

Respiration, nitrogen fixation, and mineralizable nitrogen spatial and temporal patterns within two Oregon Douglas-fir stands

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Abstract: Substrate respiration, mineralizable nitrogen, and nitrogen fixation rates, substrate moisture content, and temperature were measured in trenched and undisturbed plots within two western Oregon Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. The stands represent two different environments and ages. Woods Creek, the site of the lower elevation mature 70-year-old stand, is located in the Willamette Valley near Philomath, Oregon. The H.J. Andrews Forest, site of the higher elevation old-growth stand, lies on the western slopes of the Oregon Cascades. Mineralizable nitrogen rates were 1.3 times higher at Woods Creek than at the H.J. Andrews Forest; nitrogen fixation was 1.3 times greater at Woods Creek than at the old-growth H.J. Andrews stand. Litter evolved more CO₂ and yielded more than 3 times the mineralizable nitrogen rates of logs and soils. Woods Creek logs had significantly higher nitrogen fixation than mineral soils ($p < 0.001$); there was greater nitrogen fixation in logs and soils sampled at 0–4 cm than at 4–20 cm ($p < 0.03$). At the old-growth H.J. Andrews Forest site, nitrogen fixation was significantly greater in logs than in soils ($p < 0.001$). Nitrogen fixation tended to be higher in samples from 0 to 4 cm within logs and mineral soils than in samples from 4 to 20 cm. There were no statistical differences in mineralizable nitrogen at the H.J. Andrews Forest between logs and mineral soils either by type or by depth at the $p < 0.05$ level. Neither site yielded a statistically significant difference in mineralizable nitrogen between trenched log and soil plots and nontrenched log and soil plots. Mineralizable nitrogen declined with depth, but this pattern was only statistically significant at Woods Creek ($p < 0.005$).

Résumé : La respiration du substrat, les taux d'azote minéralisable et de fixation de l'azote, le contenu en humidité du substrat et sa température ont été mesurés dans des parcelles isolées et des parcelles non perturbées dans deux peuplements de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de l'Ouest de l'Orégon. Ces peuplements représentent deux environnements et deux âges différents. À Woods Creek, le site de basse altitude, on retrouve un peuplement mature de 70 ans localisé dans la vallée de Willamette près de Philomath en Orégon. La forêt H.J. Andrews, le site de plus haute altitude, est composée d'un vieux peuplement et repose sur les pentes ouest des Cascades de l'Orégon. Le taux d'azote minéralisable était 1,3 fois plus élevé à Woods Creek qu'à la forêt H.J. Andrews; la fixation de l'azote était 1,3 fois plus élevée à Woods Creek qu'à la forêt surannée H.J. Andrews. La litière a libéré plus de CO₂ et avait un taux d'azote minéralisable équivalent à plus de 3 fois celui du bois mort et des sols. À Woods Creek, le bois mort fixait significativement plus d'azote que les sols minéraux ($p < 0,001$); il y avait une plus grande fixation de l'azote dans le bois mort et les sols échantillonnés à une profondeur de 0–4 que 4–20 cm ($p < 0,03$). À la forêt surannée H.J. Andrews, la fixation de l'azote était significativement plus élevée dans le bois mort que dans les sols ($p < 0,001$). La fixation de l'azote tendait à être plus élevée dans les échantillons prélevés à 0–4 cm dans le bois mort et le sol minéral que dans les échantillons prélevés à 4–20 cm. Il n'y avait pas de différences statistiques pour l'azote minéralisable à la forêt H.J. Andrews entre le bois mort et le sol minéral autant par type que par profondeur ($p < 0,05$). Aucun des deux sites n'a montré de différence statistiquement significative pour l'azote minéralisable entre le bois mort ou les parcelles de sol isolés et le bois mort ou les parcelles de sol non isolés. L'azote minéralisable diminuait avec la profondeur mais ce patron n'était significatif que Woods Creek ($p < 0,005$).

[Traduit par la Rédaction]

Introduction

Levels of substrate respiration, nitrogen fixation, and mineralizable nitrogen may not only be influenced by microclimate but may be specifically influenced by forest stand substrate type and overstory composition, forest practices, successional patterns, and geography (Harmon et al. 1986, 1990; Schlesinger 1977; Vogt et al. 1986; Sprent and Sprent 1990; Velazquez-Martinez 1990; Vitousek et al. 1982). The rate at which carbon is released as CO₂, nitrogen is fixed, and organic nitrogen is transformed to inorganic form in forest litter, logs, and soils can be controlled by either moisture, temperature, or combinations of both factors as well as by interactions with substrate

Received May 27, 1996. Accepted August 9, 1996.

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Table 1. Climate information for Woods Creek (National Oceanic and Atmospheric Administration 1985) and the H.J. Andrews Forest (Forest Science Department Databank, Oregon State University, 1991).

	Jan.–June	July–Oct.	Nov.–Dec.
Woods Creek			
Temperature (°C)	9.1	16.3	9.7
Precipitation (cm)	9.5	5.0	17.7
H.J. Andrews Forest			
Temperature (°C)	5.2	13.6	2.0
Precipitation (cm)	19.4	7.4	35.4

properties (Meentemeyer and Berg 1986; Moore 1986; Zak et al. 1989; Myrold 1987). Living roots have also been shown to impact total substrate respiration, nitrogen fixation, and mineralizable nitrogen in conjunction with substrate moisture and temperature (Bowden et al. 1993). These decomposition-dependent processes, substrate respiration, nitrogen fixation, and mineralizable nitrogen, however, have not been examined concurrently in different successional stages in Oregon Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests when substrate moisture and temperature have been monitored.

In order to isolate the effect of living roots, trenching was introduced as part of the study design. As a result, the relationship of substrate respiration, nitrogen fixation, and mineralizable nitrogen to moisture content and temperature within Douglas-fir stands was determined at sites that contained both trenched and control plots.

Study area

Western Oregon's maritime climate is characterized by temperatures with narrow diurnal fluctuations, relatively wet winters, and drier summers. The study sites lie in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) vegetation zone that extends from British Columbia to southern Oregon (Franklin and Dymess 1973). Douglas-fir stands comprise a large portion of this zone.

Plots 3 × 5 m, with northerly aspects and slopes <20%, were located within two Douglas-fir stands aged 70–80 and 450 years, respectively. The younger Douglas-fir stand (elevation 543 m) was situated 24 km southwest of Philomath, Oregon at 44°28'30"N latitude, 123°29'W longitude in the Woods Creek watershed. The overstory was composed of Douglas-fir. The understory vegetation was composed of swordfern (*Polystichum munitum* (Kaulf.) Presl), Canadian bunchberry (*Cornus canadensis* L.), and various mosses. Approximately 5.5 Mg·ha⁻¹ woody debris >2.5 cm in diameter is typical for the Woods Creek vicinity (Fogel and Hunt 1979).

Woods Creek forest floor, composed of O₁ and O₂ horizons, averaged 3–5 cm in depth. The O₁ horizon contains visually recognizable, undecomposed needles as well as bud scales, insect frass, and moss. The O₂ layer is characterized by both dark, crusty, distinguishable organic matter containing fungal mycelia and indistinguishable, moist, slightly sticky humus.

Woods Creek mineral soils are gravelly loams (Slickrock Series) derived from weathered sandstone (Knezevich 1975). The A₁ horizon is soft, very friable, and slightly plastic, ex-

tending from 0 to 15 cm in depth. The A₃ horizon is slightly hard, friable, with 20% pebbles and ranges from 15 to 35 cm. Average C/N ratios are 21.0 and 17.7 for the A₁ and A₃ horizons, respectively (Huddleston 1982).

Temperature and precipitation for the sites are reported for 6-, 4-, and 2-month periods, respectively, so that seasonal differences between the sites can be demonstrated. Site differences, for example, exist in winter snowfall. Meteorological summaries for Corvallis, Oregon, located 32 km from the Woods Creek site, are depicted in Table 1 (National Oceanic and Atmospheric Administration 1985).

The old-growth stand (elevation 937 m) was located 104 km east of Eugene, Oregon, at 44°15'30 N, 122°09'30 W in the H.J. Andrews Experimental Forest. At the H.J. Andrews Forest site, stands were composed predominantly of Douglas-fir with western hemlock and scattered western redcedar (*Thuja plicata* Donn ex D. Donn). Plots were situated in a blueberry (*Vaccinium* spp.), twinflower (*Linnaea borealis* L.), and Oregon-grape (*Berberis nervosa* Pursh) understory. H.J. Andrews old-growth stands near the site are reported to have a range of fallen coarse debris from 115 to 143 Mg·ha⁻¹ (Harmon et al. 1986; Sollins et al. 1987). Grier and Logan (1977) and Sollins et al. (1987) defined coarse woody debris as material >15.0 cm in diameter.

H.J. Andrews soils near the chosen stand were classified as Dystrichrepts with A horizons characterized as loam to loamy sand (Brown 1975). Litter O₁₁ horizons range from 6 to 4 cm and consist of leaves, twigs, and cones. Slightly decomposed O₁₂ horizons occur from 4 to 0 cm. Soil A₁ horizons occur between 0 and 13 cm. Soil A₃ horizons underlie A₁ horizons from 13 to 28 cm. The A horizon C/N ratios can vary from 24 to 28. Soil organic matter (SOM) has been measured as 24–25% of the total soil matrix; soil pH ranges between 4.33 and 4.88 (Aguilera et al. 1993).

Based on a 27-year record, in situ average monthly precipitation and temperature at the H.J. Andrews Forest site are reported in Table 1 (Forest Science Department Databank, Oregon State University, 1991).

Methods

Research design

Stands were selected based on whether the sites represented either uniform Douglas-fir old-growth or mature successional stages, as well as the presence of suitable undisturbed, well-decayed logs. Since no stands could be found in close proximity that met both these criteria, i.e., that had not undergone disturbance, sites were widely separated. Both sites had a history of past research.

Within each site, the study utilized a split plot design with whole plot effects (substrate and trenching treatment) and subplot effects (depth). The whole plot had a 2 × 2 factorial structure and the subplot had a one-way treatment structure. The experimental units at each site consisted of eight log and eight mineral soil plots. At each site, the study involved sampling and two depths, 0–4 and 4–20 cm, randomly within log and soil plots. Litter was sampled overlying either log or soil plots.

Field assessment

The 3 × 5 m plots were chosen to conform to the shape of the well-decayed logs at the sites. The log plots were cut to 5 m length if the logs were longer in their natural state. The size of plots was based on the need to achieve substrate uniformity, create the potential for

determining differences in plots with severed roots, and preserve structural integrity of the plots as much as possible during destructive seasonal sampling. All logs were decay class 4 or 5 (Triska and Cromack 1980).

Destructive plot sampling was chosen as an appropriate sampling method because it is difficult to accurately assess the area or patterns of CO₂ diffusion to collection chambers either buried in substrates or located on the surface. Living moss was considered an integral part of the litter layer.

Trenching was undertaken to isolate the direct and indirect effects of roots on CO₂ production, mineralizable nitrogen rates, and nitrogen fixation. The trenching treatment was assigned to four of the eight randomly selected plots in litter, logs, and mineral soils. Trenching involved excavating ditches 30 cm deep and 15 cm wide peripheral to each selected 15-m² plot. Roots within the trenched areas were severed. However, it is likely that roots growing laterally at depths >30 cm and then vertically into the center of the plot were not severed by the trenches. The effect of these roots is not known. Aboveground understory vegetation on trenched plots was removed and kept clean by periodic clipping.

Substrate moisture content, CO₂ evolution, nitrogen fixation, and mineralizable nitrogen were sampled monthly from May to November during 1989 and 1990. August substrate temperature data were not collected in 1989 on one site, but full collection of substrate temperature data occurred from May to November in 1990. Sampling at Woods Creek, the younger Douglas-fir site, began in May, but snow remaining on the old-growth site prevented sampling until June. Data collection at the sites occurred near the first of each month.

Substrate moisture contents were calculated gravimetrically and later converted to volumetric moisture contents, using fresh sample weights taken in the field. The moisture content samples were dried at 70°C for 72 h in a forced draft Cenco oven. Substrate temperatures were measured on each plot and for each depth on the plots using a dial probe thermometer. Readings were taken between 09:00 and 12:00 on the sampling dates.

CO₂ evolution field methods

Respiration measurements followed the Sollins et al. (1987) technique with modification. Samples of 216 cm³ from each plot were placed immediately in 500-cm³ sealed Mason jars for 5 h and incubated at field temperature. The Mason jar lids contained serum stoppers that permitted 10-mL gaseous samples to be withdrawn with a syringe and placed in Vacutainers (Beckton Dickenson) for later processing on a gas chromatograph (GC).

The 10-mL gaseous samples were withdrawn immediately after placing the samples in the sealed containers. After 5 h, a second 10-mL sample was withdrawn from the Mason jar and placed in an appropriately labelled Vacutainer. Prior to utilizing the Vacutainers, tests were run to determine contamination by naturally occurring amounts of CO₂. Vials were also tested for leakage by inserting a known amount of CO₂ and testing for a decline in the amount over time. Leakage and contamination were considered negligible; the number of Vacutainers that did not retain a vacuum was <1%. Replicate sampling easily overcame the potential problem of contamination.

The first gaseous sample extracted from the incubation jar was termed the initial sample; it represented preincubation levels of CO₂. The second sample, designated as the termination sample, represented CO₂ evolved during the incubation period. Net amounts of CO₂ evolved were determined by subtracting the initial sample from the termination sample. At Woods Creek, Griffiths et al. (1990), in a seasonal study of ectomycorrhizal mats in mineral soil, found that respiration rates were constant up to 4 h using an initial 1-h resting period and unsieved mineral soil samples. In preliminary tests, we found rates constant up to 6 h; therefore, a 5-h sampling period was considered appropriate. Since each sample comprised 216 cm³, the headspace of each Mason jar sample was considered theoretically the same. As a result, no adjustment was made in the total amounts of CO₂

in relation to the amount taken from the Vacutainer for analyses on the GC.

Soil samples sieved through a 2-mm mesh were used for respiration measurements in this study. Soils were sieved to insure that the samples contained only mineral soil. Fine roots sieved from soil samples were replaced after 2-mm sieving occurred. Roots were retained within the soil and litter samples because the root respiration pool was considered an inherent part of litter, log, and soil substrate respiration. It was also possible that CO₂ evolved from plots that had severed roots might be different from CO₂ in plots with roots that had not been severed. Litter and log samples were taken as intact cores with roots enclosed. The values given for substrate CO₂ respiration, therefore, include both root and microbial respiration.

Laboratory analyses: CO₂ evolution

CO₂ evolution was measured on a GC (Hewlett Packard 5730A) fitted with a thermal conductivity detector. The column was packed with Poropak R; the carrier gas was helium. Gaseous 0.5-mL samples were injected into the chromatograph from Vacutainers. Net amounts of CO₂ evolved during the 5-h incubation period were calculated by subtracting the sample taken at the beginning of the 5-h period from the sample taken after 5 h. The sum was divided by the dry weight of the substrate sample and the number of hours of incubation. These calculations expressed CO₂ in micromoles per gram per hour. Litter, log, and soil bulk densities were calculated using sample weights and the standard 216-cm³ sample core volume. Final CO₂ values were expressed as micromoles per cubic centimetre per hour.

Nitrogen fixation field methods

Nitrogen fixation was measured using an acetylene reduction assay (ARA) (Heath et al. 1988; Sollins et al. 1987). Each Mason jar headspace was flushed with air using a bicycle pump before incubation procedures began to ensure that trapped natural ethylene and accumulated CO₂ would be removed.

The presence of preexisting natural ethylene in substrate samples was tested in a pilot sampling procedure at the initiation of the research project. Natural ethylene amounts were below the detection level of the GC. As a result, it was not considered a significant factor biasing the ARA. Consequently, amounts of natural ethylene present at the moment of sample extraction from the substrate were measured as part of the total initial gas sample taken at the onset of the 5-h incubation period and then subtracted from combined natural ethylene and acetylene-derived ethylene accumulated over the incubation period.

Samples contained in the sealed Mason jars were transported in ice chests to a controlled-environment laboratory incubator set at mean field temperatures. Commercially generated acetylene, refiltered to remove impurities before being transferred to a rubber air bladder, was injected with a syringe into each Mason jar through a serum stopper in the jar lid as soon after sample collection as possible. Acetylene was injected to achieve a 10% atmosphere within the jar. Gaseous samples (10 mL) were withdrawn with a syringe at the beginning and end of the 5-h incubation period.

The samples taken at both the initiation and completion of the 5-h period were transferred to Vacutainers for later processing on a GC. No adjustment was made for amounts of ethylene taken from the Mason jar and placed in the Vacutainers because all Mason jar headspaces were considered the same size due to the use of the 216-cm³ standard sampling container.

Laboratory analyses: nitrogen fixation

Ethylene and acetylene were measured with a Hewlett Packard 5830 GC fitted with a flame ionization detector and a stainless steel column 2 m × 2.1 mm packed with Poropak R on 80–100 Chromosorb W. The oven temperature was set at 70°C. N₂ carrier gas flow rate was adjusted to 40 mL·min⁻¹. Acetylene served as an internal standard (McNabb and Geist 1979). Samples of 0.1 mL were injected into the

Table 2. Mean (SE) nitrogen fixation, mineralizable nitrogen, and respiration in litter, logs, and mineral soils ($N = 32$) for Woods Creek and the H.J. Andrews Forest.

	Nitrogen fixation ($\text{nmol C}_2\text{H}_4 \cdot \text{cm}^{-3} \cdot \text{h}^{-1}$)		Mineralizable nitrogen ($\mu\text{mol NH}_4^+ \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)		Respiration ($\mu\text{mol CO}_2 \cdot \text{cm}^{-3} \cdot \text{h}^{-1}$)	
	Control	Trenched	Control	Trenched	Control	Trenched
Woods Creek						
Litter	13.7 (3.4)	15.5 (11.3)	25.6 (2.0)	24.6 (2.5)	15.1 (1.7)	7.1 (1.0)
Logs, 0–4 cm	12.6 (2.9)	13.1 (3.7)	8.1 (1.7)	6.8 (0.9)	1.2 (0.2)	2.4 (0.8)
Logs, 4–20 cm	6.7 (1.2)	13.3 (3.6)	5.9 (0.7)	5.7 (0.7)	1.0 (0.1)	1.3 (0.4)
Mineral soils, 0–4 cm	1.2 (0.3)	0.6 (0.1)	8.2 (0.9)	7.7 (0.7)	1.9 (0.6)	0.8 (0.1)
Mineral soils, 4–20 cm	0.4 (0.1)	0.2 (0.0)	4.1 (0.5)	4.6 (0.3)	0.3 (0.1)	0.4 (0.1)
H.J. Andrews Forest						
Litter	8.9 (0.9)	7.4 (1.6)	20.6 (1.9)	23.0 (2.2)	6.2 (1.0)	3.5 (0.6)
Logs, 0–4 cm	9.7 (4.7)	3.3 (0.6)	4.4 (0.5)	4.7 (0.5)	1.6 (0.2)	0.7 (0.1)
Logs, 4–20 cm	5.6 (1.1)	4.5 (0.5)	3.5 (0.4)	5.9 (2.3)	1.3 (0.1)	0.6 (0.1)
Mineral soils, 0–4 cm	1.2 (0.3)	0.6 (0.1)	3.2 (0.5)	6.0 (0.9)	1.2 (0.4)	0.7 (0.2)
Mineral soils, 4–20 cm	0.8 (0.2)	0.3 (0.1)	6.7 (2.3)	5.4 (7.1)	0.2 (0.1)	0.1 (0.0)

GC from the Vacutainers. Ethylene standards were used to calibrate the GC. Net amounts of ethylene were determined by subtracting the gaseous sample value extracted at the onset of the 5-h incubation from the sample collected at the termination of the incubation period.

Mineralizable nitrogen field methods

Two bulk litter samples were collected at random from all plot surfaces each month. Surface gravels and litter >3 cm in diameter were not included in the litter sample. Two log and soil plot bulk samples were also taken from excavations randomly selected at 0–4 and 4–20 cm depths, respectively, during each sampling period. The samples, enclosed in plastic bags, were transported to the laboratory in ice chests and stored in a cold room for a maximum of 2–3 days before processing in the laboratory.

Laboratory analyses: mineralizable nitrogen

Mineralizable nitrogen (ammonium concentration) was determined by a KCl extraction and incubation method (Waring and Bremner 1964). The KCl extraction was conducted under anaerobic conditions. In the laboratory, two subsample sets at field moisture contents were taken from each bulk sample. Soil samples were passed through a 2-mm sieve before weighing and processing. The objective was to determine substrate mineralizable nitrogen comparisons on the <2 mm fraction between samples that received no incubation and substrate samples after incubation for 7 days. One subsample set was used for initial mineralizable nitrogen determination and the second sample for mineralizable nitrogen determination after incubation.

Replicate 5-g litter, log, and soil samples were weighed into labelled plastic urine cups. A solution of 60 mL of 2 M KCl was placed in the receptacles containing the samples chosen for immediate processing, while the sample group to be incubated received 30 mL of distilled water. Care was taken to completely submerge samples in the solutions in order to maintain anaerobic conditions. Calculations were adjusted for any additional solution amounts that were necessary to insure anaerobic conditions. The initial or control samples were shaken before they were filtered into vials and before processing on the autoanalyzer. Samples in distilled water were placed in an incubator set at 40°C for 7 days; 30 mL 4 M KCl was added to incubated samples immediately upon removal from the incubator and before the samples were filtered and autoanalyzed. After processing on an Alpkem Rapid Flow Analyzer (R.F.A.-300), the initial amount of mineralizable nitrogen (as ammonium concentration) was subtracted from the amount accumulated after incubation. Gravimetric moisture contents were determined for each sample. Samples for substrate moisture contents were dried at 105°C for 48 h. Net amounts of nitrogen

mineralized were expressed as the hourly rate of ammonium produced per sample dry weight. Mineralizable nitrogen values were expressed on a dry weight basis because of field moisture variation in the bulk samples. Final values were converted to micromoles per gram per hour.

Data analyses

Sites were analyzed separately owing to the different age classes and different environments existing at each location. Only the second year of the two data collection years was used in the analyses. This option was undertaken because of potential lack of stability in CO_2 evolution, nitrogen fixation, and mineralizable nitrogen due to trenching. Differences in the variables were measured using SAS (SAS Institute Inc. 1989). Repeated measures analysis of variance (ANOVA) was used to measure differences in respiration, nitrogen fixation, and mineralizable nitrogen according to treatment. ANOVA tested for differences in CO_2 evolution by treatment and depth on the two sites. Because of the number of variables involved, it was necessary to run litter ANOVA separately from log and soil substrate analyses to accommodate personal computer SAS programming and memory limitations. Only log and soil substrates were compared by depth. Mean and standard error data are given for all three substrates (Tables 1–6).

Log transformations of data were necessary because of nonnormal distribution of residuals (Kleinbaum and Kupper 1978). Substrate moisture content and CO_2 evolution were expressed on a volume basis to standardize for differences in bulk density between logs and soils.

Results

Substrate respiration rates

Respiration patterns at Woods Creek and at the H.J. Andrews Forest were similar; log respiration at the H.J. Andrews Forest was slightly less than one half that found at Woods Creek (Table 2). Respiration from litter on soil plots at Woods Creek was over 2 times greater than on soil plots at the H.J. Andrews Forest. H.J. Andrews Forest respiration levels varied significantly within logs and soils depending on depth ($p = 0.006$). At both sites, CO_2 evolution was lower at 4–20 cm than at 0–4 cm, and amounts of CO_2 evolved at these depths changed depending on substrate type (Table 2).

Moisture content

Moisture content varied with substrate composition, sampling

Table 3. Mean (SE) volumetric moisture in litter, logs, and mineral soils ($N = 32$) for Woods Creek.

	Volumetric moisture (%)	
	Control	Trenched
Litter on logs	11 (1)	12 (1)
Logs, 0–4 cm	27 (1)	31 (1)
Logs, 4–20 cm	32 (1)	31 (1)
Litter on mineral soils	14 (1)	12 (1)
Mineral soils, 0–4 cm	20 (1)	22 (1)
Mineral soils, 4–20 cm	20 (1)	22 (1)

depth, and trenching (Tables 3 and 4). Litter contained the lowest mean volumetric moisture content (14%) followed by soils (21%) and logs (31%), respectively. At both Woods Creek and the H.J. Andrews Forest, most volumetric moisture in soil litter was lower than in log litter. Moisture levels were often greater at 4–20 cm than at 0–4 cm when data were expressed by dry weight. Normalizing moisture content by volume reduced mean moisture differences between 0–4 and 4–20 cm, but normalization did not affect overall significant differences in moisture content by depth. In Pacific Northwest mineral soils, however, seasonal drying trends continue until mid-October and moisture content levels at the two depths were observed to reverse after fall precipitation began.

Although ANOVA results for log and soil substrate moisture content yielded significant p -values for differences in volumetric moisture contents by depth at Woods Creek, statistical analyses main effects cannot be recognized because of significant third-level interaction terms (Table 5).

Trenching effects on moisture content

At both Woods Creek and the H.J. Andrews Forest, most moisture content levels in trenched plots were slightly greater than in control plots, but only the H.J. Andrews site had significantly different moisture contents between logs and soils. Woods Creek contained an overall mean of 20% volumetric moisture compared with 24% in trenched plots. Volumetric moisture contents in the H.J. Andrews Forest were 17% in control plots compared with 24% in trenched plots. Different moisture levels existed by depth (Tables 3 and 4).

Subsurface temperature

Temperature differences between soil and log substrates were relatively small (Tables 6 and 7). Lower temperatures in most log samples than in soils or litter may be caused by high log moisture content that acted as a heat sink. ANOVA was not conducted with both temperature and moisture variables in the model in conjunction with depth. However, simple t -tests performed on the log of temperature data showed that there were no significant differences within sites, treatments, or substrates when temperatures at 0, 0–4, and 4–20 cm depths were compared in pairs. t -Tests were also conducted to determine if there were differences based only on site and substrate type. Woods Creek logs averaged 1°C cooler than soils in both the litter layers (litter on the surface of logs) and at 0–4 cm depths within logs. At the H.J. Andrews Forest, the pattern was reversed in that logs averaged 1°C higher in temperature than soils.

Table 4. Mean (SE) volumetric moisture in litter, logs, and mineral soils ($N = 32$) for the H.J. Andrews Forest.

	Volumetric moisture (%)	
	Control	Trenched
Litter on logs	15 (2)	17 (2)
Logs, 0–4 cm	28 (2)	34 (2)
Logs, 4–20 cm	31 (2)	35 (1)
Litter on mineral soils	12 (2)	14 (2)
Mineral soils, 0–4 cm	18 (1)	23 (1)
Mineral soils, 4–20 cm	19 (1)	21 (1)

Substrate nitrogen fixation rates

Woods Creek

At Woods Creek, nitrogen fixation had higher yields in litter > logs > soils; activity declined with sampling depth (Table 5). Trenching did not have a statistically significant impact on nitrogen fixation at this site if significance is considered $p < 0.05$. Activity differed significantly between logs and mineral soils ($p < 0.0001$) as well as between 0–4 and 4–20 cm sampling depths ($p < 0.03$) at the lower elevation site (Table 5).

Woods Creek mean nitrogen fixation in litter was slightly more than in samples between 0 and 4 cm depths in logs. Logs averaged 7–8 times greater nitrogen fixation activity per unit volume than mineral soils. Although trenching was not statistically significant, mean nitrogen fixation in trenched logs sampled between 4 and 20 cm was approximately twice that of fixation in undisturbed logs at the same depth (Table 5).

H.J. Andrews Forest

Patterns of nitrogen fixation were similar in some, but not all, respects between the two sites (Table 5). Litter had the greatest nitrogen fixation level compared with logs and soils. At both sites, nitrogen fixation was higher in logs than in mineral soils, but at the H.J. Andrews Forest, there was no significant depth main effect (Table 2). Significant interactions occurred between sampling depth and substrate ($p = 0.01$) as well as between trenching and depth ($p < 0.01$). Regardless of whether the substrate consisted of logs or mineral soils, samples from 4–20 cm depths had 40–50% less nitrogen fixation than samples taken at 0–4 cm.

Substrate mineralizable nitrogen rates

Woods Creek

At both Woods Creek and the H.J. Andrews Forest sites, mineralizable nitrogen changed with sampling depth, substrate type, and, to a lesser extent, plots where the roots had been severed by trenching (Table 2). Litter yielded the greatest amount of mineralizable nitrogen regardless of site. Woods Creek litter on control plots had 3.1 times more mineralizable nitrogen than logs sampled at 4 cm. ANOVA performed on Woods Creek mineralizable nitrogen data collected from litter that covered log plots, compared with litter covering soil plots (Table 7), showed that there were no significant differences between the two litter types at Woods Creek. More than 90% of the time ($p = 0.071$), differences in mineralizable nitrogen from either litter from soil or log plots depended on whether

Table 5. ANOVA *p*-values for moisture, CO₂ evolution, mineralizable nitrogen, and nitrogen fixation in logs and soils for Woods Creek and the H.J. Andrews Forest.

	Volumetric moisture (%)	CO ₂ evolution ($\mu\text{mol CO}_2\text{ cm}^{-3}\text{ h}^{-1}$)	Mineralizable nitrogen ($\mu\text{mol NH}_4^+\text{ g}^{-1}\text{ h}^{-1}$)	Nitrogen fixation ($\text{nmol C}_2\text{H}_4\text{ cm}^{-3}\text{ h}^{-1}$)
Woods Creek				
Substrate	0.002	0.005	0.013	0.001
Trenching	0.182	0.832	0.685	0.704
Substrate \times trenching	0.647	0.723	0.266	0.103
Depth	0.042	0.002	0.005	0.026
Substrate \times depth	0.124	0.025	0.926	0.645
Depth \times trenching	0.005	0.625	0.213	0.397
Depth \times substrate \times trenching	0.016	0.673	0.854	0.460
H.J. Andrews Forest				
Substrate	0.001	<0.001	0.407	<0.0001
Trenching	0.051	0.117	0.382	0.488
Substrate \times trenching	0.882	0.050	0.765	0.806
Depth	0.020	0.006	0.390	0.834
Substrate \times depth	0.041	0.006	0.826	0.014
Depth \times trenching	0.064	0.753	0.213	0.009
Depth \times substrate \times trenching	0.196	0.359	0.854	0.878

the plots were trenched or not. There were also statistically significant differences in amounts of mineralizable nitrogen between the sampling depths of 4 and 20 cm in log and soil substrates at the Woods Creek site ($p < 0.005$).

H.J. Andrews Forest

Total mineralizable nitrogen from H.J. Andrews Forest undisturbed litter was 20% less than mineralizable nitrogen from undisturbed litter at Woods Creek (Table 1). In contrast with the statistically insignificant difference between mineralizable nitrogen generated from soil and log litter plots at Woods Creek, H.J. Andrews mineralizable nitrogen from litter on the surface of log plots had significantly higher values than that from litter on the surface of soil plots ($p < 0.007$). Mineralizable nitrogen amounts from log and mineral soil sampled at 4 and 20 cm, respectively, were not statistically significant at the H.J. Andrews site (Table 2).

Effects of trenching on mineralizable nitrogen

Severing living roots in 50% of the plots on each site did not radically change mineralizable nitrogen levels in these plots compared with the control plots. In fact, neither site had statistically significant differences in mineralizable nitrogen between log and soil plots where the perimeters were trenched and those plots that were not trenched. However, Woods Creek log and litter samples had reduced mineralizable nitrogen levels within trenched plots. Conversely, at the H.J. Andrews Forest, mineralizable nitrogen levels increased slightly in all trenched plots except mineral soil plots sampled at 20 cm.

Discussion

In this study, mineralizable nitrogen, nitrogen fixation, and respiration rates were greater in the lower elevation 75- to 80-year-old Douglas-fir stand than in the higher elevation 450-year-old stand. Forest floors yielded greater mineralizable nitrogen levels than either logs or mineral soils at both sites.

Traditionally, higher microbial activity has been found in forest floors and well-decayed logs than in mineral soils; substrate decomposition rates are controlled by moisture, temperature, substrate amounts, and substrate quality (Clarholm et al. 1981). Our findings for respiration in forest substrates support results found by Witkamp (1969), Edwards (1975), Edwards and Sollins (1973), and Wildung et al. (1975). Substrate composition may account for the strength of negative and positive correlations of CO₂ evolution with moisture content. Woods Creek has milder subsurface temperatures during the early spring and fall as well as greater substrate moisture content during the summer. This information suggests that the Coast Range Woods Creek environment may be more conducive for mineralization processes than the Oregon Cascade H.J. Andrews Forest.

Substrate composition

Living moss, decaying swordfern fronds, and Douglas-fir debris <3 cm in diameter were major litter components at Woods Creek, the source of higher CO₂ evolution compared with the H.J. Andrews Forest. Moss maintains greater subsurface moisture during the season than conifer needles and renders litter initially more moist (Chrosciewicz 1989). Moss substrates under coniferous stands can also have higher biologic activity than mineral soil substrates (Klingensmith and Van Cleve 1993). Mosses may not only retain an N₂ pool but may act as a substrate for nitrogen fixation (Dawson 1983).

More western hemlock and redcedar in the canopy of the H.J. Andrews site compared with the Woods Creek site also may have had some effect on total litter nitrogen fixation and respiration. A study of simulated forest floors composed of western hemlock needles showed that these needles had lower nitrogenase activity than Douglas-fir needles. The differences in nitrogenase activity were considered to be due to differences in needle phenolic content between conifer species (Silvester 1989).

Table 6. Mean (SE) temperature in litter, logs, and mineral soils ($N = 32$) for Woods Creek.

	Temperature (°C)	
	Control	Trenched
Litter on logs	9.5 (0.4)	10.0 (0.4)
Logs, 0–4 cm	9.2 (0.3)	9.6 (0.4)
Logs, 4–20 cm	9.3 (0.3)	9.4 (0.4)
Litter on mineral soils	10.9 (0.6)	11.1 (0.6)
Mineral soils, 0–4 cm	10.7 (0.5)	10.8 (0.5)
Mineral soils, 4–20 cm	10.5 (0.5)	10.5 (0.5)

Litter at the H.J. Andrews Forest contained greater proportions of coniferous debris <3 cm in diameter and deeper O₂ horizons than litter found at Woods Creek. Nonconiferous litter generates slightly higher levels of respiration than litter composed of conifer needles (Flanagan and Van Cleve 1977). In other studies similar to this one, O₂ horizons produced either lower respiration and (or) lower nitrogen fixation compared with O₁ horizons (Edwards and Sollins 1973; Moore 1986; Sollins et al. 1987). Reduced biologic activity may be due to lower sugar and carbohydrate levels in the O₂ horizons.

Coniferous litter can contain almost twice as much cellulose as lignin (Stump and Binkley 1993). Since cellulose is easier to degrade than lignin, one could expect higher levels of fixation and respiration where labile nitrogen may be unavailable but nitrogen is more readily degradable.

Agents of decomposition

Fallen log residence time is less at Woods Creek than at the H.J. Andrews Forest and an activity-limiting log decomposition stage may have been reached at the H.J. Andrews site. A shift in decomposers may occur, depending on the stage of decomposition, from white rots that degrade both lignin and cellulose to basidiomycetes that degrade cellulose preferentially, thus affecting labile carbon and nitrogen (Means et al. 1992). As decomposition progresses, therefore, labile nitrogen and carbon may become limiting (Griffiths et al. 1993).

It is possible that differences in nitrogen fixation between sites were due to specific differences in nitrogen-fixing bacteria species associated with different ectomycorrhizae. Niu (1987) found statistically significant differences in acetylene reduction rates between the nitrogen-fixing bacteria from *H. setchelli* and *G. monticola* in Douglas-fir soils of the Woods Creek area. One important aspect of nitrogen-fixing community dynamics is whether or not nitrogen fixation is suppressed by the presence of certain levels of available nitrogen. Research in this field to date has not yet provided a clear answer to this question.

Since greater fine-root volumes have been measured at the H.J. Andrews Forest than at Woods Creek (S.M. Hope, unpublished data), higher overall substrate respiration at Woods Creek is probably due to higher microbial respiration rates rather than fine-root respiration rates. This finding also supports the premise that nitrogen-fixing populations may be larger and (or) more metabolically active at Woods Creek rather than the H.J. Andrews Forest.

Table 7. Mean (SE) temperature in litter, logs, and mineral soils ($N = 32$) for the H.J. Andrews Forest.

	Temperature (°C)	
	Control	Trenched
Litter on logs	11.5 (0.8)	11.6 (0.9)
Logs, 0–4 cm	11.1 (0.8)	11.2 (0.8)
Logs, 4–20 cm	10.9 (0.8)	10.8 (0.7)
Litter on mineral soils	10.1 (0.8)	10.1 (0.8)
Mineral soils, 0–4 cm	9.7 (0.7)	10.0 (0.8)
Mineral soils, 4–20 cm	9.7 (0.7)	9.9 (0.7)

Moisture content effects

In fall, the mineral horizons of soils at 0–4 cm at both Woods Creek and the H.J. Andrews were observed to be moister than of soils at 4–20 cm. It is possible that litter CO₂ production and, consequently, mineralizable nitrogen as well as nitrogen fixation are influenced by the movement of a wetting front during drying phases and by the amount and distribution of incoming precipitation. Cooper (1985) reported the formation of a dry lower duff layer during seasonal measurements of moisture and temperature in litter layers within clearcuts. Higher levels of microbial activity in logs than in soils also may be attributed to the presence of log nitrogen-enhanced interstitial water that may be available to microorganisms during summer drought (Yavitt and Fahey 1985).

Moisture content increases found on both sites after trenching probably reflect the elimination of roots as a source of moisture uptake. The H.J. Andrews site in midsummer had relatively low moisture contents, and relatively high temperatures may have limited microbial activity. Fisher and Gosz (1986) found that increases in soil moisture corresponded to increases in nitrogen mineralization on trenched plots. The result of artificially increasing moisture at the New Mexico site resulted in a microbial flush that may correspond to the H.J. Andrews October increases in mineralizable nitrogen when precipitation rose in the fall.

Very little difference in temperature occurred between trenched and control plots in our Oregon study. The presence of increased moisture in trenched plots may have had an effect on respiration by lowering CO₂ diffusion rates and increasing anaerobic conditions. Moisture increases have typically been found on trenched plots (Horn 1985; Shirley 1945). It is likely that reduced CO₂ evolution with depth is the result of combined moisture, biotic, and abiotic factors.

Treatment type

The effects of trenching on the sites were complex in that the treatment involved the combined impact of decreased litter production from understory plants and decreased live respiration on trenched plots. Lower respiration found on some trenched plots compared with nontrenched plots may be related to several factors. Reduced root respiration is an expected consequence after trenching. Reduced root respiration might be a likely cause for lower CO₂ evolution rates on trenched H.J. Andrews plots because of differences in fine-root biomass between sites. In addition to greater amounts of understory at the H.J. Andrews Forest, logs had older residence times (approximately

150 years) at this site as well as greater root permeation within logs compared with the Woods Creek site. However, root respiration within individual 216-cm² substrate samples was minimal.

Another possible explanation for reduced CO₂ evolution levels in the trenched plots is that incoming litter, an available carbon source, was lower on the trenched plots due to clipping and removing the understory vegetation. Removing the understory vegetation on trenched plots was done to eliminate living roots as a confounding factor in the experimental design.

Treatment effects

If potential amounts of labile nitrogen within plots were related to root uptake via mineralization by mycorrhizal mats, the elimination of roots might result in higher mineralizable nitrogen levels in trenched plots. At Woods Creek, trenching reduced the amount of mineralizable nitrogen slightly; we found less root volumes in Woods Creek litter, logs, and mineral soils than at the H.J. Andrews site (S.M. Hope, unpublished data). At the H.J. Andrews site, there were slight increases in mineralizable nitrogen in trenched plots. Since nitrogenase levels were reduced by trenching at the H.J. Andrews site, these findings support the explanation offered by Aguilera et al. (1993) concerning the potential importance of mineralizable nitrogen uptake by roots at old-growth sites such as the H.J. Andrews Forest.

Mean nitrogen fixation was lower in both Woods Creek and H.J. Andrews trenched soil plots as well as in H.J. Andrews trenched logs. These differences may also be indirectly attributable to living roots and ectomycorrhizae affecting labile carbon and nitrogen. Dead root tissue may provide an available source of nitrogen in an environment where nitrogen is tightly held and, as a result, suppress nitrogenase activity. It is also possible that root exudates and enzyme activity by-products provide a source of nitrogen for nitrogen fixation, but this production level may not have been sufficient to cause statistical differences between treatment types.

Summary

Mineralizable nitrogen and respiration were greatest in litter, decayed logs, and mineral soils, respectively. Most samples from 0–4 cm depths in logs and soils had greater nitrogen fixation than samples from 4–20 cm depths. Substrate respiration and mineralizable nitrogen also declined with depth within decayed logs and mineral soil substrates. Moisture content appeared to limit both respiration and mineralizable nitrogen at the H.J. Andrews site in midsummer. At the Woods Creek site with higher litter, log, and mineral soil moisture contents during summer, mineralizable nitrogen levels may be impacted more by summer temperatures than moisture content. Although trenched soil plots had lower mean moisture levels at Woods Creek, no statistical differences existed in CO₂ evolution within nontrenched and trenched soil plots.

Significant differences in volumetric moisture content were found between well-decayed fallen log and soil plots at both Woods Creek and the H.J. Andrews Forest ($p < 0.05$). Moisture levels increased with depth in logs, but soil moisture levels between depths were almost identical. Litter had the lowest mean moisture contents; samples taken from 20 m in logs contained the highest mean moisture contents. The H.J. Andrews

plots that were trenched contained higher moisture levels ($p < 0.05$) than nontrenched plots.

Acknowledgements

J. Entry of Oregon State University, Corvallis, provided help during the planning and laboratory analysis phases of this project. M. Harmon, Forest Sciences Laboratory, Corvallis, and K. Mattson and R. Griffiths, both of Oregon State University, supplied useful information concerning CO₂ evolution measurement. W. Alexander helped with the field sample collections. T. Sabin provided assistance in planning and conducting statistical analyses. Partial financial support is acknowledged from Long Term Ecological Research (LTER), H.J. Andrews Forest, Grant BSR 8514325. H.J. Andrews Forest meteorological data were provided by the Department of Forest Science, Oregon State University, Forest Science Databank, a cooperative partnership with U.S. Forest Service, Pacific Northwest Research Station. Reviews by D. Perry, R. Griffiths, K. Tanino, W. McComb, J. Entry, P. Homann, J. Boyle, and K. Cromack as well as several anonymous individuals are gratefully acknowledged.

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