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Forest floor-mineral soil interactions in the internal nitrogen cycle of an old-growth forest

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Abstract. Seasonal patterns and annual rates of N inputs, outputs, and internal cycling were determined for an old-growth mixed-conifer forest floor in the Sierra Nevada Mountains of California. Rates of net N mineralization within the forest floor, and plant N-uptake and leaching of inorganic N from the forest floor were 13, 10, and 9 kg-N ha^{-1} yr^{-1}, respectively. The Mediterranean-type climate appeared to have a significant effect on N cycling within this forest, such that all N-process and flow rates showed distrinct seasonal patterns. We estimated the forest floor supplies less than one-third of the total aboveground plant N-uptake in this forest. The rate of net nitrification within the forest floor was always low (<1 kg-NO_3^--N ha^{-1} $30d^{-1}$). Mean residence times for organic matter and N in the forest floor were 13 and 34 years, respectively, suggesting that this forest floor layer is a site of net N immobilization within this ecosystem. We examined the influence of the forest floor on mineral soil N dynamics by injecting small amounts of ^{15}N-enriched $(NH_4)_2SO_4$ solutions into the surface mineral soil with the forest floor present (+FF) or removed (−FF). K_2SO_4-extractable NO_3^--N, total inorganic-N, and total-N pool sizes in the mineral soil were initially increased after forest floor removal (after 4 months), but NO_3^--N and total inorganic-N were not significantly different thereafter. Microbial biomass-N and K_2SO_4-extractable total-N pool sizes were also found to be larger in mineral soils without a forest floor after 1 and 1.3 years, respectively. Total ^{15}N-recovery was greater in the +FF treatment compared to the −FF treatment after 1-year (about 50% and 35%, respectively) but did not differ after 1.3 years (both about 35%), suggesting that the forest floor delays but does not prevent the N-loss from the surface mineral soil of this forest. We estimated using our ^{15}N data that fungal translocation from the mineral soil to the forest floor may be as large as 9 kg-N ha^{-1} yr^{-1} (similar in magnitude to other N flows in this forest), and may account for all of the observed absolute increase of N in litter during the early stages of decomposition at this site. Our results suggest that the forest floor acts both as a source and sink for N in the mineral soil.

Introduction

Nitrogen (N) availability limits tree production in many forest ecosystems

(Cole & Rapp 1981; Binkley & Hart 1989). In cold temperate and boreal coniferous forests, large quantities of organic matter frequently accumulate over the mineral soil (Cole & Rapp 1981; Vogt et al. 1986), and a significant proportion of the total ecosystem N can occur within this layer (Gessel et al. 1973; Cole 1981). Forest ecologists have loosely called the sum of these organic horizons (L + F + H) overlying the mineral soil the "forest floor" (Waring & Schlesinger 1985). Some studies suggest that the importance of the forest floor as a source of N for tree growth increases as a stand develops (Wells & Jorgensen 1975; Jorgensen et al. 1980; Grier et al. 1981), with the forest floor potentially supplying a major portion of the N growth requirement in mature stands (Jorgensen et al. 1980).

Despite the large stock of N contained in the forest floor of many forests, N availability assessments frequently do not include the forest floor layer (Binkley & Hart 1989). The lack of inclusion of the forest floor in these assessments may be due to the belief that the forest floor in coniferous forests is generally a site of net N immobilization. This hypothesis is supported by:

- the significantly longer mean residence times of N relative to organic matter in the forest floor of these forests compared to other forest ecosystems (Vogt et al. 1986);
- fertilization studies using ^{15}N that show from 13—56% of the applied-N is retained within the forest floor (Binkley and Hart 1989);
- low rates of inorganic-N flux from the forest floor (Bringmark 1980); and
- short-term ^{15}N-tracer studies that indicate inorganic N is rapidly converted to insoluble forms within the forest floor (Weber & Van Cleve 1981, 1984).

The present study was designed to assess the role of the forest floor in the N cycle of a mature mixed-conifer forest using two different approaches. The first was a budget approach where we measured N turnover within the forest floor as well as N inputs to and N outputs from the forest floor layer. The second was an experimental manipulation approach where we removed the forest floor from a plot within the forest and measured the effect on N cycling in the surface mineral soil with the aid of ^{15}N-tracer techniques. The objective of the latter approach was to quantitatively assess the interaction between forest floor and mineral soil layers in controlling the fate of N in this forest.

Materials and methods

Study site

The study site was an old-growth (> 100 years-old) mixed-conifer forest comprised of: white fir (*Abies concolor* {Gord. & Glend.} Lindl.), incense-cedar (*Calocedrus decurrens* {Torr.} Florin), Douglas-fir (*Pseudotsuga menziesii* {Mirb.} Franco.), ponderosa pine (*Pinus ponderosa* Laws.), sugar pine (*Pinus lambertiana* Dougl.), and California black oak (*Quercus kelloggii* Newb.). This forest stand is located in Blodgett Research Forest, Georgetown, California, at an elevation of 1300 m on the western slopes of the Sierra Nevada Mountains (38° 52' N, 120° 40' W). In this region, the mean daily maximum temperatures range from 9 °C in winter to 27 °C in summer; mean daily minimum temperatures range from 0 °C in winter to 14 °C in summer. Annual precipitation is 170 cm, about 85% of which falls primarily as snow between October and March. Mean monthly maximum and minimum air temperatures and monthly precipitation totals during the study period are shown in figure 1. The mineral soil is a well-drained, sandy-loam Ultic Haploxeralf, formed on granodiorite parent material. There is a substantial mor-type organic horizon (forest floor) that overlies the mineral soil. This horizon (about 10 cm thick) consists of three distinct sublayers that we have grouped into two fractions: O1 (L) layer, and O2 (F + H) layer, ranging from 2—4 cm and 6—8 cm thick, respectively.

Forest floor net N production and apparent N uptake by vegetation

Estimates of net N mineralization and nitrification were made using an in-field buried-bag technique (Eno 1960; Ellenberg 1977; Pastor et al. 1984). A 60-m transect was randomly located, with sampling locations placed every 10 m, to give seven locations. On each sampling date, the transect was move 1 m. There were a total of seven incubation periods over the one-year duration of the study, which was conducted from January through December 1986. At each sampling location, a 400 cm^2 block of the forest floor was removed using a square template. This subsample was then sliced in half: one-half was used to determine initial pool sizes of NH_4^+ and NO_3^- and water content, and the other was enclosed in a 38 μm (1.5 mil) thick polyethylene bag, sealed at the top, and returned to the same hole from which it originated. The rest of the hole was back-filled with adjacent forest floor material, and a small amount of litter was used to cover the bag.

After the incubation period (40—66 d), forest floor samples were removed and kept on ice until returning to the laboratory. Buried-bags having visible tears were not analyzed. Forest floor materials coarser than 1-cm diameter were removed by hand, and the remaining materials were chopped into pieces less than 5 cm in length and mixed using scissors and a Waring blender to allow accurate subsampling and extraction of inorganic N. Inorganic-N concentrations in forest floor samples were determined by extracting 10—20 g field-moist subsamples with 75 mL of 2 *M* KCl.

N uptake by trees and other minor understory vegetation from the forest floor was estimated from the buried-bag incubation data using the concepts developed by Nadelhoffer et al. (1984, 1985). Nadelhoffer et al. assumed that net N mineralization rates in incubated forest soils are good estimates of plant-available N in surrounding field soils. They also assumed that inorganic N in soil gained via throughfall or lost via leaching and denitrification are small relative to monthly net mineralization rates. Previous studies of denitrification from the forest floor in a 60-year-old mixed-conifer forest site located nearby our study site indicate that denitrification potential from the forest floor and surface mineral soil is very low in these forests (R. B. Strauss, unpublished data, 1983), suggesting tht N loss from denitrification is small. We used throughfall data collected in 1979 (J. G. McColl, unpublished data) from another old-growth mixed-conifer stand located in the same region at a similar elevation, and measured rates of inorganic-N leachate flux from the forest floor (explained below) to correct our 1986 estimates of N uptake by vegetation. N supplied to vegetation by the surface mineral soil (0—7.5 cm) during 1986 was also estimated using this method from data published previously (Hart & Firestone 1989). This allowed the assessment of the relative importance of the forest floor as a source of N for plant growth.

N mobilization from the forest floor

Inorganic-N flux from the forest floor was determined using an in-field ion exchange resin (IER) method (Hart & Gunther 1989). IER bags were placed at the forest floor — mineral soil interface adjacent to buried-bag incubations (total of seven per sampling period). These IER bags were the top resin bag used for surface mineral soil incubations (0—7.5 cm depth, 5-cm diameter soil cores) in the resin-core incubation method (DiStefano & Gholz 1986; Hart & Gunther 1989). The IER bags were made by placing 30 mL (7.8-g oven-dry equivalent) of cation + anion exchange

beads (J. T. Baker #M-614 16—50 mesh, mixed-bed ion exchange resins that had been pre-extracted with 2 *M* KCl; Hart & Binkley 1984) in nylon stockings that contained a 5-cm diameter rubber tubing ring, and were then tied shut. Only downward percolating solution is sampled because:

— a PVC collar around the resin bag prevents lateral water flow; and
— upward movement of NH_4^+ and NO_3^- to the IER bag is likely to be insignificant in the well-drained soil of this forest since movement of ions to ion exchange resins is highly dependent on water flow (Binkley 1984; Hart & Firestone 1989).

After the incubation period (40—66 d), IER bags were air-dried in the laboratory, and resin beads extracted with 100 mL of 2 *M* KCl. We estimated the flux of N from the forest floor by dividing the amount of N accumulated on the resin bags by the surface area of the resin bag (approximately 18.3 cm^2). This value was then converted to a kg-N ha^{-1} basis. In a similar manner, values for N accumulation on the bottom resin bag from the same resin-core incubation (Hart & Firestone 1989) were used to estimate leaching from the surface mineral soil (0—7.5 cm depth).

Forest floor and litterfall mass and N content

We estimated the mass of the forest floor using the subsamples from the buried-bag experiment described previously; this gave us a total sample size of 98. Forest floor materials > 1 cm diameter were not included in the mass estimate. The subsamples were over-dried at 65 °C and weighed. Ash-free (organic matter) mass was determined on ground ($\leqslant 425$ μm) subsamples by ashing in a muffle furnace at 550 °C for 6 h. N content in the forest floor was determined using the subsamples obtained during the forest floor removal experiment described below.

We measured annual fine litterfall mass from September 1987-August 1988 using 10 litter traps located along the same transect used in the buried-bag study. The sampling area of each trap was about 0.25 m^2. Litter was removed from the traps several times over the 1-year period, and all litter >1 cm diameter was discarded. Ash-free litterfall mass was determined in a similar manner as for the forest floor materials. N content of litterfall was determined using composited samples from the 10 littertraps for each collection period. N content of the litter subsamples were determined using a salicylic acid-thiosulfate modification of a micro-Kjeldahl method that includes NO_2^- and NO_3^- (Bremner & Mulvaney 1982). The annual rate of N input from litterfall was then calculated by summing the product of mass and N content for each collection period.

Forest floor removal experiment

In early June 1986, the forest floor was removed by hand from half of a 2 m by 10 m plot (giving two subplots of dimensions 2 m by 5 m). Twelve 10-cm diameter aluminum cylinders were driven into the subplot containing the forest floor (hereafter referred to as the +FF treatment), and the subplot where the forest floor had been removed (hereafter referred to as the −FF treatment). The cylinders were of sufficient length to include the 0—10 cm mineral soil layer in each subplot. Into each cylinder, 74 atom % ^{15}N-enriched $(NH_4)_2SO_4$ solution (95 mL, 6.1 μMoles-N L^{-1}) was injected at 2-cm mineral soil depth. About 8.1 mg of N (6.0 mg of ^{15}N) was added per cylinder (or about 10 kg-N ha^{-1}). A total of 19 injections were made into each cylinder using 18-gauge Quincke (Babcock) Spinal Needles (Popper and Sons, Inc., New Hyde Park, NY). A template and guide block were used to help uniformly distribute the label laterally within the cylinder, and insure that injections were made at the correct soil depth. Needles were rinsed with deionized water between each injection to minimize contamination of the forest floor.

Approximately every 4 months over a 1.3-year period, 3 cylinders were selected at random and removed from both the +FF and −FF subplots. All soil cylinders were frozen (−18 °C) until analyzed. Immediately after thawing, the cylinders were divided into 0—4 cm and 4—10 cm mineral soil layers. In the +FF cylinders, the forest floor was also subdivided into 01 and 02 layers. In each of these layers, the total amount of ^{15}N recovered was determined using the modified micro-Kjeldahl digestion method. For the mineral soil layers, the amount of ^{15}N and $^{14}N + {}^{15}N$ was determined in K_2SO_4-extractable and $CHCl_3$-labile pools. Two 20-g, field-moist soil subsamples from each soil layer were weighed into beakers. One subsample was extracted immediately with 75 mL of 0.5 *M* K_2SO_4. The other subsample was fumigated with distilled $CHCl_3$ vapor for 24 h, and then extracted immediately with 75 mL of 0.5 *M* K_2SO_4. Total-N in filtered extracts of fumigated and unfumigated soils was determined using the modified micro-Kjeldahl digestion method. Chloroform-labile N was determined as the difference in the total-N content of fumigated and unfumigated soil extracts (Brookes et al. 1985). A 1-day fumigation period appears to release all of the $CHCl_3$-labile N in these soils (Davidson et al. 1989). Chloroform-labile N and ^{15}N were converted to microbial biomass N and ^{15}N by dividing by a k_N factor of 0.25, which is the mean value determined for this soil (Davidson et al. 1989). K_2SO_4-extractable organic-N was calculated by subtracting inorganic-N concentrations from N concentrations in total-N digests of K_2SO_4 extracts.

In early September of 1988, 6 additional cylinders were driven into the

soil, all containing the forest floor layer. ^{15}N in solution (same solution as used previously) was injected into the mineral soil of 3 of these cylinders in an identical manner as described above, and the cylinders were immediately removed and taken back to the laboratory. These samples were used to estimate total ^{15}N recovery at "time-zero" (from O1, O2, and 0—10 cm layers), and the amount of ^{15}N contamination of the forest floor layer that might have occurred when the label was injected through the forest floor into the mineral soil. The other 3 unlabeled cylinders were used to determine background levels of ^{15}N in forest floor and mineral soil layers; the background atom % ^{15}N content was 0.37 ± 0.01% (s.e.) for all layers.

Inorganic N and ^{15}N analyses

All KCl and K_2SO_4 extracts of soil and resin were shaken for 1 h on a mechanical shaker, filtered (Whatman 1), and analyzed using a Lachat flow-injection analyzer. The filter paper was pre-leached with approximately 50 mL of 2 *M* KCl or 0.5 *M* K_2SO_4 to remove any NH_4^+ and NO_3^- initially present. Ammonium was determined using the indophenol blue method (Kenney & Nelson 1982; QuikChem Systems 1986) and nitrate by diazotiation after reduction to nitrite by zinc or cadmium (Keeney & Nelson 1982; QuikChem Systems 1987).

Kjeldahl digests of litter, soil, and soil extracts were prepared for N isotopic mass ratio analysis using the diffusion method of Brooks et al (1989). Isotopic enrichments of ^{15}N were determined by Isotope Services, Los Alamos, New Mexico.

Statistical analyses

All data were log transformed prior to statistical analyses. Two-way analyses of variance (ANOVA) were used to test for significant sample date and treatment (+FF or −FF) effects on soil moisture, N pool sizes, and ^{15}N enrichments (Steel & Torrie 1980). *T*-tests were used to test for significant differences in ^{15}N recovery due to treatment for K_2SO_4-extractable, microbial biomass, and total N pools for each sample date. A one-way ANOVA was used to test for significant differences in the amount of ^{15}N excess (above background quantities) contained in the forest floor over time. All statistical analyses were performed at the $p = 0.05$ level (unless otherwise noted) using Statgraphics microcomputer statistical software (STSC Inc. 1986).

Results and discussion

Forest floor N fluxes and turnover

Net N mineralization in the forest floor was highly seasonal, being greatest during January—February, declining until June—July (when there was net immobilization), and then generally increasing with the onset of fall precipitaiton (Fig. 2a). The highest rates of net N mineralization occurred when the forest floor was wet and cold, and the lowest rates when the forest floor was warm and dry (Fig. 1 and 2a). We had hypothesized that net N mineralization rates would be greatest in the sping and fall, when forest floor materials were both moist and warm together (Fig. 1). We have observed previously that most of the hot-water soluble N is released from freshly fallen litter within the first few months after being deposited on the forest floor, primarily during late fall (Hart 1990). This input of labile substrate may in part account for high rates of net N mineralization during the early part of the year. Another possibility is that actual (gross) rates of N transformations did follow our hypothesized seasonal pattern, but that gross N immobilization was higher during fall and spring periods

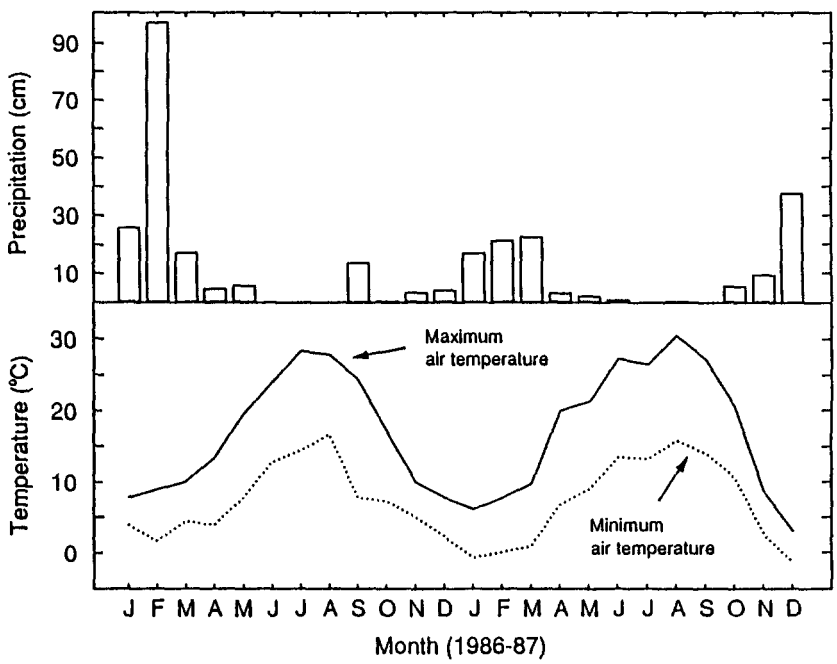

Fig. 1. Monthly precipitation (bars) and mean monthly maximum and minimum air temperatures recorded at Blodgett Forest Research Station during the study period.

resulting in lower net rates. This latter explanation is supported by ^{15}N pool dilution data that show higher gross N immobilization rates yet similar gross mineralization rates in April compared to February in the O2 layer at this site, measured during this same year (Davidson et al., submitted).

Rates of net nitrification were always low (< 1 kg-N ha^{-1} ha^{-1} $30d^{-1}$) in the forest floor, being greatest during the spring and fall (Fig. 2a). However, $^{15}NO_3^-$ pool dilution studies suggest that gross nitrification rates are an order of magnitude or more greater than net rates in the O2 layer, and also appear to be highest during fall and spring (Davidson et al., submitted). Our estimate of annual net mineralization in the forest floor is similar to the annual rate found for the surface mineral soil (0—7.5 cm) published previously (Hart & Firestone 1989), being about 13 and 16 kg-N ha^{-1} yr^{-1}, respectively.

In addition to buried-bag estimates of N availability, we assessed the relative supplying power of the forest floor to provide N to trees by calculating and comparing mean residence times for forest floor mass, organic matter, and nitrogen using the following equation (Olson 1963; Gosz et al. 1973; Vogt et al. 1986):

$$T = H/L$$

where T is the mean residence time of mass (MRTM), organic matter (MRTOM), or N (MRTN) in the forest floor (years), H is the forest floor mass, organic matter, or N content (kg ha^{-1}), and L is the mass, organic matter, or N content of annual fine litterfall (kg ha^{-1} yr^{-1}) (Table 1). This equation assumes that the forest floor is in steady state (i.e., annual litter input equals annual forest floor decomposition). The MRTOM is the forest floor of our site was calculated at about 13 years, half the MRTM (Table 1). The difference between mass and organic matter was due to the large amount of mineral soil that had been incorporated into the O2 horizon, and emphasizes the importance of expressing forest floor MRT values on an ash-free basis. Indeed, some of the variation in MRT for forest floor mass observed worldwide may actually be due to inconsistences among studies in the exclusion of mineral matter in forest floor mass estimates (see appendices in Vogt et al. 1986). The MRTN value for the forest floor is over 2.5 times that of MRTOM, suggesting that microbial immobilization of N is substantial within this forest floor layer (Vogt et al. 1986). Nevertheless, although N is retained for much longer periods of time than organic matter within the forest floor, N is still cycled rapidly within this layer. This is indicated by comparable rates of net mineralization in forest floor and mineral soil layers, and even more significantly by the fact that gross rates of N mineralization in this forest

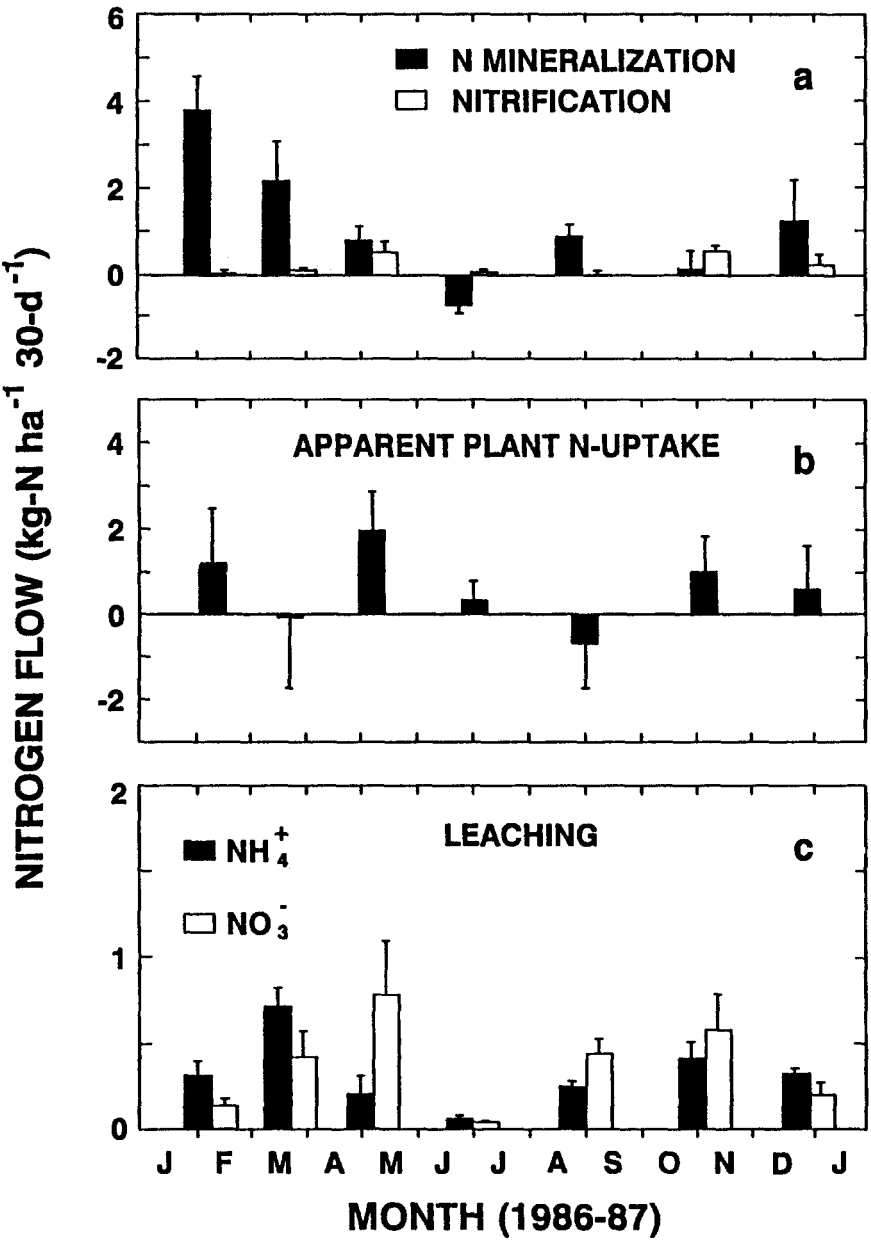

Fig. 2. Seasonal patterns in N flows within and from an old-growth mixed-conifer forest: (*a*) forest floor net nitrogen transformations; (*b*) apparent plant N-uptake from the forest floor; and (*c*) inorganic-N leaching from the forest floor. Vertical bars denote one standard error of the mean.

Table 1. Annual litterfall, stocks and mean residence times of mass (M), organic matter (OM), and nitrogen (N) in the forest floor.

Component	M	OM	N	Mean residence time M	OM	N
	(kg ha^{-1})			(years)		
Forest Floor	106320 (5810)	52950 (2900)	810 (170)	26 (2)	13 (1)	34 (8)
Annual Litterfall	4120 (290)	3970 (280)	24 (2)			

Mean and (standard error); n = 10 and 98 for annual litterfall and forest floor mass and organic matter estimates, respectively; n = 10—12 for N content estimates.

floor (O2 layer) are over 30 times greater than net rates (Davidson et al., submitted).

The inclusion of fine root inputs to the forest floor in our mean residence time (MRT) calculations would result in lower MRT values than those noted above. Vogt et al. (1983) found in young and mature *Abies amabilis* stands in the Pacific Northwest (PNW) region of the United States that inclusion of fine roots reduced estimates of MRT for organic matter and nitrogen in the forest floor by about 75%. However, the predominant location of fine roots in these stands are within the forest floor layer, and fine root turnover within the forest floor is about 3 times greater than aboveground litterfall inputs. The forest floor layer of the mixed-conifer forest in the present study has a relatively low abundance of fine roots. This pattern may be due to seasonal drying of the forest floor causing a deeper depth-distribution of fine roots, as has been found in other Mediterranean plant communities (Lamont 1983). In a nearby 60-year-old mixed-conifer forest, J. Schimel (pers. comm. 1990) found a mean of 260 and 890 kg dry-weight of live fine roots ha^{-1} in the forest floor and upper mineral soil, respectively. If we assume a similar value for fine root biomass in the forest floor of our mixed-conifer stand, and that the entire fine root biomass pool turns over annually, fine root mass inputs to the forest would be only about 6% of aboveground fine litterfall. Therefore, inclusion of fine root inputs would probably only slightly reduce our forest floor turnover estimates in this mixed-conifer stand.

An independent estimate of the MRTOM within the forest floor was obtained using the reciprocal of the first-order decay rate constant for ponderosa pine needle litter decomposition (Waring & Schlesinger 1985),

determined using a litterbag technique at our study site (Hart 1990). The litterbag-based MRTOM is about 13 years, which is the same value as that calculated using the steady-state assumption (Table 1). Because the litterbag estimates are based only on needle-litter decay, the good agreement between these two estimates of organic matter turnover in the forest floor further indicates that fine roots likely play only a minor role in forest floor dynamics in this mixed-conifer forest.

Apparent plant uptake (as calculated from buried-bag data) and leaching of inorganic N (measured using IER) both exhibited a bimodal seasonality, with rates of these processes being greatest during spring and fall (Fig. 2b and c). These seasons are also the periods during which water flow through the forest floor should be the greatest (Fig. 1), and where biological activity in the Mediterranean-type climate should be the highest (Jackson et al. 1988). Leaching of NO_3^- from the forest floor occurred during periods when net nitrification in the forest floor was highest (Fig. 2a and c). The pattern for NH_4^+ was different, which showed the highest rate of leaching from the forest floor after the period of maximum net NH_4^+ production (January—February), but before the apparent maximum N-uptake from the forest floor by plants (April—May) (Fig. 2a—c). We estimated that the annual N-uptake by plants from the forest floor was about 10 kg-N ha^{-1} yr^{-1} (negative uptake values were treated as 0 values; see Nadelhoffer et al. 1984). This value is similar to the rate of N uptake from the surface (0—7.5 cm) mineral soil (about 11 kg-N ha^{-1} yr^{-1}) estimated using the same method (data not shown).

Estimates of plant N-uptake based on buried-bag values could underestimate actual N-uptake for several reasons. Plant root severing during forest floor and soil sampling might result in greater net N immobilization than would occur under undisturbed conditions (Adams et al. 1989), resulting in lower net N mineralization rates and apparent plant N-uptake values. Furthermore, in Nadelhoffer et al.'s (1984) method it is assumed that plants do not compete successfully for inorganic N, such that only N not immobilized by microbes is considered available to plants. Recent studies using ^{15}N in an annual grassland suggest that plant roots can be significant competitors for both NH_4^+ and NO_3^- (Jackson et al. 1989; Schimel et al. 1989). If tree roots are also significant competitors for inorganic N in forest ecosystems, our estimates of plant N-uptake would also be too low. In two young (< 20 year-old) New Zealand *Pinus radiata*, Dyck et al. (1987) found that the *in situ* core method (similar to Nadelhoffer et al. 1984) underestimated annual plant N-uptake relative to the traditional biomass harvest technique. In an even younger ($\leqslant 4$ year-old) *P. radiata* plantation in South Australia, Smethurst and Nambiar (1989) recently found that the *in situ* soil-core method and the biomass

harvest method gave similar annual estimates of plant N-uptake; however, the soil-based method generally produced higher seasonal estimates. It is apparent from these results that more field studies are needed to assess the reliability of the soil-core technique for estimating plant N-uptake, particularly in older-aged stands.

We have estimated total aboveground plant N-uptake from the forest floor and mineral soil in the following manner. If we assume that total aboveground plant uptake is equal to annual N-increment (ANI) associated with bole and branch wood plus annual loss through litterfall (Cole & Rapp 1981), and that ANI at our site is equal to the mean value reported for the 13 International Biological Program temperate coniferous forest sites (about 11 kg-N ha^{-1} yr^{-1}), we calculate total plant uptake for aboveground plant biomass at our site is about 35 kg-N ha^{-1} yr^{-1}. Based on this estimate of total aboveground plant N-uptake from our forest, the forest floor supplies less than one-third of the total aboveground plant N-uptake. Including belowground plant N-uptake would further reduce our estimate of the proportion of plant-N derived from the forest floor in this forest. Although this is a significant proportion of the total aboveground plant N-uptake, it is much less than has been found for 60—90 year-old Douglas-fir forests in the PNW, where nearly all of the annual aboveground plant N-uptake is supplied by the forest floor (Cole 1981). As noted above, low abundance of fine roots within the forest floor of this forest may be responsible for the relatively low proportion of the total aboveground plant N-uptake supplied by the forest floor relative to wetter PNW forests.

Forest floor removal experiment

Forest floor removal generally increased K_2SO_4-extractable inorganic-N in the 0—4 cm mineral soil layer, but had no significant effect on K_2SO_4-extractable organic-N (Table 2). However, forest floor removal resulted in large increases in inorganic N pool sizes only during the October 1986 sampling period, when the NO_3^--N pool size was over 3 times greater and the total inorganic-N pool size was over 2 times greater in the −FF treatment soils compared to +FF treatment soils (Table 2). A substantial increase in the NO_3^- pool size also occurred during this period at the 4—10 cm depth (4.5 and 0.4 mg-N kg^{-1} for the − and +FF treatments, respectively; data not shown). This was also the sample date when soil moisture content in the −FF treatment surface mineral soils greatly exceeded that of the +FF treatment soils (0.459 and 0.284 kg^{-1} H_2O kg^{-1} dry soil, respectively; Table 2). Therefore, these differences in mineral soil

Table 2. K_2SO_4-extractable ammonium, nitrate, and organic N pool sizes and soil moisture in surface (0—4 cm) mineral soils[a]

Date	Treat.[b]	NH_4^+-N	NO_3^--N	Sum	Org.-N	Soil moisture
		- - - - - - - - - - - - mg kg^{-1} - - - - - - - - - - - -				($kg\ kg^{-1}$)
Oct. '86	+FF	14.4	6.0	20.4	9.9	0.284
		(3.9)	(3.7)	(3.1)	(2.0)	(0.017)
	−FF	26.1	20.4	46.5	4.0	0.459
		(7.8)	(9.3)	(4.3)	(3.2)	(0.040)
Jan. '87	+FF	24.1	1.5	25.6	25.2	0.374
		(4.1)	(0.0)	(4.2)	(0.9)	(0.019)
	−FF	27.2	2.5	29.7	18.2	0.398
		(10.1)	(0.9)	(10.0)	(2.3)	(0.046)
May '87	+FF	16.9	0.7	17.6	18.1	0.329
		(3.9)	(0.1)	(3.7)	(1.2)	(0.029)
	−FF	18.2	2.5	20.7	18.3	0.406
		(5.4)	(1.1)	(6.4)	(1.3)	(0.076)
Oct. '87	+FF	2.8	1.4	4.1	7.0	0.072
		(0.5)	(0.0)	(0.5)	(1.5)	(0.001)
	−FF	7.4	2.9	10.3	19.1	0.065
		(0.2)	(0.3)	(0.3)	(0.8)	(0.002)
Significant effects:[c]						
Treatment		*	*	*	ns	*

[a] Mean (and standard error), $n = 3$. All data were log transformed prior to statistical analyses; means and standard errors shown are for untransformed data.

[b] +FF = forest floor present, −FF = forest floor removed.

[c] ns and * denote not significant and significant at $p = 0.05$, respectively, by ANOVA: date was significant for all variables; there was a significant treatment * date interaction for K_2SO_4-extractable organic-N.

N pool sizes as a result of forest floor removal may be mediated indirectly by forest floor influences on water relations in the underlying mineral soil.

Forest floor removal generally increased both K_2SO_4-extractable total-N and microbial-N pool sizes in the 0—4 cm mineral soil layer, but did not significantly alter the atom percent ^{15}N enrichments (A%Enr.) of these pools (Table 3). In the 4—10 cm soil layer, forest floor removal had no significant effect on the size of either of these two pools or their ^{15}N enrichments (data not shown). Greater, rather than smaller, microbial-N pool sizes following forest floor removal suggest that heterotrophic microorganisms within the mineral soil were not dependent on carbon originating from the forest floor for their maintenance and growth (Table 3). Apparently, increases in extractable total-N and microbial-N pools within mineral soil were also due to altered soil moisture dynamics, as discussed above.

Table 3. K_2SO_4-extractable and microbial biomass N pool sizes and atom % ^{15}N enrichments (A%Enr.) in surface (0—4 cm) mineral soils.[a]

Date	Treat.[b]	K_2SO_4-extr. N mg kg^{-1}	A%Enr.	Microbial N mg kg^{-1}	A%Enr.
Oct. '86	+FF	30.3	1.81	140	2.36
		(1.9)	(0.57)	(15)	(0.52)
	−FF	50.5	2.60	192	2.32
		(5.1)	(0.06)	(22)	(0.19)
Jan. '87	+FF	50.7	2.06	114	2.37
		(4.0)	(0.17)	(27)	(0.36)
	−FF	47.9	2.81	163	2.31
		(12.1)	(0.26)	(24)	(0.26)
May '87	+FF	35.7	1.67	149	2.19
		(4.1)	(0.15)	(11)	(0.23)
	−FF	39.1	1.15	308	1.57
		(5.7)	(0.20)	(45)	(0.13)
Oct. '87	+FF	11.1	1.09	113	1.33
		(2.1)	(0.17)	(19)	(0.25)
	−FF	29.4	1.18	155	1.77
		(0.8)	(0.19)	(9)	(0.42)
Significant effects:[c]					
Treatment		*	ns	*	ns

[a] Mean (and standard error), $n = 3$. All data were log transformed prior to statistical analysis; means and standard errors shown are for untransformed data.

[b] +FF = forest floor present, −FF = forest floor removed.

[c] ns and * denote not significant and significant at $p = 0.05$, respectively, by ANOVA; date was significant for all variables; there was a significant treatment * date interaction for K_2SO_4-extractable N.

Seasonal patterns of ^{15}N recovery in K_2SO_4-extractable total-N and microbial-N pools in the mineral soil appeared to be inversely related, suggesting that there is a substantial exchange of N between these two pools (Fig. 3a and b). This rapid exchange hypothesis is supported by the similar A%Enr. of these pools in the 0—4 cm (Table 3) and 4—10 cm soil (data not shown) layers over the duration of the study.

There were few differences in the fate of ^{15}N in the mineral soil as a result of forest floor removal (Fig. 3a—c). In May 1987, there was a significantly greater amount of ^{15}N recovered in the K_2SO_4-extractable and microbial biomass fractions in the mineral soil of the +FF treatment compared to the −FF treatment (Fig. 3a and b). However, no other significant differences in ^{15}N recovery as a result of treatment were found for these pools. Total ^{15}N recovery was generally low in both treatments (Fig. 3c). Even when soil cylinders were removed immediately after label

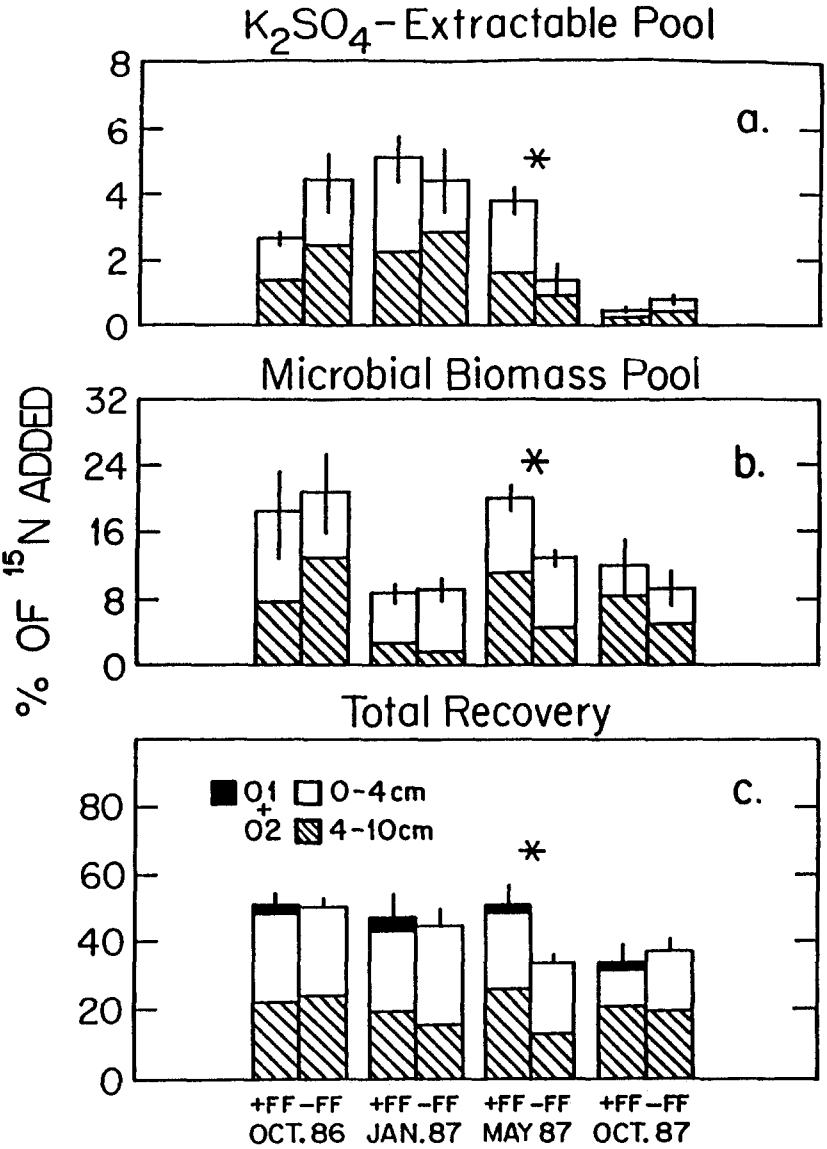

Fig. 3. Recovery of ^{15}N added to the surface mineral soil in (*a*) K_2SO_4-extractable, (*b*) microbial biomass, and (*c*) total soil N pools when the forest floor was present (+FF) or removed (−FF). Vertical bars denote two (a and b) or one (c) standard error(s) of the mean. Asterisks denote significantly different ^{15}N recoveries between treatments during that sample date using a *t*-test ($p = 0.05$).

addition ("time-zero" samples), only 84% (±2%) of the added label was recovered in the 0—10 cm mineral soil layer. The low time-zero recovery may have been due to leaching of some of the injected ^{15}N solution down

old root channels below this 10-cm soil depth. Total ^{15}N recovery during the first sampling date in October 1986 was only about 50% in both treatments, and label recovery remained at about this level through January 1987 (Fig. 3c). By May 1987, total ^{15}N recovery in the −FF treatment had decreased to about 35%, and was significantly lower than recovery in the +FF treatment, which remained at about 50% (Fig. 3c). This difference was short-lived, however, because total ^{15}N recovery in the +FF treatment dropped to about 35% by October 1987, similar to the recovery in the −FF treatment (Fig. 3c). This result suggests that the presence of the forest floor layer delays but does not prevent N loss from the surface mineral soil of this forest. This effect of forest floor removal may be due to alteration of soil moisture dynamics and/or its effects on mineralization-immobilization processes in the mineral soil.

Temperature fluctuations in the mineral soil might also have increased as the result of forest floor removal, potentially altering soil N-cycling processes. However, soil temperatures (measured at a 4-cm depth) were similar within +FF and −FF plots for all sampling dates (data not shown). Furthermore, because this stand has a closed-canopy, we would not expect a large change in the temperature dynamics of the mineral soil following forest floor removal.

There was a significant effect of sample date on the amount of ^{15}N recovered in the forest floor throughout the 1.3 year duration of the experiment, ranging from 1—4% of the initial amount added (Fig. 3c). Total ^{15}N recovery in the forest floor was significantly different from the time-zero value (which was about 0.1% of added ^{15}N) during all sample dates except that of October 1987. There was a significant difference ($p = 0.07$) in the amount of ^{15}N recovered in the O1 compared to the O2 forest floor horizons; the amount of ^{15}N recovered in the O2 layer generally equalled or exceeded ^{15}N recovery in the O1 layer (data not shown).

In a similar study in a nearby 60-year-old mixed-conifer forest, Schimel and Firestone (1989) also recovered a small amount ($< 2.5\%$) of the ^{15}N label in the forest floor over a month period when the label was added to the mineral soil. Although these values are small amounts of ^{15}N, they may represent a much greater flux of $^{14}N + {}^{15}N$ from the mineral soil to the forest floor. In order to calculate this flux we needed to make several assumptions. The first was that the mechanism of transport of ^{15}N from the mineral soil to the forest floor was fungal translocation. The second was that we could characterize the fungal-N pool actively transporting N by using the $CHCl_3$-labile N fraction in the 0—4 cm mineral soil layer. And finally, that the A%Enr. of the transporting pool was equal to the A%Enr. of the $CHCl_3$-labile N pool in October 1986 (2.36%; Table 3).

This final assumption implicitly states that all transport of N from the mineral soil to the forest floor occurred between June and October of 1986, that fungi rapidly took up the added label in June, and that their A%Enr. during this period was always 2.36%. We assumed that all of the annual transport of N from the mineral soil to the forest floor occurred between June and October, because total ^{15}N excess in the forest floor did not increase significantly after October 1986 (Fig. 3c). Given these assumptions, we calculated the total-N flux from the mineral soil to the forest floor using the following equation:

Fungal Translocation N-flux (μg)=
Total ^{15}N excess recovered in the forest floor in October 1986 (μg)/ (A%Enr./100) of $CHCl_3$-labile N pool in October 1986.

These values were then converted to a kg-N ha^{-1} basis. Our calculated values of total-N flux are:

Mineral soil to:	kg-N ha^{-1} yr^{-1}
O1 layer	4 (±2)
O2 layer	5 (±2)
Total	9 (±2)

These results imply that the total-N flux was about 40 times greater than the flux of ^{15}N alone (equivalent to the reciprocal of the A%Enr. of the $CHCl_3$-labile N pool).

Our calculated N fluxes due to fungal translocation would be overestimates if the ^{15}N A%enr. of the N being transported was greater than 2.36%. This may have occurred if N was transported to the forest floor soon after addition of the label to the mineral soil (in early June), when the soil was still relatively moist preceding the summer dry period. However in a nearby mixed-conifer forest, Schimel and Firestone (1989) found that the amount of ^{15}N recovered in the microbial biomass was similar 1 day and 31 days after addition of small amounts of $^{15}NH_4^+$ to surface mineral soil. Their results suggest that even if transport occured in June, the ^{15}N A%enr. of the microbial biomass was probably similar to that found in October, and thus would not substantially affect our N-flux estimates. The ^{15}N A%enr. of the $CHCl_3$-labile N pool may also be lower than that of the fungi transporting N if the $CHCl_3$-labile N pool included N from a large non-active (unenriched in ^{15}N) microbial population with

that of the active (^{15}N-enriched), N-transporting fungal population. This is also unlikely, because the similarity in the ^{15}N A%enr. of K_2SO_4-extractable and $CHCl_3$-labile N pools suggests that significant exchange of N was occurring between the solution phase and the majority of the microbial biomass (Table 3).

We have observed that freshly fallen ponderosa pine needles in litterbags placed in this site show a maximum net increase in N equivalent to about 4 kg-N ha^{-1} yr^{-1} between April and January during the first year of decomposition (Hart 1990). Several possible sources for observed absolute increases in N in decomposing litter have been reported, such as: throughfall and insect frass (Bocock 1963), fungal translocation from other mineral soil or forest floor layers (Staff & Berg 1977; Berg & Söderström 1979; Fahey et al. 1985), N fixation (Granhall & Lindberg 1977), and additions by flowers, pollen, bud scales, and other fine particulate matter (Gosz et al. 1973; Jorgensen et al. 1980). N leachate from freshly fallen litter on top of previous year's litter (about equal to the maximum net increase in litter contained in litterbags; Hart 1990) may be an additional source of accumulation during the early stages of litter decomposition at our site. We cannot unequivocally rule out any of these possibilities as sources of N for the observed immobilization of N into O1 litter during decomposition at our site. However, it is interesting that our estimated fungal translocation-N flux from the mineral soil to the O1 layer could account for all of the observed icrease in litter-N.

N balance

We have summarized the various flows of N in the forest floor and surface mineral soil (Fig. 4). N has been compartmentalized into organic and inorganic pools in the forest floor and surface mineral soil layers. We did not measure leaching of organic N from the forest floor and from the mineral soil. These two fluxes were determined by difference assuming steady-state conditions for total N (organic-N + inorganic-N) within each layer. Furthermore, we have assumed that fine root N inputs to the forest floor and upper mineral soil layers are small, and have not included these N flows in our model (see discussion above). Nevertheless, if we did include fine root N inputs to our N-flow model our calculated rates of organic-N leaching would increase proportionately.

Given errors of measurement, our N-flow model appears internally consistent. For example, total-N inputs to the organic pool within the forest floor is 33 kg-N ha^{-1} yr^{-1}, while total output is 30 kg-N ha^{-1} yr^{-1} (Fig. 4). Similar balances can be found for the inorganic-N pools, although

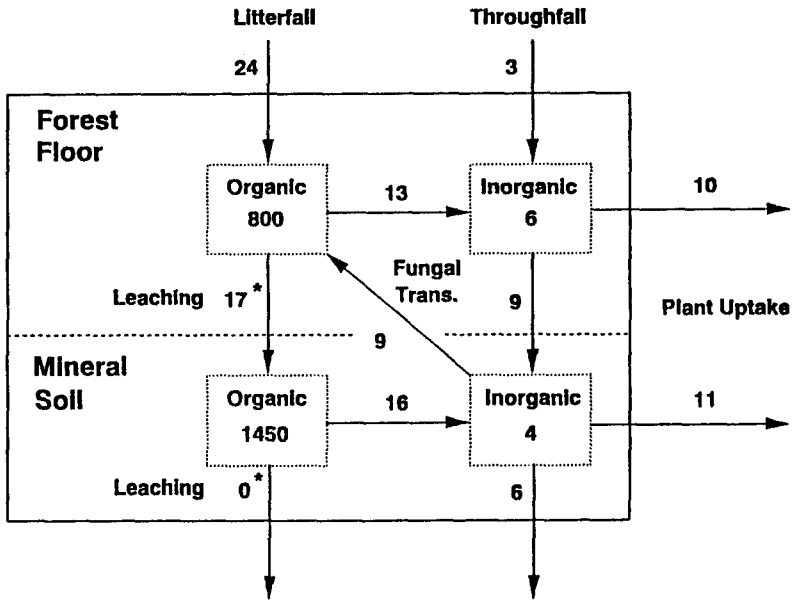

Fig. 4. Nitrogen-flow model for the forest floor and surface (0—7.5 cm) mineral soil in an old-growth mixed-conifer forest. Nitrogen in fine litterfall was determined using littertraps, and measuring mass and N concentration of litterfall. Nitrogen input in throughfall was estimated using funnel collectors in a similar forest, located in the same region and at comparable elevation. Net flows from organic to inorganic pools were determined using buried-bags. Leaching of inorganic N was estimated using ion exchange resins. Plant uptake (apparent) was calculated from buried-bag data. Fungal translocation (abbreviated fungal trans.) from the mineral soil to the forest floor was estimated from increases in ^{15}N content of the forest floor after addition of ^{15}N to the mineral soil. Leaching of organic-N (values followed by an asterisk) were determined by difference assuming steady-state conditions for total (organic + inorganic) N within each soil layer. Nitrogen-pool size data for the mineral soil are from Hart & Firestone 1989 (see text). All pool sizes and flows are expressed in kg-N ha^{-1} and kg-N ha^{-1} yr^{-1}, respectively.

these pools are seldom thought of as being in a steady-state. However, in this non-aggrading, relatively undisturbed old-growth forest, annual mean inorganic N pool sizes are fairly constant (data not shown).

Several interesting points are highlighted in our N-flow model, such as: N flow via fungal transport from the mineral soil to the forest floor is a substantial N flux within this ecosystem, being about equal in magnitude to other N fluxes, such as apparent plant uptake and leaching; annual net N mineralization, expressed relative to the total stock of organic N (so-called mineralizable-N; Powers 1990), is greater in the forest floor (1.6%) than in the surface mineral soil (1.1%); and leaching of organic N from the forest floor also appears to be a substantial N flow, equal to about two-times the inorganic-N leachate flux.

Fahey et al. (1985), using a N-budget approach, suggested that most of the absolute increase in N content of the litter layer (O1) of an old-growth lodgepole pine forest (*Pinus contorta* spp. *latifolia* Engelm.) originated from fungal translocation from the O2 layer (about 4 kg-N ha^{-1} yr^{-1}). This rate of N movement was also the same order of magnitude as other N transfers within their lodgepole pine ecosystems (e.g., plant uptake was estimated at about 11 kg-N ha^{-1} yr^{-1}). It is possible that some of the N incorporated in the O1 layer in these lodgepole pine stands originated from the surface mineral soil, especially considering that the O2 layer in these forests showed little net N mineralization, while net mineralization in the surface mineral soil (0—15 cm) was about 8 kg-N ha^{-1} yr^{-1} (Fahey et al. 1985).

Mineralizable-N values, when determined under similar conditions of temperature and moisture, have been suggested as a good index of organic matter (substrate) quality (Nadelhoffer et al. 1983; Binkley & Hart 1989; Powers 1990). In the present study, differences between temperature and moisture regimes of the forest floor and underlying surface mineral soil are unlikely to have been great enough to account for the rather large differences in mineralizable-N values found between these two soil layers. Hence, the average quality of organic matter in the forest floor apparently exceeds that of the mineral soil. A greater mineralizable-N value for the forest floor compared to the surface mineral soil is surprising given the higher C:N ratio of the forest floor layer (38 and 26, respectively; forest floor value calculated from Table 1 assuming organic matter contains 58% C, and mineral soil value taken from Hart and Firestone 1989). Unfortunately, few studies have assessed separately N mineralization rates in forest floors and mineral soil (Binkley & Hart 1989), so it is difficult to gauge whether this pattern occurs in other forests.

High leaching rates of water-soluble organic N from the forest floor have previously been reported in lodgepole pine (Fahey et al. 1985) and Douglas-fir forests (Sollins and McCorison 1981). In both of these studies, leaching of soluble organic-N from the forest floor greatly exceeded leaching losses of inorganic N. The estimated higher rate of organic-N compared to inorganic-N leaching in our study (17 and 9 kg-N ha^{-1} yr^{-1}, respectively) is also supported by the much larger pool sizes of K_2SO_4-extractable organic-N in the O2 forest floor layer relative to inorganic-N pools (ranging from 9—16 times larger, data not shown).

Conclusions

The forest floor appears to supply less than one-third of the total above-

ground plant N-demand in this old-growth forest. The mean residence time (MRT) of N in the forest floor was over 2.5 times longer than the MRT of organic matter, suggesting a strong capacity for retention of N within this soil horizon. Nevertheless, a greater proportion of the total organic-N pool is mineralized annually within the forest floor compared to the surface mineral soil. Small amounts of ^{15}N applied to the mineral soil was lost from the upper soil horizon sooner when the forest floor was removed than when it was present. Rapid exchange of N appeared to occur between microbial biomass-N and soluble-N pools of the mineral soil. Fungal transport of N from the mineral soil to the overlying forest floor was of a similar magnitude as several other internal N-flows, and could account for all of the net increse in litter-N observed during the early stages of decomposition in this forest. The forest floor appears to act both as a source and a sink for N in the mineral soil of this forest.

Unfortunately, we did not have any replication at the stand level in this study, so the results presented cannot be generalized to other old-growth forests. Furthermore, the forest floor removal experiment was only replicated within one relatively small plot, and therefore extrapolation of the results from this experiment to the stand level must be made with caution. Nevertheless, the results of this study do suggest that forest floor — mineral soil interactions may have a profound effect on N cycling within forest ecosystems.

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