

Comparison of methods for estimating soil nitrogen transformations in adjacent conifer and alder-conifer forests

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Nitrogen transformations were examined in two pairs of adjacent, 55-year-old forests dominated by conifers (primarily Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)) and by conifers and nitrogen-fixing red alder (*Alnus rubra* Bong.). Nitrogen availability was examined in aerobic and anaerobic incubations in the laboratory, and with resin-core and buried-bag incubations in the field. Rates of nitrogen mineralization and immobilization were examined in the field incubations using [¹⁵N]ammonium. Net nitrogen mineralization in a year-long series of resin-core incubations of forest floor plus 0-0.15 m depth soil was about 9 kmol·ha⁻¹·year⁻¹ for the two alder-conifer stands, but almost nil in the conifer stand at the low-productivity Wind River site, and 2.1 kmol·ha⁻¹·year⁻¹ in the conifer stand at the high-productivity Cascade Head site. The ¹⁵N pool dilution experiment showed that buried-bag incubations demonstrated more differences among stands than did resin cores; resin cores typically gave greater rates than buried bags. Previous estimates of nitrogen budgets were coupled with net mineralization estimates to examine how well the estimated fluxes balanced at an ecosystem scale. This tabulation of the complete nitrogen cycles showed substantial discrepancies, prompting caution in interpretation of some of the differences among the stands.

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Les transformations de l'azote ont été examinées pour deux paires de peuplements adjacents, âgés de 55 ans et dominés par des conifères, principalement du sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et par des conifères et aulne rouge (*Alnus rubra* Bong.) qui fixe l'azote. La disponibilité de l'azote a été déterminée par des incubations aérobiques et anaérobiques au laboratoire, et, avec des carottes avec résines et des incubations de sachets enfouis, au champ. Les taux de minéralisation et d'immobilisation d'azote ont été examinés dans des incubations au champ par l'utilisation de ¹⁵NH₄. Des séries d'incubation de carottes avec résines pour une période de 1 an, ont indiqué que la minéralisation nette de l'azote dans la couverture morte plus les 15 premiers cm du sol a été d'environ de 9 kmol·ha⁻¹·an⁻¹ pour les deux peuplements aulne-conifères, mais presque nulle dans le peuplement coniférien de productivité faible à la station de Wind River, et de 2,1 kmol·ha⁻¹·an⁻¹ dans le peuplement coniférien à forte productivité de la station de Cascade Head. L'expérience de dilution du pool de ¹⁵N a montré que les incubations de sacs enfouis présentaient de plus fortes différences entre les peuplements que les carottes avec résines; les carottes avec résines ont donné des taux plus élevés que les sachets enfouis. Les estimés antérieurs des bilans azotés ont été couplés avec les estimés de minéralisation nette afin d'évaluer la qualité des flux calculés à l'échelle de l'écosystème. Cette tabulation des cycles complets de N a montré des écarts substantiels, commandant la prudence dans l'interprétation des différences entre les peuplements.

[Traduit par la rédaction]

Introduction

Soils beneath N-fixing alder typically have more total N and greater availability of N than soils under conifers (Tarrant and Miller 1963; Bollen and Lu 1968; Franklin *et al.* 1968; Cole *et al.* 1978; Bormann and DeBell 1981; Binkley 1983; Binkley *et al.* 1984; Van Miegroet and Cole 1984). Nitrogen availability in soils from such stands has been characterized under laboratory conditions of constant moisture and temperature on well-mixed soil samples; this approach may identify differences in substrate quality that are important for N mineralization, but the artifacts caused by sample mixing and artificial environmental conditions may obscure important effects of alder on N turnover (Binkley and Hart 1989). We characterized N availability and turnover by several methods in two pairs of stands, each containing one conifer stand and one alder-conifer stand. One pair was on a low-productivity site with low total N in the ecosystem, and the other was on a high-productivity site with very high N capital. We examined the differences between stands among methods of

assessing N transformations; some possible artifacts of methods on rates of N transformations using ¹⁵N pool dilution techniques; and whole-ecosystem N budgets to determine if independent fluxes provided a well-balanced budget.

Site description

Both study sites were established and maintained by researchers of the USDA Forest Service, including C. Berntsen, J. Booth, S. Greene, L. Isaac, W. Meyer, R. Miller, M. Nance, and R. Tarrant. One study site, located within the Wind River Experiment Forest, is in southwestern Washington, at about 625 m elevation and 45°49'N latitude. Precipitation averages 2500 mm/year, with about 75% falling as snow between November and March. A snowpack of 1-2 m is common. The soil is an unclassified silty clay loam Andic Haplumbrept developed in Tertiary andesitic or rhyolitic parent materials, with some pumice and basaltic gravel of Pleistocene origin (Miller and Tarrant 1983). The site was on the eastern edge of the 120 000 ha Yacolt Burn, which occurred in 1902, and also experienced wildfires in 1922 and 1927. The terrain is rolling, with slopes ranging from 0 to 60%. The site index for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)

in the absence of red alder (*Alnus rubra* Bong.) is 25 m at 50 years. The area was planted with 2-year-old seedlings of Douglas-fir (from an off-site seed source) in 1929, at a density of 1700 trees/ha. In 1933, a 22 m wide strip was interplanted with 2-year-old red alder seedlings (also from an off-site seed source) at a density of 3000/ha, to provide a firebreak across the plantation.

A second study site was located at the Cascade Head Experiment Forest, at about 180 m elevation, near the coast of Oregon at 45°03'N latitude. Precipitation averages 2400 mm/year, with little snow. Temperatures average about 20°C in July and 10°C in January; freezing temperatures are uncommon. The well-drained Typic Dystrandept belongs to the Astoria silty clay loam series, developed from tuffaceous siltstone overlying basalt. The experimental plots are located within an 8-ha stand that occupies moderate slopes of about 15% with a generally southwesterly aspect. The site index for Douglas-fir in the absence of alder is 40 m at 50 years. The land had been farmed and was abandoned in 1925. By 1935, the naturally regenerated, 8-year-old stand contained about 4500 conifers/ha (a mixture of Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.)) and 3000 red alder/ha. A 0.2-ha plot (no. 11) was established as a control in 1935, and a 0.2-ha plot (no. 17) was thinned to a density of about 2800 stems/ha by removing all alders and many of the smaller conifers.

Methods

Laboratory incubations

Ten sampling locations were established randomly in each stand (Binkley *et al.* 1992). For each stand, 10 sieved samples from the 0–0.15 m depth (excluding forest floor materials) were assayed for net N mineralization in the laboratory using both anaerobic (10-g samples incubated in 50 mL deionized water for 7 days, extracted with 50 mL 4 M KCl; extracts analyzed for ammonium) and aerobic (10-g samples incubated in capped cups at field capacity for 30 days, extracted with 100 mL 1 M KCl; extracts analyzed for ammonium and nitrate) methods (see Binkley and Hart 1989). Net mineralization was calculated as the differences between concentrations of ammonium + nitrate in paired subsamples before and after incubation.

Resin-core incubations

In the field, we used a sequence of incubations of unsieved soil (forest floor plus 0–0.15 m depth mineral soil) in open, 40 mm diameter PVC tubes with resin bags at the bottom (resin cores, after DiStefano and Gholz 1986; Strader *et al.* 1989). The resin bags contained 14 mL of strongly acidic cation exchange resin (Dowex 50W-X8), with a cation exchange capacity of about 28 mmol ion charge (mmol_c) per bag; and 14 mL of strongly basic anion resin (J.T. Baker) with an anion exchange capacity of about 18 mmol_c/bag. The resins were saturated with NaCl before use to reduce interference with colorimetric analyses (we have subsequently found no interference problems with the Lachat Continuous Flow Analyzer System). Because the resin cores were open to water flow, the products of mineralization could leach from the soil column into the resin bags. However, the textural discontinuity between the resin bag and soil allowed the moisture content inside the cores to remain about 5–10% higher than in the surrounding soil (e.g., 0.35 g water/g dry soil outside the cores, and 0.37–0.39 g water/g dry soil inside the cores). After incubation, subsamples (10-g dry-mass equivalent) of soil in the cores were extracted in 100 mL of 2 M KCl, and the resin bags were extracted with 100 mL of 2 M KCl. This extraction procedure recovered all the exchangeable ammonium and nitrate from the soil samples, but only about 80% (±3%) of the ammonium and nitrate from the resins (as determined by recovery of spikes). Therefore, the resin-bag values were divided by 0.8 to account for the incomplete recovery. Ten resin cores were used in each stand for each sampling period. Net mineralization was calculated as the postincubation quantity of ammonium and nitrate in both the soil and resin bags, minus the quantity in the preincubation soil, as determined from paired subsamples. Annual net mineralization within the forest floor plus

0.0–0.15 m mineral soil was calculated by summing the net mineralization through the year: 2-month intervals from spring to fall, and up to a 5-month interval in winter. The conversion from rates per core to an area basis used bulk density data from Binkley and Sollins (1990). The series of incubations spanned from late 1985 through early 1987, providing one or two estimates of mineralization for each set of months.

We assessed the contribution of deeper soil to mineralization in June 1987, with 10 samples per stand. Sharpened tubes (0.35 m long) were pounded into the soil to 0.15 m, and then removed. A resin bag was placed at the bottom of the core, and the tube was pounded in an additional 0.15 m. The tube was removed, and another resin bag was placed in the bottom of the tube. The resulting core contained a sequence of forest floor to 0.15 m soil, a resin bag, 0.15 to 0.30 m soil, and another resin bag. After 30 days, the cores were removed, and the soils and resin bags were extracted as described above.

Buried-bag incubations

We also compared the forest floor to 0.15 m depth resin cores with a version of the more traditional method of buried-bag incubations. Ten resin cores in each stand were paired with 10 soil cores in PVC tubes that were placed intact into plastic bags and incubated for 30 days. Soils within the tubes inside bags remained less disturbed than if they had been transferred out of the tubes into bags.

¹⁵N pool dilution

A final experiment examined the effect of the resin core and buried-bag methods on immobilization of ¹⁵NH₄⁺. Five resin cores and five buried bags were used to estimate gross mineralization, immobilization, and net mineralization in each stand. At the beginning of the incubation period, 10 mL of water containing 100 µg of 99.3% ¹⁵NH₄Cl-N was injected with a syringe at a depth of about 10 mm below the bottom of the forest floor. After 30 days, the samples were extracted with KCl as described above. A diffusion procedure was used to recover both ammonium and nitrate in the KCl extract for analysis by mass spectrometry. Thirty millilitres of KCl extract was combined with 0.4-g DeVarda's alloy (to reduce nitrate to ammonia) in a 125-mL specimen cup. A scintillation vial containing 1 mL of 0.5 M HCl was placed in the cup, and the cup was capped and placed in an oven at 60°C for 18 h. At that time, the caps were removed and 2.0 mL of 3 M NaOH was added to convert ammonium in the KCl extract to ammonia, which was trapped as ammonium in the acidic solution in the scintillation vial. After 10 min, the cups were capped and placed in the oven at 90°C for 5 days. The procedure was repeated with the same scintillation vials and a second 30 mL aliquot of the KCl extract to increase the amount of N obtained for mass spectrometry analysis. The scintillation vials were then evaporated to dryness in a drying oven, and sent to Isotope Services, Inc. in Los Alamos, New Mexico, for analyses. Extracts of nonspiked soils averaged 0.375% ¹⁵N.

We used the equations of Kirkham and Bartholomew (1954) to calculate gross mineralization (ammonium produced from organic N) and immobilization (ammonium or nitrate immobilized by microbial or inorganic processes) from the ¹⁵N data:

$$[1] S = \frac{N_t - N_0}{t} \log_{10} \left(\frac{{}^{15}N_0 N_t}{{}^{15}N_t N_0} \right) / \log_{10} \left(\frac{N_t}{N_0} \right)$$

and

$$[2] I = \frac{N_t - N_0}{t} \log_{10} \left(\frac{{}^{15}N_0}{{}^{15}N_t} \right) / \log_{10} \left(\frac{N_t}{N_0} \right)$$

TABLE 1. Nitrogen availability among stands as gauged by a variety of net nitrogen mineralization indexes

Site and forest	Laboratory (mmol/kg)				In field resin cores (kmol·ha ⁻¹ ·year ⁻¹)		
	Anaerobic ammonium	Aerobic			Ammonium	Nitrate	Sum
		Ammonium	Nitrate	Sum			
Wind River							
Conifer	1.8 (0.2) <i>a</i>	0.2 (0.1) <i>a</i>	0.0 (0.0) <i>a</i>	0.2 (0.1) <i>a</i>	0.32	-0.28	0.04
Alder-conifer	7.1 (0.9) <i>b</i>	4.5 (0.7) <i>b</i>	1.1 (0.2) <i>b</i>	5.6 (0.7) <i>b</i>	1.93	7.07	9.00
Cascade Head							
Conifer	8.2 (1.0) <i>a</i>	4.1 (0.3) <i>a</i>	0.1 (0.0) <i>a</i>	4.2 (0.3) <i>a</i>	1.09	1.03	2.12
Alder-conifer	8.6 (0.9) <i>a</i>	4.6 (0.6) <i>a</i>	0.6 (0.1) <i>b</i>	5.2 (0.6) <i>a</i>	0.62	8.24	8.86

NOTE: Data are the means with 1 SE in parentheses ($n = 10$). Conifer and alder-conifer means (within a column and site) followed by the same letter are not significantly different ($p \leq 0.10$).

where

S is gross N supply rate (mmol·m⁻²·day⁻¹)

I is gross N immobilization rate (mmol·m⁻²·day⁻¹)

N_0 is total inorganic N (tracer plus nontracer) on day 0 (mmol·m⁻²)

N_t is total inorganic N at day t (mmol·m⁻²), with $t = 31$ days

$^{15}N_0$ is excess ^{15}N in inorganic pool on day 0 (mmol·m⁻²)

$^{15}N_t$ is excess ^{15}N in inorganic pool at day t (mmol·m⁻²)

Net mineralization was calculated as the difference between S [1] and I [2].

Our experiment violated three assumptions of these simple equations: the labelled N was not distributed uniformly throughout the cores; the rates of microbial N transformations were probably not constant during the long incubations; and some of the labelled N immobilized by microbes may have been remineralized during the incubations. Most studies using ^{15}N pool-dilution techniques use very short incubation periods (such as 1 day) to minimize any artifacts introduced by violation of these assumptions (cf. Davidson *et al.* 1992). Because our goal was to compare methods that use 30-day incubations, we chose to use these equations as the simplest approach to calculate the likely differences in the processes of mineralization and immobilization between stands and between methods. We recognize that the calculated rates of mineralization and immobilization may differ substantially from actual, varying rates during the incubation period, but expect the comparisons between methods and stands to be sound. We hope this first step of contrasting the effect of methods of in-field incubations prompts more detailed examination in the future.

Statistical analysis

We analyzed the effect of stand (within location), and the method of incubation, by t -tests with a probability of a type I error of 0.1 (Systat, Inc. 1985).

Results and discussion

Net mineralization rates

The assay methods gave very different patterns in net N mineralization (Table 1). Anaerobic incubations in the laboratory (7-day values extrapolated to a hectare basis for comparison) indicated mineralization of 2.6 kmol·ha⁻¹·year⁻¹ of N in the conifer stand at Wind River, which was 9 times the rate for aerobic incubations. The aerobic incubations in the laboratory, and resin-core incubations in the field, both gave very low values for this stand. The pattern of net mineralization in the field showed periods of both positive and negative rates (Fig. 1). The methods gave roughly similar

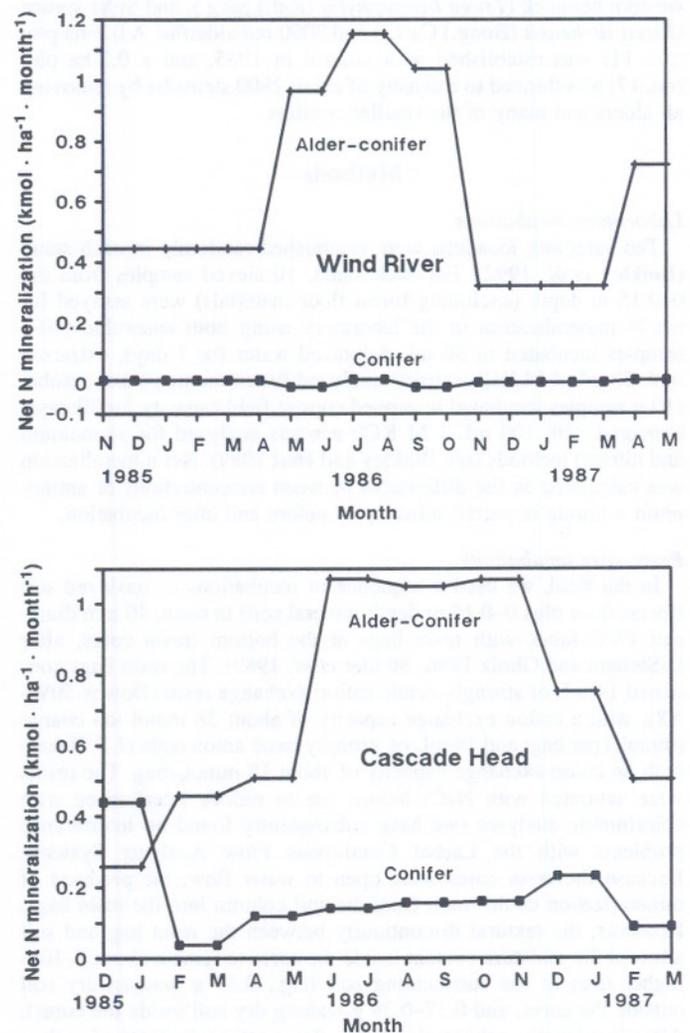


FIG. 1. Seasonal course of net nitrogen mineralization from resin-core incubations of forest floor and mineral soil to a depth of 0.15 m.

values for net mineralization in the alder-conifer stand at Wind River. The resin cores showed much more nitrification (80% of net mineralization) than was apparent in the aerobic incubations in the laboratory (20% of net mineralization). The resin core estimate was very high, with an average of 9.0 kmol·ha⁻¹·year⁻¹ (125 kg·ha⁻¹·year⁻¹).

TABLE 2. Net nitrogen mineralization by depth in resin cores during June 1987

Site and forest	Depth (m)	Net N mineralization (kmol/ha)		
		Ammonium	Nitrate	Sum
Wind River Conifer	0–0.15	0.16 (0.09)	–0.02 (0.00)	0.14 (0.09)
	0.15–0.30	0.03 (0.03)	0.00 (0.00)	0.03 (0.03)
	Sum	0.19	–0.02	0.17
Alder–conifer	0–0.15	1.71 (0.16)	0.51 (0.16)	2.22 (0.23)
	0.15–0.30	0.86 (0.06)	0.09 (0.03)	0.95 (0.09)
	Sum	2.57	0.60	3.17
Cascade Head Conifer	0–0.15	0.49 (0.14)	0.11 (0.05)	0.60 (0.15)
	0.15–0.30	0.23 (0.06)	0.01 (0.01)	0.24 (0.06)
	Sum	0.72	0.12	0.84
Alder–conifer	0–0.15	1.00 (0.22)	0.89 (0.16)	1.89 (0.34)
	0.15–0.30	0.38 (0.06)	0.24 (0.07)	0.62 (0.08)
	Sum	1.38	1.13	2.51

NOTE: Data are the means of 10 samples per stand and depth, with 1 SE in parentheses.

TABLE 3. Comparison of net mineralization values for resin cores and buried bags (forest floor to 0.15 m depth) incubated in June 1987

Site and forest	Method	Net mineralization (kmol/ha)		
		Ammonium	Nitrate	Sum
Wind River Conifer	Resin core	0.38a	0.07a	0.45a
	Buried bag	0.03b	–0.08b	–0.05b
Alder–conifer	Resin core	1.91a	1.36a	3.27a
	Buried bag	1.47a	0.49b	1.96b
Cascade Head Conifer	Resin core	0.11a	0.15a	0.26a
	Buried bag	0.43b	0.11a	0.54b
Alder–conifer	Resin core	0.69a	1.55a	2.24a
	Buried bag	1.06a	0.99a	2.05a

NOTE: All differences between conifer and alder–conifer forests were significant for both methods for ammonium, nitrate, and the sum of ammonium + nitrate. Resin-core and buried-bag means (within a column and forest type) followed by the same letter are not significantly different ($p \leq 0.10$).

The anaerobic method gave higher values than the aerobic method in both stands at Cascade Head. The resin-core method again gave higher nitrate values than the aerobic laboratory method.

Soil below 0.15 m showed substantial net mineralization (Table 2) in three of the four stands, with about 30% of the mineralization in June 1987 occurring in the 0.15–0.30 m depth (and 70% in the forest floor to 0.15 m depth). The conifer stand at Wind River was an exception, showing only negligible mineralization below 0.15 m. If these proportions for each stand held across all months, net mineralization in resin cores across the entire 0.0–0.30 m depth would be 0.05 kmol·ha⁻¹·year⁻¹ (0.7 kg·ha⁻¹·year⁻¹) for the Wind River conifer stand; 12.5 kmol·ha⁻¹·year⁻¹ (175 kg·ha⁻¹·year⁻¹) for the Wind River alder–conifer stand; 2.9 kmol·ha⁻¹·year⁻¹ (40 kg·ha⁻¹·year⁻¹) for the Cascade Head conifer stand; and 12.5 kmol·ha⁻¹·year⁻¹ (175 kg·ha⁻¹·year⁻¹) for the Cascade Head alder–conifer stand.

Comparing net mineralization by the resin-core and buried-bag methods, we found no consistent differences between the two (Table 3). The Wind River conifer stand showed negative net mineralization in buried bags, but 0.45 kmol·ha⁻¹ net mineralization in resin cores. Mineralization in resin cores in the Wind River alder–conifer stand was 1.65 times the value for buried bags. The conifer stand at Cascade Head, on the other hand, mineralized (net) only half as much N in resin cores as in buried bags, and no difference was observed between the two methods in the alder–conifer stand. The buried bags, however, generally showed less nitrification than the resin cores.

Transformation rates from ¹⁵N pool dilution

The ¹⁵N pool dilution experiment showed that resin-core estimates of N fluxes generally exceeded estimates obtained from buried-bag incubations (Table 4). Differences between the methods were generally highly significant ($p < 0.01$) for gross mineralization and net mineralization, but not significant ($p > 0.1$, except one case) for immobilization. We expected that microbial immobilization might differ between incubation methods, because the resin-core method would allow some of the inorganic N to leach to the resin bag before immobilization occurred (Binkley and Hart 1989). This potential difference appeared unimportant; net mineralization was about three-quarters of gross mineralization across sites and methods. We do not know how critical any violation of the assumptions inherent in these calculations may have been; however, these calculations do indicate that the differences we observed between the two incubation methods were derived from effects on rates of gross mineralization rather than immobilization.

N fluxes and ecosystem budgets

In an ecosystem N budget, the rate of net N mineralization in the soil must balance the N taken up by vegetation and the N lost from the system (through leaching or denitrification). We used data from the N budget for these stands (Binkley *et al.* 1992) to see if resin-core estimates of N mineralization matched the estimates for uptake plus losses. For the conifer stand at Wind River, soil uptake (0.1 kmol·ha⁻¹·year⁻¹)

TABLE 4. Nitrogen transformation rates calculated from ^{15}N pool dilution experiment (from 31-day incubations)

Site and forest	Method	N transformation ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)		
		Gross mineralization	Gross immobilization	Net mineralization
Wind River				
Conifer	Resin core	74 (9) <i>a</i>	45 (5) <i>a</i>	28 (4) <i>a</i>
	Buried bag	21 (3) <i>b</i>	23 (3) <i>b</i>	-2 (1) <i>b</i>
Alder-conifer	Resin core	173 (22) <i>a</i>	64 (14) <i>a</i>	109 (32) <i>a</i>
	Buried bag	96 (15) <i>b</i>	48 (5) <i>a</i>	48 (11) <i>b</i>
Cascade Head				
Conifer	Resin core	114 (20) <i>a</i>	47 (4) <i>a</i>	67 (20) <i>a</i>
	Buried bag	62 (11) <i>b</i>	40 (4) <i>a</i>	22 (8) <i>b</i>
Alder-conifer	Resin core	115 (29) <i>a</i>	59 (20) <i>a</i>	56 (12) <i>a</i>
	Buried bag	140 (13) <i>a</i>	48 (5) <i>a</i>	93 (12) <i>b</i>

NOTE: Data are means with 1 SE ($n = 5$) in parentheses. Means for each method (within a column and forest type) followed by the same letter are not significantly different ($p \leq 0.10$).

plus losses ($0.1 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) exceeded the resin-core estimate of N mineralization ($0.1 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) by $0.1 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, indicating that the mineralization estimate was too low to account for the N that must have been available to supply uptake for aboveground biomass plus losses. We have no information on belowground production and N requirement, but Vogt *et al.* (1986) reported an average requirement of about $4.3 \text{ kmol} \cdot \text{N} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (60 kg/ha) for the production of belowground biomass in cool, temperate forests. Therefore, inclusion of the N required for belowground production would have further increased the deficit in the net mineralization value.

For the alder-conifer stand at Wind River, uptake for aboveground biomass ($3.2 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) was lower than the estimated rate of N fixation ($5.4 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$), so that uptake of N from the soil would be $-2.2 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (representing fixed N that would supply belowground production). Losses of N totaled about $0.5 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$. The estimate of net N mineralization from resin cores ($12.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) exceeded the N needed for plant uptake and losses by $10.8 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, a difference that is likely far greater than the N required for belowground production.

In the Cascade Head conifer stand, net nitrogen mineralization in resin cores ($2.9 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) exceeded uptake ($1.7 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) plus losses ($1.0 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) by $0.2 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$. This appears to be a close balance for the overall N budget, but again the requirement for belowground production would likely be much greater than $0.2 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, indicating the calculated N budget is unbalanced. For the alder-conifer stand, N fixation ($6.1 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) again exceeded soil uptake for aboveground production ($5.9 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$); adding losses ($2.8 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) yields a total need for $2.6 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ from mineralization, compared with the resin-core estimate of $12.5 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, leaving a discrepancy of $9.9 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$.

We conclude that the resin-core measure of N mineralization likely underestimated the true rates in the conifer stands, and overestimated the rates in the alder-conifer stands. This incubation method probably identified the major differences

in net mineralization among sites and stands, but it failed to provide rates of N supply that would balance the N budgets of these stands. Such uncertainties in mineralization estimates have implications for construction of complete ecosystem N budgets. For example, Nadelhoffer *et al.* (1985) and Aber *et al.* (1985) calculated fine-root production in a wide range of forests by subtracting N leaching flux plus the flux of N into aboveground biomass from net N mineralization measured with buried bags. Any mineralized N not accounted for by the flux into aboveground biomass or leaching was assumed to have gone into production of fine roots. The complete N cycles for our four stands showed sobering discrepancies that we cannot reasonably attribute to the N flux for fine-root production. The substantial differences we found between the net mineralization rates in resin cores and buried bags, by conventional and ^{15}N pool dilution approaches, also suggest caution. Dyck *et al.* (1987) came to a similar conclusion after finding that in-field measurements of N mineralization were inadequate for estimating fine-root production in four stands of radiata pine (*Pinus radiata* D. Don).

Some studies have found encouraging (or discouraging) relationships between net mineralization estimates from *in situ* incubations and tree uptake (Aber *et al.* 1986; Nadelhoffer *et al.* 1985; Dyck *et al.* 1987; Smethurst and Nambiar 1989; Raison *et al.* 1990). Our results provide no evidence that resin cores provide better estimates of net mineralization than simpler *in situ* methods such as buried bags and closed-top tubes. The extra effort required for resin cores (including at least twice the analytical work) may not be worthwhile. In the absence of evidence favoring more complex methods, we have chosen in our current studies to use the closed-top tube method (Raison *et al.* 1987; Adams *et al.* 1989; Binkley and Hart 1989), which is similar to the buried-bag method used in this study except the core is not removed from the soil and sealed in a bag, and the soil remains less disturbed.

We conclude that the goal of "closing" the N budget was not possible in our stands, because of difficulty in estimating N fluxes accurately and because of the cumulative effects of summing inaccurate estimates into a single budget. We think that methods of estimating net mineralization will require substantially more testing (especially using ^{15}N techniques to

examine the components of net mineralization) before the accuracy of hectare-level rates can be determined. Preliminary plans have been proposed for a coordinated, international project to examine the ability of *in situ* methods to predict tree-available N (Binkley *et al.* 1990) that would be a step toward the goal of "closing" the N cycle in forest ecosystems (Landsberg *et al.* 1991).

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