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The nitrogen cycle in lodgepole pine forests, southeastern Wyoming

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Abstract. Storage and flux of nitrogen were studied in several contrasting lodgepole pine (*Pinus contorta* spp. *latifolia*) forests in southeastern Wyoming. The mineral soil contained most of the N in these ecosystems (range of 315–860 $g \cdot m^{-2}$), with aboveground detritus (37.5–48.8 $g \cdot m^{-2}$) and living biomass (19.5–24.0 $g \cdot m^{-2}$) storing much smaller amounts. About 60–70% of the total N in vegetation was aboveground, and N concentrations in plant tissues were unusually low (foliage = 0.7% N), as were N input via wet precipitation (0.25 $g \cdot m^{-2} \cdot yr^{-1}$), and biological fixation of atmospheric N (< 0.03 $g \cdot m^{-2} \cdot yr^{-1}$, except locally in some stands at low elevations where symbiotic fixation by the leguminous herb *Lupinus argenteus* probably exceeded 0.1 $g \cdot m^{-2} \cdot yr^{-1}$).

Because of low concentrations in litterfall and limited opportunity for leaching, N accumulated in decaying leaves for 6–7 yr following leaf fall. This process represented an annual flux of about 0.5 $g \cdot m^{-2}$ to the 01 horizon. Only 20% of this flux was provided by throughfall, with the remaining 0.4 $g \cdot m^{-2} \cdot yr^{-1}$ apparently added from layers below. Low mineralization and small amounts of N uptake from the 02 are likely because of minimal rooting in the forest floor (as defined herein) and negligible mineral N (< 0.05 $mg \cdot L^{-1}$) in 02 leachate. A critical transport process was solubilization of organic N, mostly 'fulvic acids'. Most of the organic N from the forest floor was retained within the major tree rooting zone (0–40 cm), and mineralization of soil organic N provided NH_4 for tree uptake. Nitrate was at trace levels in soil solutions, and a long lag in nitrification was always observed under disturbed conditions. Total root nitrogen uptake was calculated to be 1.25 $gN \cdot m^{-2} \cdot yr^{-1}$ with estimated root turnover of 0.37-$gN \cdot m^{-2} \cdot yr^{-1}$, and the soil horizons appeared to be nearly in balance with respect to N. The high demand for mineralized N and the precipitation of fulvic acid in the mineral soil resulted in minimal deep leaching in most stands (< 0.02 $g \cdot m^{-2} \cdot yr^{-1}$). These forests provide an extreme example of nitrogen behavior in dry, infertile forests.

Introduction

Nitrogen inputs exceed outputs in many terrestrial ecosystems, leading to net accumulation (Clark and Rosswall, 1981), at least during the interval between large episodic losses resulting from catastrophic disturbances. However, inputs

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often are small compared to the magnitude of tree N requirements, and mineralization of above- and below-ground detritus usually provides most of the ionic N for plant uptake (Melillo, 1981). Although ecosystem input-output budgets provide information on N accumulation during the aggrading phase of stand development (Bormann et al., 1977), identifying aggrading and degrading N pools within the forest is essential for providing a basis to understand tree growth patterns and to predict responses to perturbations. In this study we identify several mechanisms governing the accumulation and release of N from storage pools during the aggrading phase in forests dominated by *Pinus contorta* ssp. *latifolia* (Engelm ex Wats) Critchfield. Specifically, we address mechanisms operating in the forest floor and mineral soil. A secondary objective was to evaluate the relative magnitude of solution fluxes of N in organic and inorganic forms.

Forests dominated by *Pinus contorta* are common in the montane landscape over a large area in western North America and may be N deficient because of 1) limited inputs via precipitation and fixation and 2) periodic losses associated with fires. We initiated field studies of nitrogen cycling in several *P. contorta* stands in the Medicine Bow Mountains, southeastern Wyoming. Because all the measurements described below could not be made in every stand, we describe some patterns of site to site variability as well as the dynamics of N in a typical 80–110 yr old aggrading ecosystem dominated by *P. contorta*.

The climate in the study area is characterized by long, cold winters and short, cool summers, with mean daily maximum and minimum temperatures in July of ~ 20°C and 4°C, respectively. Mean annual precipitation is ~ 60 cm, with about two-thirds coming in the form of snow From October to May. Measurements of N storage and flux were made in seven lodgepole pine stands, and detailed descriptions of the various sites can be found in earlier publications (Yavitt and Fahey, 1982; Fahey, 1983; Knight et al., 1985). Soils are either Inceptisols (lithic cryocrepts) or Alfisols (typic cryoboralfs), with clay content (% of < 2 mm fraction) at the 0–10 cm depth ranging from 12.6–38%. Most of the measurements discussed in this report were made in three stands (Fox Park, Nash Fork, Dry Park), whose site characteristics are summarized in Table 1.

Methods

Above and below ground biomass data, obtained by Pearson et al. (1984) from five stands in the study area, were multiplied by nitrogen concentrations in the various tissues to estimate N storage in biomass. Tissues were ground to pass a 20-mesh screen and analyzed by the method of Isaac and Johnson (1973). Accompanying measurements of tissue standards (U.S. Bureau of Standards 'orchard leaves') were within 5% of known values.

Nitrogen accumulation in aboveground biomass was estimated by a

Table 1. Vegetation and soil characteristics of three *Pinus contorta* ecosystems, southeastern Wyoming

	Fox Park	Nash Fork	Dry Park
Age (yr)	80	110	110
Tree density (stems/ha)	2200	1850	2217
Above ground biomass (Mg/ha)	111.1	144.1	142.2
Below ground biomass (Mg/ha)	32.7	40.8	38.7
Total leaf area index	9.1	9.9	7.3
Forest floor mass (Mg/ha)	32.8	30.7	2387
Surface soil features (0–15 cm)			
bulk density (g/cm^3)	nd	1.28	1.40
organic matter (%)	7.9	7.4	8.3
total nitrogen (%)	0.10	0.08	0.11
clay (% of < 2 mm fraction)	nd	15.4	12.6

nd = not determined

dendrochonologic method (Pearson, 1982). This method combines measured allometric relations between basal area and biomass components (leaves, twigs, branches, boles, bark, woody roots) in a stand (Pearson et al., 1984), with measurements of basal area increment in that stand obtained from tree cores taken in six 200 m^2 plots. These estimates were obtained for five stands.

Detailed soil sampling was done at five sites, with 10 samples taken at each of four depths. Total N was determined on two replicate subsamples ($n = 20$ for each depth and stand) by a microkjeldahl method (Schuman et al., 1973).

From 1979 through 1982 (May to October), bulk precipitation and throughfall (10 replicates) for chemical analysis were collected from two stands using polyethylene bottles fitted with funnels. Throughfall volume (i.e., net rainfall beneath canopy) was estimated from rainfall measurements using an empirical relationship derived from about 40 rainstorms with 25 collectors per stand: throughfall cm = 0.63 (rainfall volume in cm)$^{1.18}$ ($r^2 = 0.98$, $p < 0.001$; Fahey, 1979). Because of their large data requirements, more precise models of throughfall volume (Rutter et al., 1972) have not been attempted in our study area. Snowpack samples were collected at the time of maximum snow accumulation directly into polyethylene bottles from large clearings and beneath the canopy of two stands in 1979–1982 ($n = 30$ for each stand and year), and N concentrations in snow were multiplied by snowpack water content to estimate flux to the forest floor surface in snowmelt.

Dinitrogen fixation in woody litter and in the understory herb *Lupinus argenteus* was assayed with the acetylene reduction technique (Hardy et al., 1973) in summer 1982. Wood samples (~ 5 gm) were placed in 250-ml serum bottles capped with a stopper. After 10% (by volume) of the air was removed, samples received 25 ml of acetylene and were incubated for ca 4 h at 20°C. Ethylene production at the end of the incubation period was determined with a Perkin–Elmer gas chromatograph (Model Sigma 3B) using a 2 m column of 80–100 mesh Poropack T at 60°C and a helium carrier gas flow of 15 ml/min.

Fifteen wood samples were assayed on each sampling date. Root nodules of lupine were assayed for acetylene reduction at about three-week intervals from July–October. On each date, nodules were obtained by excavating most of the root system of 8–10 plants using a hand trowel. Whole plants were taken to the laboratory (< 1 h travel time) where nodules were clipped from the root system, leaving about 2 cm of root attached to each nodule to assure adequate carbon reserves during incubation. An entire set of nodules from an individual plant was incubated in a 125-ml serum bottle for 90 min with an atmosphere of 10% acetylene; ethylene production was assayed as des-described above. Controls (without acetylene) were included in all assays to determine background ethylene production. Biomass of lupine and its root nodules was estimated in two sites by measuring plant density in 100 m^2 plots and multiplying an average biomass/plant, the latter being based upon about 200 plants.

Litterfall, forest floor accumulation, and short-term (< 2 yr) decomposition were measured by Fahey (1983). In addition, long-term decomposition of leaf litter was measured by confining older forest floor material (~ 3 yr old), consisting of decaying leaves and associated fungi and micro-litter, in mesh bags (hole size = 4 mm^2) and placing them in the 01 horizon (Yavitt and Fahey, submitted). Age of the old litter material at the start was estimated by comparing N concentrations in the litter with an inverse linear relationship between N concentration and the percent of original biomass remaining using data of Fahey (1983). This approach is well-suited for these *P. contorta* ecosystems because both dry weight and tissue N concentration of decaying needles change linearly during middle stages of decomposition (3–6 yr; Yavitt and Fahey, submitted).

Forest floor leachate was sampled with alundum plate lysimeters (Cole, 1958) placed beneath the 02 horizon in three stands (sample size ranged from 6–10 stand). For this study, the 02 horizon was defined as the organic layers above the rooted soil. Tension (12–15 KPa) was applied and samples were collected periodically (every 1–4 days) during the snowmelt period. Volume obtained was recorded for each lysimeter so that N concentrations could be described as a function of total water flux. Porous cup lysimeters (Parizek and Lane, 1970) were installed at 0.3–0.4 m and 1.4–1.8 m depth in six stands, with samples collected under tension (12 KPa) during the snowmelt drainage period. Nitrogen fluxes via soil solution were calculated using a stand-level hydrologic model (Knight et al., 1985) that computed soil water fluxes.

Net nitrogen mineralization in the soil from three stands was estimated with an in situ approach (Eno, 1960) from August 1982–August 1983. Ten soil cores per stand were carefully extracted from 0–15 cm depth in the mineral soil with a hand trowel, minimizing disruption of soil structure. Samples were placed in polyethylene bags, sealed, and inserted back into the soil for incubation. Five nonincubated samples were collected at the start of

each incubation interval for nitrate and ammonium analysis; these data also were used to infer inorganic N pool sizes. Following 3 wk incubations, the bags were collected for chemical analysis. Mineralization data were collected only twice during the winter period (November–May), but incubations were carried out continuously during the snow-free period. To calculate total soil N mineralization, we applied the rate obtained from 0–15 cm to the major rooting zone (0–40 cm) with a correction for declining mineralization with depth proportional to the decline in soil organic matter. Soil organic matter levels dropped abruptly at the 30–40 cm depth in all the stands. We did not assay N mineralizaton in the 02 layer. This horizon, as defined in the present study, did not contain tree roots; thus, net mineralization in the 02 could be quantified by measuring forest floor leaching with lysimeters.

For water samples, nitrate plus nitrite was determined by diazotization after cadmium reduction (Rand, 1976) and ammonium by the phenol-hypochlorite method (Solorazano, 1969), both analyses being done on a Scientific Instruments continuous flow analyzer. A micro-Kjeldahl method usually was used to measure organic N plus ammonium (Jackson, 1958); however, for samples with low organic N concentrations (< 0.20 mg/l), such as snowpack water, total N was measured as nitrate after alkaline persulfate digestion in a sealed ampule (D'Elia et al., 1977). Dissolved organic carbon was determined by coulometric titration on a Coulometrics, Inc. (Wheatridge, CO) model 5010, following a sealed ampule persulfate digestion (Huffman, 1977). Total Kjeldahl N in soils was measured colorimetrically with the continuous-flow analyzer following digestion with an intimate mixture of K_2SO_4-$CuSO_4$-pumice (Schuman et al., 1973). Total N in tissue samples was digested with H_2SO_4-H_2SeO_3-H_2O_2 (Issac and Johnson, 1976) and analyzed for ammonium by the same colorimetric procedure. Soil from mineralization bags was homogenized and subsamples were extracted with 2 N KCl for 14 h. Extracts were analyzed for ammonium and nitrate by continuous flow analysis and concentrations expressed on a soil dry mass basis.

Results and discussion

Ecosystem pools

About three-fourths of the total N in vegetation was above ground in two typical 110 yr old lodgepole pine stands (Table 2). Nitrogen concentration in foliage was low (mean = 0.7%) compared to other coniferous species (Rodin and Bazilevich, 1967; Lang et al., 1982) and may be lower than the optimal level for growth of conifers (Gessel, 1962). Bole and branch wood had low N concentrations (0.035% and 0.17%, respectively) but high N storage as a result of their large masses. Our values for N storage in fine roots (Table 2) must be considered preliminary because of difficulties in distinguishing live and dead roots in this size-class.

Table 2. Nitrogen distribution (g/m^2) in two typical 110-yr-old *Pinus contorta* ecosystems, southeastern Wyoming

Compartment	Nash Fork	Dry Park
Tree biomass		
Foliage	6.8	5.8
Branch + twig	6.0	5.7
Bole + bark	5.7	5.4
Total above ground	18.5	16.9
Root crown	0.7	0.8
Lateral roots (> 2 mm)	0.8	0.5
Fine roots (< 2 mm)	4.0	3.8
Total below ground	5.5	5.1
Detrital biomass		
01 horizon	9.8	8.8
02 horizon	30.4	17.0
Total forest floor	40.2	25.8
Dead wood	8.6	16.7
Total above ground detritus	48.8	42.5
Soil organic matter	490	650
Ecosystem total	563	717

Nitrogen storage in above ground detritus was greater than in living biomass. Most of the N in the forest floor was in the 02 horizon (Table 2), and high N storage also was noted in dead boles that were lying on or incorporated into the forest floor. These boles were inherited from the previous forest generation that was killed by fire. Large amounts of woody detritus remain following stand-replacement fires, later becoming a sink for N (Hungate, 1940; Fahey, 1983).

The mineral soil contained by far the largest N pool (Table 2), with a range of values for our seven sites from 315–860 $g \cdot m^{-2}$. Sites with low N content had shallow, porous soils, whereas high soil N storage was associated with deep glacial tills with relatively high clay and organic matter contents. Soil organic N in our sites is near the upper end of the range of 69–1380 $g \cdot m^{-2}$ reported by Cole and Rapp (1980) for a variety of coniferous and deciduous forests.

The inorganic N pool in the rooting zone of lodgepole pine soils was very small during the growth season (mean of six stands = 0.25 $g \cdot m^{-2}$) and composed mostly of ammonium. Inorganic N storage was significantly higher in an old-age stand on fine soil (French Creek, 0.60 $g \cdot m^{-2}$) than at the other sites. The only significant seasonal change in organic N pools was a decline in late fall and mid-winter to levels less than 0.01 $g \cdot m^{-2}$. These inorganic N values are much lower than those observed in a northern hardwoods ecosystem in New Hampshire (2.6 $g \cdot m^{-2}$, Bormann et al., 1977).

Inputs

Atmospheric deposition. Volume-weighted mean total N concentration in summer bulk rainfall was about four times higher than in winter snowpack

Table 3. Volume-weighted mean nitrogen concentrations in ecosystem solutions for the Nash Fork *Pinus contorta* stand, southeastern Wyoming. For precipitation and throughfall, non-weighted standard errors are in parenthesis

Solution type	NH_4-N ($mg\,l^{-1}$)	NO_3-N ($mg\,l^{-1}$)	Organic N ($mg\,l^{-1}$)
Snowpack			
open	0.07(0.01)	0.08(0.01)	0.04(0.00)
forest	0.08(0.01)	0.13(0.01)	0.06(0.00)
Summer rain			
bulk precipitation	0.20(0.03)	0.30(0.03)	0.27(0.03)
throughfall	0.20(0.03)	0.52(0.04)	0.58(0.06)
Forest floor leachate			
summer	0.05	< 0.01	1.48
spring snowmelt	0.04	0.01	1.28
Soil solution			
root zone (40 cm)	0.03	0.01	0.48
subsoil (180 cm)	0.02	< 0.01	0.08

(Table 3), so that N input was about two times higher for summer rain than winter snow (0.17 vs. 0.08 $g \cdot m^{-2} \cdot yr^{-1}$). Lewis and Grant (1979) reported similar inorganic N concentrations in bulk precipitation at a mountain watershed in the Colorado Rocky Mountains. In contrast, Likens et al. (1977) measured a weighted mean nitrate concentration in bulk precipitation of 1.47 $mg \cdot L^{-1}$ at Hubbard Brook, New Hampshire where high deposition of pollutants occurs. Thus, precipitation inputs of N are quite low in the lodgepole pine ecosystem because of the relatively unpolluted atmosphere and the predominance of extremely dilute snow in the annual net precipitation budget.

Ammonium concentrations did not change significantly during passage of rainfall through the forest canopy, but levels of nitrate and organic N increased to 0.52 and 0.58 $mg \cdot L^{-1}$, respectively (Table 3). We expected higher organic N levels in throughfall than bulk rain as a result of tissue leaching (Tukey, 1970), but the significant increase in NO_3 concentration was surprising because others have noted nitrate removal from canopy throughfall (e.g. Verry and Timmons, 1977). About 60% of this increase results from evaporative concentration of rainfall while in residence on canopy surfaces. Moreover, phyllosphere populations appear to be small in this ecosystem (personal observation) and their N demand probably is small. Other potential sources of added NO_3 are dry deposition of gaseous HNO_3 (Lovett and Lindberg, 1983) and leaching of nitrate accumulated in leaf tissue. However, we measured extremely low nitrate values in a 2 N KCl extract of freshly-ground, green needles, so that the latter explanation seems unlikely.

We were able to account for much of the between-storm variation in throughfall N concentration using a regression model with rainfall magnitude

and the time interval between storms as independent variables (e.g. NO_3 (in $mg \cdot L^{-1}$) = 0.042* (interval between storms in days) − 0.10* (rainfall magnitude in cm) + 0.39; $n = 258$, $R^2 = 0.49$). Values for the standard error of the estimate (in $mg \cdot L^{-1}$) were 0.05 for NH_4^+, 0.07 for NO_3^- and 0.11 for organic N. These regression models were applied to 11 yr precipitation records for the study area (Wyoming Water Resources Institute, unpublished) to calculate an average annual N flux of $0.27\,g \cdot m^{-2}$ to the forest floor by canopy throughfall.

Table 4. Acetylene reduction rates in a *Pinus contorta* ecosystem (Fox Park site) in 1982. A. highly decomposed woody litter and B. nodules of *Lupinus argenteus*. Note the difference in units between the two tables

A. Date	n	(nmoles-gdw^{-1} − 24 h^{-1} ± $S_{\bar{x}}$) C_2H_2 reduction rate	(°C) Temperature	(%) Gravimetric moisture
20 June	6	4.5 ± 1.1	8.5	235
1 July	8	24.6 ± 7.2	11.5	195
7 July	6	32.7 ± 9.1	14.0	180
31 July	6	8.8 ± 2.6	13.0	133
15 August	6	1.6 ± 0.3	17.5	99
15 September	4	0.5 ± 0.3	10.0	84

B. Date	n	(μmole-gdw^{-1} − h^{-1} ± $S_{\bar{x}}$) C_2H_2 reduction rate	Soil temperature	Phenology
1 July	4	3.1 ± 0.9	11.5	Bud burst
31 July	4	3.3 ± 0.5	13.0	Initiation of of flowering
31 August	9	17.5 ± 2.8	17.5	Flowering and peak biomass
22 September	5	8.7 ± 1.0	11.5	Seed set
3 October	5	3.8 ± 1.2	7.5	Leaf senescence

Nitrogen fixation. Nitrogen input was expected from atmospheric nitrogen fixation by non-symbiotic bacteria in dead wood and forest floor layers (Cornaby and Waide, 1973) and by the symbiosis on the roots of the legume *Lupinus argenteus*. In woody litter a maximum acetylene reduction rate of 32.7 nmoles · gram dry mass^{-1} · day^{-1} was measured (Table 4A). Lower rates in the spring probably resulted from cold soil temperature, whereas low water potentials probably inhibited nitrogenase activity in the fall. The maximum rate of acetylene reduction observed in decaying lodgepole pine wood was comparable to values reported for chestnut by Cornaby and Waide (1973) but higher than those for Douglas-fir (Larsen et al., 1978). Because high nitrogenase activity in decaying wood was restricted to a brief interval in early summer, estimated N input via this pathway was small. Assuming a 3:1

conversion ratio between moles of C_2H_2 reduced and moles of N_2 fixed, estimated N input via fixation for a typical stand with $2000\,g \cdot m^{-2}$ of dead wood is less than $0.02\,g \cdot m^{-2} \cdot yr^{-1}$. Other workers have noted that the ratio of C_2H_2 reduced to N fixed in dead wood is higher than 3:1 (Roskoski, 1981; Silvester et al., 1982), and therefore this value probably represents an overestimate.

High nitrogenase activity (Table 4B) indicated that significant amounts of N_2 were fixed by the *Lupinus argenteus* symbiosis. A midsummer maximum in acetylene reduction potential suggested that in the early spring symbiotic microbes had to compete with shoot growth for photosynthate, and maximum N_2 fixation rates did not occur until peak leaf biomass was attained. Declining nitrogenase activity in the fall was associated with declining soil water potential and leaf senescence, with a probable reduction in translocation of freshly synthesized photosynthate to root nodules (Small and Leonard, 1969; Lawrie and Wheeler, 1973).

Table 5. Carbon to nitrogen ratios of organic matter in solution and solid phases of lodgepole pine ecosystems, southeastern Wyoming. For soil solutions a range of values is given, representing significant seasonal changes

Solid phases[a]	C:N	Solution phases	C:N
Foliage	70	Bulk precipitation	10
Leaf litterfall	135	Throughfall	22
Forest floor 01	62	01 leachate	90
Forest floor 02	33	02 leachate	20–70
Soil organic matter	34	Root-zone solution	50–70
Bole wood (fresh)	1400	Subsoil solution	50–70
Decayed wood	240	Dead wood solution	50

[a] For all solid phases except soil organic matter (SOM), carbon was assumed to be 50% of organic matter. For SOM, carbon was assumed to be 40% of organic matter.

Using the conventional 3:1 conversion ratio (Hardy et al., 1973) and assuming that 24 h fixation rate was a combination of peak daytime rates (Table 4) and basal nighttime rates ($2.5\,\mu M \cdot g$ dry $mass^{-1} \cdot h^{-1}$), we estimated seasonal fixation rate for lupine of 0.14 mg N_2/gram of nodules. This value is comparable to other understory symbiotic fixers (Binckley, 1981; Lawrie, 1981).

Shoot N content in lupine plants was high (mean of 12 plants = 0.04 g/plant), indicating a potential for significant input via N_2 fixation; however, this species was not abundant in the study area, being restricted to a few stands where lupine density was about 1000 plants/ha. In these stands nodule biomass averaged $0.76\,g \cdot m^{-2}$, and total annual N input via fixation was

calculated to be only about 0.01 $g \cdot m^{-2}$. Significant input via N_2 fixation probably occurs in some lodgepole pine stands where lupine density may exceed 10 000 stems/ha and fixation of about 0.1 $g \cdot m^{-2} \cdot yr^{-1}$ is likely.

Internal recycling and transformation

In the following sections we examine a variety of internal N transformations, drawing upon information from several studies performed in different lodgepole pine stands. We attempt to unify this information by discussing N fluxes for a hypothetical 80–110 yr old stand on a loamy soil, but we also address some of the causes of spatial variability among stands in this forest type.

Retranslocation. Nitrogen concentrations in older foliage (4–5 yr age class at Nash Fork and Dry Park, mean = 0.66% dry mass) were significantly higher than for leaf litterfall in all the stands (for Nash Fork and Dry Park, mean = 0.37% dry mass), suggesting that retranslocation of N occurs prior to leaf abscission. Assuming the difference to be due entirely to this process, annual retranslocation for a typical 110 yr-old stand is calculated to be about 0.28-$g \cdot m^{-2}$ (47% of litterfall flux). However, lodgepole pine usually retains dead needles for at least several months before leaf fall, so that much of this apparent retranslocation could be the result of canopy leaching. Thus, it seems likely that actual values for retranslocation are considerably lower than that calculated above.

Litterfall and forest floor accumulation. Although somewhat variable among sites, N deposition in total litterfall was about 0.6 $g \cdot m^{-2} \cdot yr^{-1}$ for typical 80–100 yr-old stands, with 80% in leaf litter (Fahey, 1983). The contribution of woody debris became more important in older stands. Because decaying leaf litter is an important N sink during the initial 2 yr of decay (Fahey, 1983), we required estimates of N accumulation in decaying leaf litter during subsequent years. Surprisingly, N continued to accumulate in decaying leaves for 6–7 yr following leaf fall in two stands, and at the end of this interval N content was over 180% of the initial values (Figure 1). Others have noted N accumulation in decaying leaf litter (Gosz et al., 1973; Lousier and Parkinson, 1978; Edmonds, 1979; Staaf, 1980), but amounts were lower than for lodgepole pine. Low tissue N content as well as limited opportunity for forest floor leaching (see below) probably contribute to this high accumulation rate.

Accumulation of N in decaying leaf litter up to the 7 yr age class represents an annual addition of about 0.5 $g \cdot m^{-2}$ to the 01 horizon, an amount nearly as large as litterfall input. Most of this accumulation probably is associated with fungal translocation, as net retention of precipitation N appears to be relatively small (see below).

Forest floor leaching. Concentrations of inorganic N in forest floor leachate were extremely low (< 0.05 mgN $\cdot L^{-1}$), with most of the dissolved N being

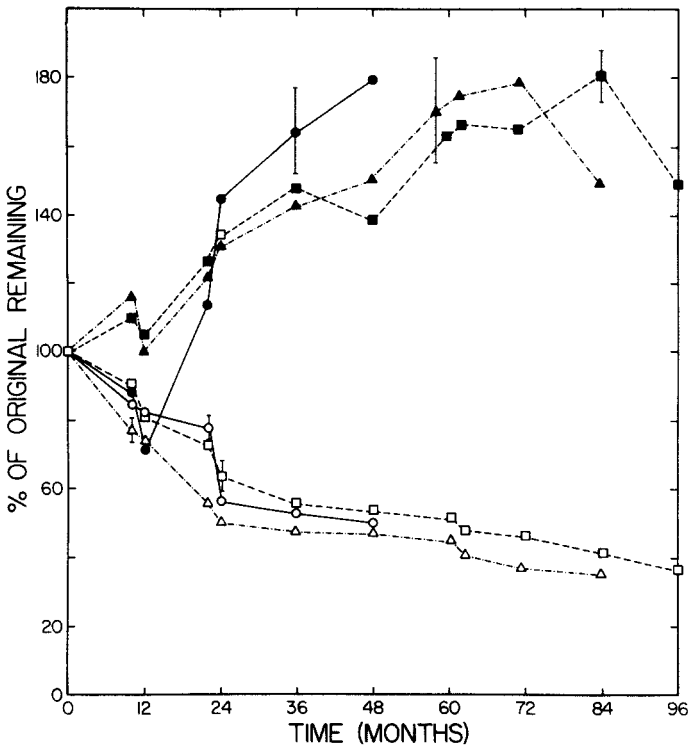

Figure 1. Dry mass loss and changes in nitrogen content of decaying leaf litter in three lodgepole pine stands, southeastern Wyoming.

organic forms (Table 3). Similar results have been reported for Douglas-fir ecosystems in Oregon (Sollins and McCorison, 1981). Based on over 200 samples of leachate, collected from three stands over 2 yr, we have estimated net annual N flux from forest floor to mineral soil during snowmelt leaching to be $0.26\,g \cdot m^{-2}$ (Yavitt and Fahey, submitted). Most of the inorganic N in snow water was retained in the forest floor, apparently by efficient heterotrophic uptake, because tree roots were uncommon in these layers.

Because summer leaching events are sporadic in the study area, a field simulation of this process was carried out, and leaching flux was estimated using a multiple regression model with throughfall magnitude and interval between leaching storms as independent variables (Yavitt and Fahey, 1984). This simple model explained much of the variation in total N concentrations of forest floor leachate in summer ($R^2 = 0.63$, $n = 70$, $p < 0.001$), and we estimated net annual N flux of $0.20\,g \cdot m^{-2}$ based on 11 yr rainfall records for the study area (Wyoming Water Resources Institute, unpublished). Because summer rains rarely are sufficient to cause leaching beyond the upper 20–30 cm of mineral soil, we assumed for the calculations below that all transported N was retained in the major rooting zone (0–40 cm).

Mineral soil leaching. We estimated N transfer from the surface mineral soil (0–40 cm) to the sub-soil (40–150 cm) and from sub-soil to deep soil and groundwater as the product of N concentration in soil solutions (collected with tension lysimeters) and soil water flux (estimated with a hydrologic model; Knight et al., 1985). Much of the dissolved organic N, derived from the forest floor, was lost from solution during passage through the upper mineral soil; mean concentration of total N in tension lysimeter solution at 30–40 cm depth ranged from 0.15–0.55 $mg \cdot L^{-1}$ among six stands, compared with a volume-weighted mean value of 1.28 $mg \cdot L^{-1}$ in forest floor leachate (Table 3). Lowest values were observed in two stands on fine textured soils, whereas highest total N values in soil solution were in coarse soils, suggesting precipitation on mineral and organic colloids (Yavitt and Fahey, in press). However, slower soil water movement in the fine soils (Fahey, unpublished data) also could allow more heterotrophic oxidation of dissolved organics. For a typical 80–110 yr old stand on loamy soil, annual retention of organic N in the surface mineral soil during snowmelt leaching was calculated to be about 0.10 $g \cdot m^{-2}$.

Gross transport of N to the subsoil during snowmelt in this typical stand was calculated to be 0.13 $g \cdot m^{-2} \cdot yr^{-1}$, based on model estimates of soil water flux (Knight et al., 1985). Total N concentration in sub-soil solution was very low in all the stands studied (< 0.10 $mg \cdot L^{-1}$). Combined with high retention of percolating snow water in the soil profile, the net result was extremely low annual N outflow to groundwater (i.e., below 140–180 cm depth, about 0.01 $g \cdot m^{-2}$; Knight et al., 1985).

Soil N mineralization and nitrification. Annual soil N mineralization in our typical stand was estimated to be 0.80 $g \cdot m^{-2}$, with all the net mineralization occurring during the snow-free period (May–October). Peak rates of N mineralization, observed in midsummer prior to extreme soil water depletion (20 $mg \cdot m^{-2} \cdot d^{-1}$), were comparable to values from other temperate zone forests (Melillo, 1981), but N mineralization in spring and fall was very low (3 $mg \cdot m^{-2} \cdot d^{-1}$). Most of the mineralized N remained in the form of ammonium, as only about 5% of the inorganic N in buried bags was in the nitrate form. The annual N mineralization rate in the lodgepole pine ecosystem was very low compared with other warmer and moister forest sites (Rapp et al., 1979; Nadelhoffer et al., 1983; Pastor et al., 1984). The apparent high demand for mineral N in our soils could result in rapid immobilization of mineralized N, so that our calculated net N mineralization rates could be lower than gross N mineralization, but they may represent accurately amounts of nitrogen available to plants.

In rooted soil intense competition probably exists for mineralized N, involving heterotrophs, autotrophic nitrifiers and plant roots (Keeney, 1980; Vitousek et al., 1982). Although we observed little evidence for nitrification in our short-term buried bags, long-term (6 month) studies of soil column

leaching in the absence of roots indicated high nitrate accumulation (Yavitt and Fahey, in press). It is probable that nitrifier populations are extremely substrate limited in these soils and that they respond slowly to increased NH_4 availability (i.e. buried bag result), but with continued availability of NH_4, autotrophic nitrifying populations build up and oxidize virtually all the available substrate (column study result). The apparent low availability of NO_3, coupled with predominantly oxidizing conditions, probably minimizes denitrification and gaseous N losses in this ecosystem.

Vegetation uptake. Annual N uptake by trees in a typical stand was estimated as the sum of annual litterfall ($0.60\,g \cdot m^{-2}$), canopy leaching ($0.10\,g \cdot m^{-2}$) and biomass increment ($0.18\,g \cdot m^{-2}$). The latter value was estimated using a dendrochronologic approach (see Methods; Pearson, 1982) and includes both above- and below-ground biomass increment. This sum ($0.88\,g \cdot m^{-2}$) is similar to the estimated soil N mineralization rate ($0.80\,g \cdot m^{-2} \cdot yr^{-1}$), which is consistent with the observation of Melillo (1981) that apparent soil N mineralization and demand of aboveground vegetation are similar.

Calculations of total annual root N uptake also must take into account fine root production and turnover. Considering the relatively high storage of N in the fine root (< 2 mm diameter) biomass of our lodgepole pine stands (Table 2), fine root turnover rate is probably much slower than in some other forest types. For example, Vogt et al. (1982) estimated that one-third of the fine roots turn over annually in *Abies amabilis* stands in Washington. At this turnover rate and in the absence of retranslocation from decaying roots, annual N uptake required to supply fine root growth alone would be about $1.1\,g \cdot m^{-2}$, much larger than the annual N mineralization. Thus, efficient N retranslocation from dying fine roots or relatively slow root turnover must be hypothesized for these lodgepole pine ecosystems. McClaughterty et al. (1982) reached a similar conclusion for a coniferous plantation in New England.

Nitrogen budget

Integration of the foregoing information into a nitrogen budget for a typical 80–110 yr old lodgepole pine stand demonstrates some internal consistencies in our data and leads to several interesting conclusions about N movement in lodgepole pine ecosystems. To develop the N budget we combined our measurements of N storage and flux in the Nash Fork stand and then back-calculated several unmeasured fluxes so that three assumptions about N cycling were satisfied:

1. Several storage compartments (Figure 2) were assumed to remain constant from year to year, including all solution compartments in the forest floor and soil and the solid phase of the 01 horizon.

2. Nitrogen accumulation in the 02 layer was assumed to be $0.11\,g \cdot m^{-2} \cdot yr^{-1}$. This value was estimated from our information on total N

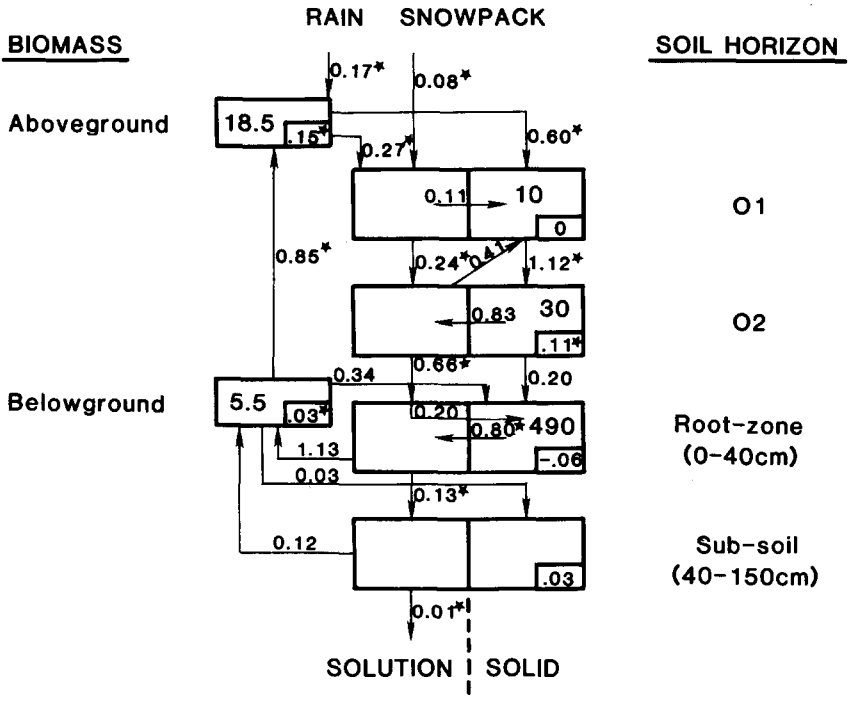

Figure 2. Nitrogen storage (large figures in boxes, $g \cdot m^{-2}$) and flux ($g \cdot m^{-2} \cdot yr^{-1}$) for a typical 110 yr old lodgepole pine ecosystem, southeastern Wyoming. Values in small boxes represent annual changes in N storage ($g \cdot m^{-2} \cdot yr^{-1}$). Flux values with stars were measured, whereas other fluxes were back-calculated (see text for explanation).

accumulation in the 02 layer during 80–110 years of ecosystem development following intense crown fire (Table 2), a sigmoidal pattern of N accumulation, and detailed information on forest floor N dynamics (Fahey, 1983; Yavitt and Fahey, 1984; Yavitt and Fahey, submitted).

3. Annual transport of dissolved organic N from the 02 to the soil root zone ($0.62\,g \cdot m^{-2} \cdot yr^{-1}$) is much larger than that from the root zone to the sub-soil ($0.12\,g \cdot m^{-2} \cdot yr^{-1}$). We assumed that 60% of this organic N is mineralized rapidly ($0.30\,g \cdot m^{-2} \cdot yr^{-1}$) and available for plant uptake, and the remainder ($0.20\,g \cdot m^{-2} \cdot yr^{-1}$) is retained in the solid phase of the soil. Although we cannot verify these assumptions (with the exception of the constant storage in soil solution phase), the resulting N budget provides a useful framework for describing N movement in this ecosystem, and allows us to evaluate the possible effect of errors in the assumptions above on the N budget.

Surprisingly, total N input to the 01 horizon in snow, throughfall, and litterfall was much smaller than outflow by leaching and solid phase transport (Figure 2). [Nitrogen leaching from 01–02 was calculated from the proportion

of total forest floor N leaching attributed to the 01 (40%; Yavitt and Fahey, 1984). The solid matter transfer represents decaying litter entering the 8 yr age class, the time at which tissue becomes fragmented and N mineralization begins (Yavitt and Fahey, submitted)]. This observation requires unmeasured input to the 01 layer, the most likely source being the relatively N-rich 02 layer. We suggest that the large apparent N deficit in the solid-phase of the 01 horizon is met by transport from the 02 horizon ($0.41\,g \cdot m^{-2} \cdot yr$) and by retention of precipitation N ($0.11\,g \cdot m^{-2} \cdot yr^{-1}$; Figure 2). Ingham and associates (pers. commun.) have detected significant N translocation by microarthropods in the forest floor from one of our sites (Fox Park), and fungal growth and translocation are other likely mechanisms of N movement.

In the 02 horizon, the solution phase receives $0.24\,g \cdot m^{-2} \cdot yr^{-1}$ from the 01, but loses $0.66\,g \cdot m^{-2} \cdot yr^{-1}$ to the mineral soil, mostly as organic N, in addition to the $0.41\,g \cdot m^{-2} \cdot yr^{-1}$ transported to the 01 layer. These figures indicate that $0.83\,g \cdot m^{-2} \cdot yr^{-1}$ is released to the 02 solution, predominantly in organic forms, but probably also including some mineralized N transported to the 01, or via mycorrhial hyphae to the soil root zone. Net N mineralization in the 02 must be very low based upon the forest floor leaching results (Table 3).

Nitrogen transport from 02 solid phase to the mineral soil is calculated to balance the 02 budget, allowing for an accumulation rate of $0.11\,g \cdot m^{-2} \cdot yr^{-1}$. The value for solid phase transport ($0.20\,g \cdot m^{-2} \cdot yr^{-1}$; Figure 2) agrees with an independent estimate based upon forest floor N accumulation and long-term litter decay measurements (Yavitt and Fahey, submitted).

As pointed out earlier, inflow of dissolved organic N to the mineral soil far exceeded outflow (Figure 2), indicating precipitation and mineralization in the soil root zone. Rapid mineralization of this organic N would not be detected by the buried-bag method (i.e., addition and mineralization of organic N occurring during the 3 week incubation period). With the additional $0.80\,g \cdot m^{-2} \cdot yr^{-1}$ mineralized in the buried bags, total root uptake of about $1.13\,g \cdot m^{-2} \cdot yr^{-1}$ is required to balance the budget for the root-zone solution.

Nitrogen flux to the subsoil ($0.13\,g \cdot m^{-2} \cdot yr^{-1}$) is not balanced by subsoil leaching ($0.01\,g \cdot m^{-2} \cdot yr^{-1}$), suggesting retention of about $0.12\,g \cdot m^{-2} \cdot yr^{-1}$. Because about 10% of tree roots are in the sub-soil (Pearson et al., 1984), we propose that this retained N goes to tree uptake at the rate of 10% of uptake from the major root-zone, and resulting in total root uptake of about $1.25\,g \cdot m^{-2} \cdot yr^{-1}$. Most of this absorbed N ($0.85\,g \cdot m^{-2} \cdot yr^{-1}$) is transported to aboveground tissues, and combined with woody root increment of $0.03\,g \cdot m^{-2} \cdot yr^{-1}$ this leaves about $0.37\,g \cdot m^{-2} \cdot yr^{-1}$ in fine root turnover. Assuming that 10% of the turnover is for roots in the sub-soil, about $0.34\,g \cdot m^{-2}$ of organic N is returned annually to the root-zone solid phase. These calculations would suggest slow depletion of N from the large

soil organic matter pool in the major rooting zone ($-0.06\,g \cdot m^{-2} \cdot yr^{-1}$, Figure 2) in this aggrading forest.

It is useful to consider the effects on these budget calculations of altering some of the original assumptions. For example, if the rate of N accumulation in the 02 layer is larger than $0.11\,g \cdot m^{-2} \cdot yr^{-1}$, then mobilization of organic N from the 02 solid phase must be lower than $0.83\,g \cdot m^{-2} \cdot yr^{-1}$, and the apparent deficit in the 01 horizon could not be supplied completely from the 02 solution phase. This would imply N transport from the root-zone to the 02 solution by fungi or invertebrates, and suggests more rapid depletion of soil organic N.

We assumed that about 40% of the organic N, which was lost from solution during passage through the mineral soil, had been added to the solid phase compartment by precipitation (Figure 2). If this figure was higher, then lower root uptake and consequently lower root turnover would be indicated. In contrast, if we have underestimated gross N mineralization with the buried-bag method, then higher root uptake and root turnover would be required.

Decaying wood remains a significant sink for N even in 80–110 yr old stands. Although some organic N is leached from decaying wood, its high water-holding capacity probably limits total water flux and most incoming N is retained for long periods. Budget calculations for dead wood also suggest that fungal translocation probably occurs, but roots are common in the decayed wood, and the magnitude of this flux certainly is smaller than for translocation to litter in 80–110 yr old stands (Yavitt and Fahey, submitted). This flux is more prominent at earlier stages of ecosystem development following fire, peaking at stand ages of about 30–60 yr (Fahey, 1983).

No consistent relationships were observed between C:N ratios of solid and solution phase organic matter (Table 5). Throughfall C:N ratio (22) was much lower than that of foliage (70), and contrasted markedly with results of Sollins and McCorison (1981) for throughfall in a Douglas-fir ecosystem in western Oregon (C:N = 120). In the forest floor and soil, solution phase C:N values generally were higher than for the corresponding solid phases and were very similar to those reported by Sollins and McCorison (1981).

The lodgepole pine ecosystems continue to retain most of the incoming N even after 100 + yr of succession following fire. In our typical stand, N outflow to deep soil and groundwater was less than 5% of input (Figure 2). Rapid assimilation of mineral N, precipitation of organic solutes in the mineral soil, and limited opportunity for deep percolation of water help to account for this effective immobilization. Moreover, periodic wildfires reduce aboveground N storage drastically (Raison, 1979), maintaining the lodgepole pine landscape in an oligotrophic state, and thereby enhancing N retention.

In conclusion, the four most critical processes affecting N flux in lodgepole pine ecosystems (Figure 2) appear to be: 1) translocation of N to the 01 layer; 2) dissolution of organic N in the 02 layer; 3) precipitation and

mineralization of organic N in the mineral soil; and 4) root N uptake and fine root turnover. Future studies of N cycling in this infertile ecosystem, perhaps the most extreme case yet reported (Miller et al., 1979; Vitousek 1982), could focus profitably on control of these four sets of processes, as well as the distribution and ecology of the major N_2 fixers, *Lupinus argenteus* and *Shepherdis canadensis*.

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References

Binkley, D. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B.C. Canadian Journal of Forest Research 11:281–286.

Bormann, F.H., G.E. Likens and J.M. Melillo. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science 196:981–983.

Clark, F.E. and T. Rosswall. 1981. Terrestrial nitrogen cycles, processes, ecosystem strategies and management impacts. Ecological Bulletin (Stockholm) 33.

Cole, D.W. 1958. An alundum tension lysimeter. Soil Science 85:293–296.

Cole, D.W. and M. Rapp. 1980. Elemental cycling in forest ecosystems. In: D.E. Reichle (ed.), Dynamic properties of forest ecosystems. pp 341–409. Cambridge University Press, Malta.

Cornaby, B.W. and J.B. Waide. 1973. Nitrogen fixation in decaying chestnut logs. Plant and Soil 39:445–448.

D'Elia, C.F., P.A. Steudler and N. Corwin. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnology and Oceanography 22:760–764.

Edmonds, R.L. 1979. Decomposition and nutrient release in Douglas fir needle litter in relation to stand development. Canadian Journal of Forest Research 9:132–140.

Eno, C.F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Science Society of America Proceedings 24:277–279.

Fahey, T.J. 1979. Water and nutrient cycling in lodgepole pine forest. Ph.D. Dissertation, University of Wyoming, Laramie. 179 p.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53:51–72.

Gessel, S.P. 1962. Progress and problems in mineral nutrition of forest trees. In: T.T. Kozlowski (ed.), Tree growth. pp 221–235. Roland Press, New York, NY.

Gosz, J.R., G.E. Likens and F.H. Bormann. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecological Monographs 42:173–191.

Hardy, R.W.F., R.C. Burns and R.D. Holsten. 1973. Applications of the acetylene-ethylene assay for measurement of nitrogen fixation. Soil Biology and Biochemistry 5:47–81.

Huffman, E.W.D. 1977. Performance of a new automatic carbon dioxide coulometer. Microchemical Journal 22:567–573.

Hungate, R.E. 1940. Nitrogen content of sound and decayed coniferous woods and its relation to loss in weight during decay. Botanical Gazette 102:382–392.

Isaac, R.A. and W.C. Johnson. 1976. Determination of total nitrogen in plant tissue, using a block digestor. Journal of the Association of Official Analytical Chemists 50:98–100.

Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

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

Knight, D.H., T.J. Fahey and S.W. Running. 1985. Water and nutrient outflow from contrasting lodgepole pine forests in Wyoming. Ecological Monographs 55:29–48.

Lang, G.E., W.A. Reiners and G.A. Shellito. 1982. Tissue chemistry of *Abies balsamea* and *Betula papyrifera* var. *cordifolia* from subalpine forests of northeastern United States. Canadian Journal of Forest Research 12:311–318.

Larsen, M.J., M.F. Jurgensen and A.E. Harvey. 1978. N_2 fixation associated with wood decayed by some common fungi in western Montana. Canadian Journal of Forest Research 8:341–345.

Lawrie, A.C. 1981. Nitrogen fixation by native Australian legumes. Australian Journal of Botany 29:143–157.

Lawrie, A.C. and C.T. Wheeler. 1973. The supply of photosynthetic assimilates to nodules of *Pisum sativum* L. in relation to the fixation of nitrogen. New Phytologist 72:1341–1348.

Lewis, W.M., Jr. and M.C. Grant. 1979. Changes in the output of ions from a watershed as a result of the acidification of precipitation. Ecology 60:1093–1097.

Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton and N.M. Johnson. 1977. Biogeochemistry of a forested ecosystem. Springer, New York, NY.

Lousier, J.D. and D. Parkinson. 1978. Chemical element dynamics in decomposing leaf litter. Canadian Journal of Botany 56:2795–2812.

Lovett, G.M. and S.E. Lindberg. 1983. Dry deposition of nitrate to a deciduous forest canopy. Bulletin of the Ecological Society of America 64:64.

McClaugherty, C.A., J.D. Aber and J.M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystem. Ecology 63:1481–1490.

Melillo, J.M. 1981. Nitrogen cycling in deciduous forests. In: F.E. Clark and T. Rosswall (eds.) Terrestrial nitrogen cycles. Processes, ecosystem strategies, and management impacts. pp 427–442. Ecological Bulletin 33, Swedish Natural Science Research Council, Stockholm.

Miller, H.G., J.M. Cooper, J.D. Miller and O. Pauline. 1979. Nutrient cycles in pine and their adaptation to poor soils. Canadian Journal of Forest Research 9:19–26.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1983. Leaf litter production and soil organic matter dynamics along a nitrogen availability gradient in southern Wisconsin (USA). Canadian Journal of Forest Research 13:12–21.

Parizek, R.R. and B.E. Lane. 1970. Soil-water sampling using pan and deep pressure-vacuum lysimeters. Journal of Hydrology 11:1–21.

Pastor, J., J.D. Aber, C.A. McClaugherty and J.M. Melillo. 1984. Above-ground production and N and P cycling along a nitrogen-mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256–268.

Pearson, J.A. 1982. Biomass distribution and ecosystem development in lodgepole pine forests of the Medicine Bow Mountains, Wyoming. Ph.D. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

Pearson J.A., T.J. Fahey and D.H. Knight. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Canadian Journal of Forest Research 14:259–265.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant and Soil 51:73–108.

Rand, M.C. 1976. Standard methods for the examination of water and waste water. American Public Health Association, Washington, DC, USA. 14th edition.

Rapp, M., M.U. LeClerc and P. Loissant. 1979. The nitrogen economy in a *Pinus pinea* L. stand. Forest Ecology and Management 2:221–231.

Rodin, L.E. and N.E. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh, Scotland.

Roskoski, J.P. 1981. Comparative C_2H_2 reduction and $^{15}N_2$ fixation in deciduous wood litter. Soil Biology Biochemistry 13:83–85.

Rutter, A.J., D.A. Kershaw, P.C. Robins and A.J. Morton. 1972. A predictive model of rainfall interception in forests, I. Derivation of the model from observations in a plantation of Corsican pine. Agricultural Meteorology 9:367–384.

Schuman, G.E., M.A. Stanley and D. Knudsen. 1973. Automated total nitrogen analysis of soil and plant samples. Soil Science Society of America Proceedings 37:480–481.

Silvester, W.B., P. Sollins, T. Verhoeven and S.P. Cline. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. Canadian Journal of Forest Research 12:646–652.

Small, J.G.C. and O.A. Leonard. 1969. Translocation of ^{14}C labelled photosynthate in nodulated legumes as influenced by nitrate nitrogen. American Journal of Botany 56:187–194.

Sollins, P. and F.M. McCorison. 1981. Nitrogen and carbon solution chemistry of an old growth coniferous forest watershed before and after cutting. Water Resources Research 17:1409–1418.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenol-hypochlorite method. Limnology and Oceanography 14:299–301.

Staaf, H. 1980. Release of plant nutrients from decomposing leaf litter in a south Swedish beech forest. Holoarctic Ecology 3:129–136.

Tukey, H.B., Jr. 1970. The leaching of substances from plants. Annual Review of Plant Physiology 21:305–324.

Verry, E.S. and D.R. Timmons. 1977. Precipitation nutrients in the open and under two forests in Minnesota. Canadian Journal of Forest Research 7:112–119.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119:553–572.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Mellilo and W.A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs 52:155–177.

Vogt, K.A., C.C. Grier, C.E. Meier and R.L. Edmonds. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology 63:370–380.

Yavitt, J.B. and T.J. Fahey. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. Canadan Journal of Forest Research 12:745–752.

Yavitt, J.B. and T.J. Fahey. 1984. An experimental analysis of solution chemistry in a lodgepole pine forest floor. Oikos 43:222–234.

Yavitt, J.B. and T.J. Fahey. (in press). Organic chemistry of the soil solution during snowmelt leaching in *Pinus contorta* forest ecosystems, Wyoming, USA, In: Planetary Ecology: selected papers from the 6th International Symposium on Environmental Biogeochemistry. The Ronald Press, New York.

Yavitt, J.B. and T.J. Fahey. Forest floor leaching and litter decay in lodgepole pine ecosystems. Submitted to Journal of Ecology.