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

DAN BINKLEY

Department of Forest Sciences, Colorado State University, Fort Collins, CO 80523, U.S.A.

AND

RANDY BELL AND PHILLIP SOLLINS

Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

Received June 25, 1991

Accepted January 17, 1992

BINKLEY, D., BELL, R., and SOLLINS, P. 1992. Comparison of methods for estimating soil nitrogen transformations in adjacent conifer and alder-conifer forests. Can. J. For. Res. 22: 858-863.

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.

BINKLEY, D., BELL, R., et SOLLINS, P. 1992. Comparison of methods for estimating soil nitrogen transformations in adjacent conifer and alder-conifer forests. Can. J. For. Res. 22 : 858-863.

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 conifers 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 Printed in Canada / Imprimé au Canada

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)

Comparison of methods for estimating soil altrogen transformation in adjacent confer and alder-confer forests

DAN BORGERS

separament of Provest Scientists, Colorado Matter Digitersting, Port Callury, CG 80522, U.S.A

10141

KARRY BELLARD PRILLIP SOLERS

¹ pariment of Divert Science, Program State University, Convolute, OR 973, J. U.S.A.

Rectaved June 23, 1993

Accepted January 17, 1992

Hissa EV, D. Britt, R., and Scittasi, P. 1992. Comparison of methods for equivaling and altrogun transformation of adjaces. The confer to a structure of the structure of the second structure of the

Nitrogen emisterninitiens were examined in two pairs of adjacent, 55-year and obtaits dominated by montane international and an antilongias in (Pearcolonge metalent (Nitrba Pranco)) and by confere and minogenerizing and alter (Alam robus Rivey) Nitrogen a statistic case examined in serebic and anaetobic inclubations in the labor of a robus each out robus (E-Mincubation on the toold Rates of antiogen minimalization and remobilization to recommed in the field immediately (PM-Jammanian. Net manogen minimalization and security) series of misin occe containing of the context field (E-M depth suit are should 9 kind hai 1 year 1 br the two inder-context stands, but streads all or the context field (E-M depth suit are should 9 kind hai 1 year 1 br the two inder-context stands, but streads all or the context field (E-M depth suit are should 9 kind hai 1 year 1 br the two inder-context stands, but streads all or the context field (E-M depth suit are should 9 kind hai 1 year 1 br the two inder-context stands, but streads all or the context field (E-M productive). What Rever site, and 2.1 kind hai 1 year 1 in the context stands, but all the hail or the context field (E-M productive). What Rever site, and 2.1 kind hai 1 year 1 in the context stands, but all the hail or the context field (E-M productive). What Rever site, and 2.1 kind hai 1 year 1 in the context stands, but all the hail or the context in the correst productive). What Rever site, and 2.1 kind hail on the context stands are the field (E-M depth depth dilation experiment showed the buried has buried in the left (E-M depth dilation of the correst stands). The stands of the correst productive of the standard of the standard in the standed at a consecution of the statistic of the information of the standard of the standard in the statistic of the standard of the statistic of the statistic discrepancies, prompting condor or therefore a the consecution of the statistic of the information of the statistic discrepancies, prompting condor or therefore a the consecu

Buotuitt, D., Burt, R., et Soli itse, P. (1921) Comparison of methods for asternative and merogen mani-sen above in acceleration of conference of the second s

Les mantionnations de l'avoits ont été catatitées pour dans pour de parpierants adjauents àgin de 30 inter et trainée par des confiders procipationen du sapin de l'ongéns (Providence) matters (Mirb.) Franco) es par des confiders et autor rouge Editais seine Bong) qui fits l'arons ha disponibilité de l'autor, a de de unitation de contaction de autor matterification au incontener, et anne des carettes area retrines et des incolutions de samp que l'influence d'autor, au matterification d'autoritation et annes par articles area retrines et des incolutions de samp que l'influence d'autor, an matterification d'autoritation et annes par articles area retrines et des incolutions de matterification de l'autor d'autor matterification de la carettes area dette que art ète commune dans des autorances de temp que l'influence de l'autor de matterification de l'autor matterification de la carettes area dettes particules de la des activités de l'autor de la carette de la devine de la devine configure, mais programa aufle d'an les amplianements antistication de productivité l'autor de la devine devine devine du pool de ¹N à montré que les autores de deux entréficier de productivité de la station de l'autor des devines devine devine du pool de ¹N à montré que les autoritations de deux productivité de la station de file de devines devines devine du pool de ¹N à montré que les autoritations de deux productivité de la station de file de des activités devines devines de devines devines de de devines de devines devines de l'autor autor caretter avec les materies de autoritation de prise des activités de devines de devines de devines de devines de devines devines devines de l'autor autor de la devine devine de devine de devines de devines de devines de devines de devines devines de l'autor autor de devines avec les materies de universification autor de devines de devines devines devines de devines devines devines devines avec les materies de devines de devines de devines de devines devines devinés devines devines devines de dev

increduction

some sense is sensed of Mitamachik under condex (Tarrant and greater availability of Mitamachik under condexy (Tarrant to d Millor (1965; Bollen and La 1965; Frankfun et al. 1965; Scile et al. 1978; Bornann und Delbell (1984; Birkfrey (1985; Minkfrey et al. 1978; Pan Magreet and Cole (1986); Mirroger availability in nots from such stands has near characterized differences to solitions of constant monther and sempermuse on well mixed soil complex; this approach may identify excitation, but the artifacts caused by sample mixing and differences in minarate quality that are reported for Minneffects of alder on Mitamover (Birkfoy and Inter 1989); We effects of alder on Mitamover (Birkfoy and Inter 1989); We in two pairs of stands, cach constituing one confirm mand and constitute and the ortifacts constitute and the 1989); We and the topological conditions are observe incontent and the optime of stands, cach constituting one confirm mand and an two pairs of stands, cach constituting one confirm mand and a two pairs of stands, cach constituting one confirm mand and a two pairs of stands, cach constituting one confirm mand and a two pairs of stands, cach constituting one confirm mand and a high-productivity state with very high W confirm was on fired the differences between stands among methods of

sing N (ransionantions; some positive antipats of performance) of a state of the solution of t

Sile description

Bach analy and were established and measurable to reach an a the USDA Forescience in the formation in the USDA Forescience in the Multicriation of the Multi

1304

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-yearold 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 buriedbag 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:



and

2]
$$I = \frac{\frac{N_t - N_0}{t} \log_{10} \left(\frac{1^5 N_0}{1^5 N_t}\right)}{\log_{10} \left(\frac{N_t}{N_0}\right)}$$

TABLE 1. Nitrogen availabilit	y among stands as gauge	d by a variety of	net nitrogen mineraliza	ation indexes
-------------------------------	-------------------------	-------------------	-------------------------	---------------

		Laboratory (Ref to establish to RSVE excerning t				
Site and forest	Annahia	Aerobic			In field resin cores $(\text{kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1})$		
	ammonium	Ammonium	Nitrate	Sum	Ammonium	Nitrate	Sum
Wind River	BOTH CHILD HOLD	01 104 1891	sart and	and the second	in the assistance of the	Successores.	
Conifer	1.8 (0.2)a	0.2 (0.1)a	0.0 (0.0)a	0.2 (0.1)a	0.32	-0.28	0.04
Alder-conifer	7.1 (0.9)b	4.5 (0.7)b	1.1 (0.2)b	5.6 (0.7)b	1.93	7.07	9.00
Cascade Head		en AL O upportable	a na si sila	Land Lands			
Conifer	8.2 (1.0)a	4.1 (0.3)a	0.1 (0.0)a	4.2 (0.3)a	1.09	1.03	2.12
Alder-conifer	8.6 (0.9)a	4.6 (0.6)a	0.6 (0.1)b	5.2 (0.6)a	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 ($p \le 0.10$).

where

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

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

No is total inorganic N (tracer plus nontracer) on day 0 $(mmol \cdot m^{-2})$

 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 \cdot 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 15N 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 resincore 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).

		Net N mineralization (kmol/ha)					
Site and forest	Depth (m)	Ammonium	Nitrate	Sum			
Wind River		and the second s	the state of the s	Date State			
Conifer	0–0.15 0.15–0.30 Sum	0.16 (0.09) 0.03 (0.03) 0.19	-0.02 (0.00) 0.00 (0.00) -0.02	0.14 (0.09) 0.03 (0.03) 0.17			
	Sulli	0.19	-0.02	0.17			
Alder–conifer	0–0.15 0.15–0.30 Sum	$ \begin{array}{c} 1.71 & (0.16) \\ 0.86 & (0.06) \\ 2.57 \end{array} $	0.51 (0.16) 0.09 (0.03) 0.60	2.22 (0.23) 0.95 (0.09) 3.17			
Cascade Head							
Conifer	0–0.15 0.15–0.30 Sum	0.49 (0.14) 0.23 (0.06) 0.72	0.11 (0.05) 0.01 (0.01) 0.12	0.60 (0.15) 0.24 (0.06) 0.84			
Alder-conifer	0-0.15 0.15-0.30	1.00 (0.22) 0.38 (0.06)	0.89 (0.16) 0.24 (0.07)	$1.89 (0.34) \\ 0.62 (0.08)$			
	Sum	1.38	1.13	2.51			

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

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

a	ingenes to nei Mercerer	Net mineralization (kmol/ha)					
forest	Method	Ammonium	Nitrate	Sum			
Wind River	Bannin V.	mats form ad	roid hove	a strong to			
Conifer	Resin core	0.38a	0.07 <i>a</i>	0.45a			
	Buried bag	0.03 <i>b</i>	-0.08b	-0.05b			
Alder-conifer	Resin core	1.91a	1.36a	3.27 <i>a</i>			
	Buried bag	1.47 <i>a</i>	0.49b	1.96b			
Cascade Head							
Conifer	Resin core	0.11 <i>a</i>	0.15a	0.26a			
	Buried bag	0.43 <i>b</i>	0.11 <i>a</i>	0.54b			
Alder-conifer	Resin core	0.69 <i>a</i>	1.55a	2.24a			
	Buried bag	1.06 <i>a</i>	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 ($p \le 0.10$).

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 buriedbag methods, we found no consistent differences between the two (Table 3). The Wind River conifer stand showed negative net mineralization in buried bags, but $0.45 \text{ kmol} \cdot ha^{-1}$ 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 $(0.1 \text{ kmol} \cdot \text{ha}^{-1} \cdot \text{year}^{-1})$

		N transformation (mmol $\cdot m^{-2} \cdot day^{-1})$					
Site and forest	Method	Gross mineralization	Gross immobilization	Net mineralization			
Wind River	0.0100.0	(10.0) 10.0	62.0				
Conifer	Resin core	74 (9)a	45 (5)a	28 (4)a			
	Buried bag	21 (3) <i>b</i>	23 (3)b	-2(1)b			
Alder-conifer	Resin core	173 (22)a	64 (14)a	109 (32)a			
	Buried bag	96 (15)b	48 (5)a	48 (11)b			
Cascade Head	0						
Conifer	Resin core	114 (20) <i>a</i>	47 (4) <i>a</i>	67 (20)a			
	Buried bag	62 (11) <i>b</i>	40 (4) <i>a</i>	22 (8)b			
Alder-conifer	Resin core	115 (29) <i>a</i>	59 (20)a	56 (12)a			
	Buried bag	140 (13) <i>a</i>	48 (5)a	93 (12)b			

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

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 ($p \le 0.10$).

plus losses (0.1 kmol·ha⁻¹·year⁻¹) exceeded the resin-core estimate of N mineralization (0.1 kmol·ha⁻¹·year⁻¹) by 0.1 kmol·ha⁻¹·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 kmol N·ha⁻¹·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 kmol·ha⁻¹·year⁻¹) was lower than the estimated rate of N fixation (5.4 kmol·ha⁻¹·year⁻¹), so that uptake of N from the soil would be $-2.2 \text{ kmol·ha}^{-1} \cdot \text{year}^{-1}$ (representing fixed N that would supply belowground production). Losses of N totaled about 0.5 kmol·ha⁻¹·year⁻¹. The estimate of net N mineralization from resin cores (12.5 kg·ha⁻¹·year⁻¹) exceeded the N needed for plant uptake and losses by 10.8 kmol·ha⁻¹·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 kmol·ha⁻¹·year⁻¹) exceeded uptake (1.7 kmol·ha⁻¹·year⁻¹) plus losses (1.0 kmol·ha⁻¹·year⁻¹) by 0.2 kmol·ha⁻¹·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 kmol·ha⁻¹·year⁻¹, indicating the calculated N budget is unbalanced. For the alder–conifer stand, N fixation (6.1 kmol·ha⁻¹·year⁻¹) again exceeded soil uptake for aboveground production (5.9 kmol·ha⁻¹·year⁻¹); adding losses (2.8 kmol·ha⁻¹·year⁻¹) yields a total need for 2.6 kmol·ha⁻¹·year⁻¹ from mineralization, compared with the resin-core estimate of 12.5 kmol·ha⁻¹·year⁻¹, leaving a discrepancy of 9.9 kmol·ha⁻¹·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 ¹⁵N 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 ¹⁵N 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).

Acknowledgements

For help in the field and laboratory, we thank Ute Riesenkonig, Don Sachs, and Carol Glassman. Steve Hart, Xiaoming Zou, and Tim Strickland assisted with the ¹⁵N experiment and data analysis. Insights provided by R. Yanai, D. Valentine, S. Hart, and I. Burke greatly improved the manuscript. Funding was provided by National Science Foundation grant BSR-841678 and by McIntire–Stennis project 0133245. This paper is a contribution of the H.J. Andrews Ecosystem Research Group.

- Aber, J., Melillo, J., Nadelhoffer, K., et al. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologia, 66: 317–321.
- Adams, M.A., Polglase, P.J., Attiwill, P.M., and Weston, C.J. 1989. *In situ* studies of nitrogen mineralization and uptake in forest soils; some comments on methodology. Soil Biol. Biochem. 21: 423–429.
- Binkley, D. 1983. Ecosystem production in Douglas-fir plantations: interaction of red alder and site fertility. For. Ecol. Manage. 5: 215–227.
- Binkley, D., and Hart, S. 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. 10: 57-112.
- Binkley, D., and Sollins, P. 1990. Factors determining differences in soil pH in adjacent conifer and alder–conifer stands. Soil Sci. Soc. Am. J. 54: 1427–1433.
- Binkley, D., Lousier, J.D., and Cromack, K., Jr. 1984. Ecosystem effects of Sitka alder in a Douglas-fir plantation. For. Sci. **30**: 26–35.
- Binkley, D., Powers, R.F., Pastor, J., and Nadelhoffer, K. 1990. Protocol for testing measures of nitrogen availability in forest soils. *In* Impact of intensive harvesting on forest site productivity. *Edited by* W. Dyck and C. Mees. Forest Research Institute Rotorua, New Zealand. Bull. 159. pp. 111-126.
- Binkley, D., Sollins, P., Bell, R., et al. 1992. Biogeochemistry of adjacent conifers and alder/conifer stands. Ecology, 73. In press.
- Bollen, W.B., and Lu, K.C. 1968. Nitrogen transformations in soils beneath red alder and conifers. *In* Biology of alder. *Edited by* J. Trappe, J. Franklin, R. Tarrant, and G. Hansen. USDA Forest Service, Portland. pp. 141–148.
- Bormann, B., and DeBell, D. 1981. Nitrogen content and other soil properties related to age of red alder stands. Soil Sci. Soc. Am. J. 45: 428–432.

- Cole, D., Gessel, S., and Turner, J. 1978. Comparative mineral cycling in red alder and Douglas-fir. *In* Utilization and management of alder. *Edited by* D. Briggs, D. DeBell, and W. Atkinson. USDA For. Serv. Gen. Tech. Rep. PNW-70. pp. 327–337.
- Davidson, E.A., Hart, S.C., and Firestone, M.K. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology. In press.
- DiStefano, J., and Gholz, H. 1986. A proposed use of ion exchange resin to measure nitrogen mineralization and nitrification in intact soil cores. Commun. Soil Sci. Plant Anal. **17**: 989–998.
- Dyck, W., Mees, C., and Hodgkiss, C. 1987. Nitrogen availability and comparison to uptake in two New Zealand *Pinus radiata* forests. N.Z. J. For. Sci. 17: 338–352.
- Franklin, J., Dyrness, C., Moore, D., and Tarrant, R. 1968. Chemical soil properties under coastal Oregon stands of alder and conifers. *In* Biology of alder. *Edited by* J. Trappe, J. Franklin, R. Tarrant, and G. Hansen. USDA Forest Service, Portland, Oreg. pp. 157-172.
- Kirkham, D., and Bartholomew, W.V. 1954. Equations for following nutrient transformations in soil, using tracer data. Soil Sci. Soc. Am. Proc. 18: 33–34.
- Landsberg, J.J., Kaufmann, M.R., Binkley, D., et al. 1991. Evaluating progress towards closed forest models based on fluxes of carbon, water and nutrients. Tree Physiol. 9: 1–15.
- Miller, R.E., and Tarrant, R.F. 1983. Long-term response of Douglasfir to ammonium and nitrate fertilizer. For. Sci. **29**: 127–137.
- Nadelhoffer, K., Aber, J., and Melillo, J. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology, 66: 1377–1390.
- Raison, R.J., Connell, M.J., and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral-N in situ. Soil Biol. Biochem. 19: 521–530.
- Raison, R.J., Khanna, P.K., Connell, M.J., and Falkiner, R.A. 1990. Effects of water availability and fertilization on nitrogen cycling in a stand of *Pinus radiata*. For. Ecol. Manage. **30**: 31–44.
- Smethurst, P.J., and Nambiar, E.K.S. 1989. An appraisal of the in situ soil-core technique for measuring nitrogen uptake by a young *Pinus radiata* plantation. Soil Biol. Biochem. **21**: 939–942.
- Strader, R., Binkley, D., and Wells, C. 1989. Nitrogen mineralization in high elevation forests of the Appalachians. I. Regional patterns in southern spruce-fir forests. Biogeochemistry, 7: 131–145.
- Systat, Inc. 1985. SYSTAT: the system for statistics. Systat, Inc., Evanston, Ill.
- Tarrant, R.F., and Miller, R. 1963. Soil nitrogen accumulation beneath a red alder–Douglas-fir plantation. Soil Sci. Soc. Am. Proc. 37: 231–234.
- Van Miegroet, H., and Cole, D. 1984. The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J. Environ. Qual. 13: 586–590.
- Vogt, K., Grier, C., and Vogt, D. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv. Ecol. Res. 15: 303–377.

economic the components of net annualization) octoor the accuracy of hectare level rates can be determined. Preliminacy plans have been proposed for a coordinated, international project to axamine the ability of in star methods to predict tree-available M (Binkloy et al. 1990) that would be a map toward the poal of "closing" the M cycle in forest ecosystems (Landsbergles et al. 1991).

A channel wingements

For help in the field and biomatory, we thank U is Riesenlowing Oon Eachs, and Carol Glassman, Share Hart, Emeraing Zoa, and Tim Strickland metoded with the ¹⁵N experiment and data analysis. Insights provided by R. Yanai, D. Valentins, S. Hart, and I. Bucke genuity reproved the monuscript. Funding was provided by National Science Foundation (card BSR-841618 and by Melature-Stemma project 0133245. This paper is a contribution of the H.I. Andrews Ecosystem Research Gamp.

- Aber, L. Melillo, L. Nadelhoffer, K. et al. 1985. Fina reactureawar in fronst eleasystems in relation to quantity and form of nitregoa availability: a comparison of two methods: Octologia, 662 377–321. Adams, M.A., Polgiase, P.L. Annolli, P.M. and Weston, C.L 1989, In the indicator introgen mirror izzation and uptation in forest with some compares of methodology. Soil Bird Hitschem 20, 403–429. Heatdory, D. 1981. Ecosystem production in Douglas for giorateirase internation of red alder and site fortility. For Bool, Manage, 58 2015–229.
- Bulley, D., and Hart, S. 1939. The evenponents of air-regen availbility assessments in forced with Adv. Sol. Soc. 10, 57, 112
- Binkley, D., and Sollins, P. 1990. Factors determining differences in soil pH in pdjarmt conffer and addet-donifer annula. Soil Sci. Soc. Am. 4, 581 (427) (147).
- Binkley, D., Lousiei, J.D., and Grumari, K., B. 1966. Borsystem Fflects of Siller alder in a treightenin plantation. For, Sci., 36, 26–35.
- Binales, D., Powen, R.F., Zantos, And Statelhoffian, K. 1990, Protonol for multing meanings of antrogon rivallability in florget suffic, in Impact of intensive horizonting on faces: site productly groups fation by W. Dyrk and C. Firene Forcest Research instituan Restricts, New Network, Bull. 159, op. 111-126.
- Buskley, D. Sollins, P. Boll, R. et al. 1992. Biogeoglamizity of adjacent conferent and addressoniter frauds. Boology, 73. In press
- between real biller and construct in Biology of aidin. Edited by https://www.icenter.com/construction/icenter/ https://www.icenter.com/construction/ construction/ on tail-148
- Bormann, B., and Delbell, D. 1981, Mithegon content and other solf proporties related to and of and adder standar. Soli Sol: Dec. Am. J. 45, 428–413.

- Fole, D., Freatel, S., and Turnar, J. 1978. Computative material spotness in red atler and Douglas-fit. In Utilitzation and international relater frame for Di Briege, D. Deffell, and W. Alkinson, India's For Serv. Den. Tech. Ren. PNW 30, ed. 322-331.
- Deviation, F.A., Hart, S.C., and Freestone, M.E. 2002. Internal cyclifter of always in soils, of a mature confidency forest. F. chapter in parts
- (institution) X. and Chook M. Posta, A proposition and the formation in market resting to anomality outcoper maneralization and with freethous in market and process (Commun. Soil Ser. Plant Anal. 17, 2019 2018).
- Dyck, W., Micek C., and Hadghba, C. 1987. Electron evaluation and comparison in up also in two New Zentana Plans and the forests N.Z. J. For. 8rt. 17, 338–353.
- Franktin, J., Dyares, C., Moore, D., and Terrar, S. 1998. Chambals and progenics under constal Orogon stands of sciences, contexts in Biology of idea, Science for J. Trappe, J. Proceeding 8, 10 process.
- and G. Banerri, O.S. Virontal Service, Witzinkovice, e. 1975. Kikkhem, D. and Brenndeantw, W. V. 1954. Equations for following matricest structures in and, saling functor that Soft Serv
- Landsberg, J.J., Kaufrecht, M.R., Birfdieg, D. & ed. (1991; Bepticities programs forwards closed foreast models based on Parses of carlingwater and marifems. Proc. Pressol, 9: 1–15.
- Stitler, R.E. and Factari, R.F. 1983. Long-term processed Disequirefit to formitonian and aitesis fostilizer. For Set 28: 127–137.
- Madolholfer, K., Aber, J., and Mahino, J. 1992. Proceeds, not prime production, and and attragen availability a new hypothesis. Ecology 66 (1977) 1900.
- Ruisson, R.J., Connell, M.J., and Khanno, P.K. (1977) Methodishies for subsymp fluxes of web matches in vitational Red (Nation), 19, 521–330.
- Raison, R.J., Stanana, R.K., Consult, M.J., and E.H. Iner, K.M. 1990 Effects of water availability and furthization on introgen cycling in a stand of Phone architect For Ecol. Manager. 31: 11–44.
- Simultunet, P.J., and Sambury, E.K.S. (1989) An approximated in site and constant to measuring attropying spectra symmetry of mellonic attraction. Soil Block Bitterberg, 24: 949–940.
- Statistic, E., Birklay, O., and Wells, C. 1959. Nitrogen mean linearch in right elevation incerts of the Applications. I: Regional process in right elevation. In Journal, Brownia, B. 2011.
- Sympto, Ion. 1985. EVENET the system for staticities System for . Eventstee, Hi
- Farrati, R.F., and Muller, R. 1963. Soil airogen neu landarion bantaris. a red Milder-Douglos-fit plantation. Soil Sci. Soc. Am. Proc. 37. 234-214.
- Van Mildernet, H., and Cole, D. 1984. The impact of nitrificance on soil addression and cannot leaching in a red attlet of oversion. I. Environ, Qual. 13: 586–590.
- Augt, K., Gehr, C. and Vogt, D. 1986. Production, turnevect 2nd matricest dynamics of above- and belowground demination works forests. Adv. Ecol. Roy. 13: 101–177.