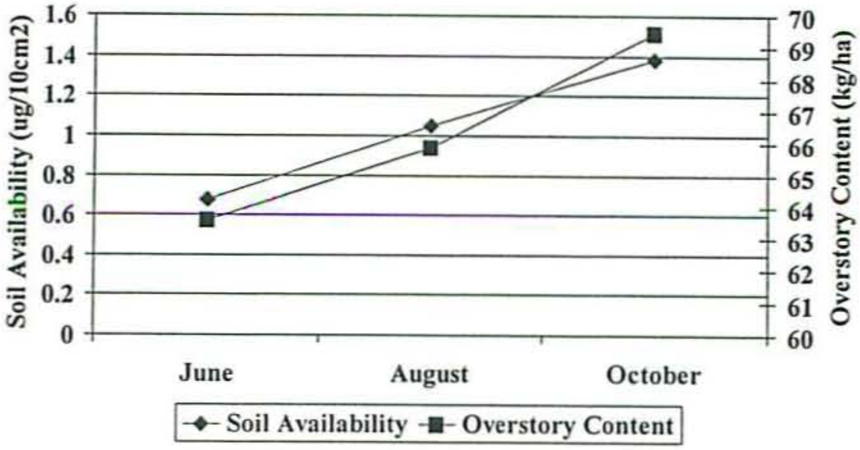


Figure 1-16. Comparison of soil calcium availability as measured by ion exchange resins with overstory calcium content during the course of the growing season in a north Idaho conifer stand. Boron displayed a similar pattern.

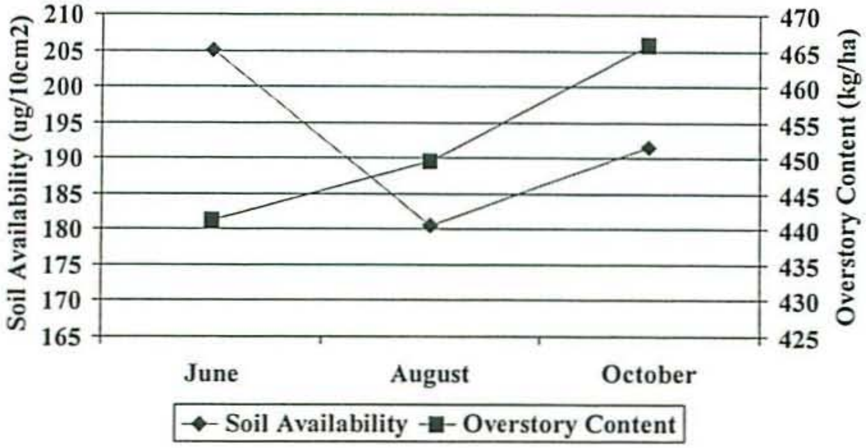
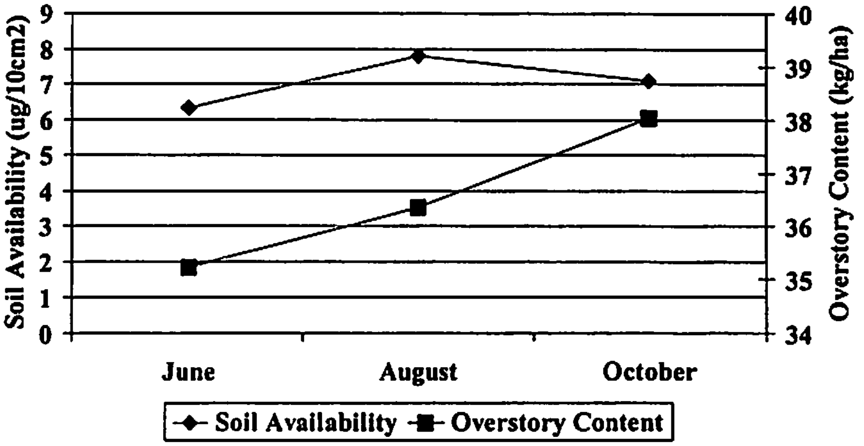


Figure 1-17. Comparison of soil sulfur availability as measured by ion exchange resins with overstory sulfur content during the course of the growing season in a north Idaho conifer stand. Manganese and copper displayed similar patterns.



Correlation analysis of upper crown foliage from dominant/ codominant Douglas-fir trees with soil ion-exchange values showed significant correlations for N, P, K, Mn and B (Table 1-2). For NH_4^+, P, Mn and B, the correlations were positive. For NO_3^- and K, the correlations were negative. Total N, which represented the sum of NO_3^- and NH_4^+, showed a negative correlation in the A and Bw horizons, and a positive correlation in the 2Bt horizon, reflecting the influence of NO_3^- on total N in the upper two horizons, and that of NH_4^+ in the 2Bt horizon. All elements which showed significant correlations were significant in the Bw soil horizon and one or two other horizons, except NH_4^+, which was significantly only in the 2Bt horizon.

Table 1-2. Pearson correlation coefficients between foliar nutrient concentration of upper crown foliage from dominant crown classes of Douglas-fir and soil ion-exchange data for four soil horizons in a north Idaho conifer stand.

	A Horizon		Bw Horizon		2Bt Horizon		2BC Horizon	
	r	*p*	r	*p*	r	*p*	r	*p*
NO3	-0.72	0.10	-0.77	0.07				
NH4					0.77	0.07		
Total N	-0.83	0.04	-0.73	0.09	0.77	0.07		
P	0.83	0.04			0.93	<0.01	0.87	<0.01
K	-0.94	<0.01	-0.81	0.05				
Mn			0.73	0.10	0.86	0.03		
B			0.86	0.03			0.91	0.01

DISCUSSION

Block Effects

Results of analysis for block effects showed that soil-ion exchange resins were useful in detecting soil nutrient availability conditions which might help explain past differences in fertilization response. The results of soil ion-exchange analysis showed that all significant differences between blocks occurred as interactions with time and with horizon. Nitrate estimates on the eastern block were significantly lower than the western block both early in the growing season and also in the upper soil horizons. Tree demand for nitrogen is highest early in the growing season, as trees break bud and begin new growth (Waring and Schlesinger, 1985). The upper soil horizons, along with the O horizon, are thought to be the most important storage compartments for nitrogen in forest ecosystems (Peterson et al., 1984; Waring and Schlesinger, 1985; Entry and Emmingham, 1995). Therefore, the finding of significantly lower nitrate-N both early in the growing season and in the upper horizons on the eastern block was interesting, as this suggests that the stronger growth response to N-fertilization on this block may have been due to less-available soil N prior to treatment, and that this deficiency was especially pronounced during the most crucial part of the growing season. Unfortunately, the reasons why NO_3^- levels might differ between blocks was less clear. The growth response differences observed years ago during the N fertilization trials suggested that N differences between blocks did exist, and the soil data collected during the current study indicate that these differences still persist today. During the observed growing season, soils on the western block were slightly warmer, moister and less acidic than the eastern block. While these differences were minor, all were in the range suitable for nitrification to occur. It is conceivable that if these differences persisted over a number of years that they could have a cumulative effect on available soil N. Unfortunately, there were no obvious stand or site characteristics that would allow us to determine this without carrying out detailed site-specific soil measurements.

While several other ions besides NO_3^- showed significant block by time effects, only Mn showed distinct block differences, with the eastern block showing lower Mn values. Potassium showed a significant block by horizon effect, with the highest estimates occurring in the upper soil horizons on the western block. Both Mn and K were lower on the eastern than on the western block. However, if the latter two nutrients were present in sufficient quantities for tree growth, then the difference between blocks would be inconsequential in explaining past response differences to N-fertilization. While not statistically significant, S and P showed higher values on the eastern block, and NH_4^+ showed greater values on the western block. Since S is important to photosynthetic processes (Marschner, 1995), perhaps greater S availability on the eastern block allowed those trees to show greater N-fertilization response, or conversely, that the lower S levels on the western block inhibited growth responses to N-fertilization. Foliar diagnostics showed that the eastern block Douglas-fir had marginally greater S concentrations than the western block, and also that both blocks were deficient in S according to established foliar critical levels (Webster and Dobkowski, 1983). Sulfur deficiency might explain the lack of additional response beyond the 224 kg treatment, since S might have become the factor limiting additional response once the N deficiency was met.

Changes With Soil Depth

Nutrient availability results by soil horizon supported the hypothesis that soil ion-exchange resins could be used to detect differences in nutrient availability with depth, as great as 90 cm below the soil surface. Horizon effects were significant for N, K, Mg, P, Fe, Mn and B. The finding of greater N in the upper horizons was expected, as N availability is heavily dependent on the quantity and quality of organic matter present. Both the A and Bw horizons showed greater organic matter amounts than the lower horizons. The finding that NO_3^--N was greater in the upper horizons, while NH_4^+-N dominated the lower horizons may relate in part to the clear presence of 2:1 clay minerals in the lower horizons found during mineralogical analysis, as the NH_4^+ ion has an affinity for being adsorbed to and fixed within these minerals (Scott et al., 1960; Liu et al., 1997; Brady and Weil, 1999). Furthermore, conditions for nitrification deteriorate with soil depth, such that much accumulation of NO_3^- would not be expected in the lower horizons.

Potassium was also significantly greater in the upper than in the lower horizons. This result was expected since K^+ is a very mobile ion in forest ecosystems, tending to accumulate in the upper horizons due to plant uptake and subsequent litter fall, and remain in the soil system due to its affinity to clay minerals (Cole et al., 1967; Waring and Schlesinger, 1985;

Klemmedson, 1994; Ranger et al., 2001). Magnesium was significantly greater in the lower two horizons, somewhat contrary to expectations since Mg has often been shown to decrease with depth (Cole et al., 1967; Klemmedson, 1994; Brais et al., 1995). In this case, the source of Mg at lower depths could have been biotite in the mica schist, though petrographic analyses indicated that biotite comprised only about 5% of that schist. Magnesium is readily adsorbed to clay surfaces, so Mg could be expected to be retained as secondary clay minerals formed (Foth and Ellis, 1997; Brady and Weil, 1999). Vermiculite and montmorillinite were detected in the clay fraction of the 2BC horizon, both of which may incorporate Mg as a structural component. The Mg^{2+} ion adsorbs to clays more strongly than K^+, and thus is less likely to be circulated to the upper horizons through plant uptake (Foth and Ellis, 1997). Also, Mg can be susceptible to leaching under acid conditions, so due to the somewhat acidic soils at the study site, some downward movement through the profile might also be expected.

Phosphorus, Fe and Mn all showed similar patterns throughout the profile, occurring at greatest quantities in the Bw horizon, and less in the A, 2Bt and 2BC horizons. The similarity between P and Fe may be explained in part by the affinity of P for Fe-oxides and Fe- and Al-bearing short-range order minerals. Soil mineralogical testing revealed that Fe-oxides were present across both the Bw and 2BC horizons, and Fe- and Al-bearing short-range order minerals were predominant in the Bw horizon. Hence, greater P availability measured in the horizon associated with greater quantities of the short-range order minerals is reasonable. Greater Fe measured in the three lower horizons probably relates both to the formation of Fe-oxides and amorphous minerals across all horizons, and to the presence of Fe-bearing minerals in the parent materials. Manganese is often associated with Fe as they show similar chemical behavior in soils (Foth and Ellis, 1997; Kabata-Pendias, 2001). Both elements are associated with organic matter, and Mn is known to accumulate in upper soil horizons due to fixation by organic matter. For Mn, there was no significant difference between the A and Bw horizons, which were both higher in organic matter than the deeper horizons.

Boron was significantly greater in the 2BC than in any of the upper horizons, none of which differed significantly from each other. Boron is known to adsorb to freshly precipitated Fe- and Al-hydroxides (Foth and Ellis, 1997), which were likely to be found at depth since soil moisture increased with depth. Boron is also associated with the clay fraction in sedimentary rocks (Kabata-Pendias, 2001), and clay-bearing sedimentary rocks were the likely protolith for the mica schist parent material on the study site. Furthermore, B is very mobile compared to other micronutrients, and is likely to leach downward through the soil profile.

Changes During the Growing Season

Results of statistical analysis of ion-exchange data by time supported the hypothesis that ion-exchange resins were capable of detecting seasonal differences in soil nutrient availability at the study site. Ion-exchange data for all elements showed significant seasonal variation. Ammonium, NO_3^- and the major cations generally tended towards decreased uptake over the course of the growing season. Phosphorus, Fe and Mn remained constant or increased slightly early in the season, then decreased later. Soil S, B and Cu fluctuated over the growing season. These findings may have been due to changes in soil temperature and moisture during the growing season (Schaff and Skogley, 1982; Skogley and Schaff, 1985; Yang et al., 1991). However, other researchers have shown that ion-exchange resins used *in* *situ* can detect temporal changes in nutrient availability due to plant uptake (Hart and Binkley, 1985; Binkley et al., 1986; Krause and Ramial, 1987; Lundell, 1989; Huang and Schoenau, 1997). These short-term changes in nutrient availability due to plant uptake describe the buffering capacity of the soil. Thus, the findings of seasonal variation in nutrient availability in this study were likely due to a combination of seasonal changes in soil temperature and moisture, and soil buffering capacity.

Comparison of Soil Ion-Exchange Data with Tree Chemistry

The findings of this study with regards to temporal changes in nutrient availability were generally reasonable, and supported findings of other researchers using ion-exchange resins *in situ* (Hart and Binkley, 1985; Krause and Ramial, 1987; Lundell, 1989; Binkley et al., 1992). Graphical comparison of seasonal fluctuations in ion-exchange values with fluctuations in vegetation nutrient contents provided a useful visualization of the effect of plant uptake on soil nutrient availability. Overstory nutrient content always exhibited a pattern of increase during the growing season, while soil nutrient availability as measured by ion-exchange resins sometimes decreased and sometimes increased. The most likely explanation for the dichotomy in patterns is simply that those elements which showed decreasing soil availability coincident with increasing overstory content were those for which nutrient demand was greatest, and soil nutrient supply capacity most limited. This could also be interpreted as indicative of low soil buffering capacity for those elements. Accordingly, the finding of increasing plant content and decreasing soil supply for N, Mg and K suggests that those elements were potentially growth-limiting nutrients by the end of the growing season. Several elements showed this same pattern temporally, including Ca and B early in the season, which is plausible since the overstory and understory were both actively producing new growth at that time. Sulfur, Mn and Cu showed the same pattern late in the season, suggesting that perhaps under conditions such as decreased soil moisture, these elements could become limiting. Conversely, P and Fe showed increased soil availability coincident with increased overstory content. Therefore, it is likely that these elements were not growth-limiting factors at the experimental site.

Correlation analysis was performed on all elements for which both foliar chemistry and soil ion-exchange data were available. The findings of significant correlations between tree foliage N and P concentrations and soil ion-exchange N and P values were similar to findings of other researchers (Smith, 1979; Binkley et al., 1986). In addition, significant correlations occurred for K, Mn and B. These correlations occurred in various soil horizons, however all elements which showed significant correlations were significant in the Bw horizon, and one or two other horizons. This suggested that the Bw horizon was the most useful horizon for monitoring seasonal effects of soil ion-exchange nutrient availability on vegetation nutritional status at this study site.

Correlation results were also useful for comparison with the graphical illustrations of tree nutrient contents and soil ion-exchange data shown in Figures 1-14 through 1-17. Nitrogen and K showed negative correlations between tree foliage chemistry and soil ion-exchange, indicating that tree uptake of these elements likely contributed to decreased soil availability. This finding concurred with the graphical comparison of soil nutrient availability and overstory nutrient content shown in Figure 1-14, and again emphasized the likelihood of short-term soil nutrient deficiencies of these elements. The strong positive correlation between foliar P concentration and ion-exchange P availability concurred with the graphical comparison shown in Figure 1-15, and suggested that tree uptake of P occurred coincident with soil P-availability. The positive correlations between tree foliage chemistry and soil ion-exchange shown by B and Mn only partially agreed with the temporal comparisons illustrated in Figures 1-16 and 1-17. This may have been due to the inclusion of all four soil horizons in those graphical comparisons, which could have obscured visualization of the correlation relationships which occurred for only one or two horizons. For Mg, Ca, S, Cu and Fe, no significant correlation occurred between tree foliage nutrient concentrations and ion-exchange values. This would be consistent with expectations for elements showing variable availability throughout the season, such as those illustrated in Figures 1-16 and 1-17. In other words, lack of correlation between soil ion-exchange data and foliar nutrient concentrations indicated that plant uptake rates varied from soil nutrient availability rates during the growing season. This may have been related to soil temperature and moisture conditions, which were more favorable for plant uptake at particular times of the year than others, or may simply indicate that the plant requirement for those elements had been met, and plant uptake was therefore not tied to soil availability.

CONCLUSIONS

The experimental site was examined for physical and chemical characteristics which might explain differences in past fertilization response. Geochemical and petrographic analyses of rocks from the two experimental blocks did not reveal strong differences which would explain growth response differences during the earlier fertilization trials. Soil mineralogical testing also revealed similarities between the two blocks. However, ion-exchange resin analysis showed significantly lower NO_3^- in the upper horizons on the eastern block than on the western block, and somewhat greater S on the eastern block. Both of these factors could explain the eastern block's greater response to 224 kg ha^{-1} N-fertilization, supporting the hypothesis that soil ion-exchange resins could be used *in situ* to detect differences in soil nutritional status which may help explain past response to fertilization.

Results of ion-exchange analysis also supported the hypothesis that ion-exchange resins could be used to detect changes in soil nutrient availability with soil depth for multiple elements. Using ion-exchange resins, significant differences were detected between horizons for N, Mg, K, P, Fe, Mn and B. Nitrogen and K were both greater in the upper soil horizons, and were related to organic matter, plant uptake and adsorption to clay minerals. Magnesium performed contrary to expectations by showing an increase with depth, but this may have been attributable to parent material influence and secondary clay minerals. Phosphorus, Fe and Mn all showed greater quantities in the Bw horizon than the other three horizons. The P findings were explained through the affinity of P for Fe- and Al- oxides and short-range order minerals, both of which were prevalent in the Bw horizon, and also the presence of organic matter in the upper soil horizons. Iron was related both to its presence in the soil parent materials at depth, and the formation of secondary Fe-bearing minerals throughout the profile. Manganese behaved similarly to Fe, but probably accumulated in the upper horizons due to organic matter fixation. Boron was highest in the 2BC horizon, which was explained primarily by the presence of clay minerals and greater soil moisture at depth.

Ion-exchange resins used *in situ* were successful in detecting temporal differences in soil nutrient availability for all elements tested, including macronutrients, micronutrients and Al. Changes over time were consistent with expectations based on soil temperature and moisture, and plant uptake patterns. Comparison of ion-exchange data with overstory nutrient content suggested that decreases in soil availability coincident with increasing plant content were indicative of nutrients under high demand and low supply. Thus, N, Mg, K, early-season Ca and B, and late-season S, Mn and Cu all were potentially limiting nutrients. Foliar diagnostics supported this contention for S and N. This use of ion-exchange data showed interesting potential for diagnosing forest nutrient deficiencies.

Correlation analysis of tree foliar nutrient concentrations with soil ion-exchange availability provided useful insights into plant-soil nutritional relationships, and complemented the graphical comparisons of overstory content and ion-exchange data. The significant negative correlations demonstrated by N and K suggested potential short-term deficiencies of those elements. The significant positive correlations of P, Mn and B indicated that those elements were likely taken up by trees as they became soil-available. Other elements showed no significant correlations for any soil horizon, which likely indicated that these elements were not consistently required by Douglas-fir trees during the growing season, or that their availability was not a limiting factor to the growth of Douglas-fir trees at the experimental site.

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Forest nutrient cycling in a north Idaho conifer stand II: Seasonal changes in chemistry and biomass of Douglas-fir and grand fir foliage, understory vegetation, litterfall and forest floor

Abstract. The macronutrient, micronutrient and Al contents of various forest ecosystem components during one growing season were evaluated during this study. Differences in overstory foliar P and Cu contents and litterfall N and S may help explain past fertilization response at this site. Needle characteristics of overstory trees showed significant differences by species, crown class, crown position, foliar age class, and sampling date. Dry weight and nutrient contents of grand fir needles were about twice that of Douglas-fir needles. This implied that grand fir placed higher nutrient demands on the site than Douglas-fir for all elements, and that species composition is an important component of forest nutrient management. Needles from dominant trees were heavier than subordinate trees, and needles higher in the crown were heavier than needles lower in the crown. These findings were consistent with the degree of foliage exposure to sunlight, and elemental foliar contents generally followed the same patterns. Older needles generally were heavier and had higher nutrient contents than younger needles. Older needle contents either did not change or slightly decreased between June and August, and then slightly increased between August and October. New foliage contents always increased between August and October. Understory shrubs contained significantly more Mn than forbs, while forbs contained more N and K than shrubs. Total understory contents of N, P, K and S were lower in October than in June or August, and other understory elemental contents showed the same trends. Litterfall dry weight and elemental contents were greater between August and October than between

June and August. Forest floor content of most elements was within expected ranges, however Ca content seemed quite high compared to other studies, particularly when viewed in conjunction with forest floor biomass. High Ca content of grand fir foliage may have influenced forest floor Ca content, and forest floor contents may also have been influenced by the August to October litterfall, which was notably higher in Ca and several other elements compared to earlier-season litterfall. Evaluation of sampling methods and data to be used in nutrient cycling model development is also discussed.

INTRODUCTION

Many forests in the Inland Northwest of the United States are nutrient deficient, which limits stand growth potential (Shafii et al., 1989; Moore et al., 1991; Chappell et al., 1999; Garrison et al., 2000). Nutrition has also been linked to various disease and insect outbreaks throughout the Inland Northwest (Entry et al., 1991; Mika et al., 1993; Garrison-Johnston et al., 2001). Harvesting practices may have negative impacts on forest nutrient pools if large portions of the overstory branches and foliage are removed (Freedman, 1981; Timmer et al., 1983; Johnson, 1983; Bigger and Cole, 1983; Wiensczyk, 1992; Proe et al., 1996; Olsson et al., 1996; Knoepp and Swank, 1997). Forest fertilization is a management tool frequently used to increase forest yields, but may also have detrimental effects if forest nutrient balances are affected (Entry et al., 1992; Mika et al., 1993; Moore et al., 1994; Mandzak and Moore, 1994). Many forest nutrition studies focus largely on nitrogen (N), probably because this element has most often been identified as a growth-limiting factor in forest stands (Heilman and Gessel, 1963; Powers, 1980; Peterson et al., 1984; Moore et al., 1991; Tiedemann et al., 1998; Chappell et al., 1999). Other studies, principally those dealing with forest nutrient cycling, provide information on additional elements, primarily macronutrients (Cole et al., 1967; Turner, 1975; Clayton and Kennedy, 1985; Rustad and Cronan, 1989). Most forest nutrition studies do not provide information on micronutrients or non-nutritional elements such as Al.

Adequate measurement of the nutrient content of the various biotic components of the forest ecosystem is important to constructing a representative forest nutrient cycling model. While foliar diagnostic tests for forest nutrient deficiencies typically involve only current year's growth from the upper portion of the crown after fall bud set, significant differences in foliar chemistry can occur between species, crown classes, position within the crown and foliar age (Lavender and Carmichael, 1966; Krueger, 1967; van den Driessche, 1974; Webber, 1977; Ballard and Carter, 1985). Furthermore, seasonal shifts in nutrient allocation in response to a tree's physiological demands can be significant (Hom and Oechel, 1983; van den Driessche, 1974; Fife and Nambiar, 1984; Nambiar and Fife, 1991 ; Kiiskila, 1996). Understory vegetation also can be an important component of the forest ecosystem nutrient cycle, particularly in lower-density forest stands (Moore and Deiter, 1992; Klinka et al., 1996; Nelson, 2000; VanderSchaaf et al., 2002). Litterfall is an important mechanism of nutrient transfer from over- and understory vegetation to the forest floor, and both litter quality and quantity are important to forest nutrient availability (Trofymow et al., 1991; Prescott et al., 1993; Vesterdal and Raulund-Rasmussen, 1998; Dijkstra, 2003). We estimated the macronutrient, micronutrient and Al contents of these forest ecosystem components at various points in time for subsequent use in forest nutrient cycling models (Garrison-Johnston, 2003b).

During the early 1980's, fertilization trials were established in numerous Douglas-fir stands throughout the Inland Northwest in order to determine which site characteristics might be associated with different levels of fertilization response (Moore et al., 1991; Mika and VanderPloeg, 1991; Shen et al., 2000). While response was found to be associated with parent material and vegetation series, the precise mechanisms responsible for the variation in response were unclear. We undertook a detailed study of the nutrient dynamics at one of these sites in an effort to detect possible causes of the variation in fertilization response, as well as to develop an improved understanding of seasonal nutrient dynamics.

For this study, we selected a site known as Mallory Creek, located in northern Idaho. This site was one of several which showed high within-site variability during the Douglas-fir fertilization trials. This stand of primarily Douglas-fir and grand fir was located on a mica-schist rock type in a western redcedar (*Thuja plicata*) vegetation series. The stand was 32 years old at the time of fertilization in 1982. During the fertilization trials, the stand was treated as a split-plot design with the stand partitioned into two blocks, where each block received three fertilization treatments consisting of an unfertilized control, 224 kg ha^{-1} nitrogen and 448 kg ha^{-1} nitrogen. The two blocks were separated by a stream, with one block occurring on the east side of the creek and the other occurring on the west. The blocks were well-matched for slope, aspect, elevation and other characteristics. Six years following fertilization, the block on the eastern side showed the strongest response to nitrogen fertilization, with gross volume growth responses of 22% and 11% to the 224 kg and 448 kg N treatments, respectively (Mika and VanderPloeg, 1991; IFTNC, 1993). The western block showed 15% and 12% responses to the same treatments. These results indicated that the 224 kg treatment did address an N deficiency on both blocks, and that the deficiency was greater on the eastern block. The decrease in response on both blocks following the 448 kg treatment suggested that the N deficiency was met, and that some other factor besides N was limiting growth. Furthermore, the lower response to the 448 kg treatment may indicate a detrimental effect of additional N fertilization, perhaps in the form of a nutrient imbalance or shift in physiological processes away from wood production.

A detailed analysis of overstory foliage elemental contents throughout the tree crowns and over the growing season for the two principal forest tree species on our study site was performed. Seasonal dynamics of understory vegetation and litterfall chemistry was also examined, as well as late-season forest floor chemistry. Possible differences between experimental blocks which might explain the past variation in response to fertilization are explored. An understanding of seasonal changes in plant nutrient levels contributes to a better understanding of forest nutrient status and cycling, and such information should help improve forest nutrient management practices. This information will later be used in the construction of forest nutrient cycling models for macronutrients, micronutrients and Al.

MATERIALS AND METHODS

Site Characteristics

The Mallory Creek study site was located 14 miles northeast of Bovill, Idaho in the Inland Northwest of the United States, with latitude approximately 46° 50' and latitude 116° 16', Boise meridian. The elevation was approximately 1036 m. The study stand was approximately 50 ha in area, and located on generally southern-facing, slightly undulating hillslopes, with aspects ranging between 170 and 230°, and slopes ranging from 15 to 25%. Average annual precipitation between 1971 and 2000 was approximately 92 cm yr^{-1}, based on weather station data from nearby Elk River, Idaho (ISCS, 2003). Precipitation during 1999, the year of this study, measured slightly higher than normal at the Elk River weather station, with rainfall averaging 98 cm yr^{-1}. Weather station estimates of precipitation between June and September totaled about 13 cm, and on-site rain gauges at the Mallory Creek site also measured approximately 13 cm of precipitation during the study period. Air temperatures between 1971 and 2000 at Elk River ranged from –0.2 to 13.2° C, with a mean of 6.6°C (ISCS, 2003). During 1999, Elk River air temperatures averaged 6 °C , and ranged from a minimum of 0 °C to a maximum of 12 °C. From June through August of 1999, the mean air temperature at Elk River was 16 °C, with a minimum of 7 °C and a maximum of 24. Air temperatures measured at the Mallory Creek study site during the 1999 study period were normal, ranging from 3 °C to 28 °C, and averaging 16 °C.

The study stand was approximately 50 years old at the time of the current study, and no management activities had occurred on the site since the mid-1970's. Approximate quadratic mean diameter of the unfertilized portion of the stand in 1999 was 26 cm, site height was 20 m, and gross volume was approximately 357 m^3 ha^{-1} (IFTNC, 1993). Total basal area was estimated to be 44 m^2 ha^{-1}, consisting of 85% Douglas-fir (*Pseudotsuga menziesii*), 10% grand fir (*Abies grandis*), 2% western redcedar (*Thuja plicata*), 2% western white pine (*Pinus monticola*) and 1% western larch (*Larix occidentalis*). The understory consisted primarily of common snowberry (*Symphorocarpus albus*), western goldthread (*Coptis occidentalis*) and bunchberry dogwood (*Cornus canadensis*). The habitat type was identified as cedar-ginger (*Thuja plicata-Asarum caudatum*) (Cooper et al., 1991).

The blocking scheme of the 1982 fertilization trials was used during the current study. Sampling for elemental contents of most above-ground components occurred in mid-June, mid-August and mid-October, and was timed to correspond to bud-break, mid-growing season, and the onset of dormancy as indicated by tree bud set.

Sampling Procedures

Eight trees were selected for chemical analysis on each block for overstory analysis, including two dominant/codominant and two subordinate crown class trees from both Douglas-fir and grand fir, the major species on the site. Trees were climbed during the June and August sampling dates, and one branch each was removed from the upper crown, mid-crown, and base of the live crown. Each branch was bagged, placed on ice and brought to the laboratory for processing. At the lab, current, one-year-old and two-year-old needles were separated from the branches and dried at 70°C for 48 hours. A subset of needles was counted and dried separately, and weighed to estimate average needle dry weight. The June sampling period corresponded with bud-break, thus only one-year and two-year-old needle samples were processed. After drying, needles were ground in preparation for chemical analysis.

Understory biomass estimates and chemical analysis samples were obtained using clip plots. Five circular plots, each 1 m^2 in area, were randomly located within each block during the June, August and October sampling dates. Each plot was clipped to the ground level and separated by growth form. Since grasses were very sparse in the understory, their small biomass was combined with the forb component. Samples were placed on ice and brought to the laboratory for processing. The forb and shrub samples for each plot were dried at 70°C for 48 hours and weighed to obtain biomass estimates. Samples were then ground for chemical analysis in a Wiley mill so as to pass a 40-mesh screen.

Six forest floor samples were collected on each block in October. Each forest floor sample consisted of all identifiable organic material down to, but not including, mineral soil. Two samples were collected 1 to 2 m uphill from each of the three soil pits on each block. Each sample was 225 cm^2 in area, and individually measured for thickness in order to calculate sample volume. Samples were placed on ice and brought to the laboratory for processing. Each sample was dried and weighed, and then ground in a Wiley mill so as to pass a 40-mesh screen.

Five litter traps were installed on each block in June. Each trap was .19 m^2 in size and constructed of a plastic lattice tray lined with fine-mesh wire screen. The traps were randomly located throughout each block and fixed in place. Traps were emptied during the August and October sampling dates. All materials in each trap were placed on ice and brought to the laboratory, where they were dried and weighed to obtain biomass estimates. Samples were then ground in a Wiley mill so as to pass a 40-mesh screen.

All ground samples were sent to MDS Harris Laboratory in Lincoln, Nebraska and analyzed for N, phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), sulfur (S), zinc (Zn), manganese (Mn), copper (Cu), iron (Fe), boron (B), and aluminum (Al). Nitrogen levels were determined using a standard micro-Kjeldahl procedure (Bremner and Mulvaney, 1982). All other elements were analyzed by inductively coupled plasma spectrometry following digestion in nitric acid (Huang and Schulte, 1985).

DATA ANALYSIS

Overstory foliage was analyzed for needle weight and nutrient content (mg 100 needles^{-1}). A split-plot factorial 222.38 design was utilized, with two blocks (eastern and western), two species (Douglas-fir and grand fir), and two crown classes (dominant/codominant and subordinate) representing the plots. Two trees per block, species and crown class represented the experimental units. Three crown positions (upper, middle and lower) represented one split on the experimental units. Since the June sampling period did not include current year foliage, for analytical purposes the collection date and foliar age classes were treated as a single 8-way split. This split includes June one-year and two-year-old foliage, and August and October current, one-year and two-year-old foliage. The tree foliar elemental content data were analyzed using multivariate analysis with the following statistical model:

$$\begin{aligned} Y_{ijklmo} = {} & \mu + \alpha_j + \gamma_l + \delta_m + (\alpha\gamma)_{jl} + (\alpha\delta)_{jm} + (\gamma\delta)_{lm} + (\alpha\gamma\delta)_{jlm} + \pi_{i(jlm)} + \beta_k + (\alpha\beta)_{jk} + \\ & (\beta\gamma)_{kl} + (\beta\delta)_{km} + (\alpha\beta\gamma)_{jkl} + (\alpha\beta\delta)_{jkm} + (\beta\gamma\delta)_{klm} + (\alpha\beta\gamma\delta)_{jklm} + (\beta\pi)_{ki(jlm)} + \phi_o + \\ & (\alpha\phi)_{jo} + (\phi\gamma)_{ol} + (\phi\delta)_{om} + (\alpha\phi\gamma)_{jol} + (\alpha\phi\delta)_{jom} + (\phi\gamma\delta)_{olm} + (\alpha\phi\gamma\delta)_{jolm} + (\phi\pi)_{o(jlm)} \\ & + (\beta\phi)_{ko} + (\alpha\beta\phi)_{jko} + (\beta\gamma\phi)_{klo} + (\beta\delta\phi)_{kmo} + (\alpha\beta\gamma\phi)_{jklo} + (\alpha\beta\delta\phi)_{jklm} + \\ & (\alpha\beta\gamma\delta\phi)_{jklmo} + (\beta\phi\pi)_{ko(jlm)} + \varepsilon_{jklmo} \end{aligned} \tag{1}$$

Where: μ = population grand mean

α_j = effect of block (j=1..p and p=2 blocks)

γ_l = effect of species (l=1..r and r=2 species)

δ_m = effect of crown class (m=1..t and t=2 crown classes)

β_k = effect of crown position (k=1..q and q=3 crown positions)

ϕ_o = effect of collection date by foliage age class (o=1..u and u= 8 collection date by foliage age class combinations)

Other model terms represent interactions of the above effects

ε_{jklmoh} = residual error

In order to make statistical comparisons of collection date and foliage age class effects on nutrient content of overstory foliage, a cell means approach was used (Kirk, 1995). Values for June were compared to August and October using only the one- and two-year-old foliage, while comparisons between August and October used all three age classes. Similarly, for age-class we compared current-year foliage to one- and two-year-old foliage using only the August and October values, while comparison of one-year-old to two-year-old foliage was made using data from all three collection dates.

Understory vegetation was analyzed using a 2.23 split-plot design, with the eastern and western blocks representing two plots, and each of the five clip plots on each block split by growth form (forb, shrub) and time (June, August, October). The following statistical model was used to analyze the understory vegetation:

$$Y_{ijkl} = \mu + \alpha_j + \pi_{i(j)} + \beta_k + (\alpha\beta)_{jk} + (\beta\pi)_{ki(j)} + \gamma_l + (\alpha\gamma)_{jl} + (\gamma\pi)_{li(j)} + (\beta\gamma)_{kl} + (\alpha\beta\gamma)_{jkl} + (\beta\gamma\pi)_{kli(j)} + \varepsilon_{ijkl} \qquad (2)$$

Where: μ = population grand mean

α_j = effect of block (j=1..p and p=2 blocks)

$\pi_{i(j)}$ = effect of plot within block (i=1..n and n=5 clip plots within each block)

β_k = effect of growth form (k=1..q and q=2 growth forms)

$(\alpha\beta)_{jk}$ = effect of block x growth form interaction

$(\beta\pi)_{ki(j)}$ = effect of growth form x plot(block) interaction

γ_l = effect of time (l=1..r and r=3 time periods)

$(\alpha\gamma)_{jl}$ = effect of block x time interaction

$(\gamma\pi)_{li(j)}$ = effect of time x plot(block) interaction

$(\beta\gamma)_{kl}$ = effect of growth form x time interaction

$(\alpha\beta\gamma)_{jkl}$ = effect of block x growth form x time interaction

$(\beta\gamma\pi)_{kli(j)}$ = effect of growth form x time x plot(block) interaction

ε_{ijkl} = residual error

In order to detect differences in total clip plot biomass and nutrient content, we also analyzed these data with the growth form split removed. This entailed summing nutrient contents and dry weights of both forbs and shrubs by clip plot, and then analyzing these data using the same statistical approach described in Equation (3) for litterfall, with $\pi_{i(j)}$ representing the effect of clip plot within block, and β_k representing the time effect for q=3 collection dates.

Litterfall was analyzed using a split-plot 2.2 design. The eastern and western blocks again treated as plots, and the five litter traps on each block were the experimental units. The litter traps were emptied in August and October, for a total of two time periods. The following statistical model was used to analyze the litter trap data:

$$Y_{ijkl} = \mu + \alpha_j + \pi_{i(j)} + \beta_k + (\alpha\beta)_{jk} + (\beta\pi)_{ki(j)} + \varepsilon_{ijkl} \qquad (3)$$

Where: μ = population grand mean

α_j = effect of block (j=1..p and p=2 blocks)

$\pi_{i(j)}$ = effect of litter trap within block (i=1..n and n=5 traps within each block)

β_k = effect of time (k=1..q and q=2 collection dates)

$(\alpha\beta)_{jk}$ = effect of block x time interaction

$(\beta\pi)_{ki(j)}$ = effect of time x trap (block) interaction

ε_{ijk} = residual error

The forest floor was analyzed for block differences. Because the number of observations was the same as the number of nutrients being examined, multivariate testing was not possible. A univariate analysis of variance was performed using the following statistical model:

$$Y_{ij} = \mu + \alpha_j + \varepsilon_{i(j)} \tag{4}$$

Where: μ = population grand mean

α_j = effect of block (j=1..p and p=2 blocks)

$\varepsilon_{i(j)}$ = residual error

All analyses were performed using SAS statistical software (SAS Institute Inc., 1989). For all statistical models, exploratory data analysis included testing for multivariate normality using a graphical test (Khattree and Naik, 1995). Homogeneity of variance was examined visually using side-by-side box plots, and also tested using the 'pool=test' option in SAS's Discrim Procedure. Where initial tests indicated that the data were not normally distributed, logarithmic transformations were applied. This generally improved the graphical tests for multivariate normality, however in most cases the data still did not show homogeneity of variance. Therefore, a repeated measures analysis was performed to produce adjustment factors for use during subsequent univariate testing. Multivariate and univariate tests were performed using the General Linear Models (GLM) Procedure. Contrast statements were included during tree foliar analysis for cell means testing of collection date and foliar age class. Multivariate tests were performed using Wilk's likelihood ratio test statistics. For all effects that were not multivariately significant, a Bonferroni adjustment was applied such that a p-value of 0.008 was necessary to detect significance at p=0.10 during univariate testing. For those effects that lacked homogeneity of variance, the univariate F-tests were also adjusted using the Greenhouse-Geisser epsilon produced during repeated measures analysis. For effects that were not testable for sphericity or multivariate significance due to insufficient degrees of freedom, a significance level of p=0.10 was used during univariate testing. Least squares means and t-tests for differences between means were produced using the Mixed Procedure in SAS. For reporting purposes, means for all variables that had been logarithmically transformed were reverted exponentially using an adjustment for bias (Baskerville, 1972). Tree foliar data were presented in mg 100 needles^{-1}, while understory, forest floor and litterfall were presented in kg ha^{-1}.

RESULTS

Overstory Foliage

No significant difference in needle weight occurred between blocks. However there were significant needle weight differences between species, crown classes and crown positions (Table 2-1). Grand fir needles were about twice as heavy as Douglas-fir needles, and needles from dominant trees were significantly heavier than those from subordinate crown class trees. Needle weights increased from lower to upper crown for both species. Foliar age classes and collection dates also had significantly different needle weights (Figure 2-1). One- and two-year-old needle weights decreased from June to August, while all needle age classes increased in weight between August and October. For all time periods, two-year-statistics. For all effects that were not multivariately significant, a Bonferroni adjustment was applied such that a p-value of 0.008 was necessary to detect significance at p=0.10 during univariate testing. For those effects that lacked homogeneity of variance, the univariate F-tests were also adjusted using the Greenhouse-Geisser epsilon produced during repeated measures analysis. For effects that were not testable for sphericity or multivariate significance due to insufficient degrees of freedom, a significance level of p=0.10 was used during univariate testing. Least squares means and t-tests for differences between means were produced using the Mixed Procedure in SAS. For reporting purposes, means for all variables that had been logarithmically transformed were reverted exponentially using an adjustment for bias (Baskerville, 1972). Tree foliar data were presented in mg 100 needles^{-1}, while understory, forest floor and litterfall were presented in kg ha^{-1}.

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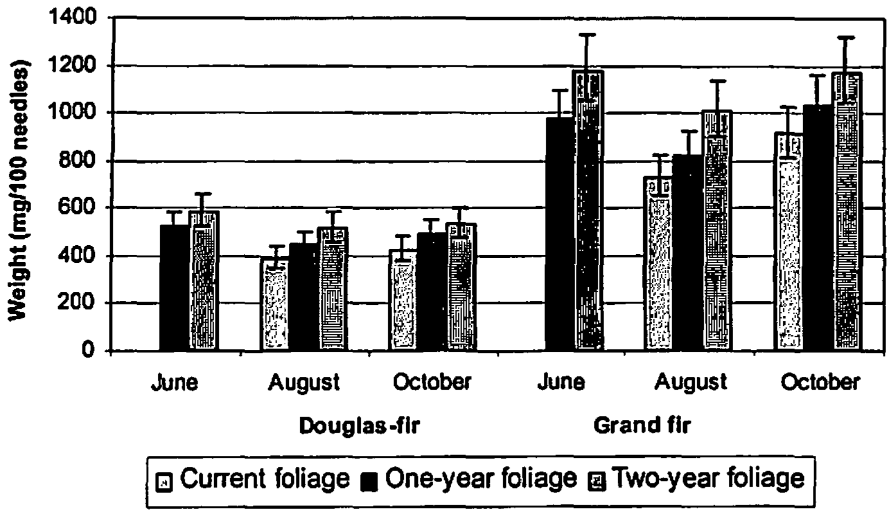
Table 2-1. Mean needle weights (mg 100 needles^{-1}) by species, crown class and crown position in a north Idaho conifer stand.

Species		
Douglas-fir		486
Grand fir		969
Crown Class		
Dominant/codominants	Douglas-fir	601
	Grand fir	1239
Subordinates	Douglas-fir	392
	Grand fir	758
Crown Position		
Lower	Douglas-fir	414
	Grand fir	838
Middle	Douglas-fir	502
	Grand fir	929
Upper	Douglas-fir	552
	Grand fir	1172

Figure 2-1. Needle weights (mg 100 needles^{-1}) by foliar age class and collection date during the 1999 growing season for Douglas-fir and grand fir foliage in a north Idaho conifer stand.



Significant block, species and crown class effects on foliar chemical contents occurred for several elements (Table 2-2). Grand fir foliar contents were greater than Douglas-fir foliar contents for all elements studied. Greater foliar P and Cu contents were detected on the eastern block than the western block. Foliar elemental contents of dominant trees were greater than subordinate trees for N, P, K, Mg, S, Zn, Mn, B and Al.

Table 2-2. Mean foliar elemental contents (mg 100 needles^{-1}) by block, species and crown class in a north Idaho conifer stand. Statistically significant within-effect comparisons (p=0.10) are in bold, italicized type.

	Block		Species		Crown Class	
Element	East	West	Douglas-fir	Grand fir	Dominant/ Codominant	Intermediate/ Suppressed
Nitrogen	7.8208	7.8545	***5.7346***	***12.0932***	***9.6724***	***6.3509***
Phosphorus	***0.9691***	***0.7813***	***0.6377***	***1.3826***	***1.0401***	***0.7280***
Potassium	4.9056	4.8567	***3.4675***	***7.7586***	***5.9121***	***4.0298***
Magnesium	0.8811	0.8879	***0.5896***	***1.4899***	***1.0074***	***0.7766***
Calcium	6.0153	6.8316	***3.7952***	***13.1335***	7.0649	5.8167
Sulfur	0.0142	0.0153	***0.4539***	***0.9390***	***0.7333***	***0.5155***
Zinc	0.2503	0.1992	***0.0069***	***0.0207***	***0.0136***	***0.0078***
Manganese	0.6573	0.6095	***0.1896***	***1.0934***	***0.5239***	***0.2804***
Copper	***0.0105***	***0.0104***	***0.0018***	***0.0043***	0.0024	0.0025
Iron	0.4724	0.3872	***0.0323***	***0.0954***	0.0446	0.0531
Boron	0.0021	0.0027	***0.0113***	***0.0260***	***0.0206***	***0.0109***
Aluminum	0.0441	0.0426	***0.0887***	***0.7521***	***0.2817***	***0.1782***

Several elements showed interactions between block, species and crown class. Block-by-species interactions were significant for Mg, Mn, Fe and B (Figure 2-2). For these elements, Douglas-fir foliar contents on the western block were generally greater than for the eastern block, while grand fir contents were generally greater on the eastern block. Exceptions were Douglas-fir Mn content and grand fir B content, which did not differ between blocks. Species-by-crown class interactions were significant for P, S, Mn and Cu (Figure 2-3). In all cases, dominant grand fir had the highest nutrient contents, while within species, dominant Douglas-fir P and Mn contents did not differ from subordinates. Foliar S content of subordinate Douglas-fir was greater than for dominants, while foliar Cu content was less. Block-by-crown class interactions were significant for Fe and B (Figure 2-4). In both cases, east block dominant trees had greater contents, while on the west block subordinate trees had greater contents. For Fe, this interaction was due primarily to the high foliar content of dominant grand fir on the eastern block and subordinate grand fir on the western block (Figure 2-5). This three-way interaction was not apparent for foliar B contents.

Figure 2-2. Block-by-species interaction of foliar nutrient content (mg 100 needles $^{-1}$) of (a) magnesium, (b) manganese, (c) iron and (d) boron in Douglas-fir and grand fir trees on eastern and western study blocks during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.

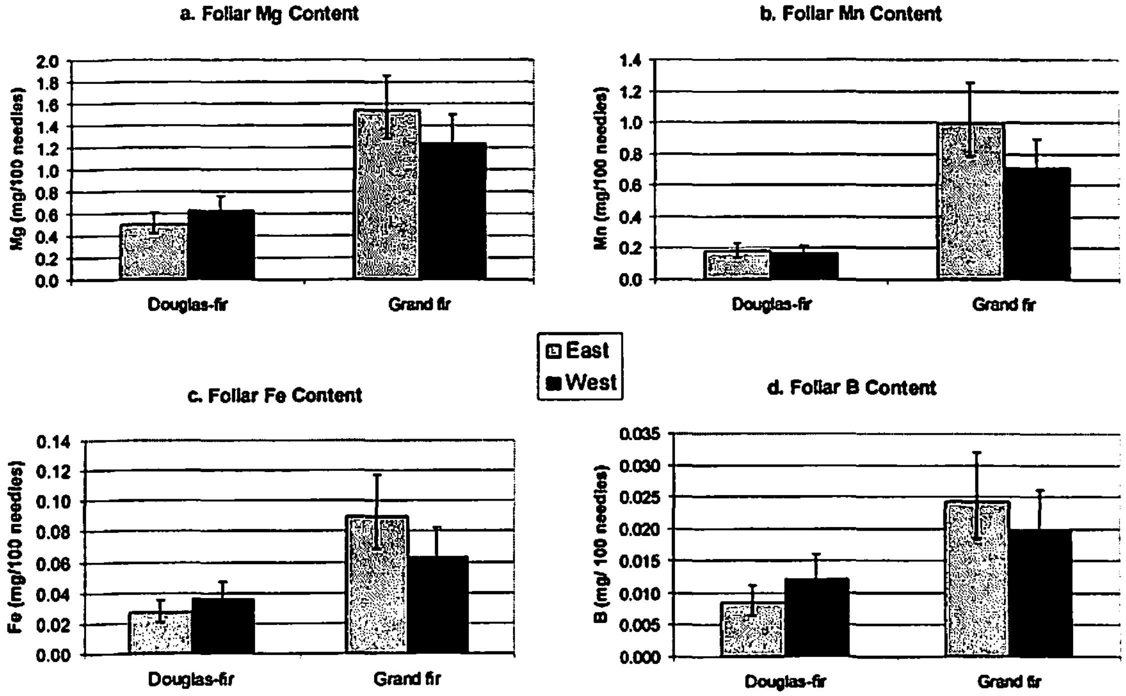


Figure 2-3. Species-by-crown class interaction of foliar nutrient content (mg 100 needles $^{-1}$) of (a) phosphorus (b) sulfur, (c) manganese and (d) copper in dominant/codominant and subordinate Douglas-fir and grand fir trees during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.

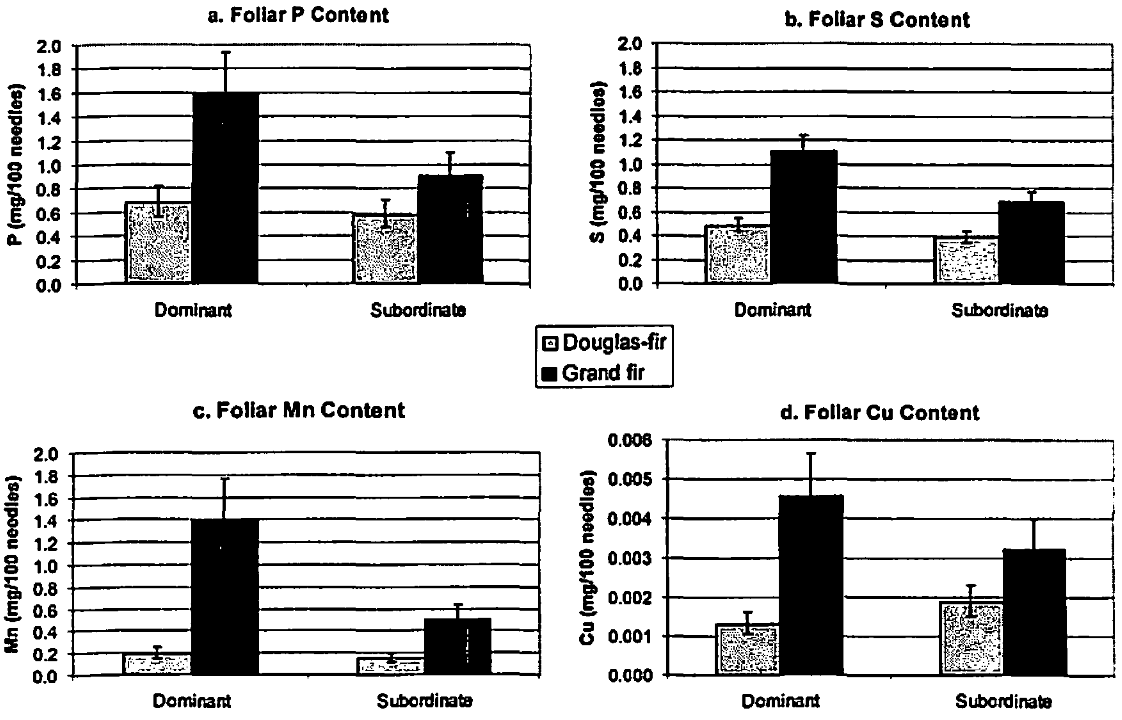


Figure 2-4. Block-by-crown class interaction of foliar nutrient content (mg 100 needles $^{-1}$) of (a) iron and (b) boron in dominant/codominant and subordinate crown class Douglas-fir and grand fir trees during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.

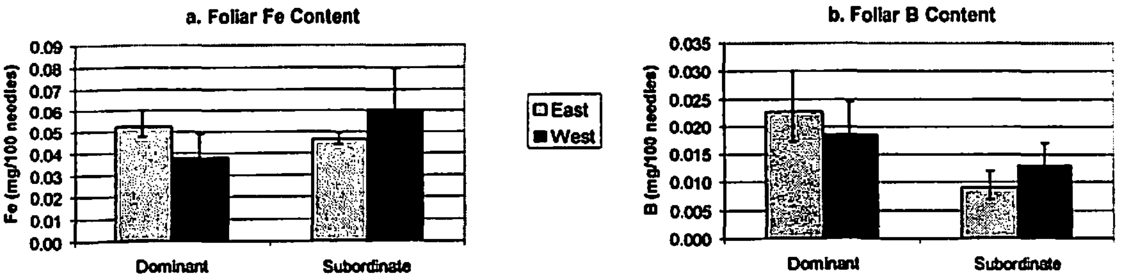
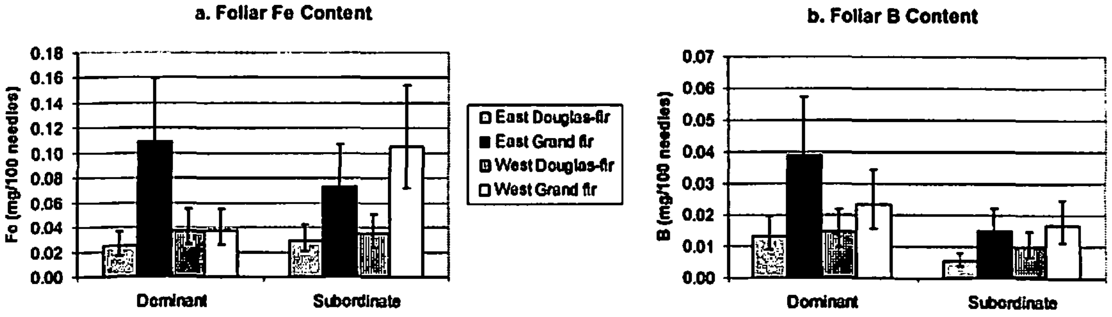


Figure 2-5. Block-by-species-by-crown class interaction of foliar nutrient content (mg 100 needles $^{-1}$) of (a) iron and (b) boron in grand fir and Douglas-fir dominant/codominant and subordinate crown class trees on eastern and western study blocks during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.

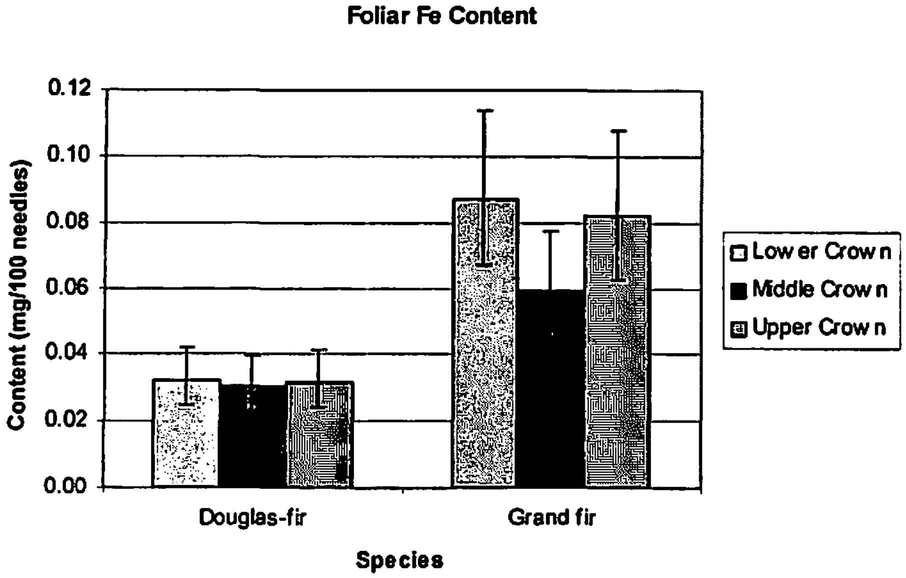


Crown position was significant for all elements except for Ca, Mn and Fe (Table 2-3). For all significant elements, nutrient contents increased from lower crown to upper crown. Calcium showed a significant five-way interaction between block, crown class, crown position, foliar age class and collection date, which was primarily due to foliar age class-by-collection date interactions among dominant trees on the eastern block. Manganese showed a significant four-way interaction between block, crown position, component and month, which was due primarily to a foliar age class-by-collection date interaction between the east and west block upper crown foliage. No obvious crown position effects were apparent for foliar Ca or Mn contents. Iron showed a significant crown position-by-species interaction, with lower crown Fe contents for grand fir greater than the middle crown and not different from upper crown (Figure 2-6). Douglas-fir foliar Fe contents were significantly lower than grand fir contents, and remained constant throughout the crown.

Table 2-3. Mean foliar elemental contents (mg 100 needles^{-1}) by crown position in a north Idaho conifer stand. Statistically significant values (p=0.10) are in bold italicized type. Elemental contents significantly different from one another by crown position are indicated by different letters in parenthesis.

Crown Position	Lower	Middle	Upper
Nitrogen	***6.3(a)***	***7.9(b)***	***9.7(c)***
Phosphorus	***0.8(a)***	***0.8(a)***	***1.1(b)***
Potassium	***4.1(a)***	***4.8(b)***	***5.9(c)***
Magnesium	***0.8(a)***	***0.8(a)***	***1.1(b)***
Calcium	6.48	6.33	6.42
Sulfur	***0.5(a)***	***0.6(b)***	***0.8(c)***
Zinc	***0.01(a)***	***0.01(a)***	***0.01(b)***
Manganese	0.36	0.37	0.42
Copper	***0.002(a)***	***0.002(a)***	***0.003(b)***
Iron	0.05	0.04	0.05
Boron	***0.01(a)***	***0.01(a)***	***0.02(b)***
Aluminum	***0.2(a)***	***0.2(b)***	***0.3(c)***

Figure 2-6. Species-by-crown position interaction of foliar iron content (mg 100 needles $^{-1}$) of grand fir and Douglas-fir foliage in the upper, middle and lower crown during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.



The foliage age class-by-collection date effect was significant for all elements (Figure 2-7). For one-and two-year-old foliage, all elemental contents remained the same between June and August except for one-year-old P content which decreased during that time. From August to October, all age classes increased in elemental content except for two-year-old N, K, Cu and Zn. One-year-old N, Mg, Ca, S, Mn, Cu, Fe and Al contents and two-year-old P, K, S, Mn, Fe, B, and Al contents were significantly greater in October than in June. Two-year-old Mg and Ca contents did not differ between June and October, and two-year-old N, Zn and Cu contents remained stable during the entire growing season.

Foliage age class was also analyzed within each collection date. In June, one-year-old foliar contents were less than two-year-old contents for Mg, Ca, S, Mn, Cu, Fe and Al, but not different for N, P, K, Zn and B. In August, current year foliar contents of N, Mg, Ca, Mn, Al, S and Fe were less than one-year-old contents, which in turn were less than two-year-old element contents. While current and one-year-old Cu contents did not differ from each other in August, both were less than two-year-old needle Cu content. August S and Fe contents were lower in current compared to two-year-old foliage, though there was no difference between current and one-year-old or between one- and two-year-old foliage. Current foliar B content was lower and K content greater in August than one- or two-year-old needle contents, but there was no difference between older foliage contents. Foliar P and Zn contents showed no difference between foliar age classes in August. In October, current foliage Ca, Mn and Al contents were less than one-year-old foliar contents, which in turn were less than two-year-old contents. While current N, Mg and B contents were lower and K content higher than both one- and two-year-old foliage in October, there was no difference between one- and two-year-old contents for those elements. Current Cu content was greater than for older needles, but one-year-old needle content was less than two-year-old content. Phosphorus and Zn needle contents did not differ between foliar age classes in October.

Figure 2-7. Foliar age class-by-collection date interaction of foliar nutrient contents (mg 100 needles $^{-1}$) of (a) nitrogen, (b) phosphorus, (c) potassium, (d) magnesium, (e) calcium and (f) sulfur in current, one-year-old and two-year-old Douglas-fir and grand fir trees during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.

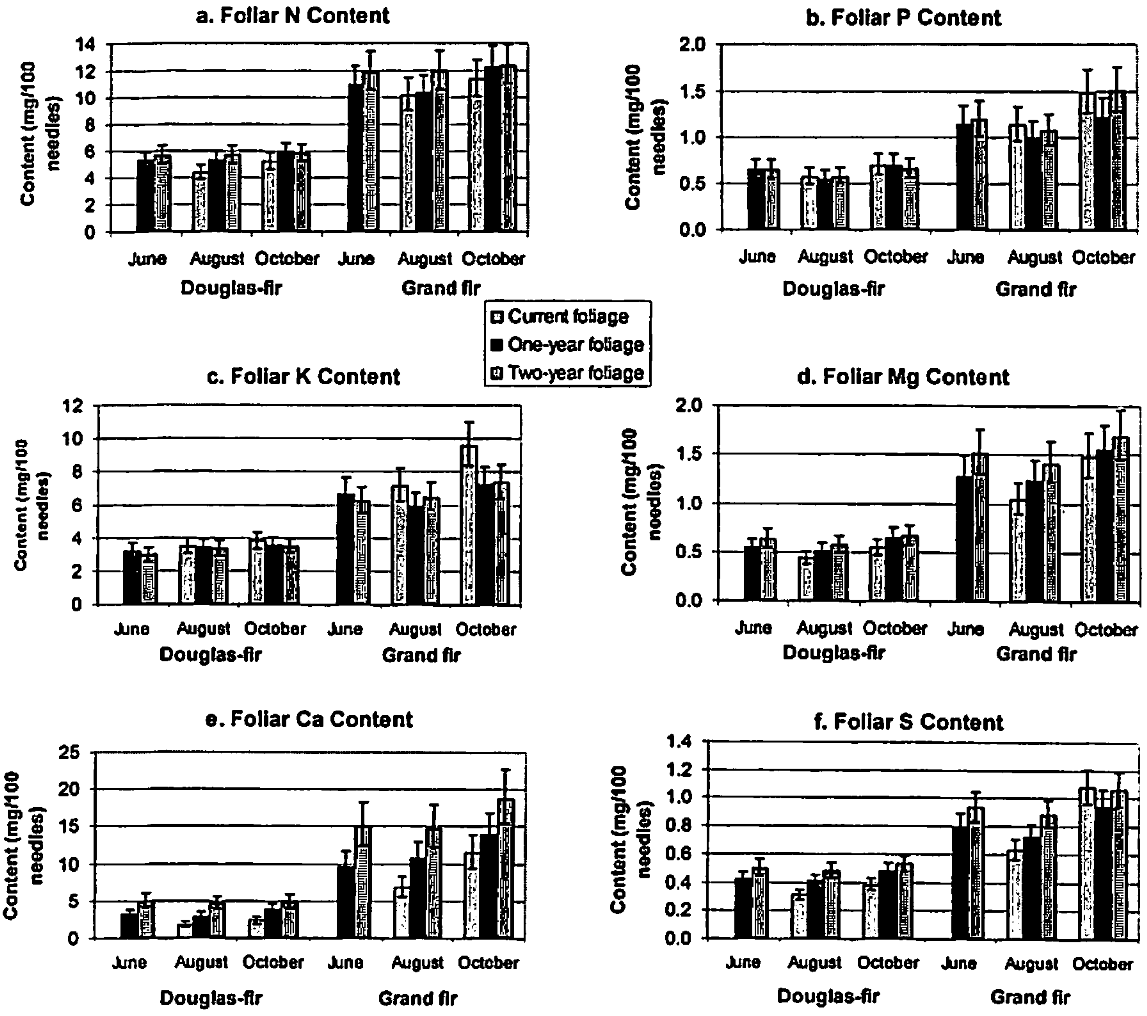
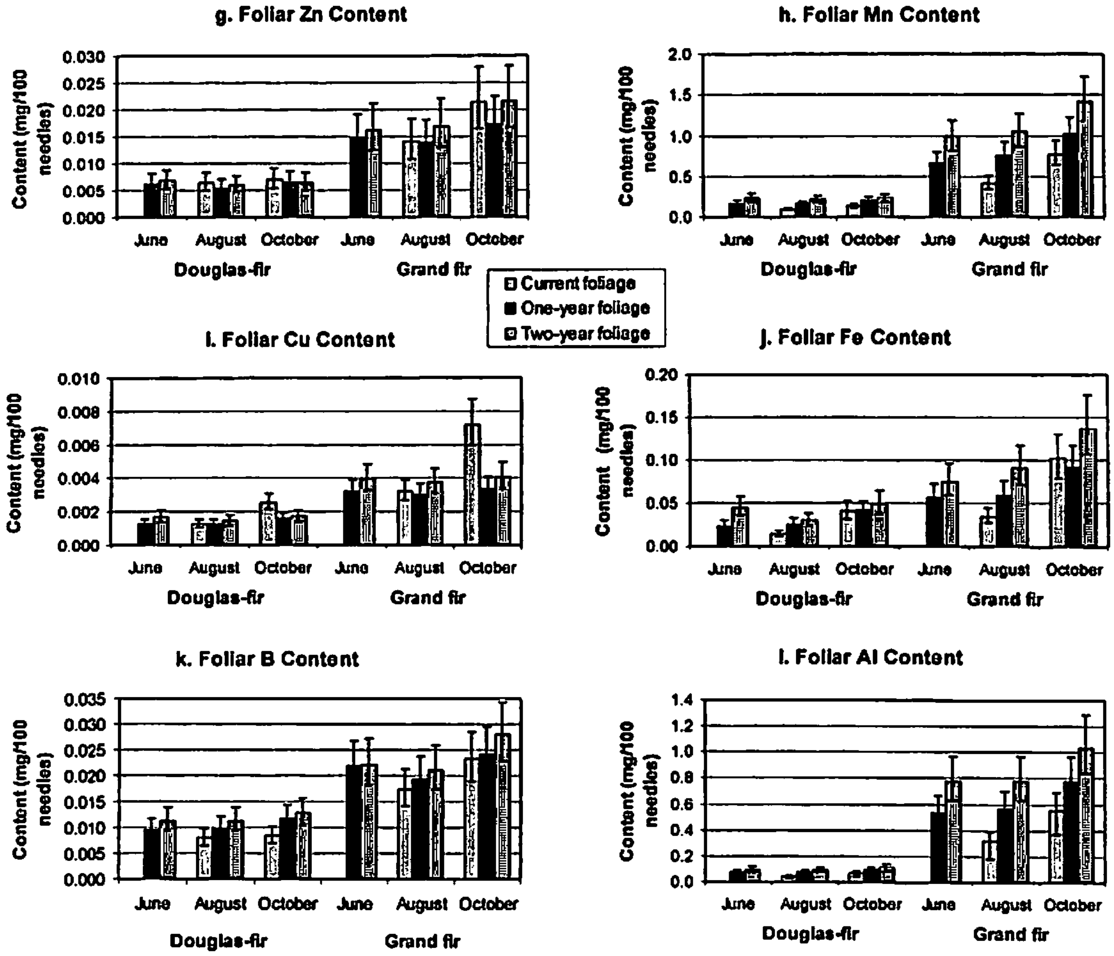


Figure 2-7 (concluded). Foliar age class-by-collection date interaction of foliar nutrient contents (mg 100 needles $^{-1}$) of (g) zinc, (h) manganese, (i) copper, (j) iron, (k) boron and (l) aluminum in current, one-year-old and two-year-old Douglas-fir and grand fir trees during the 1999 growing season in a north Idaho conifer stand. Error bars represent 10% confidence interval.



g. Foliar Zn Content

h. Foliar Mn Content

i. Foliar Cu Content

j. Foliar Fe Content

k. Foliar B Content

l. Foliar Al Content

Regardless of time of year or needle age, grand fir foliage contents were always greater than Douglas-fir contents. The charts in Figure 2-7 graphically demonstrate the age class-by-collection date-by-species effect. Foliar S and Mn were the only elements to show a significant three-way interaction between species, foliar age class and collection date (Figures 2-7f and 2-7h). In October, the current S content of Douglas-fir was lower than one-year-old content, which was lower than two-year-old content. In contrast, the October S content of current grand fir foliage was no different from two-year-old content, and both were greater than one-year-old content. Also, two-year-old Douglas-fir foliage showed no difference between the three collection dates, while S content of two-year-old grand fir foliage was greater in October than August, though neither was different from June. For Mn, Douglas-fir one-and two-year-old elemental contents did not differ from each other in October, while for grand fir the one-year-old content was lower than the two-year-old content. Although current and one-year-old foliar Mn contents for the two species behaved similarly throughout the growing season, two-year-old Douglas fir foliar Mn content remained constant while two-year-old grand fir Mn content was significantly greater in October than in June or August, which did not differ from each other.

Understory Vegetation

Analysis of variance for clip plot nutrient contents by growth form revealed no significant differences between blocks. Significant differences between growth forms were detected for N, K and Mn (Table 2-4). For Mn, shrub contents were significantly greater than forb contents. However for N and K, forb contents were greater. While not statistically significant, least squares means estimates showed shrub biomass was about 30% greater by dry weight than forb biomass.

Table 2-4. Manganese, nitrogen and potassium contents (kg ha^{-1}) and dry weight (kg ha^{-1}) of forbs and shrubs during the 1999 growing season in a north Idaho conifer stand. Dry weights were not significantly different from each other.

	Forb	Shrub
Nitrogen	2.2	1.3
Potassium	2.1	1.2
Manganese	.01	.02
Dry Weight Biomass	85.2	110.5

Analysis of variance of total understory vegetation elemental contents also showed no significant differences between blocks for any element. However, significant time effects were detected for N, P, K and S understory contents (Table 2-5). In all cases, October contents were significantly less than June and August contents, which did not differ from each other. Dry weight biomass estimates were included as well, which while not significant, also showed a tendency to be greater in June and August than in October.

Table 2-5. Mean elemental content (kg ha^{-1}) and dry weight (kg ha^{-1}) of total understory vegetation on three sampling dates during the 1999 growing season in a north Idaho conifer stand. Nitrogen, phosphorus, potassium and sulfur contents differed significantly between the three time periods (p=0.10). Elemental contents significantly different from one another by time period are indicated by different letters in parenthesis. Dry weights did not differ significantly during the growing season.

	June 15	August 15	October 15
Nitrogen	***3.38(a)***	***3.80(a)***	***1.97(b)***
Phosphorus	***0.36(a)***	***0.30(a)***	***0.16(b)***
Potassium	***2.95(a)***	***4.32(a)***	***1.87(b)***
Magnesium	0.33	0.47	0.35
Calcium	1.31	2.07	1.77
Sulfur	***0.26(a)***	***0.24(a)***	***0.14(b)***
Zinc	0.01	0.01	0.01
Manganese	0.03	0.04	0.04
Copper	0.002	0.002	0.001
Iron	0.03	0.05	0.03
Boron	0.004	0.005	0.004
Aluminum	0.03	0.04	0.03
Biomass dry weight	183.6	202.1	159.4

Litter Traps

Analysis of variance results showed that N and S litterfall contents on the east block were significantly greater than the west block (Table 2-6). Significant differences were also detected between collection dates for litterfall dry weight and all elemental contents (Table 2-7). Dry weight estimates showed that approximately 3.6 times more litter fell between August and October than between June and August. The late:early season ratio of nutrient contents for N, P, Mg and B were within 10% of this dry weight ratio. Potassium, Ca, S, Mn and Cu showed ratios more than 10% greater than the dry weight ratio, indicating greater nutrient contents during the latter half of the season. Zinc, Fe and Al showed ratios less than 10% smaller than the dry weight ratio, indicating proportionately greater chemical contents of early season litterfall for those elements.

Table 2-6. Nitrogen and sulfur contents (kg ha^{-1}) and dry weight (kg ha^{-1}) of litterfall during the 1999 growing season in a north Idaho conifer stand. Nitrogen and sulfur contents were significantly different from each other (p=0.10). Dry weights were not significantly different from each other.

Block:	Eastern	Western
Nitrogen	6.6	5.0
Sulfur	0.6	0.4
Dry Weight Biomass	839.1	733.0

Table 2-7. Elemental content (kg ha^{-1}) and dry weight (kg ha^{-1}) of litter by collection period during the 1999 growing season in a north Idaho conifer stand. Dry weights and all elemental litter contents were significantly different (p=.10) between early and late season.

	Early Season (June 15 - August 15)	Late Season (August 15 - October 15)	Ratio of Late:Early Season Litterfall
Nitrogen	3.3	9.9	3.0
Phosphorus	0.2	0.9	3.8
Potassium	1.2	5.3	4.4
Magnesium	0.3	1.3	3.9
Calcium	3.8	16.7	4.4
Sulfur	0.2	0.8	4.0
Zinc	0.02	0.04	2.1
Manganese	0.2	0.7	4.2
Copper	0.001	0.006	4.3
Iron	0.2	0.4	2.2
Boron	0.01	0.02	3.4
Aluminum	0.2	0.5	2.9
Dry Weight Biomass	344.3	1237.0	3.6

Forest Floor

No significant differences between blocks were detected for forest floor elemental content or dry weight (Table 2-8). Elemental values were highest for Ca, Fe and Al, all of which showed contents greater than 400 kg ha^{-1}. Nitrogen was the next highest at 320 kg ha^{-1}, while all other elements comprised 100 kg ha^{-1} or less of the forest floor. The smallest components of the forest floor elemental content were Zn, B and Cu, each of which comprised less than 2 kg ha^{-1} of the forest floor.

Table 2-8. Estimated nutrient content (kg ha^{-1}) and dry weight (kg ha^{-1}) of the forest floor in a north Idaho conifer stand.

Nitrogen	320.4
Phosphorus	31.1
Potassium	76.2
Magnesium	100.2
Calcium	481.2
Sulfur	29.4
Zinc	1.9
Manganese	48.4
Copper	0.5
Iron	478.0
Boron	1.4
Aluminum	407.2
Dry Weight Biomass	47909.0

DISCUSSION

Overstory Vegetation: Needle Dry Weights

Analysis of variance on needle dry weights showed no significant difference between blocks. A significant species effect was detected, with grand fir needles approximately twice the weight of Douglas-fir needles. This finding agrees with needle weight results reported for a compilation of experiments across interior northwestern U.S. (Moore et al., 2003). A significant crown class effect was also observed, with dominant tree needles significantly heavier than subordinate needles, which was also in agreement with findings by other researchers (van den Driessche, 1974; Naidu et al., 1998). A significant difference in needle weights between crown positions was detected, with upper crown needles heavier than mid-crown needles, which in turn were heavier than lower crown needles. These findings agree with those of other researchers (Smith, 1972; Bartelink, 1996). Findings related to both crown class and crown position were consistent with expectations based on their position and exposure to sunlight. Sun-exposed foliage is known to develop additional palisade mesophyll cells and harbor additional storage reserves, resulting in heavier needles as compared to shade foliage (Waring and Schlesinger, 1985).

Needle weights decreased between June and August, and then increased between August and October. The early-season decrease in needle weights was expected as resources were retranslocated to newly expanding shoots (Waring and Schlesinger, 1985). However the increase in late-season needle weight was somewhat contrary to expectations. Other studies have shown Douglas-fir needles continuing to decrease in weight during the later portion of the growing season (Smith et al., 1981; Kiiskila, 1996). In both of these studies, weight decreases were attributed to retranslocation, either prior to abscission for older needles, or prior to winter for younger age classes. In our study, the foliage age classes examined should remain on the tree so a pre-abscission weight decrease would not be expected, although a pre-dormancy weight decrease might occur. Although there was no significant species-by-collection date-by-foliar age class effect, pairwise comparisons of August and October data for all foliar age classes showed that the increase in Douglas-fir needle weight during this period at Mallory Creek was negligible, while the increase in grand fir needle weight was substantial. Consequently, the grand fir needles drove the average needle weights higher during the August to October period. Needle weights also increased with increasing foliar age class. Douglas-fir and grand fir both displayed this pattern, and there was no interaction or significant difference between the two species. A study of Douglas-fir foliage from several sites and age classes showed similar trends with respect to needle age class (Bartelink, 1996). Van den Driessche (1974) points out that year-to-year variation in foliage is not unexpected since many of the factors which influence foliar characteristics vary between years. Climate data from area weather stations indicated a steady decrease in annual precipitation from 1996 through 1999, which probably explains the yearly decrease in needle weights for the three age classes examined in our study (Idaho State Climate Services, 2002).

Overstory Vegetatation: Nutrient Contents

The combined nutrient concentrations of all elements totaled less than 5% of needle composition, on average. Therefore, needle dry weights largely influenced nutrient contents and their statistical significance. The same effects which were significant for needle weights were usually significant for nutrient contents; however the block effect, which was not significant for needle weights, was significant for P and Cu. Contents of both elements were greater on the eastern block. Copper differences were quite minor, with only 0.1 μg difference per 100 needles, which may not represent a physiologically significant difference between blocks. Phosphorus content differences were comparatively greater at almost 188 μg difference per 100 needles. Both Cu and P play important roles in photosynthesis and plant metabolism. Copper is needed for N metabolism and affects plant carbohydrate content, while P is important in starch synthesis and carbon partitioning during photosynthesis (Marschner, 1995). While neither element had foliar concentration deficiency levels on either block (Powers, 1983; Webster and Dobkowski, 1983), it is possible that the higher Cu and P contents in the eastern block foliage contributed to higher N-fertilization response for that block.

Grand fir foliage contents were greater than Douglas-fir foliage contents for all elements studied. Needle weight for grand fir was about double that for Douglas-fir, and most foliar elemental contents followed this same proportion. This implies that grand fir took up approximately twice as many elements as Douglas-fir in order to maintain the same concentrations as Douglas-fir. Exceptions were Ca, Mn and Al contents, which were approximately 3.5, 5 and 8 times greater for grand fir than Douglas-fir respectively, indicating that even greater amounts of these elements were taken up by grand fir. Calcium is known to be an important structural component of cell walls and membranes (Marschner, 1995), which could explain the greater Ca content of the heavier grand fir needles. Excess Al in plants is thought to have an antagonistic effect on Ca by reducing Ca transport (Kabata-Pendias, 2001), so another possibility is that the high Al content of the grand fir needles induced the higher Ca contents of those same needles by reducing Ca retranslocation capability. Reasons for the disproportionately greater Mn and Al contents for grand fir were less clear. Both elements show a propensity to be taken up at greater rates under particularly acid soil conditions (Marschner, 1995). We surmise that because grand fir uptake was more aggressive than Douglas-fir uptake for all elements, and because cation uptake in particular stimulates H^+ exudation by plant roots, that the grand fir rhizosphere may have developed increased acidity as compared to the Douglas-fir rhizosphere. This in turn could have led to increased Al and Mn uptake by the grand fir, perhaps creating a positive feedback cycle of increasing acidity and uptake. Aluminum is thought to control cellular colloidal properties in some plant systems (Kabata-Pendias, 2001), while Mn is involved in numerous enzymatic reactions and photosynthetic oxygen evolution (Marschner, 1995; Kabata-Pendias, 2001). Thus, species differences in physiological processes may also be responsible for the greater grand fir Al and Mn contents.

Foliar contents of N, P, K, Mg, S, Zn, Mn, B and Al were significantly greater for dominant trees compared to subordinate crown classes. Most elemental contents were about 1.3 to 1.9 times greater in dominant than in subordinate tree foliage, reflecting the needle weight difference which was about 1.6 times greater for dominants.

The block-by-species interactions for Mg, Mn, Fe and B reflected differences in the way species behaved between the two blocks. Grand fir contents were greater on the eastern block compared to the western for Mg, Mn and Fe, while Douglas-fir contents were greater on the western than the eastern block for Mg, Fe and B. As expected, grand fir contents were greater than Douglas-fir contents in all cases. The lower Mg, Fe and B contents of Douglas-fir on the eastern block could be interpreted as being indicative of lower overall availability of these elements on that block, since Douglas-fir dominates the stand. However by the same reasoning, the block-by-crown class interaction showing greater Fe and B contents of dominant trees on the eastern block could also be interpreted as indicating greater availability of these same elements on the eastern block, since dominant/codominant trees also dominate the stand. Examination of the three-way interaction between block, species and crown class for Fe clarified that within the dominant/codominant crown class, Douglas-fir trees had higher Fe contents on the western block (Figure 2-5a). Since dominant Douglas-fir trees dominated the stand, this was probably indicative of greater Fe availability on the western block. In contrast, the three-way interaction for B (Figure 2-5b) indicated no real difference in B content between the east and west blocks for dominant Douglas-fir trees.

The species-by-crown class interactions for P, S, Mn and Cu were informative. Grand fir contents were greater than Douglas-fir contents for all elements, and dominant grand fir had greater elemental contents than subordinate grand fir, as expected based on needle weights. The significant interaction shows that Douglas-fir behaved somewhat differently than grand fir. For P and Mn, there was no difference between dominant and subordinate Douglas-fir, even though dominant trees had heavier needles than subordinate trees. This indicated an accumulation of P and Mn in the foliar tissue of the subordinate trees. Similarly, subordinate Douglas-fir had greater Cu content than dominant Douglas-fir, while S content of dominant Douglas-fir foliage was greater than subordinate Douglas-fir. Soil ion exchange analyses and foliar diagnostics indicated that the site may be deficient in S (Garrison-Johnston, 2003a), hence the dominant trees may be out-competing the subordinate trees for that element. However subordinate Douglas-fir accumulated P, Mn and Cu in amounts disproportionate to subordinate tree needle weights. Because Douglas-fir is less tolerant to shading than grand fir, the subordinate Douglas-fir trees may be somewhat stressed compared to dominant trees and grand fir. Perhaps subordinate trees respond to environmental stresses in some manner requiring the accumulation of these elements in foliage. All three elements function in photosynthetic processes and various enzymatic processes (Marschner, 1995).

Foliage elemental contents of N, P, K, Mg, S, Zn, Cu, B and Al were highest in the upper crown and decreased lower in the crown for both species. Calcium, Mn and Fe did not change with crown position. These results generally reflected the needle weights, which were greatest in the upper crown and lowest in the lower crown. The N and P results in our study agree with those of Webber (1977) who showed N and P increasing with height in the crown for Douglas-fir (Webber, 1977). Our Ca, Mg and K content patterns within the crown differed from those observed by Webber (1977). Other studies have demonstrated nutrient concentration changes within the crown, with N, P, K, and Mg usually increasing with height in the crown, and Ca decreasing (Lavender and Carmichael, 1966; van den Driessche, 1974). A Ca concentration decrease higher in the crown also explained our results, as this decrease coupled with the increasing needle mass caused the nutrient content shift to be insignificant.

Nutrient contents differed with needle age and collection date for both species. While needle dry weight of one- and two-year-old foliage decreased between June and August, nutrient contents did not change during this period, except for a decrease in P content of one-year-old foliage. This result suggests that while carbohydrate reserves may have shifted to new foliage production, nutrients apparently did not, except for P. A nursery study of Douglas-fir seedlings showed that carbohydrates and P shifted from year-old to new foliage just prior to and following bud break (Krueger, 1967). A study of young field-grown Douglas-fir trees in British Columbia showed results similar to ours in that one-and two-year-old foliage contents did not change much between June and August for most elements (Kiiskila, 1996). Exceptions were N and K, both of which decreased between June and August in their study, while in our study they remained fairly constant. Another study of young field-grown Douglas-fir trees over the course of one year in Oregon showed nutrient concentrations of N, P, K and Ca in one- and two-year-old foliage increasing between April and July, while Mg concentration decreased during this time period (Lavender and Carmichael, 1966). In our study, the decrease in needle weight between June and August coupled with no change in elemental content means that elemental concentrations increased, such that less foliage weight maintained the same element content. Thus, Lavendar and Carmichael's (1966) findings for N, K and Ca were similar to ours, though those for P and Mg differed. A different study of young Douglas-fir trees in the Washington Cascade range showed that older foliage maintained fairly constant N contents throughout the spring and early summer (Smith et al., 1981). They also suggested that the short growing season of the Cascade range relative to the Oregon Coast range probably produces greater variation in carbohydrate demand and related variation in leaf weights during the growing season. Our north Idaho site is likely similar to Smith et al.'s (1998) Cascade range site in growing season length. Furthermore, perhaps some nutrient retranslocation from older foliage may have already occurred prior to our first sampling, which was at or just after bud-break. Retranslocation seems plausible in light of findings by Kiiskila (1996), who showed a number of elements in one-and two-year-old Douglas-fir foliage declined sharply prior to bud-break.

Current and one-year-old needle content of all elements and two-year needle content of all elements except K, N, Zn and Cu increased between August and October. Two-year-old needle K content increased between June and October, while N, Zn and Cu contents remained constant across the entire growing season. Needle weights increased between August and October for all foliar age classes. This suggests that most elemental concentrations either remained constant or perhaps increased in order to maintain or increase in content during that time. These results partially agree with those of an Oregon Douglas-fir seedling study, where new shoot concentrations of Ca, Mg, Mn and Fe concentrations increased, although N and P declined and K, Cu, B and Zn concentrations varied greatly (Proebsting and Chaplin, 1983). Our results also generally agree with those of Lavender and Carmichael (1966), who showed P, K, Mg and Ca concentrations increased between July and October, while N concentrations decreased slightly or remained constant. Our findings also partially agree with Kiiskila (1996), who showed all current year contents increased over the course of the growing season, though only P, K, Mg and Fe contents of older foliage increased between August and October. Older foliage content of other elements either decreased or did not change during this period in the Kiiskila (1996) study. The universal increase in elemental contents of young foliage during the latter part of the growing season in our study was likely due partly to an increase in storage reserves prior to winter dormancy, and perhaps also in preparation for the development of the next year's foliage, as well as retranslocation from abscising needles.

At each collection date, most elemental contents were greater in older foliage than in younger foliage, though some elements showed no difference in content between foliar age classes. These results generally reflected yearly needle weight variation. Notable exceptions were K in August and K and Cu in October, where current foliage contents were greater than older foliage contents, and current grand fir needle S content in October, which was greater than one-year-old S content. Interestingly, Kiiskila's (1996) study showed very similar results for Douglas-fir, with older foliage having greater nutrient contents for all elements except K, which was significantly greater in current foliage than older foliage by the October sampling (Kiiskila, 1996). A study of mature Douglas-fir in an Idaho stand also showed higher K concentration in current than in older foliage (Nelson, 2000). While the reasons for greater K and Cu content in current compared to older foliage in October and greater S content for current grand fir foliage in October in our study are unclear, we surmise that these elements were retranslocated to current foliage later in the growing season prior to bud set and dormancy. Copper affects carbohydrate content (Marschner, 1995), and hence could be affecting pre-dormancy reserves. Similarly, K and S serve in various capacities related to stomate function, glucose transformation, photosynthesis, protein synthesis and other processes which could play important roles in tree preparation for winter dormancy.

Grand fir foliage contents of all elements were greater than Douglas-fir foliage contents, regardless of time of year, crown class, crown position or needle age. This suggests that a stand composed primarily of grand fir will place a higher nutrient demand on a site than an equivalent stand of Douglas-fir growing on the same site. Other studies in the region have shown similar findings of greater grand fir nutrient contents compared to other tree species (Garrison et al., 2000; Moore et al., 2003). Other studies have also provided comparisons of foliar nutrient and biomass dynamics of various other species and sites (Clayton and Kennedy, 1980; Gower et al., 1993; Miller et al., 1993). All of these studies indicated that tree nutrient demand is related to species-specific canopy dynamics and foliar characteristics. Interestingly, species nutrient demand in those studies also reflected relative shade-tolerance, with nutrient demand increasing as shade tolerance increased. Hence, as species composition shifts from predominantly shade-intolerant species to predominantly shade-tolerant species, nutrient demand on the site should also increase. This implies that stand species composition is an important component of forest nutrient management decisions ranging from reforestation to intermediate silvicultural activities.

Understory Vegetation

Understory vegetation at the Mallory Creek study site primarily consisted of forbs and shrubs. Only Mn, N and K showed significant differences between growth forms, with Mn content of shrubs greater than forbs, and N and K content of forbs greater than shrubs. While not statistically significant, least squares means estimates indicated that shrub biomass was greater than forb biomass, which could help explain the greater Mn contents of the shrubs. Agricultural researchers have found that Mn is commonly returned to plant stems as leaves senesce (Tiffin, 1972). Therefore we might expect shrubs to retain greater amounts of Mn than forbs due to their woody tissues. Nitrogen and K, on the other hand, are involved in photosynthetic processes and therefore more likely to be associated with herbaceous tissues, which explains their higher contents in the forb component of the understory.

Total understory vegetation contents of N, P, K and S were lower in October than in June or August, which were not different from each other. No other elements showed significant differences across the growing season, though all followed a similar tendency of decreasing late in the season. Nutrient contents reflected understory biomass, which also tended to decrease later in the season. Light availability to the understory affects understory biomass production (Jameson, 1967; Riegel et al., 1995; Lieffers et al., 1999; McKenzie et al., 2000). While we did not measure incident radiation during this study, we surmise that because day length shortened and sun position moved south during the course of our measurement period, incident radiation probably decreased. Thus, the decrease in understory biomass and therefore nutrient content toward the end of the growing season was not unexpected. While few studies detailing changes in nutrient content of understory vegetation during the growing season were available, other workers have shown similar early-season peaks in nutrient content coincident with biomass (VanderSchaaf, 1999; Tremblay and Larocque, 2001). Furthermore, herbaceous vegetation is known to retranslocate some nutrients out of senescing tissue prior to abscission (Tiffin, 1972; Salisbury and Ross, 1985; Tremblay and Larocque, 2001), and some abscission did occur prior to the October sampling date, also explaining the late-season decrease in nutrient content.

Litter Traps

Litter trap nutrient contents were greater on the eastern block for N and S. Differences were small, about 1.5 kg ha^{-1} for N and 0.2 kg ha^{-1} for S. While not statistically significant, a greater amount of total litterfall was collected on the eastern block, and probably explains why significantly greater N and S contents were detected on the eastern block. Alternatively, the results may reflect higher N and S nutrient use efficiency and cycling on the eastern block (Vitousek, 1982). This could also be related to greater soil availability of these two elements on the eastern block, as reported in a companion paper (Garrison-Johnston, 2003a). Greater soil S availability could also explain the better N fertilization response for the eastern block during the earlier fertilization trials.

Significantly more litter was collected during the latter than the early half of the growing season. Similar results have been reported in other litterfall studies (Zavitkovski and Newton, 1971; Rustad and Cronan, 1989; Miller et al., 1996; Nelson, 2000). In our study, approximately 3.6 times more litter dry weight fell during the latter half of the growing season. The late to early season ratios of P, Mg and B contents generally approximated this weight-based ratio. While P and Mg show good mobility in plants and B shows poor mobility (Marschner, 1995), these three elements appeared to retranslocate at about the same rate when comparing the earlier to the later part of the season. In contrast, late season litter contents of K, Ca, S, Mn and Cu were higher than the dry weight ratio explains, while late season contents of N, Zn, Fe and Al were lower. This suggests greater early-season retranslocation efficiency for elements in the first group, and greater late-season retranslocation efficiency for those in the second group. Our results generally agreed with those of several other studies for the late to early season dry weight ratio and most elemental contents (Rustad and Cronan, 1989; Miller et al., 1996; Nelson, 2000). Our findings did not always agree for P, K and Mg litterfall contents, however variation in forest type and climatic regime probably explain those differences. Litter composition is another factor that may contribute litterfall dry weight and nutrient content seasonal differences, as early season litterfall was comprised largely of grand fir and Douglas-fir needles and bud scales, while late season litterfall contained annual shrub and forb leaves in addition to tree needles.

Forest Floor

Forest floor content of most elements generally reflected those found by other Douglas-fir forest researchers (Cole et al., 1967; Turner, 1975; Vesterdal and Raulund-Rasmussen, 1998; Nelson, 2000). Forest floor dry weight biomass and N, P and K content in a similar study in central Idaho showed about 1.5 times more dry weight and N and K contents compared to our study, but about 2.5 times greater P content (Nelson, 2000). The greater quantity of forest floor at that site was probably due to drier conditions with correspondingly lower decomposition rates. The forest floor at Nelson's (2000) site contained a significant pine component, with different decomposition characteristics and P mineralization rates. Our study site showed higher forest floor Ca content than other sites, particularly considering total forest floor biomass amounts (Turner, 1975; Vesterdal and Raulund-Rasmussen, 1998). This result suggests Ca immobilization in the forest floor at our site. This is particularly of interest in light of our finding of rapidly decreasing soil-available Ca based on our nutrient cycling model projections (Garrison-Johnston, 2003b). Prescott et al. (2000) found significant correlation between litterfall and forest floor Ca contents (Prescott et al., 2000). At our site, such a relationship would imply that Ca in litterfall was quite high, and in fact we did find that older grand fir needles had very high Ca values compared to Douglas-fir (Figure 2-7e), and perhaps could have influenced forest floor content. Other researchers have found grand fir forest floor Ca content to be significantly higher compared to Douglas-fir forest floors, also indicating that perhaps the grand fir foliage at our site influenced forest floor Ca content (Vesterdal and Raulund-Rasmussen, 1998). Furthermore, forest floor contents measured in October were probably influenced by the August to October litterfall, which was notably higher in Ca and several other elements compared to earlier-season litterfall.

Nutrient Cycling Data Compilation

Compilation of forest nutrient cycling data requires extensive measurement of various ecosystem components. We detected significant differences in species, crown class, crown position, foliar age class and time of year for overstory foliage. These results mean that all of these factors must be accounted for in construction of a nutrient cycling model. This presents a logistical challenge, particularly for studies in uneven-aged mixed-species stands. All significant species and crown classes would need to be sampled. However, variability in foliar age class and crown position could be accounted for by compositing foliage during sample processing (Carter and Lowe, 1986). The timing of sample collection depends on the time step being modeled. Perhaps a more accurate assessment of seasonal nutrient movements during our study could have been obtained by sampling at least once prior to bud flush. Fall sampling just after bud set provides a reasonable estimation of annual elemental content, since nutrients are generally more stable at that time. Furthermore, fall sampling coincides with recommended foliar diagnostic sampling protocols (van den Driessche, 1974; Ballard and Carter, 1985; Cole and Gessel, 1992; Moore et al., 2003).

Variability in understory nutrient content did occur during the growing season and between growth forms for some elements during our study. The understory as a whole represented a very small proportion of total above-ground nutrient pools because our experimental site was a mature stand. The understory component becomes more significant in less dense stands (Alaback and Herman, 1988; Klinka et al., 1996; Tremblay and Larocque, 2001), and would probably be an important component of the above-ground elemental pools early during stand development.

Litterfall also showed variability during the growing season in our study. Numerous other studies have shown similar trends, and also have shown that litterfall quantity and quality vary greatly with species composition (Attiwill, 1968; Trofymow et al., 1991; Prescott et al., 1993; Miller et al., 1996; Kavvadias et al., 2001). Assessment of annual litterfall also requires collection during the winter season, which was not conducted in this study. Forest floor elemental contents were measured at only one point during the growing season. One sample is probably sufficient for short-term nutrient model estimation, however other researchers have shown that forest floor contents change over the course of stand development (Turner, 1975). Thus, forest floor and litterfall would be important ecosystem components to evaluate during various stages of stand development.

CONCLUSIONS

Overstory and litterfall dry weights and elemental contents showed differences between blocks which might explain past N fertilization response differences. Overstory foliar P and Cu contents were greater on the eastern block than the western block, and assuming the same situation at the time of past fertilization trials, better availability of these elements might have contributed to the higher response of the eastern block to N fertilization. Greater N and S contents were detected in litterfall on the eastern block, and while this may have resulted from greater litter mass, it may also indicate higher nutrient cycling rates and nutrient use efficiency, which could also support higher fertilization response on the eastern block. No block differences were detected for understory or forest floor elemental contents.

Overstory vegetation showed significant differences by tree species, with grand fir needles weighing about twice as much as Douglas-fir needles. Elemental contents showed similar species differences, with grand fir content of most elements about double that of Douglas-fir. Grand fir Ca, Mn and Al contents were proportionately even greater than other elemental contents compared to Douglas-fir, implying greater uptake rates by grand fir for those three elements. Overall, the finding of greater nutrient content for grand fir suggests that this shade-tolerant species placed a greater nutrient demand on the experimental site than the less tolerant Douglas-fir. This implies that manipulation of stand species composition through regeneration or intermediate silvicultural operations is an important nutrient management tool.

Other significant findings related to overstory foliar chemistry dynamics were also evident. Dominant tree needles were heavier than subordinate tree needles, and needles higher in the crown were heavier than needles lower in the crown. These findings were consistent with the degree of foliage exposure to sunlight. Foliar contents for most elements followed the same patterns. We also found evidence of significant foliar age class differences and seasonal differences for Douglas-fir and grand fir. Overstory elemental content of new foliage always increased between August and October. Older tree foliar elemental contents either did not change or slightly decreased in content between June and August, and then slightly increased between August and October. Older needles generally were heavier and had higher nutrient contents than younger needles. Our findings could be explained by nutrient retranslocation to new growth and perhaps storage prior to bud formation and dormancy.

Growth form differences in nutrient contents of understory vegetation were also detected, as were seasonal differences. Understory shrubs contained significantly more Mn than did forbs, primarily due to the greater woody tissue content and seasonal foliage longevity of the shrubs. Understory forbs contained more N and K than did shrubs, due to their greater quantity of non-woody tissue. Total understory vegetation contents of N, P, K and S were lower in October than in June or August, and all elemental understory contents followed a similar trend of decreasing late in the season, reflecting lower understory biomass in the fall.

Litterfall dry weight and nutrient contents were greater during the August to October period than the earlier period, and for the most part these estimates were similar to those reported by other researchers. Forest floor content of most elements was also within expected ranges, however Ca content seemed quite high compared to other studies, particularly considering the relatively low forest floor biomass amounts. The high forest floor Ca content may be explained by the high grand fir foliar Ca content detected at our study site, and also may have been influenced by late-season litterfall, which occurred just prior to forest floor sample collection.

The significant differences in overstory nutrient contents by species, crown class, foliar age class, crown position and time of year indicate that these factors all must be accounted for during nutrient cycling data compilation. Similarly, several differences in understory growth form and time of year were detected, and litterfall elemental contents changed significantly over the course of the growing season.

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Forest nutrient cycling in a north Idaho conifer stand III: A systems analysis approach to modeling seasonal and annual nutrient dynamics of a forest ecosystem

Abstract. Overstory, understory, forest floor and soil elemental contents and litterfall flows of N, P, K, Mg, Ca, S, Zn, Mn, Cu, Fe, B and Al were measured during one growing season in a north Idaho conifer stand. These data were compiled into a systems analysis model of forest elemental cycling, and projected over a three-year period. Overstory elemental contents increased both seasonally and annually, while understory contents varied seasonally, but decreased annually. Late-season litterfall contents were greater than early-season contents, while estimated winter litterfall contents exceeded measured seasonal litterfall contents. Throughfall was not measured during this study, but proved to be a useful mechanism for transferring elements from vegetation to the forest floor as needed to meet seasonal decreases in overstory and understory elemental contents. Model simulations were performed for three overstory tree species composition scenarios. One simulation represented the actual mixed conifer overstory composition of the stand, while the other two simulations treated all overstory trees as either grand fir or Douglas-fir, with all other stand characteristics held constant. Results of the three simulations were compared to evaluate the effect of species composition on forest nutrient cycling. Grand fir overstory contents were higher than Douglas-fir or mixed conifer species compositions for all elements except Zn and Cu, which were higher for Douglas-fir. Overstory Ca, K, P and Mn contents were about 1.5 to 4 times greater for the grand fir simulation than Douglas-fir. Quantity and timing of seasonal and annual overstory elemental uptake varied with species composition, as did tree throughfall. Soil nutrient reserves for all elements except Fe and S decreased over time.

Nitrogen, P, Mg and Ca soil reserves were projected to be depleted within a few years for all species composition scenarios. Soil reserves were depleted faster under the grand fir scenario compared to Douglas-fir. Model estimates of soil nutrient pools may have been inadequate. Overall, systems analysis was a useful tool for evaluating forest elemental cycling. A better understanding of seasonal and short-term nutrient dynamics and component interactions of the experimental stand was obtained. Those boxes and flows requiring additional data collection were identified. Future research efforts should focus on tree nutrient content estimation for various species, soil nutrient pool estimation and monitoring, forest floor mineralization, and overstory and understory content changes. Tree and plant uptake might be best represented as a function of soil nutrient availability. Improved monitoring of year-round litterfall, throughfall and external inputs would be useful as well.

INTRODUCTION

Many forest nutrition studies focus largely on nitrogen (N), probably because this element has most often been identified as a growth-limiting factor in forest stands (Heilman and Gessel, 1963; Powers, 1980; Peterson et al., 1984; Moore et al., 1991; Tiedemann et al., 1998; Chappell et al., 1999). A number of studies have examined the elemental contents of overstory vegetation in forest stands for various other elements (Cole et al., 1967; Turner, 1975; Gordon, 1983; Pang et al., 1987; Miller et al., 1993; Mitchell et al., 1996). Often, the effects of forest harvesting on remaining site reserves are discussed (Timmer et al., 1983; Johnson, 1983; Bigger and Cole, 1983; Smith Jr., 1984; Clayton and Kennedy, 1985; Turner and Lambert, 1986; Moller, 2000). Quantification of stand disturbance effects on site nutrient reserves typically concentrates on soil nutrient reserves, and ranges from estimates of soil exchangeable cations to streamwater hydrologic losses (Feller and Kimmins, 1984; Tew et al., 1986; Mann et al., 1988; Olsson et al., 1996; Hopmans et al., 1987). Most forest nutrition studies do not provide information on micronutrients or non-nutritional elements such as Al. Even fewer studies attempt to integrate the nutrient dynamics of multiple ecosystem components into a nutrient cycling framework.

A systems analysis approach to compartmentalizing ecosystem components and modeling nutrient cycle interactions would provide a valuable framework for understanding and evaluating ecosystem nutrient dynamics (Pugh, 1977; Aber and Melillo, 2001; Muetzelfeld, R., 2003; Garrison-Johnston, 2003a). Such a model could describe the effects of seasonal climatic changes on stand nutrient dynamics, or the scale could be expanded to describe long-term stand development. Systems analysis allows visualization of the effects of stand nutrient content manipulations on other ecosystem components, without necessarily describing all of the finer-scale processes contributing to nutrient fluxes. Several researchers have presented similar conceptual approaches for evaluating macronutrients and Mn over the course of stand development or in response to harvesting activities (Cole et al., 1967; Turner, 1975; Gordon, 1983). Other studies present nutrient cycling information for particular ecosystem components such as overstory, understory, litterfall, forest floor or soils (Rustad and Cronan, 1989; Prescott et al., 1993; Miller et al., 1993; Olsson et al., 1996; Moller, 2000; Nelson, 2000; Tremblay and Larocque, 2001; Kavvadias et al., 2001; Dijkstra, 2003).

A systems analysis approach was selected to integrate the dynamics of soil, understory and overstory vegetation and litterfall chemistry measured at one experimental site during one growing season. This 'box and flow' method was selected for its value in synthesizing complex interactions into a simplified and comprehensible form. By describing elemental fluxes during one growing season, a better understanding will be gained of the seasonal dynamics and interactions of various ecosystem components. By extending estimates of elemental dynamics to an annual basis, a better understanding of component interactions should be developed. Furthermore, model construction provides a better focus for future research efforts in forest nutrient cycling and the evaluation of various forest management options.

MATERIALS AND METHODS

Site Selection

During the early 1980's, fertilization trials were established in numerous Douglas-fir stands throughout the inland northwest in order to determine which site characteristics might be associated with various levels of fertilization response (Moore et al., 1991; Mika and VanderPloeg, 1991; Shen et al., 2000). Because of the consequent availability of long-term tree measurements and some understanding of past fertilization response, a detailed study of the nutrient dynamics at one of these sites was undertaken to develop a seasonal nutrient cycling model.

Site Characteristics

The Mallory Creek study site was located 14 miles northeast of Bovill, Idaho in the Inland Northwest of the United States, with latitude approximately 46° 50' and latitude 116° 16', Boise meridian. The elevation was approximately 1036 m. The study stand was approximately 50 ha in area, and located on generally southern-facing, slightly undulating hillslopes, with aspects ranging between 170 and 230°, and slopes ranging from 15 to 25%. Average annual precipitation between 1971 and 2000 was approximately 92 cm yr^{-1}, based on weather station data from nearby Elk River, Idaho (ISCS, 2003). Precipitation during 1999, the year of this study, measured slightly higher than normal at the Elk River weather station, with rainfall averaging 98 cm yr^{-1}. Weather station estimates of precipitation between June and September totaled about 13 cm, and on-site rain gauges at the Mallory Creek site also measured approximately 13 cm of precipitation during the study period. Air temperatures between 1971 and 2000 at Elk River ranged from –0.2 to 13.2° C, with a mean of 6.6°C (ISCS, 2003). During 1999, Elk River air temperatures averaged 6 °C , and ranged from a minimum of 0 °C to a maximum of 12 °C. From June through August of 1999, the mean air temperature at Elk River was 16 °C, with a minimum of 7 °C and a maximum of 24. Air temperatures measured at the Mallory Creek study site during the 1999 study period were normal, ranging from 3 °C to 28 °C, and averaging 16 °C.

The study stand was approximately 50 years old at the time of the current study, and no management activities had occurred on the site since the mid-1970's. Approximate quadratic mean diameter of the unfertilized portion of the stand in 1999 was 26 cm, site height was 20 m, and gross volume was approximately 357 m^3 ha^{-1} (IFTNC, 1993). Stand density as of 1997 was estimated to be 0.457 using Drew and Flewelling's (1979) relative density index. Total basal area was estimated to be 44 m^2 ha^{-1}, consisting of 85% Douglas-fir (*Pseudotsuga menziesii*), 10% grand fir (*Abies grandis*), 2% western redcedar (*Thuja plicata*), 2% western white pine (*Pinus monticola*) and 1% western larch (*Larix occidentalis*). The understory consisted primarily of common snowberry (*Symphorocarpus albus*), western goldthread (*Coptis occidentalis*) and bunchberry dogwood (*Cornus canadensis*). The habitat type was identified as cedar-ginger (*Thuja plicata-Asarum caudatum*) (Cooper et al., 1991).

Sampling Procedures

In June of 1999, six soil pits were installed and described, and soil and parent material samples were collected. Pit locations were randomly selected, with the restriction that all pits occurred on the same elevational contour, and that they were located at least 15 m away from previous fertilization test plots. Soil samples from the six pits were composited by horizon for standard laboratory analyses (Appendix A-2). Available P and K were tested using sodium acetate extraction, while NH_4^+ and NO_3^- were analyzed using 2M KCl extraction with analysis by colorimetry (Case and Thyssen, 1996a; Case and Thyssen, 1996d). Sulfate-sulfur was analyzed by calcium phosphate extraction and ion chromatography, and B was analyzed by calcium chloride extraction and spectrophotometric determination (Case, 1996; Case and Thyssen, 1996c). Extractable Ca, Mg, K and Na were analyzed by 1N ammonium acetate extraction and ICP, and micronutrients Cu, Zn, Mn and Fe by DTPA (Case and Thyssen, 1996b; Case and Thyssen, 2000). Additionally, four horizons were selected for installation of ion-exchange resins, which were replaced every two weeks during the growing season. Results from that study are discussed in a companion paper (Garrison-Johnston, 2003a).

Sampling for elemental contents of tree foliage and understory vegetation occurred in mid-June, mid-August and mid-October, and was timed to correspond to bud-break, mid-growing season and the onset of dormancy as indicated by tree bud set. For overstory analysis, sixteen trees were selected for chemical analysis, including four dominant/codominant and four subordinate crown class trees of each of the two major species on the site, Douglas-fir and grand fir. Trees were climbed during the June and August sampling dates, and one branch each was removed from the upper crown, mid-crown and base of the live crown. Each branch was bagged, placed on ice and brought to the laboratory for processing. At the lab, current, one-year old and two-year old needles were separated from the branches and dried at 70°C for 48 hours. A subset of needles was counted and dried separately, and weighed to estimate average needle dry weight. The June sampling period corresponded with bud-break, thus only one-year and two-year old needle samples were processed. After drying, needles were ground in preparation for chemical analysis. During the October sampling, the trees were felled and destructively sampled, and foliage samples were collected and processed following the same procedures as for June and August. In addition, branch wood samples were collected from the base and mid-point of each sample branch. "Cookies" were taken from the bole of each tree at breast height (1.4 m), base of live crown and at the third whorl from the top of the tree. Branch, stem and bark samples were placed on ice for transport to the laboratory. In the lab, current-volume specific gravity measurements were performed on one set of samples using water volume displacement (Husch et al., 1982). A separate set of samples of the same tree components were dried and ground in preparation for chemical analysis.

Understory biomass estimates and chemical analysis samples were obtained using clip plots. Ten circular plots, each 1 m^2 in area, were randomly located throughout the experimental site during the June, August and October sampling dates, with the restriction that they be located at least 15 m away from the previous fertilization test plots. Each plot was clipped to the ground level and separated by growth form. Since grasses were very sparse in the understory, they were included with the forb component. Samples were placed on ice and brought to the laboratory for processing. The forb and shrub samples for each plot were dried at 70°C for 48 hours and weighed to obtain biomass estimates. Samples were then ground for chemical analysis in a Wiley mill so as to pass a 40-mesh screen.

Twelve forest floor samples were collected in October of the study season. Two samples were collected 1 to 2 m uphill from each of the three soil pits on each block. Each sample was 225 cm^2 in area, and individually measured for thickness in order to calculate sample volume. Samples were placed on ice and brought to the laboratory for processing. Each sample was dried and weighed, and then ground in a Wiley mill so as to pass a 40-mesh screen.

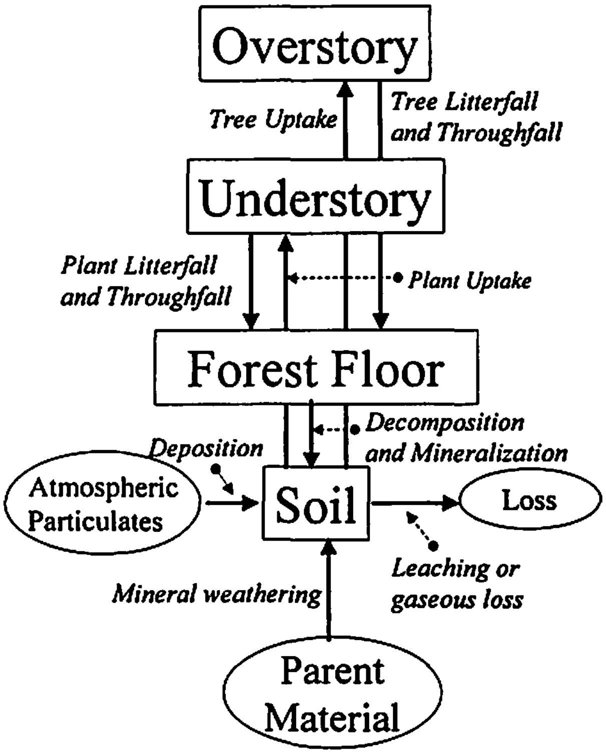
Ten litter traps were installed throughout the experimental site in June. Each trap was .19 m^2 in size and constructed of a plastic lattice tray lined with fine-mesh wire screen. The traps were randomly located throughout the stand, with the restriction that all traps be at least 15 m from old fertilization test plots. Traps were emptied during the August and October sampling dates. All materials in each trap were placed on ice and brought to the laboratory, where they were dried and weighed to obtain biomass estimates. Samples were then ground in a Wiley mill so as to pass a 40-mesh screen.

All ground samples were sent to MDS Harris Laboratory in Lincoln, Nebraska and analyzed for N, P, K, Mg, Ca, S, Zn, Mn, Cu, Fe, B, and Al. Nitrogen levels were determined using a standard micro-Kjeldahl procedure (Bremner and Mulvaney, 1982). All other elements were analyzed by inductively coupled plasma spectrometry following digestion in nitric acid (Huang and Schulte, 1985).

MODEL COMPILATION

A systems analysis approach was selected to develop a quantitative understanding of nutrient movement within the Mallory Creek ecosystem (Pugh, 1977; Aber and Melillo, 2001). The "box and arrow" conceptual model for forest ecosystem nutrient cycling developed for this study is presented in Figure 3-1. The boxes represent ecosystem compartments, while the arrows represent flows between compartments. External inputs and losses are represented as ovals. For each compartment, estimates of elemental content per hectare were obtained for three points in time corresponding to the beginning, middle and end of the growing season, which corresponded to the mid-June, mid-August, and mid-October sampling dates. Additionally, growth trends were extended to estimate compartment contents for mid-June of the following year, to allow modeling of annual nutrient cycling. Similarly, estimates of nutrient flow between boxes were obtained for each time step, corresponding to mid-June through mid-August (step 1), mid-August through mid-October (step 2), and mid-October through mid-June of the following year (step 3). By extending nutrient content estimates over the course of a full year, simulations of nutrient cycling over several years were conducted.

Figure 3-1. Conceptual nutrient cycling model developed for use in systems analysis of forest nutrient cycling in a north Idaho conifer stand.



Compartment Contents

Overstory Content

As part of the original fertilization study, tree measurement data were collected between 1982 and 1997. For the purposes of modeling seasonal nutrient dynamics during this study, the 1997 measured diameters and estimated heights and crown ratios on the unfertilized control plot were used to initiate overstory biomass predictions. Annual growth and height increments based on the prior 5 years of growth were applied to the 1997 measurements to estimate one additional year of height and diameter growth. For modeling purposes, these were subsequently referred to as Year 1 and Year 2, respectively. The assumption was made that all tree growth for the year occurred at an equal rate starting in June and ending in October; hence one-half the annual growth occurred between June and August, and one-half between August and October. In actuality, tree growth probably initiated prior to June and occurred at a more sporadic rate, however for purposes of simplifying the model and restricting growth to the time periods for which we had collected tissue chemistry, we made this assumption.

Control plot tree measurement data were used to estimate volume and mass of the tree stem, bark, branches and foliage. Diameter at breast height (d_{bh}) was estimated for the beginning, middle and end of the Year 1 growing season and start of the Year 2 growing season as described previously. For each point in time, diameter at the base of the live crown (d_{bolc}) was estimated from d_{bh} using regression equation (1) derived from measurements taken on the sixteen destructively sampled trees:

$$d_{bolc}=0.03181+(0.87251*d_{bh})-(0.00717*clrstm) \qquad R^2=0.93;\ CV=14.7 \qquad (1)$$

Where: d_{bolc} = diameter at base of live crown (m)
d_{bh} = diameter at breast height (m)
clrstm = below-crown stem length (m)

Bark thickness was measured on the cookies taken at breast height, base of live crown and at the third whorl from the top of the sixteen destructively sampled trees. These measurements were used to develop species-specific regression equations (2, 3) to predict bark thickness based on diameter at any point along the bole.

For Douglas-fir:

$$bark= 0.00105+(0.03667*d) \qquad R^2=0.79;\ CV=37.9 \qquad (2)$$

For grand fir:

$$bark=0.00092+(0.01963*d) \qquad R^2=0.90;\ CV=22.7 \qquad (3)$$

Where: bark= bark thickness (m)
d = diameter (m)

Volume of the stem below the live crown was estimated both inside and outside the bark using a modified frustrum of parabaloid form equation (4) (Husch et al., 1982).

stvol=clrstm*((x_b+x_bc)*0.55) (4)

Where: stvol = volume of below-crown stem (m^3)
clrstm = below-crown stem length (m)
x_b = cross-sectional area at breast height (m^2)
x_bc = cross-sectional area at base of live crown (m^2)

Volume of the stem within the crown was predicted in a similar fashion using a cone form equation (5) (Husch et al., 1982).

crvol=(cleng*x_bc)*0.33 (5)

Where: crvol = volume of within-crown stem (m^3)
cleng = crown length (m)
x_bc = cross-sectional area at base of live crown (m^2)

Total stem volume was calculated as the sum of the within-crown and below-crown volume estimates. Volume estimates derived in this manner were compared with estimates derived using regional volume equations (Wykoff et al., 1982). For trees greater than 0.2 m d_{bh}, an adjustment factor was applied so that the estimated volumes more closely matched regional volume predictions. For smaller trees the form equation estimates were retained. Volume inside and outside of the bark was calculated. Bark volume was calculated as the difference between volume inside and outside of the bark. Wood and bark densities measured on collected samples were applied to the volume data to calculate wood and bark mass, respectively.

Crown mass for each tree was estimated using regional biomass prediction equations based on species, crown class and diameter at breast height (Brown, 1978). Total crown mass estimates were divided by three to estimate the weight of crown thirds. The proportion of each crown third in foliage and in branches was modified using site-specific branch and foliage weights (Equations 6, 7). The purpose of this modification was to account for the finding that much of the weight of the upper crown was in foliage, while in the lower part of the crown relatively more of the weight was in branches. Branch weight was calculated as the difference between total weight and foliage weight.

Douglas-fir:

$$fprop=(0.3571609567)-(0.0303610703*d_{mp})+(0.002954372*h_{mp}) \qquad (6)$$

Grand fir:

$$fprop=(0.4740398358)-(0.0303610703*d_{mp})+(0.002954372*h_{mp}) \qquad (7)$$

Overall R^2=0.65; CV=27.9

Where fprop = proportion of crown third in foliage
d_{mp} = stem diameter at midpoint of crown third
h_{mp} = height above ground at midpoint of crown third

The volume and biomass of the tree stem, bark branches and foliage were calculated for June, August and October of Year 1 and June Year 2. Average foliar nutrient concentrations of the first two age classes of needles in June of the study season were applied to June Year 1 and June Year 2 biomass estimates to derive foliar nutrient contents for those points in time. Average foliar nutrient concentrations of the first three age classes of needles in August and October of the study season were applied to the August and October Year 1 foliar biomass estimates to calculate those foliar nutrient contents. Wood, bark and branch nutrient concentrations measured in October of the study season were applied to biomass estimates for all sampling dates. Nutrient content estimates for all control plot trees were then summed to provide an estimate of total overstory nutrient content (kg ha^{-1}) for each point in time. The June Year 1 estimates were used to initial model projections, while the August and October Year 1 and June Year 2 estimates were used to calibrate elemental uptake rates.

Three model simulations were performed in order to evaluate the effect of species composition on forest nutrient cycling. The first simulated nutrient dynamics based on the actual mixed conifer (MC) species composition of the study stand. For the other two model projections, species composition was defined as either pure grand fir (GF) or pure Douglas-fir (DF), with numbers and dimensions of study stand trees otherwise the same, and overstory contents were recalculated accordingly. Results of the three model projections were compared and evaluated for species composition effects on tree uptake, tree throughfall and soil elemental contents.

Understory Content

Understory biomass and nutrient concentrations were measured at the mid-June, mid-August and mid-October sampling dates, allowing for computation of total understory biomass and nutrient content for each of these three points in time (Garrison-Johnston, 2003b). Prediction of understory biomass for June Year 2 was made using our collected data in conjunction with regional understory biomass prediction equations based on overstory basal area (VanderSchaaf, 1999). Using this approach, understory biomass production and nutrient contents for June Year 2 were estimated to be 94.4% of the June Year 1 estimate. The elemental contents for June Year 1 were used to initiate the model, while the August and October Year 1 and June Year 2 estimates were used to calibrate elemental uptake rates.

Forest Floor Content

Forest floor biomass was measured only once, in October. Due to the mature nature of the stand under study, we assumed that a steady state had been reached with respect to forest floor inputs and outputs. Therefore this estimate was assumed to represent a constant value over the course of model projection. Forest floor elemental content values were presented in a companion paper (Garrison-Johnston, 2003b).

Soil Content

Soil nutrient contents were estimated using profile description data, bulk densities and laboratory chemical data for extractable nutrients. Soil profile and physical characteristics were provided in a companion paper (Garrison-Johnston, 2003a). The thickness of each horizon was used to estimate the volume of soil per hectare for that horizon, and bulk density was used to convert soil volume to soil mass per hectare. Soil chemical data from laboratory tests were applied to each horizon to derive estimates of total nutrient content per soil horizon. The nutrient contents of all horizons were summed to provide an estimate of total soil nutrient content per hectare for each element. These estimates were based on soil samples collected in June of the study season, and were used to initiate the model run at June Year 1.

Flows

Tree and Plant Litter

Litterfall was measured from June to August and August to October of the study season, and portions pertaining to the understory and overstory components were estimated using a combination of ocular estimates and data from a similar study (Nelson, 2000). Data from the Nelson (2000) study were also used to estimate litterfall dry weight for the October to June period. Nutrient concentrations measured during the June to August and August to October periods were applied to the respective litterfall dry weight estimates to derive the quantity of nutrients being returned to the forest floor in litterfall during each time step. These estimates were used for June to August Year 1 and August to October Year 1 respectively during model execution. The average nutrient concentrations across both collection dates were applied to the October Year 1 to June Year 2 biomass estimate to obtain nutrient contents for that time period. Tree litter values were set to remain at the same levels annually during model projection, based on the assumption that litterfall at this stage of stand development has reached a relatively steady state. Tree litterfall elemental contents also remained unchanged during the three model simulations representing different overstory species compositions, as insufficient data were available for estimating the effect of different overstory species on litterfall elemental contents. Plant litter for each time period was calculated as a percentage of total understory content at the start of that period.

Tree and Plant Throughfall

In some cases nutrient decreases between time steps in overstory and understory contents were not entirely accounted for by litterfall. Two possible mechanisms of accounting for this were considered. One consisted of creating a 'plant storage' compartment which would hold nutrients presumed to retranslocate to temporary storage in unmeasured vegetation components such as roots. The other was to create a throughfall mechanism which would allow for leaching of elements from canopy and stem to the soil compartment. We utilized the throughfall approach to account for non-litter nutrient losses from vegetation, because it is a recognized and important mechanism of nutrient transfer in forest ecosystems (Tamm, 1951; Madgwick and Ovington, 1959; Tukey and Morgan, 1964; Tukey, 1970; Parker, 1983). Throughfall varied with overstory species composition during the three model simulations. Based on changes in vegetation nutrient content and litterfall, the elements for which throughfall was implemented included N, P, K, and Mg for the MC simulation; N, P and K for the DF simulation; and N, P, K, Mg, Ca, S, and Mn for the GF simulation. Tree throughfall estimates were set to remain constant on an annual basis, based on assumptions that tree uptake and litterfall will also remain at about the same levels during this stage of stand development. Plant throughfall estimates were expected to reflect changes in plant nutrient content, and therefore were recalculated during each time step as rate percent of plant nutrient content.

Tree and Plant Uptake

Tree and plant uptake represented the movement of elements from the soil to the overstory and understory compartments, respectively. Uptake quantities were calculated based on changes in overstory and understory nutrient content, plus the quantity of nutrients required to meet litterfall estimates for each time period. In the case of a decline in total above-ground nutrient content, uptake was set to zero and the loss accounted for by litterfall and sometimes throughfall. Because our experimental stand was in a developmental stage where nutrient demand should be relatively constant from one year to the next (van den Driessche, 1974; Miller et al., 1981; Cole and Gessel, 1992; Fife and Nambiar, 1997), tree uptake flows were set to remain the same from year to year during each model simulation. Plant uptake flows were expected to be a function of plant biomass and nutrient content, and therefore were calculated as a percentage of plant nutrient content for each time step.

Deposition

Wet and dry deposition were not measured during the current study. Data from local National Atmospheric Deposition measurement sites located near Pullman, WA and Headquarters, ID were used to estimate wet deposition to our site, based on the average of the last ten years of data from two sites, one to the east and one to the west of our study site (NADP, 2003). Estimates were only available for Ca, Mg, K and N. For other elements, no deposition estimates were included in the model. Deposition estimates were entered into the nutrient cycling model as kg ha^{-1} per time period (Table 3-1). The same deposition rates were used throughout model projection.

Table 3-1. Estimated atmospheric deposition (kg ha^{-1} $period^{-1}$) of several elements during the 1999 growing season in north Idaho.

Element	June - August	August - October	October - June
Nitrogen	0.70	0.70	3.35
Potassium	0.03	0.03	0.12
Magnesium	0.01	0.01	0.07
Calcium	0.08	0.07	0.39
Sulfur	0.30	0.34	1.74

Mineralization

The term ‘mineralization’ was used loosely to describe all inputs to the soil nutrient pool derived from litter turnover and atmospheric deposition. Based on our assumption that the forest floor represented steady-state conditions, we considered that all inputs to the forest floor over the course of the year were balanced by outputs of approximately equal magnitude. Thus, the mineralization flow represented the sum of overstory and understory litter inputs plus atmospheric deposition at each time step.

Mineral Weathering

Most of the nutrients discussed in this paper are derived primarily from mineral weathering. Exceptions are N, derived primarily from the atmosphere and held in organic materials, and possibly S and B, which although geologically derived, are also tied closely with organic matter cycling (Marschner, 1995; Kabata-Pendias, 2001). We utilized a technique developed by Clayton (1979) based on weathering rind formation to provide a quick, gross estimate of weathering rates for several elements. Using this approach, the average particle diameter and volume percent of the coarse fraction (>2 mm) of the soil were utilized to predict the amount of material weathering each year. The mineralogy of the coarse fraction was then combined with estimates of relative mineral weathering rates (Clayton, 1979; Birkeland, 1999) and formula weights (Klein and Hurlbut Jr., 1993) to derive weathering estimates for several elements (Table 3-2).

Table 3-2. Total elemental supply from rock based on quantity of various minerals produced from rock weathering each year, and relative weathering rates and proportions of elements comprising each mineral.

Mineral	Total quantity weathered (kg ha^{-1} yr^{-1})	Relative weathering rate	Elemental Supply Rate by Weathering (kg ha^{-1} yr^{-1})			
			K	Ca	Mg	Fe
muscovite	190.53	0.5	1.87			
biotite	6.23	1.0	0.50		0.46	1.06
orthoclase	4.13	0.1	0.06			
oligoclase (An20)	50.06	0.5		0.76		
Total elemental supply from weathering			**2.42**	**0.76**	**0.46**	**1.06**

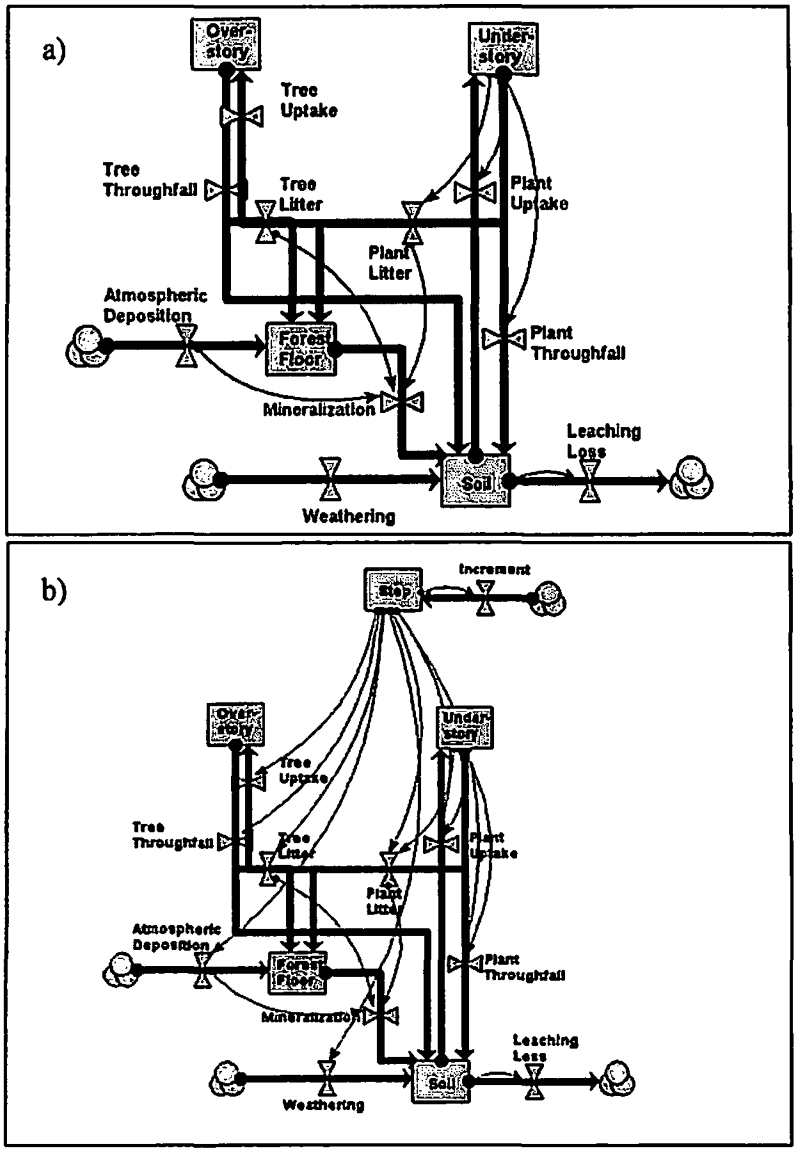
Leaching

Leaching losses from the ecosystem were not measured. We did assume that a maximum nutrient-holding capacity of the soil could exist, above which any additional input would be lost to the system through leaching. However, we did not have an adequate means of estimating this maximum soil capacity. Therefore a theoretical maximum value approximately 50% higher than the measured quantity based on June soil tests was assumed. This is an area where further study is warranted.

Model Compilation

The model data were compiled using the Simile© visual model, which employs a system dynamics approach (Muetzelfeld, 2003). This model has been successfully used to simulate various systems including individual tree growth, tree and crop interactions and wildlife population dynamics (Muetzelfeldt and Taylor, 2000; Muetzelfeldt and Taylor, 2001). The compartments, flows, inputs and outputs corresponding to the conceptual nutrient model shown in Figure 3-1 were assembled in the Simile© environment (Figure 3-2a). June Year 1 was the starting point for each model run. The June Year 1 value for each compartment was entered into the 'Equation' box provided for each model component in the Simile modeling environment. The flows between compartments were entered as either constant values or rate percent of the source compartment. In the latter case, the flows were linked to the source compartment by a feedback loop. A time step was also incorporated into the model, with Step 1 representing June to August, Step 2 representing August to October and Step 3 representing October to June (Figure 3-2b).

Figure 3-2. Forest nutrient cycling model for a north Idaho conifer stand as designed using Simile© systems analysis software. Model is shown without (a) and with (b) time step included.



Assuming that stand growth continues at the same rate as the 5 years prior to the 1997 measurements, Drew and Flewellings's (1979) relative density index approach indicates that this stand would reach the stage of imminent competition-induced mortality in approximately 7 years (Drew and Flewelling, 1979). Because this stand has likely reached a stage where nutrient limitations are affecting growth (Miller, 1981; Cole and Gessel, 1992), and our model does not have any built-in feedbacks to account for growth-limiting nutrient deficiencies, we elected to run our nutrient cycling model for only four years beyond the study year, for a total of five years. Because annual trends were the same throughout the model projection period, only the first three years of results are presented in this report. Five-year results for all compartments and flows modeled during the MC species composition simulations are shown in Appendix B-1. Five-year results for the compartments and flows affected by changes in species composition during the DF and GF model simulations are shown in Appendix B-2, including tree uptake, tree throughfall, overstory and soil elemental contents.

RESULTS

Compartments

Overstory

Comparison of the three species composition simulation results showed that overstory GF elemental contents were greater than DF contents for all elements except Zn and Cu, which were greater during the DF simulation (Figure 3-3). The MC simulation results were always intermediate between the DF and GF results. Overstory elemental content behaved about the same for all three species composition simulations, increasing during the growing season and peaking in October of each year. The exception was N during the GF simulation, which peaked in August (Figure 3-3a). Annually, a decrease in elemental content always occurred between October of any given year and June of the subsequent year, but again increased by October of the subsequent year.

The greatest difference in overstory content between species composition simulations occurred for Ca, which was about double for GF compared to DF in October Year 1, with contents of 791 and 391 kg ha^{-1}, respectively. Simulated K and P contents also differed by species composition, with October Year 1 values of 472 and 92 kg ha^{-1} for GF compared to 276 and 65 kg ha^{-1} for the DF simulation, respectively. Differences for Mn and Al were also substantial, at 49 and 29 kg ha^{-1} for GF compared to 12 and 19 kg ha^{-1} for DF respectively. While differences for other elements were not as dramatic, GF-simulated contents were greater than DF-simulated contents for most other elements. Exceptions were Zn and Cu contents of 4 and 2 kg ha^{-1} respectively for the DF simulation in October, which were approximately double the GF contents of 2 and 1 kg ha^{-1} at that time. Overstory elemental contents increased on an annual basis. By October of Year 3, simulated GF contents ranged as high as 837 kg ha^{-1} for Ca and 483 kg ha^{-1} for N, while simulated DF contents of the same elements were 418 and 446 kg ha^{-1}, respectively. Simulated GF contents in October of Year 3 were higher than DF-simulated contents for all other elements except Zn and Cu.

Positive seasonal gains in overstory content always occurred between June and October. This seasonal content gain was usually greater than annual elemental gains between October of that year and October of the subsequent year (Figure 3-4). For the simulated DF stand, annual overstory content gains between June and October of Year 1 ranged from 14 kg ha^{-1} for Ca to 1 kg ha^{-1} for S, Fe and Al, while seasonal gains of other micronutrients were undetectable. In contrast, seasonal overstory content gains between October Year 1 and October Year 2 for the simulated DF stand ranged from a high of 36 kg ha^{-1} for N to 2 kg ha^{-1} for S. Seasonal gains of 1 kg ha^{-1} for Fe and Al also occurred during the DF simulation, while changes in other micronutrients and Al were undetectable. The same trends were evident during the GF simulation as well, except that the magnitude of differences between annual and seasonal projections was even greater. Annual overstory content gains during the GF simulation ranged from 23 kg ha^{-1} for Ca to 1 kg ha^{-1} for S, compared to the greater seasonal gains of 71 kg ha^{-1} for Ca to 5 kg ha^{-1} for S. Annual changes of 1 kg ha^{-1} were detected for Mn and Al during the GF simulation, while seasonal changes for those same elements were 8 and 5 kg ha^{-1}, respectively. Neither seasonal nor annual changes in other micronutrients were detected during the GF simulation, except for a seasonal increase in Fe content of 1 kg ha^{-1}.

Figure 3-3. Overstory and soil elemental contents for the first three years of nutrient cycling model projection for a north Idaho conifer stand consisting of simulated pure grand fir (GF) and pure Douglas-fir (DF) compositions, and forest floor content of the actual mixed conifer stand. Mixed conifer overstory and soil contents were intermediate between GF and DF results. Year 1 estimates were based on measurements during one growing season. Year 2 and 3 estimates were projections based on Year 1 data.

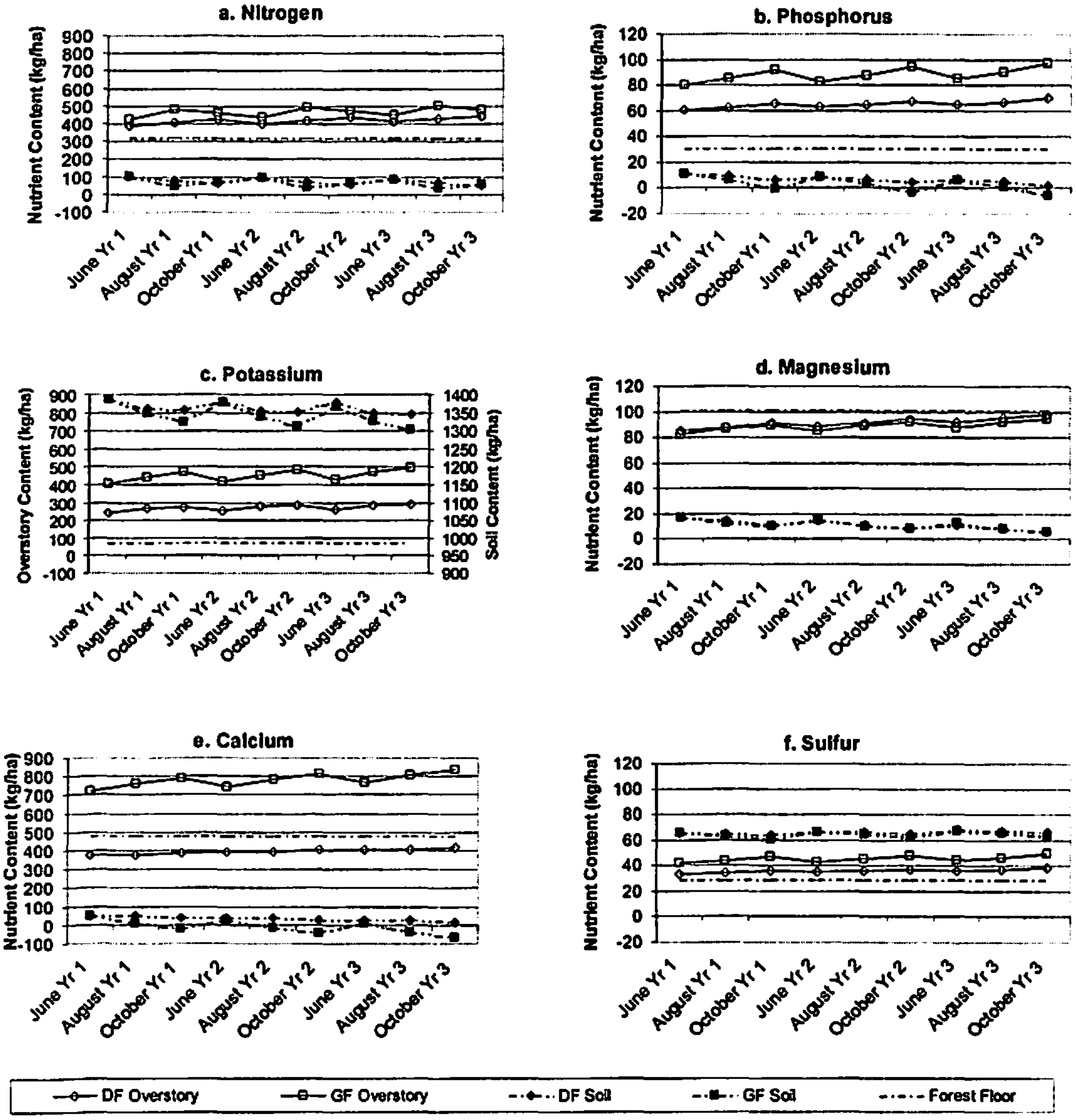


Figure 3-3 (concluded). Overstory and soil elemental contents for the first three years of nutrient cycling model projection for a north Idaho conifer stand consisting of simulated pure grand fir (GF) and pure Douglas-fir (DF) compositions, and forest floor content of the actual mixed conifer stand. Mixed conifer overstory and soil contents were intermediate between GF and DF results. Year 1 estimates were based on measurements during one growing season. Year 2 and 3 estimates were projections based on Year 1 data.

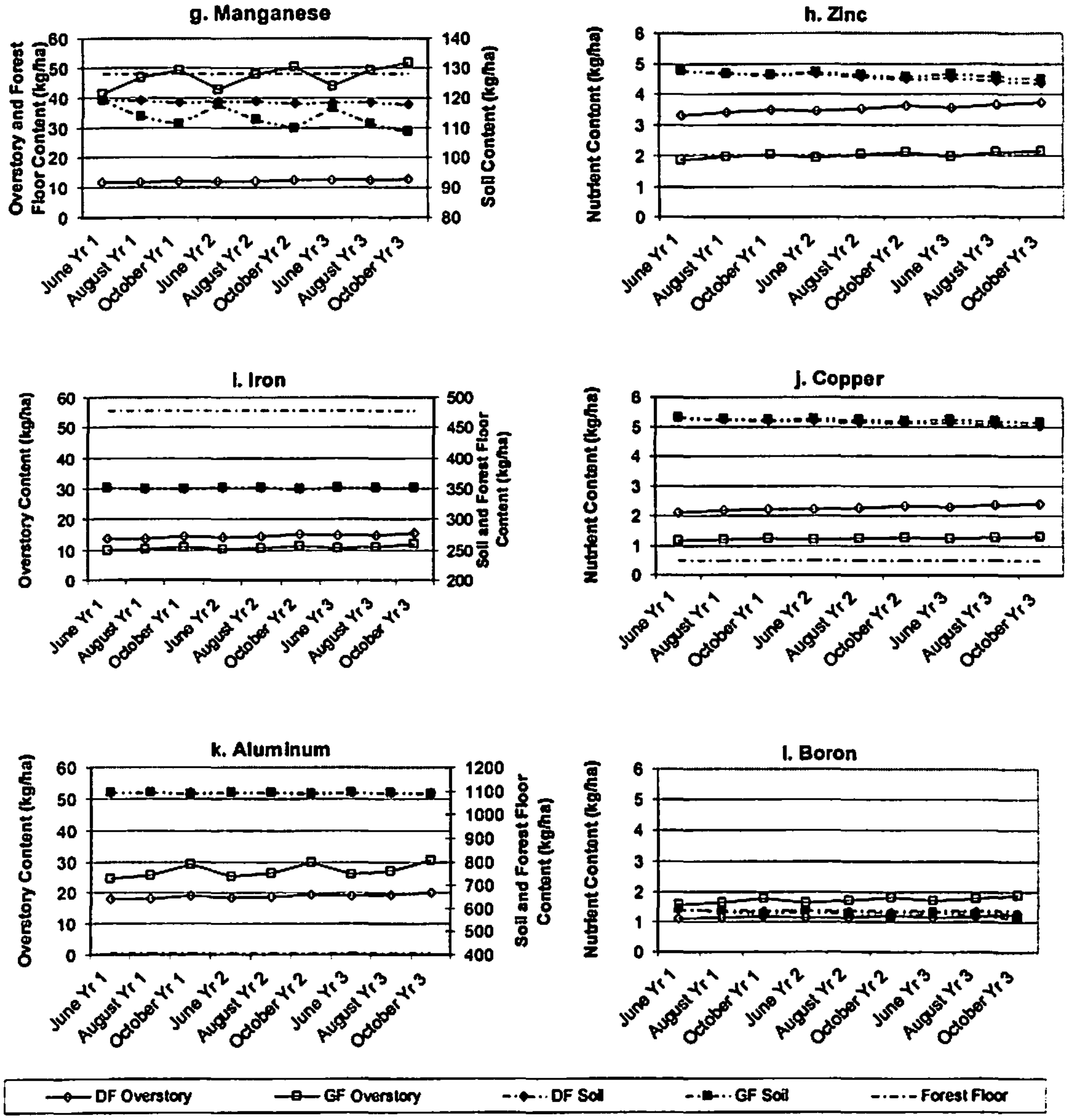
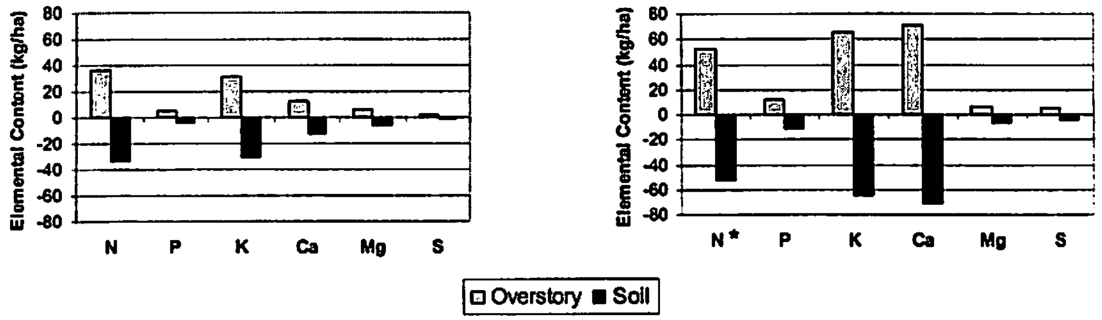
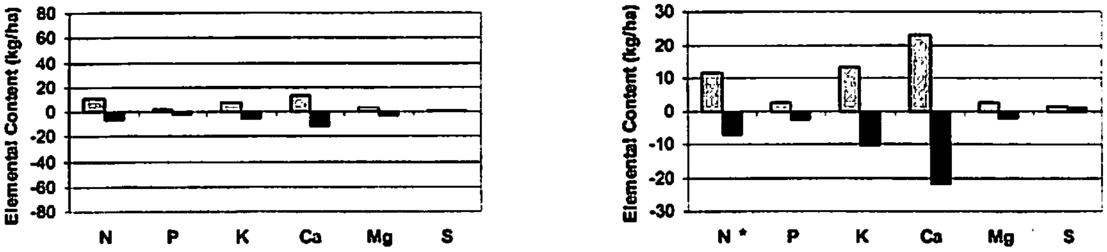


Figure 3-4. Seasonal (June Year 1 through October Year 1) and annual (October Year 1 through October Year 2) changes in overstory and soil elemental contents in a north Idaho conifer stand for simulated grand fir (GF) and Douglas-fir (DF) compositions.



c. DF Annual Change

d. GF Annual Change



* GF seasonal N changes represented June through August of Year 1, all other seasonal changes represented June through October of Year 1

Soil

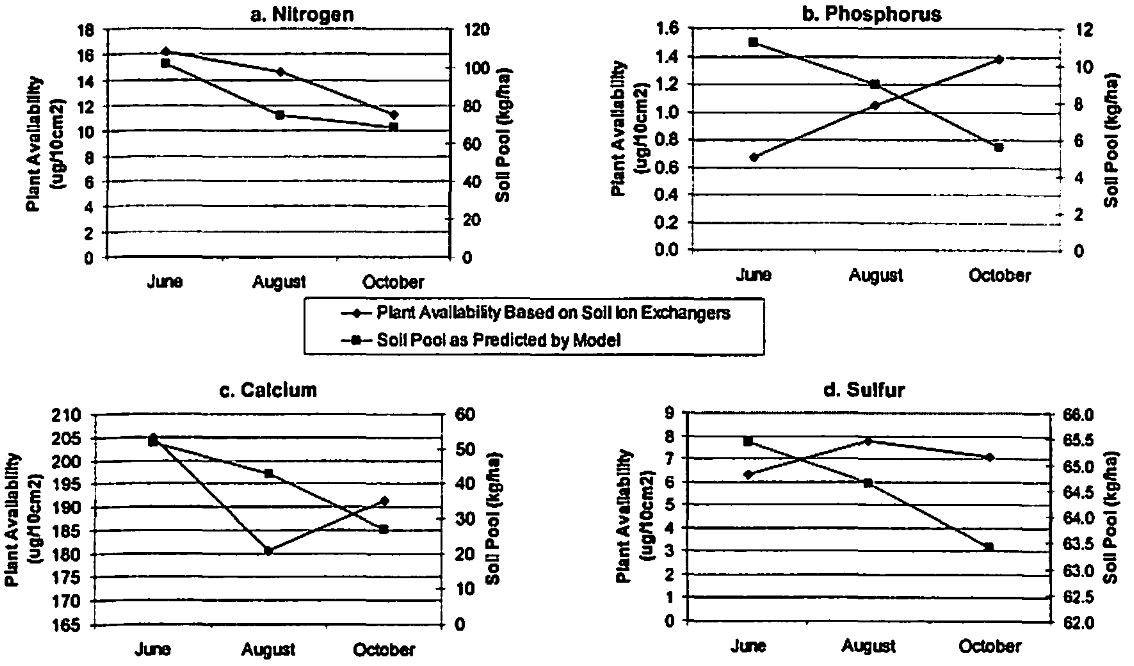
Soil nutrient content was always greatest in June, and always decreased during the growing season (Figure 3-3). On an annual basis, soil elemental content continued to decrease for all elements except S and Fe. These trends were evident during all model simulations, regardless of overstory species composition. Soil elemental contents in June Year 1 ranged from 1388 kg ha^{-1} for K to 1 kg ha^{-1} for B, and were in the order K >Al > Fe> Mn> N > S > Ca > Mg > P >Cu = Zn > B. The decrease in soil elemental contents between

June and October was generally greater than the annual decrease from October to October, regardless of overstory species composition. However, the magnitude of both seasonal and annual decreases was greater for the GF simulation than the DF simulation (Figure 3-4). The species difference was most notable for Ca, which showed seasonal decreases of 71 and 13 kg ha^{-1} during Year 1 for the GF and DF simulations, respectively. Similarly, K decreased by 64 and 31 kg ha^{-1}, P by 11 and 5 kg ha^{-1}, and S by 5 and 1 kg ha^{-1} between June and October of Year 1 for the GF and DF simulations, respectively. Manganese and Al decreased by 8 and 5 kg ha^{-1} respectively during the GF simulation, while seasonal changes for those elements were undetectable during the DF simulation. Seasonal decreases for other soil elemental contents did not differ greatly between species simulations. Soil N content decreased by 29 kg ha^{-1} for GF and 34 kg ha^{-1} for DF, while Mg decreased by 7 and 6 kg ha^{-1} for the GF and DF simulations, respectively. Seasonal decreases in soil Fe content were about 1 kg ha^{-1} for all model simulations. Seasonal Zn, Cu and B changes were detectable only in trace quantities for all model simulations. Seasonal decreases for the MC simulation were intermediate between the GF and DF simulations.

Annual changes in soil elemental contents were also greater for the GF simulation compared to the DF and MC simulations, although the magnitude of these differences was less than for seasonal comparisons (Figure 3-4). Calcium differences were still highest, showing annual decreases of 22 and 12 kg ha^{-1} for the GF and DF simulations respectively. Potassium decreased by about 10 kg ha^{-1} for the GF simulation and 5 kg ha^{-1} for DF. Other macronutrient differences were small, with P decreasing by 3 and 2 kg ha^{-1} respectively and Mg by 2 and 3 kg ha^{-1} respectively for the GF and DF simulations. Sulfur decreased by 1 kg ha^{-1} annually during all species simulations, and annual decreases in other soil elemental contents were similarly minor. However, model projections still showed long-term soil pool decreases for most elements, due to the cumulative effect of the small decreases in the soil elemental pool over time. At current rates of stand growth and with no inputs other than those already included, the MC simulation indicated that the soil N supply would be depleted in about 11 years, Mg supply in 6 years, P in 4 years and Ca in 3 years. The GF simulation predicted depletion of the same elements in 9 years for N, 7 years for Mg and 1 year for both P and Ca, while the DF simulation predicted 12, 6, 4 and 5 year durations for the same soil elemental supplies. Sulfur and Fe were the only elements to show an annual increase in nutrient content, and soil pools of these elements continued to increase over time regardless of overstory species.

Soil elemental pool estimates utilized in this model were based on standard laboratory chemical analysis of soils collected in June of the study season. Subsequent soil collections for validation of changes in the soil pool were not performed. However, soil elemental availability throughout the season was measured using ion-exchange resins (Garrison-Johnston, 2003a). Evaluation of model predictions of soil elemental availability were made by graphically comparing the estimates produced during the MC simulation to the corresponding ion-exchange estimates (Figure 3-5). For N, Mg and K, both approaches showed these elements decreasing in availability throughout the entire growing season (Figure 3-5a). For P and Fe, the model predicted a consistent decrease during the season while soil ion-exchangers showed a consistent increase (Figure 3-5b). Both approaches showed a decrease in availability of Ca and B between June and August, but while the model projected a continual decrease into the latter half of the season, the ion-exchangers showed an increase (Figure 3-5c). Conversely, ion-exchange analysis showed Mn, Cu and S availability to increase early in the season while model projections showed a decrease, but both methods showed decreasing availability of these elements during the latter half of the season (Figure 3-5d).

Figure 3-5. Comparison of soil nutrient availability as projected by nutrient cycling model versus availability as measured by ion-exchange resins in a north Idaho conifer stand.



Understory

Understory biomass represented a very small portion of the above-ground component of the forest ecosystem at the study site. Understory N, K and Ca contents were detectable throughout the growing season, while other elements were present only in trace quantities (Table 3-3). August N and K contents were significantly greater than October N and K contents, while for Ca, content did not differ between August and October (Garrison-

Johnston, 2003b). Understory macronutrient contents during August Year 1 ranged from 4 kg ha^{-1} for N and K to 2 kg ha^{-1} for Ca. Understory nutrient contents varied by only 1 to 2 kg ha^{-1} seasonally, and annual changes were also minor. As of August Year 3, understory K and Ca contents were unchanged, while understory N content decreased to 3 kg ha^{-1}. The same understory nutrient content values were used during all three model runs simulating various overstory species compositions.

Table 3-3. Nitrogen, potassium and calcium* contents (kg ha^{-1} period^{-1}) of understory compartments for first 3 years of nutrient cycling model projection in a north Idaho conifer stand. Year 1 estimates were based on measurements during one study season. Year 2 and 3 estimates were projections based on Year 1 data.

Point in time	Nitrogen	Potassium	Calcium
June Yr 1	3	3	1
August Yr 1	4	4	2
October Yr 1	2	2	2
June Yr 2	3	3	1
August Yr 2	4	4	2
October Yr 2	2	2	2
June Yr 3	3	3	1
August Yr 3	3	4	2
October Yr 3	2	2	2

*Other elements detected in trace amounts only.

Flows

Tree Litter, Throughfall and Uptake

Growing season tree litter elemental contents were generally smallest between June and August and greatest between August and October (Table 3-4). Calcium, N and K showed the greatest tree litter nutrient contents during the August to October period, ranging from 14 to 4 kg ha^{-1}. Phosphorus, Mg, S and Mn showed litterfall returns of 1 kg ha^{-1} during this period, while tree litter contents of other elements were detected only in trace quantities. Over an entire year, the greatest elemental litterfall content was predicted to occur between

October of one year and June of the subsequent year. Winter tree litter contents were again highest for Ca, N and K, and ranged from 24 to 8 kg ha^{-1}. Phosphorus and Mg showed winter tree litter contents of 2 kg ha^{-1}, while S, Mn, Fe and Al each returned 1 kg ha^{-1} in winter litterfall. Periodic tree litterfall returns during Years 2 and 3 were the same as Year 1. The same tree litterfall elemental contents were used during all three model simulations of various overstory species compositions.

Table 3-4. Elemental contents of tree litter (kg ha^{-1} period $^{-1}$) in a north Idaho conifer stand. Estimates were based on measurements during the 1999 growing season.

	N	P	K
June-Aug Yr 1	3	0	1
Aug-Oct Yr 1	8	1	4
Oct Yr 1-June Yr 2	18	2	8
June-Aug Yr 2	3	0	1
Aug-Oct Yr 2	8	1	4
Oct Yr 2-June Yr3	18	2	8
June-Aug Yr 3	3	0	1
Aug-Oct Yr 3	8	1	4
	Mg	**Ca**	**S**
June-Aug Yr 1	0	4	0
Aug-Oct Yr 1	1	14	1
Oct Yr 1-June Yr 2	2	24	1
June-Aug Yr 2	0	4	0
Aug-Oct Yr 2	1	14	1
Oct Yr 2-June Yr3	2	24	1
June-Aug Yr 3	0	4	0
Aug-Oct Yr 3	1	14	1
	Mn	**Fe**	**Al**
June-Aug Yr 1	0	0	0
Aug-Oct Yr 1	1	0	0
Oct Yr 1-June Yr 2	1	1	1
June-Aug Yr 2	0	0	0
Aug-Oct Yr 2	1	0	0
Oct Yr 2-June Yr3	1	1	1
June-Aug Yr 3	0	0	0
Aug-Oct Yr 3	1	0	0

*Zn, Cu, B and elements showing '0' value were detected in trace amounts only.

Tree throughfall was only recorded for those elements and time steps where the overstory elemental content decrease was greater than litterfall content. Tree throughfall elemental contents varied with overstory species composition during the three different model simulations (Table 3-5). The higher overstory contents of the simulated GF stand, combined with the lack of simulation-specific tree litter data, produced much higher throughfall projections for GF compared to the DF and MC simulations. For most elements, throughfall was calculated between October and June. Throughfall N for the simulated GF stand was also calculated between August and October. Total annual tree throughfall contents of K, N, P and Mg during the GF simulation ranged from 45 to 2 kg ha^{-1} yr^{-1}, and were two to three times higher than the corresponding MC and DF projections. Simulated GF throughfall contents of 24 and 3 kg ha^{-1} yr^{-1} were projected to occur for Ca and S, while no throughfall was predicted for either element during the DF and MC simulations. Conversely, Mn and Al throughfall quantities of 5 and 3 kg ha^{-1} yr^{-1} were recorded for the DF simulation, but not for the MC or GF simulations.

Table 3-5. Comparison of tree elemental throughfall* (kg ha^{-1} period^{-1}) in a north Idaho conifer stand for mixed conifer (MC), simulated pure Douglas-fir (DF) and simulated pure grand fir (GF) species composition. Uptake rates remained the same during each year of model projection.

	Nitrogen			Phosphorus			Potassium		
	MC	DF	GF	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	0	0	0	0	0	0	0	0	0
Aug-Oct Yr 1	0	0	12	0	0	0	0	0	0
Oct Yr 1-June Yr 2	7	7	2	2	1	7	21	16	45
Total Annual Throughfall	***7***	***7***	***15***	***2***	***1***	***7***	***21***	***16***	***45***

	Magnesium			Calcium			Sulfur		
	MC	DF	GF	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	0	0	0	0	0	0	0	0	0
Aug-Oct Yr 1	0	0	0	0	0	0	0	0	0
Oct Yr 1-June Yr 2	1	0	2	0	0	24	0	0	3
Total Annual Throughfall	***1***	***0***	***2***	***0***	***0***	***24***	***0***	***0***	***3***

	Manganese			Aluminum		
	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	0	0	0	0	0	0
Aug-Oct Yr 1	0	0	0	0	0	0
Oct Yr 1-June Yr 2	0	5	0	0	3	0
Total Annual Throughfall	***0***	***5***	***0***	***0***	***3***	***0***

*Zn, Cu, Fe, B and elements showing '0' value were detected in trace amounts only.

Tree uptake of macro- and micronutrients and Al reflected changes in overstory elemental content plus the amount of nutrients needed to supply litterfall for each time step. Uptake rates varied with overstory species composition (Table 3-6). Total annual overstory uptake of N, P, K, Ca and S was greater for the simulated GF stand than the DF stand, and the MC projection was intermediate. Annual uptake of Mg and Fe was about the same for all three simulations, while Al and Mn uptake was greatest for the simulated DF stand. Comparison of periodic elemental uptake during the year revealed differences in the timing of elemental uptake for the different simulated species compositions. For example, the simulated DF stand took up about half its N in the first half of the season and half in the second, while the simulated GF stand accumulated its entire annual N allotment between June and August. Conversely, the simulated GF stand accumulated Ca at a constant rate throughout the season, while the simulated DF stand accumulated most of its Ca between

August and October. Potassium, P and Al also showed somewhat disproportionate rates of uptake when comparing periodic GF and DF simulation results. Uptake rates during the MC projection were intermediate between the simulated GF and DF rates. Model projections for subsequent years utilized the same tree uptake rates.

Table 3-6. Comparison of tree elemental uptake (kg ha^{-1} period^{-1}) in a north Idaho conifer stand for mixed conifer (MC), simulated pure Douglas-fir (DF) and simulated pure grand fir (GF) species composition. Uptake rates remained the same during each year of model projection.

	Nitrogen			Phosphorus			Potassium		
	MC	DF	GF	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	30	25	56	3	2	5	30	27	39
Aug-Oct Yr 1	17	23	0	4	4	7	14	10	33
Oct Yr 1-June Yr 2	0	0	0	0	0	0	0	0	0
Total Annual Uptake	***48***	***48***	***56***	***7***	***6***	***13***	***44***	***38***	***71***
	Magnesium			**Calcium**			**Sulfur**		
	MC	DF	GF	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	3	3	5	12	4	46	1	1	2
Aug-Oct Yr 1	4	4	3	30	26	43	2	2	4
Oct Yr 1-June Yr 2	0	0	0	16	25	0	0	0	0
Total Annual Uptake	***8***	***7***	***8***	***58***	***56***	***89***	***4***	***3***	***6***
	Manganese			**Iron**			**Aluminum**		
	MC	DF	GF	MC	DF	GF	MC	DF	GF
June-Aug Yr 1	1	5	0	0	0	0	1	1	0
Aug-Oct Yr 1	2	3	1	1	1	1	2	4	1
Oct Yr 1-June Yr 2	0	0	1	0	0	0	0	0	1
Total Annual Uptake	***3***	***9***	***2***	***2***	***2***	***2***	***2***	***5***	***2***

*Zn, Cu, B and elements showing '0' value were detected in trace amounts only.

Plant Litter, Throughfall and Uptake

Plant litter contents were much smaller than tree litter contents. Plant elemental litter contents tended to be highest between August and October, and were generally undetectable between June and August (Table 3-7). October to June estimates of plant litterfall were intermediate between the June to August and August to October contents. Year 1 plant litter content ranged from 3 kg ha^{-1} for Ca to 1 kg ha^{-1} for N and K between August and October, to trace quantities for other elements. Over the three-year period modeled, plant litterfall returns declined coincident with decreased elemental uptake and decreased understory biomass production. Year 3 returns ranged from 2 kg ha^{-1} for late-season Ca return to trace quantities for most other elements. Plant throughfall contents were negligible for all elements except K. Plant K throughfall of 2 kg ha^{-1} was calculated during the August to October time step. Over the three-year projection period, plant throughfall decreased coincident with decreased plant uptake. By Year 3, August to October K throughfall content had decreased to 1 kg ha^{-1}.

Table 3-7. Nitrogen, potassium and calcium* fluxes (kg ha^{-1} period^{-1}) in plant uptake, litter and throughfall in a north Idaho conifer stand. Year 1 estimates were based on measurements during one study season. Year 2 and 3 estimates were projections based on Year 1 data.

	Plant Litter	Plant Through-fall	Plant Uptake	Plant Litter	Plant Through-fall	Plant Uptake	Plant Litter	Plant Through-fall	Plant Uptake
	Nitrogen			Potassium			Calcium		
June-Aug Yr 1	0	0	1	0	0	1	0	0	1
Aug-Oct Yr 1	1	0	0	1	2	0	3	0	2
Oct Yr 1-June Yr 2	1	0	2	0	0	1	2	0	1
June-Aug Yr 2	0	0	1	0	0	1	0	0	1
Aug-Oct Yr 2	1	0	0	1	2	0	2	0	2
Oct Yr 2-June Yr3	1	0	2	0	0	1	1	0	1
June-Aug Yr 3	0	0	1	0	0	1	0	0	1
Aug-Oct Yr 3	1	0	0	1	1	0	2	0	2

*Other elements detected in trace amounts only.

Understory plant uptake of most elements was minor. Plant uptake quantities were calculated for N, K and Ca (Table 3-7), and were detected only in trace quantities for most other elements. Understory uptake of N was greatest between October and June at 2 kg ha^{-1}, and an additional 1 kg ha^{-1} was taken up between June and August. Understory K uptake of 1 kg ha^{-1} occurred between June and August and between October and June. No understory N or K uptake was recorded between August and October. Plant uptake of Ca was 2 kg ha^{-1} between August and October and 1 kg ha^{-1} during the other two time periods. Over the three-year projection period, plant uptake of all elements decreased coincident with decreased understory plant growth.

DISCUSSION

Overstory Contents and Transfers

This study demonstrated the importance of species nutritional ecology through the simulated manipulation of overstory species composition during model projections. Overstory biomass predictions were based on tree diameter and species (Brown, 1978). Experimental manipulation of stand species composition was performed by applying either grand fir or Douglas-fir tissue chemical concentrations to the same set of plot trees to produce stand-based overstory content estimates for pure stands of both species. Resultant model projections showed large differences in stand overstory elemental contents by species. Simulated GF contents of Ca, K, P, Mn and Al were 1.5 to 4 times greater than simulated DF contents of the same elements in October of Year 1. Simulated GF contents of other elements were also greater than simulated DF contents, except for Zn and Cu which were greater for Douglas-fir. Similar species-related biomass and elemental differences occur for other forest tree species (van den Driessche, 1974; Clayton and Kennedy, 1980; Hom and Oechel, 1983; Lim and Cousens, 1986; Miller et al., 1993; Bauer et al., 1997; Moore et al., 2003). The sensitivity of the overstory box to shifts in species composition in this study suggests that accurate tree measurement and appropriate species-specific tissue sampling for chemical analysis are crucial for modeling the elemental dynamics of the above-ground portion of a forest stand. Improved sampling techniques and additional data collection for different coniferous species will be an important component of future nutrient cycling studies.

During model projections in this study, total overstory contents of all elements increased from June to August to October regardless of species composition, except for N content of the simulated GF stand, which was greatest in August and decreased slightly in October. While this general pattern of increase was due in part to our biomass estimation procedure, which divided annual height and diameter increments across the growing season and resulted in larger trees at each time step, the increase primarily reflected differences in foliar nutrient contents. Even though particular age classes of needles were found to decrease in elemental content during the season (Garrison-Johnston, 2003b), when nutrient concentrations were averaged across all age classes sampled, including the nutrient-rich current-year foliage (which was included in the August and October estimates), total foliar contents increased. Several other workers have noted similar seasonal increases in the nutrient content of coniferous foliage for N, P, K, Ca, Mg and Cu (van den Driessche, 1974; Smith et al., 1981). While very little work has been done on the seasonal fluctuations in nutrient content of the other elements reported in our study, workers studying hardwoods have found seasonal increases for B and Mn contents (Guha and Mitchell, 1966). Because we measured stem, branch and bark nutrient concentrations only in October and then applied those concentrations to June and August biomass estimates, changes in content of those tissues also increased, perhaps artificially, as a function of increased tree size over the growing season. In retrospect, measurement of tissue concentrations for these components might have resulted in a more accurate representation of total tree nutrient content during the earlier portions of the growing season.

Our model also showed a decrease in overstory content between the end of one growing season and the start of the next for all elements, regardless of overstory species composition. Since tree biomass and nutrient content of woody tissues were unchanged between the end of one season and the start of the next in our model calculations, the decline was a direct reflection of lower foliar nutrient concentrations and contents in June compared to October. Many workers have documented lower foliar nutrient concentrations and contents at the start of the growing season, particularly for N (Lavender and Carmichael, 1966; Krueger, 1967; van den Driessche, 1974; Lim and Cousens, 1986; Kiiskila, 1996; Nelson, 2000). In our study, we did not measure elemental concentrations of buds, but presumably that is where nutrients would be allocated to promote new growth, thus explaining the lower elemental content of older tissues at this time of year (Webber, 1977; Smith et al., 1981; Hom and Oechel, 1983; Proebsting and Chaplin, 1983; Nambiar and Fife, 1991; Millard and Proe, 1992). By this reasoning, overstory elemental content between October of one year and June of the subsequent year might not have changed as much as our projections showed, but rather might indicate that we underestimated June content because we did not account for new shoots. Although new shoots are minor from a biomass standpoint, they could have affected above-ground nutrient content. In terms of model functioning, however, underestimation of June overstory nutrient content would simply mean greater nutrient return to the soil compartment between October and June, and increased uptake later in the season. Thus, while underestimation of June content might increase the magnitude of uptake and return, the overall nutrient balance would remain about the same as modeled. Bark and branches are other overstory components important to sample at various times of the year for better representation of seasonal nutrient dynamics, particularly due to the contribution of cambial transport tissues to stem and branch bark. Wood concentrations were generally low and were not expected to show significant seasonal changes.

The annual increase in overstory nutrient content detected during model projection seemed reasonable on an individual tree basis, as larger trees require more nutrients to sustain growth. However the magnitude of tree nutrient content increases seemed high, particularly for nutrient-demanding species compositions such as the simulated GF stand. When extrapolated to a stand basis, the large annual elemental increases accounted for much of the rapid soil nutrient depletion observed during longer-term model projections, especially for the simulated GF stand. The assumption of stable nutrient demand of our experimental stand was based on theories of stand development as related to nutrition (Miller et al., 1981; Cole and Gessel, 1992). However, a more realistic approach in our case may have been to allow stand nutrient demand to decrease over time during model projection, as well as to vary based on species-specific nutrient demands. This would still follow stand-based nutrient demand theories if our experimental stand has reached the developmental stage typified by culmination of mean annual increment. This could be verified through examination of increment cores.

During this study, litterfall was the primary transfer mechanism of elements from the overstory to the forest floor and the soil-available pool. The greatest growing season transfers occurred between August and October, and these findings were similar to those of other researchers (Rustad and Cronan, 1989; Miller et al., 1996; Nelson, 2000). The weakest litterfall estimate was for October of the study season through June of the subsequent year, which was based on the proportion of litter falling during this time period in a similar study (Nelson, 2000). This approach resulted in elemental content estimates which were greater than the combined estimates of growing season litterfall. However, this estimate proved to be reasonable from a modeling standpoint, given the large decrease in overstory elemental content which occurred during that time period. For several elements, this litterfall estimate was still insufficient to bring overstory nutrient contents down to the predicted June levels. In those cases, the throughfall flow was employed. Ample evidence exists that both litterfall and throughfall are important mechanisms by which elements are removed from trees, particularly for conifers during the winter (Tamm, 1951; Madgwick and Ovington, 1959; Tukey, 1970; Turner, 1975; Klemmedson et al., 1990; Trofymow et al., 1991; Prescott et al., 1993; Nelson, 2000). Therefore, even though the winter litterfall estimates were the least reliable in our model, and throughfall was probably under-represented, the model nonetheless provided a reasonable representation of seasonal nutrient dynamics. Winter litterfall measurements and year-round throughfall measurements would help to refine model estimates.

The significant differences in overstory nutrient contents resulting from various species compositions suggests that significant species-related differences in litter and throughfall elemental contents may occur as well. Several studies document differences in litter elemental contents for various forest ecosystems at different times of the year (Rustad and Cronan, 1989; Klemmedson et al., 1990; Trofymow et al., 1991; Kavvadias et al., 2001). Litter and forest floor decomposition rates also vary for different forest tree species (Vesterdal and Raulund-Rasmussen, 1998; Prescott et al., 2000; Thirukkumaran and Parkinson, 2001; Dijkstra, 2003). Throughfall is affected by species as well as tissue type and age (Tamm, 1951; Madgwick and Ovington, 1959; Tukey, 1970; Parker, 1983). In this study, litterfall elemental contents were held constant during simulated model projections comparing various overstory species compositions, because data for simulation-specific litterfall simulations were not available. Throughfall elemental contents were used to equalize model projections, and were probably not indicative of actual throughfall contents during any of the simulated model scenarios. Because these transfers have such important biological significance and also vary with forest species composition, future nutrient cycling studies should include appropriate measurements of litterfall and throughfall.

Understory Contents and Transfers

Because understory plant biomass was so small compared to tree biomass in the study stand, understory elemental content and associated litterfall, throughfall and uptake quantities were minor, and most elements were detected only in trace quantities. Nitrogen, K and Ca were detected in measurable quantities in the understory. During the growing season, understory nutrient contents were greatest in August. All elements showed a late-season decrease in nutrient content, though the difference was only significant for N and K (Garrison-Johnston, 2003b). The tendency toward decreased late-season nutrient content was attributable in part to understory biomass, which also was lowest in October. Even though not statistically significant, seasonal changes in understory biomass and content are probably real from a biological standpoint, resulting from both light conditions and seasonal nutrient allocation shifts (Tiffin, 1972; Lieffers et al., 1999; VanderSchaaf, 1999; Nelson, 2000; Tremblay and Larocque, 2001).

By design, understory nutrient content in our model decreased from one year to the next as a function of overstory density. The decrease in understory production coincident with increased stand density has been well-documented, and in most cases is attributed to increased competition for resources, principally light (Jameson, 1967; Alaback and Herman, 1988; Uresk and Severson, 1989; Moore and Deiter, 1992; Riegel et al., 1995; Klinka et al., 1996; Lieffers et al., 1999; McKenzie et al., 2000). While the decrease in understory biomass with increased overstory density seems obvious, few prediction equations applicable to this study were available. One equation based on several sites and forest types throughout the inland northwest was utilized (VanderSchaaf et al., 2002).

The same litterfall and throughfall mechanisms responsible for winter decreases in overstory content play important roles in late-season nutrient transfers from understory vegetation to the forest floor (Tukey and Morgan, 1964; Tukey, 1970; Rustad and Cronan, 1989; Nelson, 2000). In our study, understory litterfall was simply estimated as a proportion of total litterfall content, rather than separating litter materials into overstory and understory components for processing and chemical analysis. Therefore, understory litterfall may have been somewhat over- or underestimated, particularly as plant litter chemistry probably differed significantly from tree litter chemistry (Nelson, 2000; Kavvadias et al., 2001; Dijkstra, 2003). As with the overstory, throughfall was not measured, but rather was utilized as a mechanism to account for non-litterfall nutrient losses from the understory, and therefore may have been poorly estimated, depending on the reliability of plant litter estimates. Because the understory was such a minor component of the simulated stand, both from a biomass and elemental content standpoint, the modeling approach used in this study was considered adequate. However, both litter and throughfall transfer mechanisms should warrant more attention in future studies of this type, particularly in younger or less dense stands where the understory comprises a greater stand component. Understory production following various levels of harvesting would be a very important component to track in long-term nutrient cycling studies, both for the value of herbaceous vegetation in retaining nutrients on-site, and the difficulties such vegetation can pose to subsequent stand establishment.

Soil Contents

The developed nutrient cycling model adequately patterned short-term overstory and understory nutrient contents, given the current stage of stand development. However, if cycling were to continue as modeled, all soil reserves except for S and Fe would eventually be depleted. This was true regardless of overstory species composition, although during the GF simulation, soil elemental content was depleted even faster than during the DF and MC simulations. This depletion is probably not an accurate long-term representation of soil elemental dynamics, though there are several plausible explanations for our model results.

As specified, no controls on nutrient uptake as a function of nutrient availability were included in the overstory and understory portions of the model. Therefore, growth limitations due to nutrient deficiency were not modeled. From a biological standpoint, we know that nutrient deficiencies, particularly N, limit growth (Moore et al., 1991; Garrison et al., 2000). These nutrient deficiencies should be addressed from a modeling standpoint. This would probably be best accomplished by making tree and plant uptake a function of soil compartment availability, rather than allowing the soil compartment to be a function of tree and plant growth, as the model currently is constructed. However, in order to accomplish this, the difficult task of measurement and prediction of accurate plant-available values for the soil compartment at different points in time would need to be addressed.

Soil data collected at one point in time was utilized for this model. Soils were analyzed using standard agricultural laboratory tests. Soils could have been sampled and analyzed over time in order to obtain periodic soil reserve estimates. However laboratory tests were not considered an adequate reflection of forest soil nutrient availability, for several reasons. Theoretically, these tests use chemical reagents to extract soil elements in the same way a crop plant would extract those elements (Foth and Ellis, 1997; Aber and Melillo, 2001). To date, most reported correlations between forest soils and forest nutrient status have been for mineralizable N and C/N ratios in response to N fertilization (Powers, 1980; Peterson et al., 1984; Carter et al., 1998). Correlations of other soil test data with forest nutrient status have not generally been successful (Peterson et al., 1984; Hart and Binkley, 1985; Binkley et al., 1992; Cade-Menum and Lavkulich, 1997). Soil ion-exchange resins used *in-situ* may give a better picture of site-specific nutrient availability, because they theoretically integrate the various site-specific conditions which affect nutrient availability to plants over time (Smith, 1979; Hart and Binkley, 1985; Binkley et al., 1986; Olness and Rinke, 1994; Skogley and Dobermann, 1996). However, a major drawback to using these data in a mass balance modeling approach is that the units are based on resin surface area rather than soil volume. Ion-exchange resin data may be useful if we can either use them to validate data obtained from standard soil tests, or make some assumptions as to the volume of soil exploited by ion-exchangers and thereby enable their use in a mass balance approach.

In this study, ion-exchange data did support the model projections for the MC stand showing decreases in soil pools of N, Mg and K throughout the growing season. This result probably indicates that soil availability of those elements did decrease during the growing season, though the actual magnitude of that decrease is uncertain. From a biological standpoint it also is reasonable that the available pool of these elements decreased coincident with plant uptake. Conversely, ion-exchange data showed P and Fe availability to increase throughout the growing season while the model projection showed their availability decreasing. For P, this may reflect the ability of ion-exchange resins to mimic plant elemental uptake, since any P which became available in the immediate vicinity of an ion-exchange resin likely adhered to the resin. Furthermore, mycorrhizae are known to play an important role in tree uptake of P, indicating that perhaps trees were able to access sources of P not detected during standard soil tests nor represented in model projections. Both factors suggest that the model did not adequately represent fluxes in soil-available P throughout the growing season. Similarly, Fe estimates may have not been adequately represented on a seasonal basis, however the model did project increases in soil Fe on an annual basis. Therefore, the timing of Fe inputs from rock weathering could be adjusted to more accurately reflect availability as shown by ion-exchange resins. Ion-exchange data and model projections for the remaining elements showed mixed results in this comparison, and likely reflected a mix of the explanations discussed for N, Mg, K, P and Fe.

Flows to and from the soil box were also evaluated for their role in projected soil nutrient depletion. As previously discussed, overstory elemental contents were sensitive to shifts in forest species composition. Therefore, by experimentally shifting the stand composition from a less nutrient-intensive species (Douglas-fir) to a more intensive species (grand fir), the demand on soil nutrient reserves was intensified. Elemental returns from the overstory to the soil through litterfall and throughfall also likely vary with forest species composition, but were not directly evaluated in this study due to lack of data. Thus, appropriate measurement and monitoring of overstory elemental content, litterfall and throughfall for various forest species will be important in improving future model performance.

Forest floor mineralization rates were not measured during this study, but may be an important source of elements to the soil nutrient pool. Nutrient cycling model projections showed that initial soil reserves of N, Mg, P and Ca, which were 102, 17, 11, and 52 kg ha^{-1} respectively, would be depleted within several years. Forest floor contents of these four elements were three to nine times as great as soil nutrient contents, measuring 320, 48, 30 and 480 kg ha^{-1}, respectively. Given that soil reserves of these four elements at our experimental site were probably not being depleted as fast as the model indicated, mineralization of elements held in the forest floor may be have been occurring, even during the short time period modeled.

Simulated soil pools of S and Fe increased on an annual basis. For both elements, increases were due to inputs exceeding plant demands. For S, the input was atmospheric while for Fe, the input was from rock weathering. Plant-available S probably did not truly increase during the growing season at our experimental site, based on ion-exchange assessment of the soil S pool and the finding of S deficiency in the trees based on foliar nutrient diagnostics (Garrison-Johnston, 2003a). However, the S sorption capacity of the Bw volcanic ash horizon of this site was approximately 4900 kg ha^{-1}, based on regional soil S sorption curves (Kimsey, In Progress). This suggests that even if the soil S pool increased over time, this S would likely be unavailable for plant uptake because of sorption, and thus the site could still demonstrate a plant S deficiency. Conversely, it is feasible that weathering input of Fe could result in a slow increase in the soil Fe pool over time. Ion-exchange analysis at our experimental site also showed an increase in available Fe over the course of the growing season (Garrison-Johnston, 2003a).

Forest Floor

In our model, the forest floor was assumed to maintain steady state conditions for the few years simulated during this study. Findings from a study in a Washington state Douglas-fir stand supported this assumption for K, P and Mg, but not for N, Ca and Mn, which continued to accumulate over time (Guha and Mitchell, 1966). The results of our nutrient cycling model projection showed that soil reserves of several elements would be depleted within a few years at our experimental site, while forest floor content for these elements were three to nine times greater than soil reserves. Thus, the forest floor seems to be an important source for continued nutrient supply at this site. The forest floor steady-state nutrient condition assumption was probably not valid, at least for some elements. Conversely, long-term utilization of forest floor reserves to sustain tree growth would lead to the 'mining' of the forest floor for these elements, unless another source were provided to the forest floor or soil nutrient pools.

Forest floor nutrient reserves are largely governed by decomposition rates of incoming litter. Litter decomposition rates, in turn, are governed by climatic and topographic conditions as well as site-specific factors such as site fertility, tree species, litter and forest floor quality and biological activity (Prescott et al., 1993; Kavvadias et al., 2001). The generally cool, moist conditions of our experimental site may have resulted in low biological activity and concurrent low litter decomposition rates, particularly given stand density and the high needle component of litterfall. This in turn would contribute to forest floor elemental accumulation over time. Better monitoring of forest floor nutrient reserves would improve estimates of forest floor accumulation or depletion rates for use in nutrient cycle modeling.

Rock Weathering

Computation methods for rock weathering rates range from solving mass balance equations at the watershed level to detailed microscopic examination of individual soil mineral particles (McClelland, 1951; Clayton, 1979; Clayton, 1984; Hodson et al., 1998; Birkeland, 1999). No single method provided a 'best' estimate for all soil types based on a comparison of methods for estimating forest soil mineral weathering rates (Kolka et al., 1996). Clayton's (1979) approach was selected for our study because of its simplicity. However, results using this procedure can vary widely given even small variations in estimated particle size and quantity of the coarse fraction, as well as component mineralogy. Inadequate determination of particle size, quantity and mineralogy may have contributed to inaccurate elemental supply estimates from rock weathering. This in turn could have contributed to the rapid depletion of soil reserves of Ca and Mg predicted by our nutrient cycling model.

Other elements in addition to those shown in Table 3-2 were likely supplied through weathering of accessory minerals such as apatite. Since accessory minerals were not detected in the coarse fraction, they were not included in weathering estimates. The likelihood of detecting accessory minerals through optical mineralogical examination of soil particles is low, given the limited occurrence of these minerals and the low probability of their remaining intact during rock weathering and soil developmental processes. However, extensive optical examination of minerals provides the best means of detecting such accessory minerals for inclusion in mineral weathering estimates.

Model Evaluation

The framework of compartments and flows developed for this model appeared adequate for evaluation of forest elemental cycling. Evaluation of the field data using this model, and additional simulations performed by changing the overstory species composition, highlighted the strengths and weaknesses in the data. Short-term seasonal estimates of overstory and understory elemental contents were reasonable, and agreed with those of other researchers. Litterfall estimates were reasonable in view of seasonal tree and plant dynamics and agreed with findings of other researchers. Throughfall was not measured during this study. A throughfall flow was used as a 'default' flow for returning excess nutrients from vegetation to the soil pool, and thus was probably not representative of actual throughfall rates. However, 'real' nutrient inputs from throughfall were accounted for in other ways in our model. Future research should be directed towards improved estimation of overstory elemental contents of various tree species, as well as related litterfall and throughfall contents. Inputs and outputs external to the system which would benefit from additional or more detailed measurements included wet and dry deposition, mineral weathering and leaching losses. Rates of change for forest floor and soil compartment estimates should also be improved for better model performance.

The nutrient modeling framework developed in this study provides a good basis for future experimental stand manipulations. Extending the basic model to handle such manipulations would require several modifications, such as provisions for increased understory development and nutrient uptake following harvesting, provision of a woody debris compartment and input flow similar to forest floor and litterfall input, estimates of nutrient release from woody debris, and estimates of soil nutrient changes and leaching thresholds following major inputs from the overstory. Numerous studies detailing the response of various ecosystem components to forest harvesting and natural disturbances have been performed (Cole et al., 1967; Gordon, 1983; Timmer et al., 1983; Johnson, 1983; Smith, 1984; Tew et al., 1986; Mann et al., 1988; Olsson et al., 1996; Mitchell et al., 1996; Nelson, 2000). The incorporation of this type of information into a systems analysis model such as ours would facilitate an understanding of component interactions and the effects of stand manipulation or disturbance on ecosystem nutrient cycling.

Forest nutrient cycling is a complex system comprised of numerous processes occurring at multiple scales. By integrating these processes into a generalized systems analysis model, we created a simple tool for visualizing stand-based nutrient cycling. Using this approach, we were able to consider the elemental dynamics of this forest stand in a manner not possible through examination of the individual boxes and flows.

CONCLUSIONS

This systems analysis approach was useful for evaluation of ecosystem elemental cycling at the experimental site. Overstory elemental contents increased both seasonally and annually, as expected due to stand developmental stage and in accordance with findings by other researchers. Experimental manipulation of the overstory species composition revealed that grand fir nutrient demand was greater than Douglas-fir nutrient demand for most elements. This resulted in more rapid depletion of soil nutrient reserves for grand fir compared to Douglas-fir stands, especially for N, P and Ca. Understory elemental contents varied seasonally, but decreased annually, also in accordance with expectations based on overstory conditions. Litterfall elemental contents during the August to October time period were greater than June through August, while contents for October of one year through June of the next year were greater than total litterfall contents measured during one growing season. Throughfall was not measured during this study, but proved to be a useful mechanism for transferring elements from vegetation to the forest floor as needed to meet seasonal changes in elemental contents of overstory and understory compartments during model execution. Throughfall was likely more active on our site than indicated by these estimates, however throughfall transfers not included in those flows were accounted for in other ways by the model.

Soil nutrient reserves were the most affected by elemental dynamics during model projections. If nutrient cycling trends were to continue as modeled, soil N, P, Mg, and Ca reserves would be depleted in just a few years. All other elements except for S and Fe were also declining, though at a slower rate. While there is some likelihood that any of these elements could be a limiting factor to growth at this site, probably these estimates of soil nutrient pools and soil nutrient dynamics were inaccurate. This could have resulted from poor estimation of forest stand-available elemental pools, poor estimation of external inputs from atmospheric or mineral weathering sources, or inadequate estimation of internal cycling rates such as forest floor mineralization or vegetation uptake.

Overall, we found systems analysis to be a useful tool for evaluating forest elemental cycling. This approach allowed us to incorporate data measurements from multiple ecosystem components into one generalized model, which was applicable to both macro- and micronutrients. Building the model for the growing season for which data was collected provided a better understanding of seasonal nutrient dynamics and component interactions of the study stand. Extending the model over a three-year period allowed identification of those boxes and flows requiring better data, as well as those components potentially most sensitive to stand manipulations and disturbances. Experimental manipulation of overstory species composition emphasized the important role of species nutritional characteristics in site nutrient demand and nutrient cycling dynamics. Future research efforts should focus on improved estimation of nutrient contents of various forest species, as well as soil nutrient pool estimation and monitoring, forest floor mineralization, and understory content changes. Tree and plant uptake might be more adequately represented as a function of soil nutrient availability. Improved monitoring of year-round litterfall, throughfall and external inputs would be useful as well.

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APPENDIX A-1: Whole-Rock Geochemistry

	GAR MG 265-1	GAR MG 265-2	GAR MG 265-3	GAR MG 265-4	GAR MG 265-5
Date	6-Mar-00	6-Mar-00	6-Mar-00	6-Mar-00	6-Mar-00
LOI (%)	3.53			7.88	1.69
			Normalized Results (Weight % Oxide):		
SiO2	69.92	72.22	73.74	74.88	71.30
Al2O3	17.29	15.39	16.30	20.26	15.97
TiO2	0.634	0.011	0.024	0.137	0.671
FeO*	5.43	0.16	0.23	1.22	3.95
MnO	0.074	0.002	0.015	0.037	0.066
CaO	0.09	0.04	0.60	0.23	0.52
MgO	1.37	0.00	0.01	0.33	1.31
K2O	4.76	†10.50	6.56	2.15	4.48
Na2O	0.37	1.67	2.51	0.73	1.60
P2O5	0.062	0.008	0.015	0.022	0.115
			Normalized Results (Weight % Element):		
Si	32.68	33.75	34.47	35.00	33.32
Al	9.15	8.15	8.62	10.72	8.45
Ti	0.380	0.007	0.015	0.082	0.402
Fe	4.22	0.13	0.18	0.95	3.07
Mn	0.058	0.002	0.012	0.029	0.051
Ca	0.06	0.03	0.43	0.16	0.37
Mg	0.82	0.00	0.01	0.20	0.79
K	3.95	8.71	5.45	1.78	3.72
N	0.28	1.24	1.86	0.54	1.19
P	0.027	0.003	0.007	0.010	0.050
Oxygen	*48.37*	*47.98*	*48.96*	*50.52*	*48.57*
			Trace Elements (ppm):		
Ni	28	3	2	13	18
Cr	58	0	0	10	48
Sc	22	8	10	6	18
V	83	11	1	22	85
Ba	516	1724	†4356	273	678
Rb	196	195	113	83	187
Sr	25	272	490	53	73
Zr	254	14	23	52	274
Y	42	4	6	9	43
Nb	16.6	2.6	3.7	6.5	16.4
Ga	23	11	13	20	19
Cu	48	6	2	10	7
Zn	43	0	2	19	51
Pb	11	†69	56	16	10
La	52	0	6	10	52
Ce	93	0	11	28	72
Th	15	0	5	4	14

Major elements are normalized on a volatile-free basis, with total Fe expressed as FeO.
"†" denotes values >120% of our highest standard.

Rock ID Key:

265-1	MCE, weathered mica schist, class 6-7*
265-2	MCE, remnant pegmatite feldspars
265-3	MCW, granitic fresh class 5, white
265-4	MCW, granitic weathered Class 6-7, orange
265-5	MCW, mica schist, class 6-7

** Weathering classes based on Clayton et al. (1979)*

Average Geochemistry By Rock Type

Normalized Results (Weight % oxide)

	Schist	Granite
SiO_2	70.61	74.31
Al_2O_3	16.63	18.28
TiO_2	0.65	0.08
FeO*	4.69	0.73
MnO	0.07	0.03
CaO	0.31	0.41
MgO	1.34	0.17
K_2O	4.62	4.36
Na_2O	0.99	1.62
P_2O_5	0.09	0.02

Normalized Results (Weight % Element)

	Schist	Granite
Si	33.0016	34.7317
Al	8.8014	9.6732
Ti	0.3913	0.0483
Fe	3.6483	0.5639
Mn	0.0544	0.0202
Ca	0.2187	0.2954
Mg	0.8077	0.1025
K	3.8357	3.6169
N	0.7330	1.2012
P	0.0387	0.0081
Cu (ppm)	27.50	6.00
Zn (ppm)	47.00	10.50

Mallory Creek Pit # 1 **Description by Mike Regan October 19, 1999**

Horizonation	Boundary		Texture					Color		Consistence	Structure		Roots
	depth (cm)	depth (in)	distictness	coarse frag.	class	%clay	% mica	dry	moist	dry	shape	grade	
A	16	6.3	A	1	sil	10	0	10YR 5/4	7.5YR 3/3	S	sbk	1	3vf,2f
Bw	38	15.0	A	1	sil	8	0	10YR 6/4	10YR 4/4	S	sbk	1	3vf,2vf
2Bt1	57	22.4	C	10	l	15	35	7.5YR 6/4	10YR 5/4	MH	sbk	2	2m,2vc
2Bt2	74	29.1	C	15	l	14	40	7.5YR 6/4	10YR 5/4	MH	sbk	2	1vf,1f,1vc
2BC	121	47.6	C	15	ls	10	75	7.5YR 6/4	10YR 5/4	SH	sbk	1	2c
2C	121+	47.6+		5	ls	7	90	7.5YR 6/4	10YR 5/4	SH	sbk	1	1vf

This Pit is located on a sideslope/backslope

The parent material is volcanic ash over colluvium and residuum from schist

This soil is classified as Coarse-loamy, paramicaceous, frigid, Andic Haploudalf.

The series that fits this classification with a Thuja plicata / Asarum caudatum vegetation community is the Poorman series.

Mallory Creek Pit # 2 **Description by Mike Regan October 19, 1999**

Horizonation	Boundary		Texture					Color		Consistence	Structure		Roots
	depth (cm)	depth (in)	distictness	coarse frag.	class	%clay	% mica	dry	moist	dry	shape	grade	
A	15	5.9	A	1	sil	10	0	10YR 5/4	7.5YR 3/3	S	sbk	1	3vf,3f,3m,3vc
Bw	32	12.6	A	1	sil	8	0	10YR 6/4	10YR 4/3	S	sbk	1	3vf,3f,3m,3vc
2BC	48	18.9	C	20	l	10	75	7.5Y 5/4	10YR 4/3	MH	sbk	2	1vf,2m,2vc
2BC2	98	38.6	C	15	sl	7	90	7.5YR 5/4	10YR 4/3	MH	sbk	1	2m,2vc
2CB	98+	38.6+		15	sl	10	85	7.5YR 5/6	10YR 4/6	MH	sbk	2	1vf

This Pit is located on a sideslope/backslope

The parent material is volcanic ash over colluvium and residuum from schist

This soil is classified as Coarse-loamy, paramicaceous, frigid, Andic Eutrudept, with a Thuja plicata /Asarum caudatum vegetation community. The series is unknown but closely resembles the Alderman series, it is paramicaceous whereas Alderman is not. It is Andic instead of Vitrandic meaning it has a less mixed or deeper ash layer, and the vegetation community is slightly wetter. Alderman has THPL/CLUN vegetation.

Mallory Creek Pit #3 **Description by Mike Regan October 19, 1999**

Horizon-ation	Boundary		Texture					Color		Consis-tence	Structure			Roots
	depth (cm)	depth (in)	distict-ness	coarse frag.	class	%clay	% mica	dry	moist	dry	type	shape	grade	
A	8	3.1	A	2	sil	10	0	10YR 5/4	7.5YR 3/2	S	gr	sbk	1	3vf,3f,2c,3vc
Bw	21	8.3	A	2	sil	8	0	10YR 6/4	10YR 3/3	S	sbk	sbk	1	3vf,3f,2c,3vc
2Bt1	41	16.1	C	5	sil	17	15	7.5Y 6/4	10YR 4/3	MH	sbk	sbk	2	3m,2vc
2Bt2	65	25.6	C	15	sil	15	15	7.5YR 7/4	10YR 5/4	MH	sbk	sbk	2	3m,2vc
2BC	75	29.5	A	10	sl	10	65	7.5YR 6/4	10YR 5/4	SH	sbk		1	3f,3c
2Cr	75+	29.5+		5	ls	6	85	7.5YR 7/6	10YR 5/6	MH	sbk	sbk	2	2f

This Pit is located on a shoulder

The parent material is volcanic ash over colluvium and residuum from schist

This soil is classified as Coarse-loamy, paramicaceous, frigid, Andic Haploudalf.
The series that fits this classification with a Thuja plicata / Asarum caudatum vegetation community is the Poorman series.

Mallory Creek Pit #4 **Description by Mike Regan October 19, 1999**

Horizon-ation	Boundary		Texture					Color		Consis-tence	Structure		Roots
	depth (cm)	depth (in)	distictness	coarse frag.	class	%clay	% mica	dry	moist	dry	type	grade	
A	10	3.9	A	1	sil	8	0	10YR 5/4	7.5YR 3/3	S	sbk	1	3vf,3f,3c
Bw	33	13.0	A	1	sil	8	0	10YR 6/4	10YR 4/4	S	sbk	1	3vf,3f,3c
2Bt/E 1	53	20.9	C	2	sil	14	10	7.5YR 6/4	7.5YR 5/4	MH	sbk	2	1m,3c
2Bt/E 2	75	29.5	C	3	sil	15	10	7.5YR 6/4	10YR 4/4	HA	sbk	2	1f
2Bt1	90	35.4	C	3	sil	20	15	7.5YR 6/4	10YR 4/4	HA	sbk	2	1f
2Bt2	120	47.2	C	5	sil	24	15	7.5YR 6/4	10YR 5/4	HA	sbk	2	1f
3Bt	120+	47.2+		10	sil	16	15	7.5YR 6/4	10YR 5/4	MH	sbk	2	1f

This Pit is located on a sideslope/backslope

The parent material is volcanic ash over loess mixed with colluvium and residuum from schist

This soil is classified as Fine-loamy, mixed, frigid, Andic Haploudalf.
The series that most closely resembles this classification with a Thuja plicata / Asarum caudatum vegetation community is the Poorman series. This soil lacks the high mica content of the Poorman soil series.
This soil also has a strong loess influence unlike the Poorman series.

Mallory Creek Pit #5 **Description by Mike Regan October 19, 1999**

Horizon-ation	Boundary		Texture					Color		Consis-tence	Structure		Roots
	depth (cm)	depth (in)	distict-ness	coarse frag.	class	%clay	% mica	dry	moist	dry	type	grade	
A	11	4.3	A	1	sil	9	0	10YR 5/4	7.5YR 3/3	S	sbk	1	3vf,3f,2c
Bw	27	10.6	A	1	sil	8	0	10YR 6/4	7.5YR 3/3	S	sbk	1	3vf,3f,2c
2E	40	15.7	C	10	sl	7	30	7.5YR 6/4	7.5YR 4/4	MH	sbk	2	3vf,3f,3vc
2Bt	51	20.1	A	10	sl	11	30	7.5YR 6/4	7.5YR 4/4	MH	sbk	2	2vf,2f
3C	82	32.3	A	15	s	5	20	7.5YR 8/2	7.5YR 6/3	L	sg	0	1m
2Cr	82+	32.3+		0	s	3	95	10YR 5/4	7.5YR 4/4	L	sg	0	1vf

This Pit is located on a sideslope/backslope

The parent material is volcanic ash over residuum from quartz monzonite and schist

This soil is classified as Coarse-loamy, mixed, frigid, Andic Haploudalf.
The series that most closely resembles this classification with a Thuja plicata / Asarum caudatum vegetation community is the Poorman series. This soil lacks the high mica content of the Poorman soil series.

Mallory Creek Pit #6 **Description by Mike Regan October 19, 1999**

Horizon-ation	Boundary		Texture					Color		Consis-tence	Structure		Roots
	depth (cm)	depth (in)	distic-ness	coarse frag.	class	%clay	% mica	dry	moist	dry	type	grade	
A	12	4.7	A	1	sil	9	0	10YR 5/4	7.5YR 3/2	S	sbk	1	3vf,3f,1vc
Bw	33	13.0	A	1	sil	8	0	10YR 6/4	7.5YR 4/4	S	sbk	1	3vf,3f,1vc
2Bt/E 1	63	24.8	C	2	sil	15	10	10YR 6/4	7.5YR 4/4	HA	sbk	2	3v,3m
2Bt/E 2	79	31.1	C	5	sil	16	15	10YR 7/4	7.5YR 5/4	HA	sbk	2	2m
2BC	79+	31.1+		10	sil	15	5	10YR 7/4	7.5YR 5/4	VH	sbk	2	1m

This Pit is located on a shoulder position

The parent material is volcanic ash over colluvium and residuum from Quartz monzonite and schist

This soil is classified as Coarse-loamy, mixed, frigid, Andic Haploudalf.
The series that most closely resembles this classification with a Thuja plicata / Asarum caudatum vegetation community is the Poorman series. This soil lacks the high mica content of the Poorman soil series.

APPENDIX A-3: Soil Chemistry

Tests performed by:

ANALYTICAL SCIENCES LABORATORY
UNIVERSITY OF IDAHO
HOLM RESEARCH CENTER
MOSCOW, ID 83844-2203

	SAT.	0.75M NaOAc			2M KCl	
	PASTE	P	K	O.M.	NO3-N	NH4-N
	pH	µg/g	µg/g	%	µg/g	µg/g
A	6.30	2.80	420.00	14.25	19.9	38.4
Bw	6.00	0.50	180.00	2.28	3.6	7.6
2Bt and 2E (schist)	5.20	0.90	74.00	0.52	0.7	2.3
2BC and 2C (schist)	5.00	0.50	52.00	0.34	0.5	2.9
3BC and 3C (granitic)	5.80	0.00	48.00	0.17	0.9	5.3

			EXTRACTABLE CATIONS		
	SO4-S	B	Ca	Mg	K
	µg/g	µg/g		µg/g	
A	10.8	0.41	20.50	1.85	1.40
Bw	16.6	0.11	3.55	0.76	0.58
2Bt and 2E (schist)	2.6	0.10	2.70	1.40	0.25
2BC and 2C (schist)	2.9	0.06	2.70	1.40	0.19
3BC and 3C (granitic)	1.4	0.00	0.48	0.03	0.04

		DTPA		
	Zn	Mn	Cu	Fe
	µg/g	µg/g	µg/g	µg/g
A	2.40	48.0	0.63	61.0
Bw	0.33	8.1	0.41	35.0
2Bt and 2E (schist)	0.21	8.0	0.42	26.0
2BC and 2C (schist)	0.18	2.0	0.30	15.0
3BC and 3C (granitic)	0.14	2.0	0.16	9.9

APPENDIX B-1: Results of Elemental Cycling Projections Over Five Years
Mallory Creek Mixed Conifer Stand

Nitrogen

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weather-ing	Atmospheric Deposition	Leaching
June Yr 1	1	397.23	3.3764	320.44	101.99	0	0.6972	0
August Yr 1	2	424.40	3.8000	320.44	75.09	0	0.6987	0
October Yr 1	3	433.20	1.9652	320.44	68.83	0	3.352	0
June Yr 2	1	408.58	3.1873	320.44	95.58	0	0.6972	0
August Yr 2	2	435.75	3.5872	320.44	68.70	0	0.6987	0
October Yr 2	3	444.55	1.8551	320.44	62.34	0	3.352	0
June Yr 3	1	419.93	3.0088	320.44	89.15	0	0.6972	0
August Yr 3	2	447.10	3.3863	320.44	62.30	0	0.6987	0
October Yr 3	3	455.90	1.7512	320.44	55.84	0	3.352	0
June Yr 4	1	431.28	2.8404	320.44	82.72	0	0.6972	0
August Yr 4	2	458.45	3.1967	320.44	55.89	0	0.6987	0
October Yr 4	3	467.25	1.6532	320.44	49.33	0	3.352	0
June Yr 5	1	442.63	2.6813	320.44	76.28	0	0.6972	0
August Yr 5	2	469.80	3.0177	320.44	49.47	0	0.6987	0
October Yr 5	3	478.60	1.5606	320.44	42.82	0	3.352	0
June Yr 6	1	453.98	2.5312	320.44	69.83	0	0.6972	0

Point in time	Step	Minerali-zation	Tree Uptake	Tree Litter	Tree Through-fall	Plant Uptake	Plant Litter	Plant Through-fall
June Yr 1	1	4.0461	30.3515	3.1815	0.0000	0.5910	0.1674	0.0000
August Yr 1	2	10.6172	17.2307	8.4307	0.0000	0.0000	1.4878	0.3470
October Yr 1	3	22.4152	0.0000	17.9194	6.7006	2.3660	1.1438	0.0000
June Yr 2	1	4.0368	30.3515	3.1815	0.0000	0.5579	0.1581	0.0000
August Yr 2	2	10.5339	17.2307	8.4307	0.0000	0.0000	1.4045	0.3276
October Yr 2	3	22.3512	0.0000	17.9194	6.7006	2.2335	1.0798	0.0000
June Yr 3	1	4.0279	30.3515	3.1815	0.0000	0.5267	0.1492	0.0000
August Yr 3	2	10.4552	17.2307	8.4307	0.0000	0.0000	1.3258	0.3093
October Yr 3	3	22.2907	0.0000	17.9194	6.7006	2.1084	1.0193	0.0000
June Yr 4	1	4.0196	30.3515	3.1815	0.0000	0.4972	0.1409	0.0000
August Yr 4	2	10.3810	17.2307	8.4307	0.0000	0.0000	1.2516	0.2919
October Yr 4	3	22.2336	0.0000	17.9194	6.7006	1.9903	0.9622	0.0000
June Yr 5	1	4.0117	30.3515	3.1815	0.0000	0.4694	0.1330	0.0000
August Yr 5	2	10.3109	17.2307	8.4307	0.0000	0.0000	1.1815	0.2756
October Yr 5	3	22.1797	0.0000	17.9194	6.7006	1.8789	0.9083	0.0000
June Yr 6	1	4.0042	30.3515	3.1815	0.0000	0.4431	0.1255	0.0000

Phosphorus

Point in time	Step	Over-story	Under-story	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	63.59	0.3557	31.07	11.23	0	0	0
August Yr 1	2	65.86	0.3038	31.07	9.02	0	0	0
October Yr 1	3	69.45	0.1635	31.07	5.57	0	0	0
June Yr 2	1	65.89	0.3358	31.07	8.95	0	0	0
August Yr 2	2	68.16	0.2868	31.07	6.73	0	0	0
October Yr 2	3	71.75	0.1544	31.07	3.28	0	0	0
June Yr 3	1	68.19	0.3170	31.07	6.67	0	0	0
August Yr 3	2	70.46	0.2707	31.07	4.45	0	0	0
October Yr 3	3	74.05	0.1457	31.07	0.98	0	0	0
June Yr 4	1	70.49	0.2992	31.07	4.39	0	0	0
August Yr 4	2	72.76	0.2556	31.07	2.16	0	0	0
October Yr 4	3	76.35	0.1376	31.07	-1.31	0	0	0
June Yr 5	1	72.79	0.2825	31.07	2.11	0	0	0
August Yr 5	2	75.06	0.2412	31.07	-0.12	0	0	0
October Yr 5	3	78.65	0.1299	31.07	-3.60	0	0	0
June Yr 6	1	75.09	0.2667	31.07	-0.18	0	0	0

Point in time	Step	Minerali-zation	Tree Uptake	Tree Litter	Tree Through-fall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.2434	2.5012	0.2312	0	0.0000	0.0122	0.0397
August Yr 1	2	0.9194	4.3715	0.7815	0	0.0000	0.1379	0.0024
October Yr 1	3	1.6314	0	1.5335	2.0265	0.2701	0.0979	0.0000
June Yr 2	1	0.2427	2.5012	0.2312	0	0.0000	0.0115	0.0375
August Yr 2	2	0.9117	4.3715	0.7815	0	0.0000	0.1302	0.0022
October Yr 2	3	1.6259	0	1.5335	2.0265	0.2550	0.0924	0.0000
June Yr 3	1	0.2420	2.5012	0.2312	0	0.0000	0.0108	0.0354
August Yr 3	2	0.9044	4.3715	0.7815	0	0.0000	0.1229	0.0021
October Yr 3	3	1.6207	0	1.5335	2.0265	0.2407	0.0872	0.0000
June Yr 4	1	0.2414	2.5012	0.2312	0	0.0000	0.0102	0.0334
August Yr 4	2	0.8975	4.3715	0.7815	0	0.0000	0.1160	0.0020
October Yr 4	3	1.6158	0	1.5335	2.0265	0.2273	0.0823	0.0000
June Yr 5	1	0.2409	2.5012	0.2312	0	0.0000	0.0097	0.0316
August Yr 5	2	0.8910	4.3715	0.7815	0	0.0000	0.1095	0.0019
October Yr 5	3	1.6112	0	1.5335	2.0265	0.2145	0.0777	0.0000
June Yr 6	1	0.2403	2.5012	0.2312	0	0.0000	0.0091	0.0298

Potassium

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weather-ing	Atmos-pheric Deposition	Leaching
June Yr 1	1	272.76	2.9507	76.18	1388.32	0	0.0338	0
August Yr 1	2	301.59	4.3188	76.18	1358.16	0	0.0319	0
October Yr 1	3	311.07	1.8725	76.18	1351.15	2.42	0.1162	0
June Yr 2	1	282.09	2.7855	76.18	1381.76	0	0.0338	0
August Yr 2	2	310.92	4.0769	76.18	1351.67	0	0.0319	0
October Yr 2	3	320.40	1.7677	76.18	1344.53	2.42	0.1162	0
June Yr 3	1	291.42	2.6295	76.18	1375.19	0	0.0338	0
August Yr 3	2	320.25	3.8486	76.18	1345.17	0	0.0319	0
October Yr 3	3	329.73	1.6687	76.18	1337.90	2.42	0.1162	0
June Yr 4	1	300.75	2.4822	76.18	1368.60	0	0.0338	0
August Yr 4	2	329.58	3.6331	76.18	1338.66	0	0.0319	0
October Yr 4	3	339.06	1.5752	76.18	1331.27	2.42	0.1162	0
June Yr 5	1	310.08	2.3432	76.18	1362.02	0	0.0338	0
August Yr 5	2	338.91	3.4296	76.18	1332.13	0	0.0319	0
October Yr 5	3	348.39	1.4870	76.18	1324.63	2.42	0.1162	0
June Yr 6	1	319.41	2.2120	76.18	1355.42	0	0.0338	0

Point in time	Step	Minerali-zation	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	1.2372	29.9732	1.1432	0.0000	1.4283	0.0602	0.0000
August Yr 1	2	5.2956	13.9542	4.4742	0.0000	0.0000	0.7895	1.6567
October Yr 1	3	8.4307	0.0000	7.8156	21.1644	1.4118	0.4989	0.0000
June Yr 2	1	1.2338	29.9732	1.1432	0.0000	1.3483	0.0568	0.0000
August Yr 2	2	5.2514	13.9542	4.4742	0.0000	0.0000	0.7453	1.5639
October Yr 2	3	8.4027	0.0000	7.8156	21.1644	1.3327	0.4709	0.0000
June Yr 3	1	1.2306	29.9732	1.1432	0.0000	1.2728	0.0536	0.0000
August Yr 3	2	5.2097	13.9542	4.4742	0.0000	0.0000	0.7036	1.4763
October Yr 3	3	8.3764	0.0000	7.8156	21.1644	1.2581	0.4446	0.0000
June Yr 4	1	1.2276	29.9732	1.1432	0.0000	1.2015	0.0506	0.0000
August Yr 4	2	5.1703	13.9542	4.4742	0.0000	0.0000	0.6642	1.3937
October Yr 4	3	8.3515	0.0000	7.8156	21.1644	1.1876	0.4197	0.0000
June Yr 5	1	1.2248	29.9732	1.1432	0.0000	1.1342	0.0478	0.0000
August Yr 5	2	5.1331	13.9542	4.4742	0.0000	0.0000	0.6270	1.3156
October Yr 5	3	8.3280	0.0000	7.8156	21.1644	1.1211	0.3962	0.0000
June Yr 6	1	1.2221	29.9732	1.1432	0.0000	1.0707	0.0451	0.0000

Magnesium

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	85.07	0.3279	100.20	17.40	0	0.0138	0
August Yr 1	2	88.24	0.4725	100.20	14.10	0	0.0149	0
October Yr 1	3	91.18	0.3457	100.20	11.30	0.4621	0.0726	0
June Yr 2	1	88.39	0.3095	100.20	14.66	0	0.0138	0
August Yr 2	2	91.56	0.4460	100.20	11.37	0	0.0149	0
October Yr 2	3	94.50	0.3263	100.20	8.57	0.4621	0.0726	0
June Yr 3	1	91.71	0.2922	100.20	11.92	0	0.0138	0
August Yr 3	2	94.88	0.4210	100.20	8.64	0	0.0149	0
October Yr 3	3	97.82	0.3081	100.20	5.83	0.4621	0.0726	0
June Yr 4	1	95.03	0.2758	100.20	9.18	0	0.0138	0
August Yr 4	2	98.20	0.3974	100.20	5.91	0	0.0149	0
October Yr 4	3	101.14	0.2908	100.20	3.09	0.4621	0.0726	0
June Yr 5	1	98.35	0.2604	100.20	6.44	0	0.0138	0
August Yr 5	2	101.52	0.3752	100.20	3.17	0	0.0149	0
October Yr 5	3	104.46	0.2745	100.20	0.35	0.4621	0.0726	0
June Yr 6	1	101.67	0.2458	100.20	3.70	0	0.0138	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.3504	3.4898	0.3198	0.0000	0.1614	0.0168	0
August Yr 1	2	1.3202	4.0495	1.1095	0.0000	0.0691	0.1958	0
October Yr 1	3	2.2468	0.0000	2.0437	0.7463	0.0943	0.1305	0
June Yr 2	1	0.3495	3.4898	0.3198	0.0000	0.1524	0.0159	0
August Yr 2	2	1.3092	4.0495	1.1095	0.0000	0.0652	0.1848	0
October Yr 2	3	2.2395	0.0000	2.0437	0.7463	0.0890	0.1232	0
June Yr 3	1	0.3486	3.4898	0.3198	0.0000	0.1438	0.0150	0
August Yr 3	2	1.2989	4.0495	1.1095	0.0000	0.0615	0.1745	0
October Yr 3	3	2.2326	0.0000	2.0437	0.7463	0.0840	0.1163	0
June Yr 4	1	0.3478	3.4898	0.3198	0.0000	0.1358	0.0142	0
August Yr 4	2	1.2891	4.0495	1.1095	0.0000	0.0581	0.1647	0
October Yr 4	3	2.2260	0.0000	2.0437	0.7463	0.0793	0.1097	0
June Yr 5	1	0.3470	3.4898	0.3198	0.0000	0.1282	0.0134	0
August Yr 5	2	1.2799	4.0495	1.1095	0.0000	0.0548	0.1555	0
October Yr 5	3	2.2199	0.0000	2.0437	0.7463	0.0749	0.1036	0
June Yr 6	1	0.3462	3.4898	0.3198	0.0000	0.1210	0.0126	0

Calcium

Point in time	Step	Overstory	Under-story	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	441.34	1.3079	481.17	51.79	0	0.0802	0
August Yr 1	2	449.56	2.0686	481.17	42.89	0	0.0741	0
October Yr 1	3	465.80	1.7656	481.17	27.03	0.7584	0.3895	0
June Yr 2	1	457.33	1.2347	481.17	37.18	0	0.0802	0
August Yr 2	2	465.55	1.9528	481.17	28.32	0	0.0741	0
October Yr 2	3	481.79	1.6667	481.17	12.44	0.7584	0.3895	0
June Yr 3	1	473.32	1.1655	481.17	22.56	0	0.0802	0
August Yr 3	2	481.54	1.8434	481.17	13.74	0	0.0741	0
October Yr 3	3	497.78	1.5734	481.17	-2.15	0.7584	0.3895	0
June Yr 4	1	489.31	1.1002	481.17	7.94	0	0.0802	0
August Yr 4	2	497.53	1.7402	481.17	-0.84	0	0.0741	0
October Yr 4	3	513.77	1.4853	481.17	-16.75	0.7584	0.3895	0
June Yr 5	1	505.30	1.0386	481.17	-6.69	0	0.0802	0
August Yr 5	2	513.52	1.6427	481.17	-15.43	0	0.0741	0
October Yr 5	3	529.76	1.4021	481.17	-31.36	0.7584	0.3895	0
June Yr 6	1	521.29	0.9805	481.17	-21.32	0	0.0802	0

Point in time	Step	Minerali-zation	Tree Uptake	Tree Litter	Tree Through-fall	Plant Uptake	Plant Litter	Plant Through-fall
June Yr 1	1	3.8808	11.8306	3.6106	0	0.9507	0.1900	0
August Yr 1	2	16.7527	30.4169	14.1769	0	2.1987	2.5017	0
October Yr 1	3	26.1550	15.7496	24.2196	0	1.0150	1.5459	0
June Yr 2	1	3.8702	11.8306	3.6106	0	0.8975	0.1794	0
August Yr 2	2	16.6126	30.4169	14.1769	0	2.0756	2.3616	0
October Yr 2	3	26.0684	15.7496	24.2196	0	0.9581	1.4593	0
June Yr 3	1	3.8601	11.8306	3.6106	0	0.8472	0.1693	0
August Yr 3	2	16.4804	30.4169	14.1769	0	1.9593	2.2294	0
October Yr 3	3	25.9867	15.7496	24.2196	0	0.9045	1.3776	0
June Yr 4	1	3.8507	11.8306	3.6106	0	0.7998	0.1599	0
August Yr 4	2	16.3555	30.4169	14.1769	0	1.8496	2.1045	0
October Yr 4	3	25.9096	15.7496	24.2196	0	0.8538	1.3005	0
June Yr 5	1	3.8417	11.8306	3.6106	0	0.7550	0.1509	0
August Yr 5	2	16.2377	30.4169	14.1769	0	1.7460	1.9867	0
October Yr 5	3	25.8367	15.7496	24.2196	0	0.8060	1.2276	0
June Yr 6	1	3.8333	11.8306	3.6106	0	0.7127	0.1425	0

Sulfur

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	35.23	0.2634	29.38	65.45	0	0.2962	0
August Yr 1	2	36.35	0.2423	29.38	64.64	0	0.3394	0
October Yr 1	3	38.03	0.1435	29.38	63.40	0	1.7419	0
June Yr 2	1	36.40	0.2487	29.38	66.67	0	0.2962	0
August Yr 2	2	37.52	0.2287	29.38	65.86	0	0.3394	0
October Yr 2	3	39.20	0.1355	29.38	64.62	0	1.7419	0
June Yr 3	1	37.57	0.2347	29.38	67.89	0	0.2962	0
August Yr 3	2	38.69	0.2159	29.38	67.09	0	0.3394	0
October Yr 3	3	40.37	0.1279	29.38	65.83	0	1.7419	0
June Yr 4	1	38.74	0.2216	29.38	69.11	0	0.2962	0
August Yr 4	2	39.86	0.2038	29.38	68.30	0	0.3394	0
October Yr 4	3	41.54	0.1207	29.38	67.05	0	1.7419	0
June Yr 5	1	39.91	0.2092	29.38	70.33	0	0.2962	0
August Yr 5	2	41.03	0.1924	29.38	69.52	0	0.3394	0
October Yr 5	3	42.71	0.1140	29.38	68.26	0	1.7419	0
June Yr 6	1	41.08	0.1975	29.38	71.55	0	0.2962	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.4903	1.3044	0.1844	0	0.0000	0.0097	0.0114
August Yr 1	2	1.1154	2.3396	0.6596	0	0.0176	0.1164	0.0000
October Yr 1	3	3.1036	0.0000	1.2800	0.35	0.1868	0.0817	0.0000
June Yr 2	1	0.4898	1.3044	0.1844	0	0.0000	0.0092	0.0107
August Yr 2	2	1.1089	2.3396	0.6596	0	0.0166	0.1099	0.0000
October Yr 2	3	3.0990	0.0000	1.2800	0.35	0.1764	0.0771	0.0000
June Yr 3	1	0.4892	1.3044	0.1844	0	0.0000	0.0086	0.0101
August Yr 3	2	1.1027	2.3396	0.6596	0	0.0157	0.1037	0.0000
October Yr 3	3	3.0947	0.0000	1.2800	0.35	0.1665	0.0728	0.0000
June Yr 4	1	0.4888	1.3044	0.1844	0	0.0000	0.0082	0.0096
August Yr 4	2	1.0969	2.3396	0.6596	0	0.0148	0.0979	0.0000
October Yr 4	3	3.0906	0.0000	1.2800	0.35	0.1572	0.0687	0.0000
June Yr 5	1	0.4883	1.3044	0.1844	0	0.0000	0.0077	0.0090
August Yr 5	2	1.0915	2.3396	0.6596	0	0.0140	0.0925	0.0000
October Yr 5	3	3.0868	0.0000	1.2800	0.35	0.1484	0.0649	0.0000
June Yr 6	1	0.4879	1.3044	0.1844	0	0.0000	0.0073	0.0085

Zinc

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	3.05	0.0072	1.95	4.79	0	0	0
August Yr 1	2	3.14	0.0063	1.95	4.70	0	0	0
October Yr 1	3	3.22	0.0050	1.95	4.62	0	0	0
June Yr 2	1	3.16	0.0068	1.95	4.68	0	0	0
August Yr 2	2	3.25	0.0060	1.95	4.59	0	0	0
October Yr 2	3	3.33	0.0047	1.95	4.51	0	0	0
June Yr 3	1	3.27	0.0064	1.95	4.57	0	0	0
August Yr 3	2	3.36	0.0056	1.95	4.48	0	0	0
October Yr 3	3	3.44	0.0045	1.95	4.40	0	0	0
June Yr 4	1	3.38	0.0061	1.95	4.46	0	0	0
August Yr 4	2	3.47	0.0053	1.95	4.37	0	0	0
October Yr 4	3	3.55	0.0042	1.95	4.29	0	0	0
June Yr 5	1	3.49	0.0057	1.95	4.35	0	0	0
August Yr 5	2	3.58	0.0050	1.95	4.26	0	0	0
October Yr 5	3	3.66	0.0040	1.95	4.18	0	0	0
June Yr 6	1	3.60	0.0054	1.95	4.24	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.0213	0.1102	0.0202	0	0.0002	0.0011	0
August Yr 1	2	0.0435	0.1170	0.0370	0	0.0052	0.0065	0
October Yr 1	3	0.0958	0.0301	0.0901	0	0.0075	0.0057	0
June Yr 2	1	0.0212	0.1102	0.0202	0	0.0002	0.0010	0
August Yr 2	2	0.0431	0.1170	0.0370	0	0.0049	0.0061	0
October Yr 2	3	0.0955	0.0301	0.0901	0	0.0071	0.0054	0
June Yr 3	1	0.0211	0.1102	0.0202	0	0.0002	0.0009	0
August Yr 3	2	0.0428	0.1170	0.0370	0	0.0046	0.0058	0
October Yr 3	3	0.0952	0.0301	0.0901	0	0.0067	0.0051	0
June Yr 4	1	0.0211	0.1102	0.0202	0	0.0001	0.0009	0
August Yr 4	2	0.0425	0.1170	0.0370	0	0.0044	0.0055	0
October Yr 4	3	0.0949	0.0301	0.0901	0	0.0063	0.0048	0
June Yr 5	1	0.0210	0.1102	0.0202	0	0.0001	0.0008	0
August Yr 5	2	0.0422	0.1170	0.0370	0	0.0041	0.0052	0
October Yr 5	3	0.0946	0.0301	0.0901	0	0.0060	0.0045	0
June Yr 6	1	0.0210	0.1102	0.0202	0	0.0001	0.0008	0

Manganese

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	16.90	0.0318	48.4033	119.06	0	0	0
August Yr 1	2	17.70	0.0398	48.4033	118.25	0	0	0
October Yr 1	3	18.58	0.0394	48.4033	117.37	0	0	0
June Yr 2	1	17.46	0.0300	48.4033	118.50	0	0	0
August Yr 2	2	18.26	0.0376	48.4033	117.69	0	0	0
October Yr 2	3	19.14	0.0372	48.4033	116.81	0	0	0
June Yr 3	1	18.02	0.0283	48.4033	117.94	0	0	0
August Yr 3	2	18.82	0.0355	48.4033	117.13	0	0	0
October Yr 3	3	19.70	0.0351	48.4033	116.25	0	0	0
June Yr 4	1	18.58	0.0268	48.4033	117.38	0	0	0
August Yr 4	2	19.38	0.0335	48.4033	116.57	0	0	0
October Yr 4	3	20.26	0.0331	48.4033	115.69	0	0	0
June Yr 5	1	19.14	0.0253	48.4033	116.82	0	0	0
August Yr 5	2	19.94	0.0316	48.4033	116.02	0	0	0
October Yr 5	3	20.82	0.0313	48.4033	115.14	0	0	0
June Yr 6	1	19.70	0.0238	48.4033	116.26	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Through-fall
June Yr 1	1	0.1782	0.9693	0.1693	0	0.0169	0.0089	0
August Yr 1	2	0.7454	1.5136	0.6336	0	0.1114	0.1118	0
October Yr 1	3	1.2221	0.0288	1.1488	0	0.0639	0.0733	0
June Yr 2	1	0.1777	0.9693	0.1693	0	0.0160	0.0084	0
August Yr 2	2	0.7391	1.5136	0.6336	0	0.1052	0.1055	0
October Yr 2	3	1.2180	0.0288	1.1488	0	0.0604	0.0692	0
June Yr 3	1	0.1772	0.9693	0.1693	0	0.0151	0.0079	0
August Yr 3	2	0.7332	1.5136	0.6336	0	0.0993	0.0996	0
October Yr 3	3	1.2141	0.0288	1.1488	0	0.0570	0.0653	0
June Yr 4	1	0.1768	0.9693	0.1693	0	0.0142	0.0075	0
August Yr 4	2	0.7277	1.5136	0.6336	0	0.0937	0.0941	0
October Yr 4	3	1.2105	0.0288	1.1488	0	0.0538	0.0617	0
June Yr 5	1	0.1764	0.9693	0.1693	0	0.0134	0.0071	0
August Yr 5	2	0.7224	1.5136	0.6336	0	0.0885	0.0888	0
October Yr 5	3	1.2070	0.0288	1.1488	0	0.0508	0.0582	0
June Yr 6	1	0.1760	0.9693	0.1693	0	0.0127	0.0067	0

Copper

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	1.96	0.0023	0.48	5.30	0	0	0
August Yr 1	2	2.01	0.0019	0.48	5.25	0	0	0
October Yr 1	3	2.06	0.0013	0.48	5.20	0	0	0
June Yr 2	1	2.04	0.0022	0.48	5.22	0	0	0
August Yr 2	2	2.09	0.0018	0.48	5.17	0	0	0
October Yr 2	3	2.14	0.0012	0.48	5.12	0	0	0
June Yr 3	1	2.12	0.0020	0.48	5.14	0	0	0
August Yr 3	2	2.17	0.0017	0.48	5.09	0	0	0
October Yr 3	3	2.22	0.0012	0.48	5.04	0	0	0
June Yr 4	1	2.20	0.0019	0.48	5.06	0	0	0
August Yr 4	2	2.25	0.0016	0.48	5.01	0	0	0
October Yr 4	3	2.30	0.0011	0.48	4.96	0	0	0
June Yr 5	1	2.28	0.0018	0.48	4.98	0	0	0
August Yr 5	2	2.33	0.0015	0.48	4.93	0	0	0
October Yr 5	3	2.38	0.0010	0.48	4.88	0	0	0
June Yr 6	1	2.36	0.0017	0.48	4.90	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0003
August Yr 1	2	0.0061	0.0552	0.0052	0.0000	0.0003	0.0009	0.0000
October Yr 1	3	0.0102	0.0000	0.0096	0.0104	0.0015	0.0006	0.0000
June Yr 2	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0003
August Yr 2	2	0.0061	0.0552	0.0052	0.0000	0.0003	0.0009	0.0000
October Yr 2	3	0.0102	0.0000	0.0096	0.0104	0.0014	0.0006	0.0000
June Yr 3	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0003
August Yr 3	2	0.0060	0.0552	0.0052	0.0000	0.0003	0.0008	0.0000
October Yr 3	3	0.0101	0.0000	0.0096	0.0104	0.0013	0.0005	0.0000
June Yr 4	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0003
August Yr 4	2	0.0060	0.0552	0.0052	0.0000	0.0003	0.0008	0.0000
October Yr 4	3	0.0101	0.0000	0.0096	0.0104	0.0013	0.0005	0.0000
June Yr 5	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0003
August Yr 5	2	0.0059	0.0552	0.0052	0.0000	0.0003	0.0007	0.0000
October Yr 5	3	0.0101	0.0000	0.0096	0.0104	0.0012	0.0005	0.0000
June Yr 6	1	0.0015	0.0514	0.0014	0.0000	0.0000	0.0001	0.0002

Iron

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	13.03	0.0345	477.97	350.99	0	0	0
August Yr 1	2	13.29	0.0504	477.97	350.71	0	0	0
October Yr 1	3	14.05	0.0347	477.97	349.97	1.067	0	0
June Yr 2	1	13.55	0.0326	477.97	351.54	0	0	0
August Yr 2	2	13.81	0.0475	477.97	351.26	0	0	0
October Yr 2	3	14.57	0.0328	477.97	350.52	1.067	0	0
June Yr 3	1	14.07	0.0307	477.97	352.09	0	0	0
August Yr 3	2	14.33	0.0449	477.97	351.81	0	0	0
October Yr 3	3	15.09	0.0309	477.97	351.07	1.067	0	0
June Yr 4	1	14.59	0.0290	477.97	352.64	0	0	0
August Yr 4	2	14.85	0.0424	477.97	352.36	0	0	0
October Yr 4	3	15.61	0.0292	477.97	351.62	1.067	0	0
June Yr 5	1	15.11	0.0274	477.97	353.18	0	0	0
August Yr 5	2	15.37	0.0400	477.97	352.91	0	0	0
October Yr 5	3	16.13	0.0276	477.97	352.16	1.067	0	0
June Yr 6	1	15.63	0.0259	477.97	353.73	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.1592	0.4112	0.1512	0	0.0238	0.0080	0
August Yr 1	2	0.3568	1.0632	0.3032	0	0.0379	0.0536	0
October Yr 1	3	0.7627	0.2169	0.7169	0	0.0436	0.0458	0
June Yr 2	1	0.1587	0.4112	0.1512	0	0.0225	0.0075	0
August Yr 2	2	0.3538	1.0632	0.3032	0	0.0358	0.0506	0
October Yr 2	3	0.7601	0.2169	0.7169	0	0.0412	0.0432	0
June Yr 3	1	0.1583	0.4112	0.1512	0	0.0212	0.0071	0
August Yr 3	2	0.3509	1.0632	0.3032	0	0.0338	0.0477	0
October Yr 3	3	0.7577	0.2169	0.7169	0	0.0389	0.0408	0
June Yr 4	1	0.1579	0.4112	0.1512	0	0.0200	0.0067	0
August Yr 4	2	0.3483	1.0632	0.3032	0	0.0319	0.0451	0
October Yr 4	3	0.7554	0.2169	0.7169	0	0.0367	0.0385	0
June Yr 5	1	0.1575	0.4112	0.1512	0	0.0189	0.0063	0
August Yr 5	2	0.3457	1.0632	0.3032	0	0.0301	0.0425	0
October Yr 5	3	0.7533	0.2169	0.7169	0	0.0347	0.0364	0
June Yr 6	1	0.1572	0.4112	0.1512	0	0.0179	0.0060	0

Boron

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	1.18	0.0043	1.38	1.42	0	0	0
August Yr 1	2	1.22	0.0052	1.38	1.38	0	0	0
October Yr 1	3	1.29	0.0036	1.38	1.32	0	0	0
June Yr 2	1	1.22	0.0041	1.38	1.38	0	0	0
August Yr 2	2	1.26	0.0049	1.38	1.34	0	0	0
October Yr 2	3	1.33	0.0034	1.38	1.28	0	0	0
June Yr 3	1	1.26	0.0038	1.38	1.34	0	0	0
August Yr 3	2	1.3	0.0046	1.38	1.30	0	0	0
October Yr 3	3	1.37	0.0032	1.38	1.24	0	0	0
June Yr 4	1	1.3	0.0036	1.38	1.31	0	0	0
August Yr 4	2	1.34	0.0043	1.38	1.26	0	0	0
October Yr 4	3	1.41	0.0030	1.38	1.20	0	0	0
June Yr 5	1	1.34	0.0034	1.38	1.27	0	0	0
August Yr 5	2	1.38	0.0041	1.38	1.22	0	0	0
October Yr 5	3	1.45	0.0028	1.38	1.16	0	0	0
June Yr 6	1	1.38	0.0032	1.38	1.23	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.0055	0.0452	0.0052	0.0000	0.0011	0.0003	0
August Yr 1	2	0.0184	0.0856	0.0156	0.0000	0.0012	0.0028	0
October Yr 1	3	0.0333	0.0000	0.0313	0.0387	0.0025	0.0020	0
June Yr 2	1	0.0055	0.0452	0.0052	0.0000	0.0011	0.0003	0
August Yr 2	2	0.0182	0.0856	0.0156	0.0000	0.0011	0.0026	0
October Yr 2	3	0.0332	0.0000	0.0313	0.0387	0.0024	0.0019	0
June Yr 3	1	0.0054	0.0452	0.0052	0.0000	0.0010	0.0002	0
August Yr 3	2	0.0181	0.0856	0.0156	0.0000	0.0011	0.0025	0
October Yr 3	3	0.0331	0.0000	0.0313	0.0387	0.0022	0.0018	0
June Yr 4	1	0.0054	0.0452	0.0052	0.0000	0.0010	0.0002	0
August Yr 4	2	0.0179	0.0856	0.0156	0.0000	0.0010	0.0023	0
October Yr 4	3	0.0330	0.0000	0.0313	0.0387	0.0021	0.0017	0
June Yr 5	1	0.0054	0.0452	0.0052	0.0000	0.0009	0.0002	0
August Yr 5	2	0.0178	0.0856	0.0156	0.0000	0.0010	0.0022	0
October Yr 5	3	0.0329	0.0000	0.0313	0.0387	0.0020	0.0016	0
June Yr 6	1	0.0054	0.0452	0.0052	0.0000	0.0009	0.0002	0

Aluminum

Point in time	Step	Overstory	Understory	Forest Floor	Soil	Weathering	Atmospheric Deposition	Leaching
June Yr 1	1	18.94	0.0284	407.15	1094.00	0	0	0
August Yr 1	2	19.34	0.0374	407.15	1093.59	0	0	0
October Yr 1	3	20.53	0.0332	407.15	1092.41	0	0	0
June Yr 2	1	19.59	0.0268	407.15	1093.35	0	0	0
August Yr 2	2	19.99	0.0353	407.15	1092.94	0	0	0
October Yr 2	3	21.18	0.0313	407.15	1091.76	0	0	0
June Yr 3	1	20.24	0.0253	407.15	1092.70	0	0	0
August Yr 3	2	20.64	0.0333	407.15	1092.30	0	0	0
October Yr 3	3	21.83	0.0296	407.15	1091.11	0	0	0
June Yr 4	1	20.89	0.0239	407.15	1092.05	0	0	0
August Yr 4	2	21.29	0.0315	407.15	1091.65	0	0	0
October Yr 4	3	22.48	0.0279	407.15	1090.46	0	0	0
June Yr 5	1	21.54	0.0226	407.15	1091.41	0	0	0
August Yr 5	2	21.94	0.0297	407.15	1091.00	0	0	0
October Yr 5	3	23.13	0.0263	407.15	1089.81	0	0	0
June Yr 6	1	22.19	0.0213	407.15	1090.76	0	0	0

Point in time	Step	Mineralization	Tree Uptake	Tree Litter	Tree Throughfall	Plant Uptake	Plant Litter	Plant Throughfall
June Yr 1	1	0.1793	0.5703	0.1703	0	0.0179	0.0090	0
August Yr 1	2	0.5118	1.6251	0.4351	0	0.0725	0.0767	0
October Yr 1	3	1.0209	0.0197	0.9597	0	0.0549	0.0612	0
June Yr 2	1	0.1788	0.5703	0.1703	0	0.0169	0.0085	0
August Yr 2	2	0.5075	1.6251	0.4351	0	0.0685	0.0724	0
October Yr 2	3	1.0175	0.0197	0.9597	0	0.0518	0.0578	0
June Yr 3	1	0.1783	0.5703	0.1703	0	0.0160	0.0080	0
August Yr 3	2	0.5035	1.6251	0.4351	0	0.0646	0.0684	0
October Yr 3	3	1.0143	0.0197	0.9597	0	0.0489	0.0546	0
June Yr 4	1	0.1778	0.5703	0.1703	0	0.0151	0.0075	0
August Yr 4	2	0.4997	1.6251	0.4351	0	0.0610	0.0646	0
October Yr 4	3	1.0112	0.0197	0.9597	0	0.0462	0.0515	0
June Yr 5	1	0.1774	0.5703	0.1703	0	0.0143	0.0071	0
August Yr 5	2	0.4960	1.6251	0.4351	0	0.0576	0.0609	0
October Yr 5	3	1.0083	0.0197	0.9597	0	0.0436	0.0486	0
June Yr 6	1	0.1770	0.5703	0.1703	0	0.0135	0.0067	0

APPENDIX B-2: Results of Elemental Cycling Projections Over Five Years

Mallory Creek Pure Species Scenarios

Nitrogen: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	387.14	101.9904	24.8715	0
August Yr 1	2	408.83	80.57401	23.1207	0
October Yr 1	3	423.52	68.41754	0	7.2306
June Yr 2	1	398.37	95.69737	24.8715	0
August Yr 2	2	420.06	74.3047	23.1207	0
October Yr 2	3	434.75	62.04548	0	7.2306
June Yr 3	1	409.6	89.39376	24.8715	0
August Yr 3	2	431.29	68.02348	23.1207	0
October Yr 3	3	445.98	55.66727	0	7.2306
June Yr 4	1	420.83	83.08015	24.8715	0
August Yr 4	2	442.52	61.73101	23.1207	0
October Yr 4	3	457.21	49.28323	0	7.2306
June Yr 5	1	432.06	76.7571	24.8715	0
August Yr 5	2	453.75	55.42792	23.1207	0
October Yr 5	3	468.44	42.89371	0	7.2306
June Yr 6	1	443.29	70.42515	24.8715	0

Nitrogen: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	427.73	101.9904	56.0315	0
August Yr 1	2	480.58	49.41401	0	12.4693
October Yr 1	3	459.68	72.84754	0	2.2206
June Yr 2	1	439.54	95.11737	56.0315	0
August Yr 2	2	492.39	42.5647	0	12.4693
October Yr 2	3	471.49	65.89548	0	2.2206
June Yr 3	1	451.35	88.23376	56.0315	0
August Yr 3	2	504.2	35.70348	0	12.4693
October Yr 3	3	483.3	58.93727	0	2.2206
June Yr 4	1	463.16	81.34015	56.0315	0
August Yr 4	2	516.01	28.83101	0	12.4693
October Yr 4	3	495.11	51.97323	0	2.2206
June Yr 5	1	474.97	74.4371	56.0315	0
August Yr 5	2	527.82	21.94792	0	12.4693
October Yr 5	3	506.92	45.00371	0	2.2206
June Yr 6	1	486.78	67.52515	56.0315	0

Phosphorus: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	60.56	11.2342	1.9212	0
August Yr 1	2	62.25	9.59611015	3.9315	0
October Yr 1	3	65.4	6.58637843	0	1.0965
June Yr 2	1	62.77	9.04411843	1.9212	0
August Yr 2	2	64.46	7.40312172	3.9315	0
October Yr 2	3	67.61	4.38553528	0	1.0965
June Yr 3	1	64.98	6.85292146	1.9212	0
August Yr 3	2	66.67	5.20918068	3.9315	0
October Yr 3	3	69.82	2.18417937	0	1.0965
June Yr 4	1	67.19	4.66067157	1.9212	0
August Yr 4	2	68.88	3.01434037	3.9315	0
October Yr 4	3	72.03	-0.0176606	0	1.0965
June Yr 5	1	69.4	2.46742772	1.9212	0
August Yr 5	2	71.09	0.81865116	3.9315	0
October Yr 5	3	74.24	-2.2199575	0	1.0965
June Yr 6	1	71.61	0.27324555	1.9212	0

Phosphorus: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	80.2	11.2342	5.3512	0
August Yr 1	2	85.32	6.16611015	7.2215	0
October Yr 1	3	91.76	-0.1336216	0	7.4465
June Yr 2	1	82.78	8.67411843	5.3512	0
August Yr 2	2	87.9	3.60312172	7.2215	0
October Yr 2	3	94.34	-2.7044647	0	7.4465
June Yr 3	1	85.36	6.11292146	5.3512	0
August Yr 3	2	90.48	1.03918068	7.2215	0
October Yr 3	3	96.92	-5.2758206	0	7.4465
June Yr 4	1	87.94	3.55067157	5.3512	0
August Yr 4	2	93.06	-1.5256596	7.2215	0
October Yr 4	3	99.5	-7.8476606	0	7.4465
June Yr 5	1	90.52	0.98742772	5.3512	0
August Yr 5	2	95.64	-4.0913488	7.2215	0
October Yr 5	3	102.08	-10.419957	0	7.4465
June Yr 6	1	93.1	-1.5767545	5.3512	0

Potassium: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	244.29	1388.3206	27.1932	0
August Yr 1	2	270.34	1360.936311	10.3542	0
October Yr 1	3	276.22	1357.534451	0	15.9344
June Yr 2	1	252.47	1382.907744	27.1932	0
August Yr 2	2	278.52	1355.60007	10.3542	0
October Yr 2	3	284.4	1352.061216	0	15.9344
June Yr 3	1	260.65	1377.485634	27.1932	0
August Yr 3	2	286.7	1350.250284	10.3542	0
October Yr 3	3	292.58	1346.582109	0	15.9344
June Yr 4	1	268.83	1372.054788	27.1932	0
August Yr 4	2	294.88	1344.887712	10.3542	0
October Yr 4	3	300.76	1341.097459	0	15.9344
June Yr 5	1	277.01	1366.615695	27.1932	0
August Yr 5	2	303.06	1339.513071	10.3542	0
October Yr 5	3	308.94	1335.607575	0	15.9344
June Yr 6	1	285.19	1361.168818	27.1932	0

Potassium: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	406.7	1388.3206	38.5032	0
August Yr 1	2	444.06	1349.626311	32.5642	0
October Yr 1	3	472.15	1324.014451	0	44.5244
June Yr 2	1	419.81	1377.977744	38.5032	0
August Yr 2	2	457.17	1339.36007	32.5642	0
October Yr 2	3	485.26	1313.611216	0	44.5244
June Yr 3	1	432.92	1367.625634	38.5032	0
August Yr 3	2	470.28	1329.080284	32.5642	0
October Yr 3	3	498.37	1303.202109	0	44.5244
June Yr 4	1	446.03	1357.264788	38.5032	0
August Yr 4	2	483.39	1318.787712	32.5642	0
October Yr 4	3	511.48	1292.787459	0	44.5244
June Yr 5	1	459.14	1346.895695	38.5032	0
August Yr 5	2	496.5	1308.483071	32.5642	0
October Yr 5	3	524.59	1282.367575	0	44.5244
June Yr 6	1	472.25	1336.518818	38.5032	0

Magnesium: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	85.33	17.4019	3.1398	0
August Yr 1	2	88.15	14.4511397	4.1195	0
October Yr 1	3	91.16	11.5827951	0	0.3763
June Yr 2	1	88.74	14.5736635	3.1398	0
August Yr 2	2	91.56	11.630999	4.1195	0
October Yr 2	3	94.57	8.75555574	0	0.3763
June Yr 3	1	92.15	11.7443985	3.1398	0
August Yr 3	2	94.97	8.80937654	4.1195	0
October Yr 3	3	97.98	5.92723208	0	0.3763
June Yr 4	1	95.56	8.91416276	3.1398	0
August Yr 4	2	98.38	5.98635523	4.1195	0
October Yr 4	3	101.39	3.09788489	0	0.3763
June Yr 5	1	98.97	6.08301055	3.1398	0
August Yr 5	2	101.79	3.16201344	4.1195	0
October Yr 5	3	104.8	0.26757149	0	0.3763
June Yr 6	1	102.38	3.25099321	3.1398	0

Magnesium: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	82.42	17.4019	4.7598	0
August Yr 1	2	86.86	12.8311397	3.2995	0
October Yr 1	3	89.05	10.7827951	0	1.8763
June Yr 2	1	85.13	15.2736635	4.7598	0
August Yr 2	2	89.57	10.710999	3.2995	0
October Yr 2	3	91.76	8.65555574	0	1.8763
June Yr 3	1	87.84	13.1443985	4.7598	0
August Yr 3	2	92.28	8.58937654	3.2995	0
October Yr 3	3	94.47	6.52723208	0	1.8763
June Yr 4	1	90.55	11.0141628	4.7598	0
August Yr 4	2	94.99	6.46635523	3.2995	0
October Yr 4	3	97.18	4.39788489	0	1.8763
June Yr 5	1	93.26	8.88301055	4.7598	0
August Yr 5	2	97.7	4.34201344	3.2995	0
October Yr 5	3	99.89	2.26757149	0	1.8763
June Yr 6	1	95.97	6.75099321	4.7598	0

Calcium: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	378.5	51.7947	4.2606	0
August Yr 1	2	379.15	50.46419	26.1469	0
October Yr 1	3	391.12	38.87132	25.1469	0
June Yr 2	1	392.0473	39.62284	4.2606	0
August Yr 2	2	392.6973	38.33493	26.1469	0
October Yr 2	3	404.6673	26.72509	25.1469	0
June Yr 3	1	405.5946	27.44688	4.2606	0
August Yr 3	2	406.2446	26.19918	26.1469	0
October Yr 3	3	418.2146	14.57333	25.1469	0
June Yr 4	1	419.1419	15.26705	4.2606	0
August Yr 4	2	419.7919	14.05731	26.1469	0
October Yr 4	3	431.7619	2.416336	25.1469	0
June Yr 5	1	432.6892	3.083564	4.2606	0
August Yr 5	2	433.3392	1.909664	26.1469	0
October Yr 5	3	445.3092	-9.74559	25.1469	0
June Yr 6	1	446.2365	-9.10337	4.2606	0

Calcium: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	719.67	51.7947	45.8006	0
August Yr 1	2	761.86	8.924189	43.0769	0
October Yr 1	3	790.76	-19.5987	0	23.7504
June Yr 2	1	742.79	30.05014	45.8006	0
August Yr 2	2	784.98	-12.7778	43.0769	0
October Yr 2	3	813.88	-41.3176	0	23.7504
June Yr 3	1	765.91	8.301482	45.8006	0
August Yr 3	2	808.1	-34.4862	43.0769	0
October Yr 3	3	837	-63.0421	0	23.7504
June Yr 4	1	789.03	-13.451	45.8006	0
August Yr 4	2	831.22	-56.2008	43.0769	0
October Yr 4	3	860.12	-84.7718	0	23.7504
June Yr 5	1	812.15	-35.2072	45.8006	0
August Yr 5	2	854.34	-77.9211	43.0769	0
October Yr 5	3	883.24	-106.506	0	23.7504
June Yr 6	1	835.27	-56.9669	45.8006	0

Sulfur: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	33.78	65.4464	1.0744	0
August Yr 1	2	34.67	64.87369	1.9996	0
October Yr 1	3	36.01	63.97189	0.17	0
June Yr 2	1	34.9	66.71865	1.0744	0
August Yr 2	2	35.79	66.14476	1.9996	0
October Yr 2	3	37.13	65.23742	0.17	0
June Yr 3	1	36.02	67.99007	1.0744	0
August Yr 3	2	36.91	67.41507	1.9996	0
October Yr 3	3	38.25	66.50251	0.17	0
June Yr 4	1	37.14	69.26072	1.0744	0
August Yr 4	2	38.03	68.68466	1.9996	0
October Yr 4	3	39.37	67.76717	0.17	0
June Yr 5	1	38.26	70.53063	1.0744	0
August Yr 5	2	39.15	69.95357	1.9996	0
October Yr 5	3	40.49	69.03143	0.17	0
June Yr 6	1	39.38	71.79984	1.0744	0

Sulfur: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	41.58	65.4464	2.3744	0
August Yr 1	2	43.77	63.57369	3.7696	0
October Yr 1	3	46.88	60.90189	0	2.7
June Yr 2	1	42.9	66.51865	2.3744	0
August Yr 2	2	45.09	64.64476	3.7696	0
October Yr 2	3	48.2	61.96742	0	2.7
June Yr 3	1	44.22	67.59007	2.3744	0
August Yr 3	2	46.41	65.71507	3.7696	0
October Yr 3	3	49.52	63.03251	0	2.7
June Yr 4	1	45.54	68.66072	2.3744	0
August Yr 4	2	47.73	66.78466	3.7696	0
October Yr 4	3	50.84	64.09717	0	2.7
June Yr 5	1	46.86	69.73063	2.3744	0
August Yr 5	2	49.05	67.85357	3.7696	0
October Yr 5	3	52.16	65.16143	0	2.7
June Yr 6	1	48.18	70.79984	2.3744	0

Zinc: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	3.3	4.787	0.1102	0
August Yr 1	2	3.39	4.697884	0.117	0
October Yr 1	3	3.47	4.619204	0.0501	0
June Yr 2	1	3.43	4.657403	0.1102	0
August Yr 2	2	3.52	4.568238	0.117	0
October Yr 2	3	3.6	4.489484	0.0501	0
June Yr 3	1	3.56	4.527784	0.1102	0
August Yr 3	2	3.65	4.438572	0.117	0
October Yr 3	3	3.73	4.359748	0.0501	0
June Yr 4	1	3.69	4.398143	0.1102	0
August Yr 4	2	3.78	4.308887	0.117	0
October Yr 4	3	3.86	4.229997	0.0501	0
June Yr 5	1	3.82	4.268482	0.1102	0
August Yr 5	2	3.91	4.179185	0.117	0
October Yr 5	3	3.99	4.100232	0.0501	0
June Yr 6	1	3.95	4.138802	0.1102	0

Zinc: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	1.86	4.787	0.1302	0
August Yr 1	2	1.97	4.677884	0.097	0
October Yr 1	3	2.03	4.619204	0	0.0199
June Yr 2	1	1.92	4.727403	0.1302	0
August Yr 2	2	2.03	4.618238	0.097	0
October Yr 2	3	2.09	4.559484	0	0.0199
June Yr 3	1	1.98	4.667784	0.1302	0
August Yr 3	2	2.09	4.558572	0.097	0
October Yr 3	3	2.15	4.499748	0	0.0199
June Yr 4	1	2.04	4.608143	0.1302	0
August Yr 4	2	2.15	4.498887	0.097	0
October Yr 4	3	2.21	4.439997	0	0.0199
June Yr 5	1	2.1	4.548482	0.1302	0
August Yr 5	2	2.21	4.439185	0.097	0
October Yr 5	3	2.27	4.380232	0	0.0199
June Yr 6	1	2.16	4.488802	0.1302	0

Manganese: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	11.92	119.0553	0.1993	0
August Yr 1	2	11.95	119.0173	1.0336	0
October Yr 1	3	12.35	118.6177	1.0888	0
June Yr 2	1	12.29	118.6871	0.1993	0
August Yr 2	2	12.32	118.6495	1.0336	0
October Yr 2	3	12.72	118.2499	1.0888	0
June Yr 3	1	12.66	118.3188	0.1993	0
August Yr 3	2	12.69	118.2816	1.0336	0
October Yr 3	3	13.09	117.882	1.0888	0
June Yr 4	1	13.03	117.9503	0.1993	0
August Yr 4	2	13.06	117.9136	1.0336	0
October Yr 4	3	13.46	117.514	1.0888	0
June Yr 5	1	13.4	117.5818	0.1993	0
August Yr 5	2	13.43	117.5455	1.0336	0
October Yr 5	3	13.83	117.1458	1.0888	0
June Yr 6	1	13.77	117.2133	0.1993	0

Manganese: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	41.41	119.0553	5.4593	0
August Yr 1	2	46.7	113.7573	3.1536	0
October Yr 1	3	49.22	111.2377	0	5.4212
June Yr 2	1	42.65	117.8171	5.4593	0
August Yr 2	2	47.94	112.5195	3.1536	0
October Yr 2	3	50.46	109.9999	0	5.4212
June Yr 3	1	43.89	116.5788	5.4593	0
August Yr 3	2	49.18	111.2816	3.1536	0
October Yr 3	3	51.7	108.762	0	5.4212
June Yr 4	1	45.13	115.3403	5.4593	0
August Yr 4	2	50.42	110.0436	3.1536	0
October Yr 4	3	52.94	107.524	0	5.4212
June Yr 5	1	46.37	114.1018	5.4593	0
August Yr 5	2	51.66	108.8055	3.1536	0
October Yr 5	3	54.18	106.2858	0	5.4212
June Yr 6	1	47.61	112.8633	5.4593	0

Copper: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	2.12	5.3034	0.0514	0
August Yr 1	2	2.17	5.253798	0.0552	0
October Yr 1	3	2.22	5.204401	0	0.0004
June Yr 2	1	2.21	5.213529	0.0514	0
August Yr 2	2	2.26	5.163904	0.0552	0
October Yr 2	3	2.31	5.114474	0	0.0004
June Yr 3	1	2.3	5.12365	0.0514	0
August Yr 3	2	2.35	5.074005	0.0552	0
October Yr 3	3	2.4	5.024543	0	0.0004
June Yr 4	1	2.39	5.033765	0.0514	0
August Yr 4	2	2.44	4.9841	0.0552	0
October Yr 4	3	2.49	4.934607	0	0.0004
June Yr 5	1	2.48	4.943873	0.0514	0
August Yr 5	2	2.53	4.894189	0.0552	0
October Yr 5	3	2.58	4.844669	0	0.0004
June Yr 6	1	2.57	4.853976	0.0514	0

Copper: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	1.17	5.3034	0.0314	0
August Yr 1	2	1.2	5.273798	0.0452	0
October Yr 1	3	1.24	5.234401	0	0.0204
June Yr 2	1	1.21	5.263529	0.0314	0
August Yr 2	2	1.24	5.233904	0.0452	0
October Yr 2	3	1.28	5.194474	0	0.0204
June Yr 3	1	1.25	5.22365	0.0314	0
August Yr 3	2	1.28	5.194005	0.0452	0
October Yr 3	3	1.32	5.154543	0	0.0204
June Yr 4	1	1.29	5.183765	0.0314	0
August Yr 4	2	1.32	5.1541	0.0452	0
October Yr 4	3	1.36	5.114607	0	0.0204
June Yr 5	1	1.33	5.143873	0.0314	0
August Yr 5	2	1.36	5.114189	0.0452	0
October Yr 5	3	1.4	5.074669	0	0.0204
June Yr 6	1	1.37	5.103976	0.0314	0

Iron: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	13.62	350.9895	0.3912	0
August Yr 1	2	13.86	350.7336	1.0132	0
October Yr 1	3	14.57	350.0393	0.3069	0
June Yr 2	1	14.16	351.5184	0.3912	0
August Yr 2	2	14.4	351.2635	1.0132	0
October Yr 2	3	15.11	350.5682	0.3069	0
June Yr 3	1	14.7	352.0473	0.3912	0
August Yr 3	2	14.94	351.7931	1.0132	0
October Yr 3	3	15.65	351.0971	0.3069	0
June Yr 4	1	15.24	352.576	0.3912	0
August Yr 4	2	15.48	352.3226	1.0132	0
October Yr 4	3	16.19	351.6258	0.3069	0
June Yr 5	1	15.78	353.1046	0.3912	0
August Yr 5	2	16.02	352.852	1.0132	0
October Yr 5	3	16.73	352.1544	0.3069	0
June Yr 6	1	16.32	353.6331	0.3912	0

Iron: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	9.74	350.9895	0.4712	0
August Yr 1	2	10.06	350.6536	1.3432	0
October Yr 1	3	11.1	349.6293	0	0.2731
June Yr 2	1	10.11	351.6884	0.4712	0
August Yr 2	2	10.43	351.3535	1.3432	0
October Yr 2	3	11.47	350.3282	0	0.2731
June Yr 3	1	10.48	352.3873	0.4712	0
August Yr 3	2	10.8	352.0531	1.3432	0
October Yr 3	3	11.84	351.0271	0	0.2731
June Yr 4	1	10.85	353.086	0.4712	0
August Yr 4	2	11.17	352.7526	1.3432	0
October Yr 4	3	12.21	351.7258	0	0.2731
June Yr 5	1	11.22	353.7846	0.4712	0
August Yr 5	2	11.54	353.452	1.3432	0
October Yr 5	3	12.58	352.4244	0	0.2731
June Yr 6	1	11.59	354.4831	0.4712	0

Boron: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	1.09	1.4245	0.0352	0
August Yr 1	2	1.12	1.393641	0.0656	0
October Yr 1	3	1.17	1.345217	0	0.0187
June Yr 2	1	1.12	1.394741	0.0352	0
August Yr 2	2	1.15	1.36393	0.0656	0
October Yr 2	3	1.2	1.315418	0	0.0187
June Yr 3	1	1.15	1.364968	0.0352	0
August Yr 3	2	1.18	1.334202	0.0656	0
October Yr 3	3	1.23	1.285607	0	0.0187
June Yr 4	1	1.18	1.335183	0.0352	0
August Yr 4	2	1.21	1.30446	0.0656	0
October Yr 4	3	1.26	1.255786	0	0.0187
June Yr 5	1	1.21	1.305385	0.0352	0
August Yr 5	2	1.24	1.274703	0.0656	0
October Yr 5	3	1.29	1.225955	0	0.0187
June Yr 6	1	1.24	1.275576	0.0352	0

Boron: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	1.57	1.4245	0.0752	0
August Yr 1	2	1.64	1.353641	0.1356	0
October Yr 1	3	1.76	1.235217	0	0.0987
June Yr 2	1	1.63	1.364741	0.0752	0
August Yr 2	2	1.7	1.29393	0.1356	0
October Yr 2	3	1.82	1.175418	0	0.0987
June Yr 3	1	1.69	1.304968	0.0752	0
August Yr 3	2	1.76	1.234202	0.1356	0
October Yr 3	3	1.88	1.115607	0	0.0987
June Yr 4	1	1.75	1.245183	0.0752	0
August Yr 4	2	1.82	1.17446	0.1356	0
October Yr 4	3	1.94	1.055786	0	0.0987
June Yr 5	1	1.81	1.185385	0.0752	0
August Yr 5	2	1.88	1.114703	0.1356	0
October Yr 5	3	2	0.995955	0	0.0987
June Yr 6	1	1.87	1.125576	0.0752	0

Aluminum: Pure Douglas-fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	17.87	1094	0.4703	0
August Yr 1	2	18.17	1093.691	1.1751	0
October Yr 1	3	18.91	1092.955	0.5797	0
June Yr 2	1	18.53	1093.342	0.4703	0
August Yr 2	2	18.83	1093.033	1.1751	0
October Yr 2	3	19.57	1092.297	0.5797	0
June Yr 3	1	19.19	1092.683	0.4703	0
August Yr 3	2	19.49	1092.375	1.1751	0
October Yr 3	3	20.23	1091.639	0.5797	0
June Yr 4	1	19.85	1092.025	0.4703	0
August Yr 4	2	20.15	1091.717	1.1751	0
October Yr 4	3	20.89	1090.98	0.5797	0
June Yr 5	1	20.51	1091.366	0.4703	0
August Yr 5	2	20.81	1091.059	1.1751	0
October Yr 5	3	21.55	1090.322	0.5797	0
June Yr 6	1	21.17	1090.707	0.4703	0

Aluminum: Pure grand fir

Point in time	Step	Overstory	Soil	Tree Uptake	Tree Throughfall
June Yr 1	1	24.66	1094	1.3003	0
August Yr 1	2	25.79	1092.861	3.8051	0
October Yr 1	3	29.16	1089.495	0	2.8503
June Yr 2	1	25.35	1093.312	1.3003	0
August Yr 2	2	26.48	1092.173	3.8051	0
October Yr 2	3	29.85	1088.807	0	2.8503
June Yr 3	1	26.04	1092.623	1.3003	0
August Yr 3	2	27.17	1091.485	3.8051	0
October Yr 3	3	30.54	1088.119	0	2.8503
June Yr 4	1	26.73	1091.935	1.3003	0
August Yr 4	2	27.86	1090.797	3.8051	0
October Yr 4	3	31.23	1087.43	0	2.8503
June Yr 5	1	27.42	1091.246	1.3003	0
August Yr 5	2	28.55	1090.109	3.8051	0
October Yr 5	3	31.92	1086.742	0	2.8503
June Yr 6	1	28.11	1090.557	1.3003	0