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FLOW AND FATE OF SOIL NITROGEN IN AN ANNUAL GRASSLAND AND A YOUNG MIXED-CONIFER FOREST

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Summary—A comparative study of N dynamics in an annual grassland and a young mixed-conifer forest, that occur on the same soil great group in California, was made by adding small amounts of $^{15}NH_4^+$ to mineral soils within field microplots and following changes in ^{15}N recoveries in soil and plant pools over 12–16 months. In annual grassland microplots, the aboveground plant biomass contained 5–6% of the added ^{15}N at the end of the growing season. One month after ^{15}N addition almost 70% of the added ^{15}N was recovered in the soil organic matter (SOM) pool, which included surface litter and roots but not microbial biomass. Laboratory incubation of sterilized soil cores indicated that as much as half of the ^{15}N recovered in the SOM pool may have been fixed abiotically. Nevertheless, substantial and rapid incorporation of ^{15}N in the SOM pool indicates a high potential for N immobilization and a rapid turnover of the microbial biomass-N pool in this soil. Recovery of ^{15}N in microbial biomass ranged from 9 to 15%; recovery in the soil solution was lower than in the microbial biomass, but showed a similar seasonal trend. Total ^{15}N recovery ranged from 72 to 85% over the study period. In forest microplots (which excluded plants), recovery of added ^{15}N was generally lower than in the grassland for all soil pools examined. Recovery of ^{15}N in SOM and microbial pools showed reciprocal trends seasonally, suggesting that there was considerable movement of N between these pools in the forest soil. Total ^{15}N recovery was only about 54% 6 months after ^{15}N addition, indicating a high potential for rapid N loss from the surface soil of this forest. Substantially lower recovery of ^{15}N in the forest soil cannot be attributed entirely to the exclusion of plant uptake because plant ^{15}N recovery in the grassland was relatively low. The low ^{15}N recovery in the forest soil might be due to the low capacity of this soil to immobilize N and protect immobilized N from being remineralized and lost from the soil via leaching or denitrification. In both ecosystems estimates of N flow from the mineral soil to decomposing surface residues (presumably via fungal translocation) was significant (0.29 and 0.02 g-N m^{-2} yr^{-1} for the grassland and forest, respectively) relative to the net internal dynamics of N within the surface detritus. Comparison of net changes in litter N and accumulation of ^{15}N during decomposition suggests that N was mineralized from litter concurrently as N was immobilized from the mineral soil in both sites.

INTRODUCTION

Between-site comparisons within the same experimental study using similar methodology can be useful in elucidating the significance of individual processes in maintaining the structure and function of ecosystems, and aid in the development of unifying concepts. We report the results of a field study that examined the flow and fate of nitrogen (N) in an ungrazed annual grassland and a young mixed-conifer plantation in California. These two ecosystems have substantially different N cycling and litter decomposition rates despite their occurrence on soils from the same soil great group.

Net annual fluxes of nutrients in annual grassland soils of California are large because the vegetation turns over every year, the soil microbial biomass is large, the grass litter is of a relatively high quality (i.e. low lignin:N ratio), and most of the litter from the previous year decomposes during a single growing season (Woodmansee and Duncan, 1980; Jackson *et al.*, 1988, 1989). Net annual fluxes of N in young mixed-conifer forests of California are comparatively small because only a small proportion of the plant biomass turns over each year, the soil microbial biomass is relatively small, conifer litter is of a low quality, and litter decomposition is extremely slow (Hart *et al.*, 1992).

We investigated N cycling processes in both of these ecosystems by applying small amounts of $^{15}NH_4^+$ to mineral soils and following the flow and fate of added N within soil and plant pools over time. In particular we wanted to estimate the gross N flux from the mineral soil to decomposing surface litter in these ecosystems. Recent work by Hart and Firestone (1991) indicated that this seldom measured N flux, apparently the result of fungal translocation, was significant relative to other N flows in an old-growth mixed-conifer forest in California.

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MATERIALS AND METHODS

Study sites

The annual grassland study site is located on the Sierra Foothill Range Field Station of the University of California, near Marysville, Calif. (39°15′N, 121°17′W), at an elevation of 200 m. The ecosystem is classified as a blue oak annual grassland savanna, composed primarily of a *Quercus douglasii* overstory (70% cover), and an annual grassland understory. Our field plots were located in the open grassland, within a fenced plot (5000 m^2) which had been grazed only once since 1983. The most abundant species in the open grassland areas in 1985 were *Bromus mollis*, *Hordeum hystrix*, *Avena barbata*, *B. madritensis*, and *Lolium multiflorum* (Jackson *et al.*, 1988). The climate is Mediterranean, with rainfall concentrated from November to February, and averaging about 60 cm annually. Air temperatures during the summer months range from a daily maximum above 30°C to a daily minimum near 20°C. Surface soil maximum daily temperatures often exceed 40°C during this period. During the winter, daily air temperatures range from 15 to 0°C. The soil (Argonaut soil series of the subgroup Mollic Haploxeralfs) was formed on highly-weathered basic igneous parent material, and the surface soil has a silt–loam texture. The total carbon (C) and N content in the upper 10 cm of mineral soil are 2740 and 230 g m^{-2}, respectively (Jackson *et al.*, 1988). A surface organic layer overlying the mineral soil persists throughout the year, ranging in depth from < 1 to 2 cm, and having a mass of about 170 g oven dry weight m^{-2} at the end of the growing season in May (Jackson *et al.*, 1988). Most of the plant roots (about 85%) and microbial biomass (about 75%) occur in the upper 10 cm of the mineral soil (Jackson *et al.*, 1988). Detailed discussions of seasonal changes in climate, plant productivity, and plant and soil N pools are described in Jackson *et al.* (1988).

The forest site is located within the Blodgett Forest Research Station of the University of California, near Georgetown, Calif. (38°52′N, 120°40′W), at an elevation of about 1300 m in the Sierra Nevada Mountains. The forest is a young (about 10 yr old at the initiation of the study) mixed-conifer plantation comprised of: white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). The current forest was established after clearcutting the previous one in 1975. Prior to planting of the young forest, logging slash was raked into piles and burned. As a result of this cultural activity, the forest floor had been partially removed and partially incorporated into the mineral soil. The climate is Mediterranean; annual precipitation averages 170 cm, 85% of which falls primarily as snow between October and March. However, snow rarely persists for extended periods. 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. Maximum daily surface soil temperatures in the summer frequently exceed 40°C, and surface soils can be frozen during the winter for short periods. The soil (Holland soil series of the subgroup Ultic Haploxeralfs) was formed on granodiorite parent material, and the surface soil has a sandy–loam texture. The total C and N contents in the upper 10 cm of mineral soil are 5510 and 220 g kg^{-1}, respectively. A description of some of the other surface soil characteristics can be found in Hart and Firestone (1989).

Field labeling and harvesting procedures

Grassland. Microplots consisted of aluminum cylinders (10 cm dia, 12 cm long) that had been driven to a depth of 10 cm into the mineral soil. Four cylinders were driven into the soil within each of three 1 × 1 m plots (total of 12 cylinders) that had been clipped to remove most of the live aboveground plant biomass in early April 1986. In early May 1986, a solution containing 8.1 mg of N as ^{15}N-enriched $(NH_4)_2SO_4$ (6.2 mg of ^{15}N) was injected into each cylinder at a 2 cm mineral soil depth, giving a N addition rate of about 1 g m^{-2}. A total of 19 injections were made into each cylinder (95 ml total solution volume) using 1.27 mm o.d. (18-gauge Babcock) spinal needles (Popper and Sons Inc., New Hyde Park, N.Y.). A template was used to uniformly distribute the ^{15}N label laterally within the cylinder (Schimel and Firestone, 1989). Injection needles were rinsed with deionized water between each injection to minimize contamination of the organic surface layer with ^{15}N.

About 1 month later (early June), subsamples of recent senescent, unlabeled grass-shoot litter (0.87 g ash-free, oven dry wt; atom % ^{15}N enrichment = 0.39%), obtained from a composite sample adjacent to the study area, were enclosed in 1 mm mesh nylon bags (7.9 × 7.9 cm) and attached to the soil surface within the cylinders using steel pins. These litterbags were used for assessing both the flow of N from the mineral soil to surface organic materials (Hart and Firestone, 1991), and the net rate of N release during decomposition of grass litter. The rate of grass addition was 110 g m^{-2}. Three cylinders were removed at this time to determine the initial ^{15}N distribution within the soil cylinder at the time of addition of the grass litterbags.

In late September, and mid-January and May the following year (1987), three cylinders were selected at random (one from each plot), returned to the laboratory, and frozen (−18°C) until analyzed. Immediately after thawing, the litterbags were removed and the soil cylinders were separated into the following components: live above ground grass (if present), surface detritus, and 0–4 and 4–10 cm mineral soil layers. The mineral soil was sieved (4 mm) and roots retained on the screen were remixed with the sieved

soil. The ash-free mass of the grass litter remaining was determined by placing subsamples in a muffle furnace at 550°C for 6 h. The total amount of N and ^{15}N recovered was determined in the litterbag, surface detritus, and soil layers. The total amount of N and ^{15}N contained in the extractable soil solution and microbial biomass were also determined.

Forest. In May 1986 four cylinders (10 × 12 cm) were driven into each of three plots (1 × 1 m) located in bare soil areas between trees. A ^{15}N-enriched $(NH_4)_2SO_4$ solution was then added to each microplot cylinder using the same addition rate and procedure described above for the grassland. About 5 months after the addition of ^{15}N (early November), unlabeled subsamples of freshly fallen ponderosa pine needle-litter (0.95 g ash-free, oven dry mass; atom % ^{15}N enrichment = 0.39%), obtained from a composite sample adjacent to the forest study area, were placed directly on the mineral soil surface within the cylinders. This gave a rate of pine needle addition of 120 g m^{-2}. A 1 mm mesh nylon screen cover was secured on top of the cylinders to keep the litter within the cylinder. As in the grassland microplots, this added litter was used to assess both the flow of N from the mineral soil to surface organic materials (in this case needle litter), and the net rate of N release from needle litter during decomposition. Three cylinders were removed at this time to determine the initial ^{15}N distribution within the soil at the time of addition of the needle litter. In mid-January, May, and the end of September the following year (1987), three cylinders were selected at random (one from each plot), returned to the laboratory, and frozen (−18°C) until analyzed. Immediately after thawing, the needle litter was removed by hand-picking, and the soil within the cylinders was separated into 0–4 and 4–10 cm layers and sieved (4 mm). Chemical analyses were the same as those conducted in the grassland cylinders (see below).

Labeled NH_4^+ was added instead of labeled NO_3^- because NH_4^+ is more rapidly assimilated by microorganisms in both of these ecosystems (Davidson *et al.*, 1992). Surface soils were initially labeled with ^{15}N 1–5 months prior to the period when most of the annual aboveground detrital input occurs (in early summer in the annual grassland and in the fall in the forest) in order for the microbial biomass to be sufficiently enriched with ^{15}N to be able to measure ^{15}N flow upward to the decomposing surface litter. Microbial assimilation of NH_4^+ is more rapid in the grassland than in the forest (Jackson *et al.*, 1989; Davidson *et al.*, 1992), so more time was allowed between the labeling of the mineral soil and the placement of the unlabeled litterbags on the soil surface in the forest site.

Abiotic NH_4^+-fixation and N-flow

Because the grassland soil was known to contain significant amounts of vermiculite (an NH_4^+-fixing clay mineral; Bartlett and Doner, 1988), a laboratory experiment was conducted to determine the capacity for abiotic fixation of $^{15}NH_4^+$ in the grassland soil. This experiment was also used to determine the potential for abiotic transport of N from the mineral soil to surface residues.

Three intact soil cores (0–10 cm) contained in aluminum cylinders (5 × 12 cm) were removed from the grassland and returned to the laboratory. The cores were placed in a desiccator and fumigated with propylene oxide for 10 days. The cores were then removed from the desiccator and ^{15}N-enriched $(NH_4)_2SO_4$ solution was added at a 2 cm depth using the same method and rate of N addition as used in the field experiment. After the addition of the label the soil water content was about 0.32% kg H_2O kg^{-1} soil (or about −33 kPa water potential). Litterbags (1 mm mesh, 3.8 × 3.8 cm) containing 0.25 g air dry wt of grass litter were placed on the soil surface (same rate of grass addition as in the field experiment), and cotton plugs were then placed over the top and bottom openings of the cylinders. The soil cores were then refumigated for 24 h, and then each was placed in a sealed 0.95 litre Mason jar fitted with a rubber septum. The cores were then kept in the dark at 22 ± 1°C for 208 days. Carbon dioxide concentrations were determined frequently in the headspace of the chambers during the incubation period by gas chromatography (Varian Aerograph 920) using a thermal conductivity detector. No significant increase in headspace CO_2 concentrations occurred throughout the incubation, suggesting that the sterilization treatment was successful and that sterility was maintained. At the end of the incubation, litterbags were removed from the soil cores, and the oven dry mass, total-N and ^{15}N content of the soil and grass litter contained within the litterbags were determined.

Biological and chemical analyses

Microbial biomass. Chloroform-labile N and ^{15}N (i.e. the additional N and ^{15}N extracted from the soil following chloroform fumigation) were determined by the direct-extraction method, using a 1 day fumigation period (Brookes *et al.*, 1985; Davidson *et al.*, 1989). Chloroform-labile N and ^{15}N were converted to microbial-N and ^{15}N by dividing the chloroform-labile values by 0.42 for the grassland soil and 0.25 for the forest soil. These conversion (k_N) values are seasonal mean values determined for each soil (Davidson *et al.*, 1989).

Total N. All total-N analyses of plant, detritus, soil, and soil extracts were conducted using a salicylic acid-thiosulfate modification of a micro-Kjeldahl method that includes NO_2^- and NO_3^- (Bremner and Mulvaney, 1982). The digests were then analyzed for NH_4^+.

Extractable NH_4^+ and NO_3^-. Soil NH_4^+ and NO_3^- were determined by extracting 20 g, field-moist subsamples with 75 ml of 0.5 M K_2SO_4. Soil suspensions (including those of chloroform-fumigated soil used to determine microbial N) were shaken for 1 h, filtered

Table 1. Fate of low additions of $(^{15}NH_4)_2SO_4$ applied to the mineral soil (2 cm depth) in an annual grassland[1]

Sampling date	Months after addition	% of added ^{15}N recovered in					
		Surface litterbag	Plant shoots	SOM[2]	Microbial biomass	K_2SO_4-extractable[3]	Total
4 June 1986	1.0	—[4]	—[5]	69.0 (7.7)	8.7 (0.8)	6.8 (0.8)	84.5 (7.4)
27 September 1986	4.8	0.04 (0.005)	—[5]	55.6 (1.7)	15.4 (3.2)	9.0 (0.6)	80.0 (0.8)
15 January 1987	8.4	0.21 (0.04)	6.4 (0.1)	54.1 (1.6)	13.3 (0.4)	6.1 (0.6)	80.1 (1.1)
20 May 1987	12.5	0.19 (0.02)	5.4 (0.4)	54.1 (4.9)	11.0 (1.5)	1.6 (0.2)	72.3 (3.0)

[1]Mean (and standard error); $n = 3$; soil was sampled to a depth of 10 cm.
[2]Soil organic matter; includes ^{15}N recovered in live and dead roots; excludes ^{15}N recovered in microbial biomass.
[3]Inorganic ^{15}N + organic ^{15}N.
[4]No litterbags were present during this sampling date.
[5]No live plants were present during this sampling date.

(Whatman No. 1), and analyzed for NH_4^+ and NO_3^- using a Lachat flow-injection analyzer. The filter paper was leached with approx. 50 ml of the extracting solution before the extracts were filtered to remove any NH_4^+ and NO_3^- present initially in the filter paper.

Nitrate was reduced to nitrite using zinc or cadmium and then determined by diazotiation (QuikChem Systems, 1987), and ammonium was determined by the indophenol-blue method (QuikChem Systems, 1986).

^{15}N analyses. Soil extracts and Kjeldahl digests of plants, litter, soils, 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, N.M., U.S.A.

Results reported for plants and plant litter are based on an oven dry (65°C), ash-free basis. All soil results are reported on an oven dry (105°C) basis.

RESULTS

Grassland

Table 1 shows the amount of ^{15}N recovered in the various soil–plant components over 1 yr. Plant shoots, representing mature plants near senescence, recovered 5–6% of the labeled N. The soil organic matter (SOM) pool, which as reported here included surface litter and plant roots but not microbial biomass, was by far the largest sink for ^{15}N, accounting for 69% of the added label in June, 1 month after addition of $^{15}NH_4^+$. Recovery of ^{15}N in the SOM pool declined to about 56% in September, and remained fairly constant thereafter. The microbial biomass was the next largest sink for ^{15}N, increasing from about 9% in June to a maximum of 15% in September following the first significant precipitation since spring. This increase in ^{15}N recovery in the microbial biomass coincided with a general increase in the microbial biomass-N pool (Table 2). Recovery of ^{15}N in the microbial biomass declined slightly throughout the rest of the growing season while microbial N continued to increase, reaching a maximum of 11.6 g m^{-2} in January (Table 2). Microbial N then declined along with soil moisture as the summer dry-season approached. Recovery of ^{15}N in the extractable soil solution (inorganic N + organic N) was lower than that in the microbial biomass, but followed a similar seasonal trend (Table 1). The relative amounts of the various N forms (NH_4^+, NO_3^-, organic) that comprise the soil solution total-N

Table 2. Surface soil (0–10 cm) characteristics on field sampling dates in the grassland site[1]

Sampling date	Soil moisture	Microbial N	KCl-extractable			
			NH_4^+-N	NO_3^--N	Organic-N	Total
	(kg kg $^{-1}$)			(g m $^{-2}$)		
4 June 1986	0.056 (0.010)	1.71 (0.12)	0.87 (0.26)	1.76 (0.38)	0.08 (0.08)	2.71 (0.73)
27 September 1986	0.271 (0.020)	7.82 (0.66)	0.70 (0.02)	4.31 (0.67)	0.00 (0.00)	5.02 (0.65)
15 January 1987	0.297 (0.012)	11.61 (0.79)	2.31 (0.20)	0.86 (0.11)	0.43 (0.05)	3.59 (0.32)
20 May 1987	0.109 (0.005)	6.37 (0.50	0.58 (0.05)	0.56 (0.10)	0.33 (0.07)	1.47 (0.09)

[1]Mean (and standard error); $n = 3$.

pool were different over the year; the organic-N component of the soil solution was generally small (Table 2). Total ^{15}N recovery in the soil–plant system decreased during the year from about 85% to 72% (Table 1).

The decomposition rate of native aboveground grass litter, as measured using the litterbag technique and the regression analysis of Schlesinger and Hasey (1981), was about 0.54 yr^{-1}. Total N in the litter decreased during the fall and winter periods from 6.5 to 4.3 g N kg^{-1} initial litter mass, and then increased to 5.8 g N kg^{-1} initial litter mass by the end of spring [Fig. 1(a)]. The amount of ^{15}N excess (^{15}N enrichment above background) recovered in the grass contained within the litterbags was fairly small, reaching a maximum of only 0.2% of the initial ^{15}N applied to the mineral soil [Table 1 and Fig. 1(b)]. However, this flux represents a larger flux of $^{14}N + {}^{15}N$ from the mineral soil to the surface litter during this same period. The total N-flux was calculated in a manner similar to that described in Hart and Firestone (1991):

> Total N-flux = change in ^{15}N excess of grass litter in litterbag/{(mean atom % ^{15}N enrichment/100) of the microbial biomass-N pool in the 0–4 cm layer over that period}.

This calculation assumes that the mechanism of transport of ^{15}N from the mineral soil to the surface litter was fungal translocation, and that the atom % ^{15}N enrichment of the fungal N pool actively transporting N can be characterized using the atom % ^{15}N enrichment of the chloroform-labile N pool in the 0–4 cm soil layer.

The atom % ^{15}N enrichment of the microbial biomass (chloroform-labile pool) in the 0–4 cm mineral soil decreased exponentially over the 1 yr period from 5.39% in June to 1.47% by the following May [Fig. 1(c)]. The resulting calculated temporal pattern of cumulative N-flux from the mineral soil to the overlying surface residues is shown in Fig. 1(d). The estimated total N-flux from the mineral soil to the litterbag grass followed a similar pattern as the

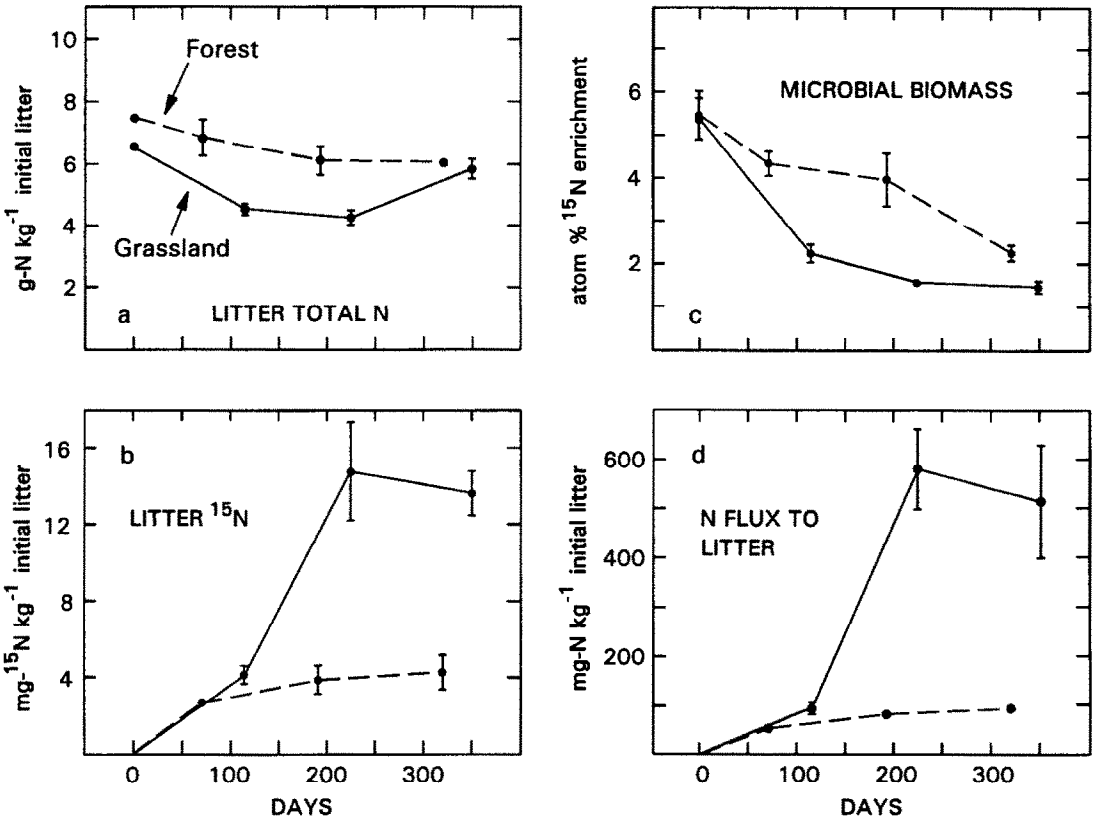

Fig. 1. Changes in total litter-N mass (a), litter ^{15}N excess (b), atom % enrichment of the microbial biomass in the upper 4 cm of mineral soil (c), and calculated cumulative N-flux from the mineral soil to the overlying litter (d) during decomposition of grass shoots in an annual grassland and ponderosa pine needles in a young mixed-conifer forest. In the grassland, the surface mineral soil was initially enriched in ^{15}N by adding $^{15}NH_4$ 1 month prior to the placement (in early May 1986) of unenriched grass shoots contained in litterbags on the soil surface. In the forest, the surface mineral soil was initially enriched in ^{15}N by adding $^{15}NH_4^+$ *c* 5 months prior to the placement (in early November 1986) of unenriched ponderosa pine needles directly on the soil surface. Vertical bars denote ±SE.

Table 3. Fate of low additions of $(^{15}NH_4)_2SO_4$ applied to the mineral soil (2 cm depth) in a young conifer forest[1]

Sampling date	Months after addition	% of added ^{15}N recovered in				
		Surface litterbag	SOM[2]	Microbial biomass	K_2SO_4 extractable[3]	Total
9 November 1986	5.4	—[4]	26.4 (8.1)	22.1 (4.7)	5.6 (0.2)	54.2 (3.9)
19 January 1987	7.8	<0.1	37.0 (1.8)	8.7 (2.6)	3.8 (1.3)	49.6 (6.4)
21 May 1987	11.8	0.1 (0.0)	26.7 (3.9)	15.4 (0.2)	2.1 (0.4)	44.3 (4.1)
26 September 1987	16.1	0.1 (0.0)	40.2 (6.5)	3.9 (0.1)	2.6 (0.3)	46.9 (5.8)

[1]Mean (and standard error); $n = 3$; soil was sampled to a depth of 10 cm; plant uptake of N was prevented.
[2]Soil organic matter; excluded ^{15}N recovered in microbial biomass.
[3]Inorganic ^{15}N + organic ^{15}N.
[4]No litterbags were present during this sampling date.

change in atom % excess in the grass, with the greatest rate of N flux occurring between January and March. Little apparent N flux from the mineral soil to the overlying litterbag grass occurred between March and May. Net changes in the total mass of N in grass litter [Fig. 1(a)] did not coincide with changes in the N flux from the mineral soil [Fig. 1(d)]. Our estimate of the maximum gross flux of N from the mineral soil to the grass litter was about 38% of the maximum observed net increase in total N in the grass litter.

Forest

Table 3 shows the amount of ^{15}N recovered in the various soil pools in the forest site. As in the grassland, the SOM pool was the largest sink for the label, ranging from 26 to 40%. However, unlike the grassland, recovery of ^{15}N in SOM was fairly dynamic, increasing between November and January, decreasing between January and May, and again increasing between May and September (Table 3). Recovery of ^{15}N in the microbial biomass over time showed the inverse of this seasonal pattern, and ranged from 4 to 22% of the added ^{15}N (Table 3). Unlike the grassland soil, the total amount of N in solution was fairly similar at all sampling dates (Table 4). However, ^{15}N recovery in the soil solution decreased over time from 5.6% of the initial amount added to this pool after 5.4 months, to 2.6% after 16 months (Table 3). Organic N comprised a larger proportion of the total N in soil solution in the forest compared to the grassland, generally being of a similar size as the NH_4^+ and NO_3^- fractions (Table 4). Total ^{15}N recovery in the soil was much lower than in the grassland, ranging from 44 to 54% over the 16 month study period (Table 3).

The calculated decomposition rate of ponderosa pine needles contained in litterbags and placed on the soil surface within the $^{15}NH_4^+$-labeled microplots was about 0.12 yr^{-1}. Total litter-N decreased over the 1 yr period from 7.5 to 6.0 g N kg^{-1} initial litter mass [Fig. 1(a)]. Over this same period, the ^{15}N excess in the litter increased to 4.2 mg ^{15}N kg^{-1} initial litter mass [Fig. 1(b)]. This amount of ^{15}N is only about 0.1% of the amount initially added to the mineral soil (Table 3). At the time of litterbag addition to the surface, the microbial biomass in the surface soil (0–4 cm) had a ^{15}N atom % enrichment of 5.4%, which 1 yr later decreased to about 2.3% [Fig. 1(c)]. The calculated annual cumulative total N-flux from the mineral soil to the decomposing needle litter on the soil surface was estimated to be about 0.95 g N kg^{-1} initial litter mass [Fig. 1(d)]. This N flux is

Table 4. Surface soil (0–10 cm) characteristics on field sampling dates in the forest site[1]

Sampling date	Soil moisture	Microbial N	KCl-extractable			
			NH_4^+-N	NO_3^--N	Organic-N	Total
	(kg kg^{-1})		(g m^{-2})			
9 November 1986	0.115 (0.004)	4.84 (0.47)	0.25 (0.06)	1.19 (0.18)	0.36 (0.09)	1.80 (0.11)
19 January 1987	0.263 (0.014)	3.33 (0.30)	0.56 (0.04)	0.43 (0.19)	0.89 (0.20)	1.88 (0.08)
21 May 1987	0.210 (0.004)	8.99 (0.20)	0.47 (0.05)	0.77 (0.17)	0.30 (0.16)	1.54 (0.19)
26 September 1987	0.038 (0.002)	3.26 (0.72)	0.47 (0.09)	0.81 (0.23)	0.59 (0.27)	1.86 (0.35)

[1]Mean (and standard error); $n = 3$.

about two-thirds of the net flux of N that was released from the needle litter over this same period [Fig. 1(a)].

DISCUSSION

Grassland

In the annual grassland recovery of ^{15}N in plants when added as $^{15}NH_4^+$ was low relative to similar studies in perennial grassland ecosystems (Tables 1 and 5), even when accounting for the fact that only ^{15}N recovered in aboveground plant biomass was measured (which is also the case for some of the other grassland studies shown in Table 5). This difference may be due to the greater capacity for immobilization of added N within the microbial biomass (chloroform-labile) or their metabolites (SOM) in annual grasslands relative to perennial grasslands. Higher rates of microbial immobilization of N may be driven by higher C availability in annual relative to perennial grasslands (Woodmansee and Duncan, 1980; Jackson *et al.*, 1988, 1990). High C availability in this annual grassland soil was indicated from laboratory incubations of intact soil cores which respired 30% of their total soil C as CO_2 over 200 days, and still had high and stable respiration rates at the end of this incubation period (S. C. Hart, unpubl. Ph.D. thesis, University of California, Berkeley, 1990). Low recovery of added $^{15}NH_4^+$ in plants relative to other studies also might be due to the fact that the label was added to the soil at the onset of the summer dry season, when plants were not actively growing. However, in this grassland plants recovered only 8–11% of the added ^{15}N in 1 day, $^{15}NH_4^+$-uptake studies during the spring, when grasses were growing rapidly (Jackson *et al.*, 1989); these plant-recovery values are still generally lower than those from ^{15}N-addition studies in perennial grasslands (Table 5).

There was a phenomenal amount of ^{15}N recovered in the SOM pool 1 month after $^{15}NH_4^+$ addition to the grassland soil, with a comparatively low recovery of ^{15}N in the microbial biomass (Table 1). All of the ^{15}N recovered in the SOM pool either had to pass through the microbial biomass (i.e. $^{15}NH_4^+$ assimilated by microorganisms and then transferred to the SOM pool via metabolites or microbial death), or been chemically fixed in a non-extractable (unavailable) form by SOM or NH_4^+-fixing clay minerals. Davidson *et al.* (1991) found over 30% of added $^{15}NH_4^+$ was non-extractable with concentrated salt solution 15 min after addition to autoclaved, intact soil cores from this same grassland. We found a mean of 33% (SE = 5%) of the added $^{15}NH_4^+$ was non-extractable with K_2SO_4 from soil cores sterilized with propylene oxide after 208 days of laboratory incubation. These results suggest that as much as half of the ^{15}N recovered in the SOM pool in the present

Table 5. Summary of recent studies on the fate of ^{15}N applied to grasslands

Vegetation (location)	N applied (g m^{-2})	Source	Duration (months)	% of added ^{15}N recovered in: Plants	SOM[1]	Microbial biomass	Extractable solution	Total soil	Total
Shortgrass praire	2.6	KNO_3	1	52	—	—	—	28	80
(Colorado, U.S.A.)[2]			49	44	—	—	—	36	80
L. perenne–T. repens	36	Urea	0.7	25	8	—	56	64	89
pasture	39	$(NH_4)_2SO_4$	0.7	15	6	—	40	46	61
(New Zealand)[3]	29	KNO_3	0.7	8	4	—	61	65	73
Tussock tundra	0.1	Urea	1.9	26	74	—	< 1	74	100
(Alaska, U.S.A.)[4]	5.1	Urea	1.9	15	85	—	< 1	85	100
Dairy pasture, mainly *L. perenne* (New Zealand)[5]	5.0	Urea	4–6	31–63	26–30	6–7	< 1	30–35	63–99
Grass–legume	14	Urea	1.9	24	10	6	< 1	15	39
association			5.8	25	19	11	< 1	29	54
(Italy)[6]			18	28	14	11	< 1	25	53
			27	29	6	12	< 1	18	47

[1]Soil organic matter.

[2]Data from Clark (1977). Label was applied in solution at a 2 cm soil depth. Plant recovery includes senescent and detrital roots. Recovery in solution was noted as being very low except after 1 month, but values were not reported. SOM values include microbial N. Total recovery was estimated from the author's data. Soil was sampled to a 36 cm depth.

[3]Data from Keeney and MacGregor (1978). Label was applied in solution to the soil surface. SOM values include microbial N. Soil was sampled to a 30 cm depth.

[4]Data from Marion *et al.* (1982). Label was applied in solution to the surface and washed into the soil with water. Plant recovery includes vascular and non-vascular plants. SOM values include microbial N and were determined by difference assuming 100% total recovery. Soil was sampled to the permafrost table (50–60 cm depth).

[5]Data from Ledgard *et al.* (1988). Label was applied to the surface in solid form. Range in recovery values reflects effects of different times of label application (May, June, or August) and duration of the experiment. Plant recovery includes cumulative harvests of aboveground biomass only. Recovery in microbial N was determined by direct extraction using a $k_N = 0.54$ (Brookes *et al.*, 1985). Soil was sampled to a 25 cm depth.

[6]Data from Nannipieri *et al.* (1985). Label was applied to the soil surface as a powder. Plant recovery includes cumulative harvests of aboveground biomass only. Recovery in microbial N was calculated using a modification of the chloroform fumigation–incubation method (Jenkinson and Powlson, 1976), with a $k_N = 0.625$. Total recovery values do not include ^{15}N in plant roots, which were not measured. Recovery of ^{15}N in soil pools was estimated assuming a soil bulk density of 1.1 Mg m^{-3}. Soil values reported here are for the 0–20 cm depth.

study may have been fixed rapidly by abiotic processes, and remained unavailable for the duration of the field study. We conclude that abiotic fixation accounts, in part, for the high retention of ^{15}N within the soil, the relatively low recovery of ^{15}N in plants, and the large amount of ^{15}N recovered in the SOM pool relative to the microbial biomass (Table 1).

Multiplying Jackson *et al.*'s (1988, 1990) estimate of the surface detrital mass (previous year's plant growth) by our calculated specific (per g of initial litter), N-flux to litter [Fig. 1(d)] results in a calculated N flux from the mineral soil to these overlying surface residues of about 0.29 g m^{-2} yr^{-1}. This flux is likely an underestimate of the actual (gross) flux because some of the ^{15}N was probably transported to the surface layer and then returned to the mineral soil over the 1 yr period. The magnitude of this flux is comparable to estimates of N outputs from deep leaching at this site (0.3 g m^{-2} yr^{-1}; M. Singer, University of California, Davis, unpubl. data, 1986), and N inputs from wet and dry deposition (0.1 g m^{-2} yr^{-1}) and from N fixation (0.1–1.0 g m^{-2} yr^{-1}) at a similar grassland site in California (Center *et al.*, 1989).

After 208 days of incubation in the laboratory, grass litter placed on the surface of sterilized soil cores showed no significant change in mass or total N (1-tailed t-test, $P > 0.10$). Furthermore, only 0.23% (SE = 0.02%) of the amount of ^{15}N added to the mineral soil was recovered in the surface grass residue. The primary processes involved in the abiotic upward transport of N are capillary flow and NH_3 volatilization-sorption. This laboratory estimate of abiotic upward transport of N within the soil does not include *in situ* environmental fluctuations which might be important controls on these processes, and thus may not be an accurate estimate of the abiotic contribution to total-N transport under field conditions. However, these results do suggest that the mechanism of N transport is largely biological, and is likely the result of translocation of N by fungal hypae (Hart and Firestone, 1991).

The N flux from the mineral soil to surface residues appeared to cease while there was a net accumulation of N in surface grass litter between January and May [Figs 1(a) and (d)]. It is possible that the mineral soil was still supplying N to the grass litter during this period, but the applied ^{15}N was no longer in a microbial pool which was actively transporting N.

Forest

Because of the relatively large biomass and low density of trees, ^{15}N-studies in forests have been conducted in tree-less plots, or in small plots containing a single seedling or tree (Table 6). Total ^{15}N recovery in plant-less forest microplots of the present study was very low, but was comparable to recovery of ^{15}N in two nearby, mature mixed-conifer forests (Table 6). In experimental systems which include trees and other associated vegetation, total ^{15}N recovery is generally higher, but recovery in vegetation is quite variable (ranging from 3 to 49%; see Table 6 and carlier review by Knowles, 1975). Differences in sampling depths, rates of application, N source, location of application within the soil profile, and the experiment duration among these studies makes it difficult to assess the effect of plants on the fate of ^{15}N in these soils. Nevertheless, it is probable that the exclusion of plants from our soil microplots, at least to some extent, altered the flow and fate of the applied ^{15}N.

The reciprocal relationship in recovery of ^{15}N in microbial and SOM pools over time suggests that significant amounts of N are being transferred between these two soil fractions (Table 3). The probable mechanism for this N flow is via microbial death (which transfers N to the SOM pool), followed by microbial growth and assimilation of N made available from the remineralization of dead microbial biomass (Smith *et al.*, 1986). An increase in ^{15}N recovery in the microbial biomass coupled with a decrease in ^{15}N recovery in SOM between June and September suggests a similar N exchange may be occurring in the grassland soil (Table 1). However, little change in ^{15}N recovery within microbial and SOM pools occurred after September, indicating a smaller magnitude of N flow between these two pools. Minor changes in ^{15}N recovery in microbial and SOM pools after September may be due to the finer texture of the grassland soil protecting ^{15}N contained within microbial biomass and metabolites from remineralization (van Veen *et al.*, 1987).

As was found in the grassland, the flow of N from the mineral soil to surface litter during decomposition appears to be a significant pathway of N flow relative to the internal N-dynamics of the residues themselves. Extrapolating our specific N-flux to litter data [Fig. 1(d)] to an areal basis in a similar manner as we did for the annual grassland using an estimate of litter mass at the forest site (200 g m^{-2}, S.C. Hart, unpubl. Ph.D. thesis, University of California, Berkeley, 1990), we estimate that the flow of N from the mineral soil to decomposing surface residues is < 0.02 g N m^{-2} yr^{-1} in this forest. This flux is much lower than estimated by Hart and Firestone (1991) for a nearby old-growth mixed-conifer forest, using similar methods. They found that N flow from the mineral soil to the litter layer (01) could account for all of the N immobilized in this layer during the first year of decomposition (about 0.4 g N m^{-2} yr^{-1}). However, the difference between these N-flux rates appears to be due simply to the much greater mass of the litter layer in the old forest (about 4000 g m^{-2}; Hart and Firestone, 1991).

We did not test the potential for abiotic transport of N from the mineral soil to decomposing surface litter in the forest as we did in the grassland. However, the primary mechanisms of abiotic flow of N upward within the soil profile (capillary flow and NH_3 volatilization-sorption) are likely to be less

Table 6. Summary of recent studies of the fate of ^{15}N applied to forests

Site treatment	^{15}N applied to	Amount added (g/m^2)	Source	Duration (months)	% of applied recovered in						
					Plants	Forest floor	SOM[1]	Microbial biomass	Extractable solution	Total soil	Total
Mixed-conifer[2]	A horizon	0.2	$(NH_4)_2SO_4$	1.3	—	1	15	17	15	34	34
Clearcut[3]	Surface	0.27	$(NH_4)_2SO_4$	5							
chopped					11	31	40	12	—	83	94
SPD					13	5	40	15	—	60	73
Mixed-conifer[4]	A horizon	1.0	$(NH_4)_2SO_4$	4	—	3	28	18	3	52	52
				16	—	1	22	12	<1	35	35
Slash pine[5]	Forest floor	5.6	$(NH_4)_2SO_4$	18	25	9	21	—	—	30	55
		22.4			27	6	12	—	—	18	45
Douglas-fir[6]	Forest floor	22.4	Urea	24	25–36	9–14	20–44	—	—	24–53	52–78
Scots pine[7]	Forest floor	10.0	$^{15}NH_4NO_3$	24	30	22	30	—	—	52	82
		10.0	$NH_4{}^{15}NO_3$	24	37	13	26	—	—	39	76

[1]Soil organic matter.

[2]Data from Schimel and Firestone (1989). Labeled-N was added to the surface mineral soil by injecting through the forest floor. The SOM fraction includes dead roots and detritus. Plant uptake was prevented. Soil was sampled to a depth of 5 cm.

[3]Data from Vitousek and Matson (1984). The two different treatments refer to contrasting methods of site preparation prior to replanting. Chopping leaves most of the structural organic residue on-site, while shearing, piling, and disking removes most of this material as well as most of the forest floor. The forest floor fraction in this table includes large (> 1 cm dia) organic residue (slash). The plants were 1–2 yr old. Soil solution recoveries of the label were not reported. Soil was sampled to a depth of 15 cm.

[4]Data from Hart and Firestone (1991). Experimental design was similar to Schimel and Firestone (1989) with ^{15}N being injected through the forest floor into the underlying mineral soil. Plant uptake was prevented. Soil was sampled to a depth of 10 cm.

[5]Data from Mead and Pritchett (1975). The stand was 11 yr old. SOM values include microbial biomass- and soil solution-N. Soil was sampled to a depth of 50 cm.

[6]Data from Heilman *et al.* (1982a, b). Ranges in values include two different sites and spring and fall applications. SOM values include microbial biomass- and soil solution-N. Soil was sampled to a depth of 38 cm.

[7]Data from Melin *et al.* (1983). SOM values include microbial biomass- and soil solution-N. No significant difference in total label recovery was found with ammonium or nitrate sources of N. Soil was sampled to a depth of 30 cm.

pronounced in the forest soil because of its coarser texture and lower pH than the grassland soil. Therefore, we presume that the majority of the upward flow of N observed in the forest soil is also due to fungal translocation.

Comparison of annual grassland and forest ecosystems

Total recovery of added $^{15}NH_4^+$ was much higher in the grassland than in the forest, and this difference cannot be attributed directly to the exclusion of plants from the forest microplots because plant uptake of ^{15}N in the grassland was low. Higher ^{15}N recovery in the grassland soil may have been, in part, the result of the abundance of NH_4^+-fixing clays which were virtually absent in the forest soil.

Higher initial rates of $^{15}NH_4^+$ immobilization into the microbial biomass in the grassland soil may have been an important mechanism for greater retention of added ^{15}N in grassland than forest microplots. Seasonal, 1 day ^{15}N-studies have shown for these same sites that the rate of microbial immobilization of NH_4^+ is from three to over ten times higher in the grassland soil (Jackson *et al.*, 1989; Davidson *et al.*, 1990, 1992). Higher rates of N immobilization by microbes may be the result of higher C availability to microorganisms in the grassland. Long-term laboratory incubations of soils from the grassland and forest sites show much higher respiration rates in the grassland (S. C. Hart, unpubl. Ph.D. thesis, *loc. cit.*), which suggests higher C availability in the grassland soil.

Protection of immobilized ^{15}N from remineralization would be expected to be higher in the grassland soil because of its higher clay content (van Veen *et al.*, 1985, 1987). Our ^{15}N data show that the microbial biomass-N pool turned over much more rapidly in the grassland soil than in the forest soil during the first 100 days after unlabeled litter was placed within the microplots. Faster microbial-N turnover rates are indicated by the faster rate of decline in ^{15}N atom % enrichment of the microbial biomass pool in the grassland than in the forest during this period [Fig. 1(c)]. However, after 100 days, the rate of microbial-N turnover declined substantially in the grassland soil, while remaining relatively unchanged in the forest soil; after 200 days the rate of microbial-N turnover in the forest soil was higher than in the grassland soil. A high degree of physical protection of microbial biomass in the grassland soil and the absence of physical protection in the forest soil would explain the lower turnover rates of microbial N in the grassland compared to the forest after 200 days. The lack of any significant physical protection of the microbial biomass in the forest soil also would be consistent with our results showing greater dynamics in the amount of ^{15}N recovered in the microbial biomass and SOM pools in the forest, as well as the generally greater amounts of K_2SO_4-extractable organic N found in the forest soil solution (Tables 1–4). The faster rates of microbial-N turnover in the grassland soil during the first 100 days in the presence of a greater concentration of clay suggests that physical protection of microbial N may only be significant after more recalcitrant microbial metabolites are produced, or after most of the easily degradable organic C substrates have been utilized. However, this conclusion is not supported by field experiments using ^{14}C, ^{15}N-labeled plant residues (Ladd *et al.*, 1981, 1985), and in laboratory studies using $^{15}NH_4^+$ (Ladd *et al.*, 1985) which show consistently lower microbial-N turnover rates in soil with finer textures.

The exclusion of plant roots from microplots in the forest site may have altered N-cycling patterns relative to the bulk soil, and thus make comparisons of the flow and fate of N with the grassland site (where plants were included) problematic. In a nearby, 5 yr old mixed-conifer plantation, only about a third of the total fine roots (and mycorrhizae) occur in the top 10 cm of mineral soil (Smith and Paul, 1988). Furthermore, in the present study we found no significant difference between inorganic-N pool sizes measured inside and outside the microplots during any of the sampling dates (data not shown). These results suggest that the exclusion of plant roots in the forest microplots may not have greatly altered N cycling in the surface soil.

Because decomposition of recent plant detritus is frequently N limited (Aber and Melillo, 1980), exogenous N-inputs to litter is paramount for decomposition processes to proceed; greater fluxes of N to decomposing litter from exogenous sources should result in accordingly faster rates of litter decomposition. Therefore, the greater rate of N flow from the mineral soil to decomposing surface litter in the grassland than the forest may in part account for the greater decomposition rates in the grassland.

In both the annual grassland and forest, N was mineralized from decomposing litter concurrently as N was immobilized from the mineral soil. A similar conclusion was found by Berg (1988) for Scots pine (*Pinus sylvestris*) needles by comparing the dilution of added ^{15}N-labeled needles by unlabeled soil-N relative to net total-N litter dynamics. Nitrogen transport from the mineral soil to decomposing surface residues was significant relative to the net changes in N within the decomposing litters themselves. Higher specific rates (per mass of initial litter) of N flow from the mineral soil to surface litter in the grassland soil may be due to the greater availability of N within the mineral soil, as well as the greater microbial biomass available for transporting N (Jackson *et al.*, 1989; Davidson *et al.*, 1990, 1992). Higher specific N-flow rates in the grassland might also be the result of placing the unlabeled litter on the soil surface over 4 months later after $^{15}NH_4^+$ addition in the forest than in the grassland. For instance, the longer period between soil labeling and litter placement in the forest site may have resulted in more of the added ^{15}N being incorporated in a pool that was

not actively involved in upward transport. However, the microbial biomass had virtually identical atom % ^{15}N enrichments in the forest and grassland surface soils at the time the unlabeled litter was added [Fig. 1(c)]. If the microbial biomass-N pool, as measured by chloroform fumigation–extraction, is the primary source pool for the N immobilized in decomposing surface litter, then the differences in the timing of litter addition relative to $^{15}NH_4^+$ addition cannot account for the large differences in N flow to the litter [Fig. 1(d)]. We suspect that this little-studied flow of N from the mineral soil to decomposing surface litter will be greatest in those ecosystems which have large accumulations of high C:N ratio litter on the soil surface, and high availabilities of N in the underlying mineral soil.

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