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Organic matter turnover in a sagebrush steppe landscape

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Abstract. Laboratory incubations of ^{15}N-amended soils from a sagebrush steppe in south-central Wyoming indicate that nutrient turnover and availability have complex patterns across the landscape and between microsites. Total and available N and P and microbial C and N were highest in topographic depressions characterized by tall shrub communities. Net and gross N mineralization rates and respiration were also highest in these areas, but microbial efficiencies expressing growth relative to respiration cost were highest in soils of exposed ridgetop sites (prostrate shrub communities). Similar patterns occurred between shrub and intershrub soils, with greater nutrient availability under shrubs, but lower microbial efficiencies under shrubs than between. Surface soils had higher soil nutrient pools and N mineralization rates than subsurface soils, but N and C turnover and microbial efficiencies were lower in those surface soils. All soils decreased in respiration, mineralization, and immobilization rates during the 30-day incubation period, apparently approaching a steady-state substrate use. Soil microbial activity of the high organic matter accumulation areas was apparently more limited by labile substrate.

Introduction

Soil organic matter accumulation and turnover processes are tightly coupled to abiotic factors that vary with topography. These factors include lithology, soil texture, and soil microclimate (Jenny 1941; Aandahl 1948; Malo et al. 1974; Schimel et al. 1985a, 1985b; Pastor et al. 1984; Gosz & White 1986; Zak 1986; Burke 1989). Topographic variation in abiotic factors creates landscape patterns that change slowly as ecosystem properties such as community structure and organic matter quantity and quality respond to erosion, weathering and climate. Dynamic ecosystem properties such as rates of organic matter turnover, plant nutrient uptake, nutrient deposition, and gaseous losses to the atmosphere are influenced by the slowly changing landscape patterns.

Landscape-scale studies of biogeochemical cycling are especially appropriate in the Wyoming sagebrush steppe. Winter winds redistribute snow across the landscape (Sturges 1979), so that effective annual precipitation can vary from a few centimeters on exposed ridgetops to 60 cm on lower lee slopes. Over the long term (geologic time scales), repeated patterns of snow distribution have led to variation in soil organic matter properties across the sagebrush landscape. The purpose of this paper is to use spatial patterns at the landscape and microsite scale to evaluate controls of N mineralization and immobilization in a sagebrush steppe. Sepcifically, we hypothesized that landscape and microsite positions that accumulate snow and hence plant biomass accumulate more organic matter, support more microbial biomass, and cycle more nitrogen than those sites that are blown snow-free.

Methods

Study site

The Stratton Sagebrush Hydrology Area (Sturges 1977a, 1977b) is located near Saratoga, Wyoming (107° 10′ W, 41° 25′ N). The climate of the area is characterized by short, dry summers and long, cold winters. Three hundred of the annual 525 mm precipitation fall as snow. Vegetation and soils are strongly patterned with topographic position (Sturges 1977b; Burke 1989), with vegetation most dense and soils deepest in topographic depressions where snow accumulates. Soils of the region are loamy sands to sands, and are classified as Argic Cryoborolls (Sturges 1986).

Overview of experimental design

We examined organic matter across three gradients: landscape variability, shrub-intershrub variability, and depth from surface soil (0–5 cm) to subsurface soil (5–15 cm). Variability at the landscape scale was addressed by sampling across an apparent productivity gradient represented by three different sagebrush vegetation types. *Artemisia tridentata* ssp. *vaseyana*, a tall shrub, dominates dense vegetation (90% shrub cover) that occurs in leeward, high snow deposition areas. *A. tridentata* ssp. *wyomingensis*, a medium-height shrub, dominates the more sparse vegetation type (50% shrub cover) that occurs in moderate snow deposition areas on relatively exposed slopes. Finally, *A. nova*, a prostrate sagebrush shrub, dominates on ridgetop or windswept, low snow deposition areas, where there is very little vegetation cover (20%). Three plots representing each vegetation type were

Table 1. Analysis schedule for incubations of soils from 3 sagebrush vegetation types, stratified by shrub-intershrub position and depth. Soils incubated in the laboratory were amended with 15-N prior to incubation.

	Incubation period (days)				
	0	5	15	30	30
Fraction measured	Laboratory				Field
Ammonium	*	*	*	*	*
Nitrate	*	*	*	*	*
Microbial biomass N		*	*	*	
Total N				*	
Inorganic ^{15}N		*	*	*	
Microbial ^{15}N		*	*	*	
Total ^{15}N recovery				*	
Available P	*			*	*
Microbial biomass P				*	
Total P				*	
Mineralized C		*	*	*	
Microbial biomass C		*	*	*	
Total C				*	

sampled. Within each plot, soil samples were collected in between- and under-shrub positions, and in surface (0–5 cm) and subsurface (5–15 cm) strata.

Soil samples from each of the vegetation/shrub-intershrub position/depth combinations were subjected to multiple chemical analyses (Table 1) using a protocol similar to Schimel (1986). Total nitrogen, total carbon, and total phosphorus were measured once for each sample. One set of subsamples was incubated in the field for 30 days to estimate in situ net N mineralization rates. Three sets of subsamples were amended with ^{15}N and were incubated in the laboratory for 5, 15, and 30 days. These samples were analyzed for potential net N mineralization, gross N mineralization and N immobilization, C mineralization, microbial biomass C and N, and the distribution of ^{15}N in each of the N fractions.

Sampling and soil preparation

Three 5 × 5 m plots within each of the three vegetation types were randomly located. In each plot, three soil cores (collected in two increments, 0–5 cm and 5–15 cm) were randomly located under shrubs and three between shrubs in August 1985. A small subsample (about 50 g) was handsorted in the field, sealed into a plastic and incubated in the field at its original depth for 30 days. The buried samples were recovered and the nitrate and am-

monium content measured for estimates of net in situ N mineralization (Ellenberg 1977) (see analytical procedures below). Available phosphorus was measured on these samples as well.

In the laboratory, the replicate samples within plots were composited, and each composite was subsampled for initial moisture and contents of NH_4^+, NO_3^-, and available P. The composites were then subsampled 14 times for incubation samples. These subsamples were amended with ^{15}N and brought up to field capacity in a joint procedure. Each of the subsamples was amended with ^{15}N as NH_4Cl (99% enriched) at a rate of 5 μg ^{15}N per gram of dry soil with a solution of 125 mg ^{15}N/liter. This amendment was approximately 0.5 mg ^{15}N per gram of nitrogen, increasing the initial ^{15}N pool by 13.6%. Additional deionized water necessary to bring the samples to field capacity (previously determined) was then added, and the samples were mixed completely.

The subsamples from each composite were separated into three groups to be incubated for 5, 15, and 30 days. Samples from each group were placed into 1-quart mason jars, with no more than 50 g of soil per jar. Each jar also contained water to maintain humidity, and a vial holding 6 mls of 1 N NaOH to serve as a CO_2 trap (Schimel 1986). The jars were incubated at 20 °C. At the end of the 5-, 15-, and 30-day incubations, one 25 g sample was analyzed for microbial biomass nitrogen and ^{15}N, two 25 g samples were analyzed for nitrate, ammonium, and their ^{15}N content, and the base traps were analyzed for CO_2. At the end of the experiment (30 days), two 5-g samples were analyzed for microbial biomass P, and one 5-g sample was analyzed for available P. One 10-g sample was used for total N, P, and ^{15}N determination, and another for total carbon analysis (Table 1).

Total carbon and CO_2

Total carbon of soil samples was measured using a wet oxidation-diffusion procedure (Snyder & Trofymow 1984). NaOH traps from the total carbon oxidation-diffusions and from the incubation jars were titrated using the procedure described by Jenkinson & Powlson (1976). Carbon mineralization (respiration) (mg/g-day) was calculated as the difference between the incubation base trap and the blank, divided by the numbers of days of incubation. An index of carbon turnover was calculated following Schimel (1986):

$$\text{C turnover (\%/day)} = \text{C mineralization} \times 100\%/\text{total C}$$

Total and available nitrogen and phosphorus

Total N and P were determined on day 30 using a sulfuric acid/mercuric oxide digestion (Vitousek & Matson 1985). Nitrate was determined separately. A subsample of the digestate was used to determine total ^{15}N content using a diffusion procedure (described below).

Available phosphorus was estimated on days 0 and 30 using a sodium bicarbonate procedure (Olsen & Sommers 1982). Nitrate and ammonium in the soil samples were measured on day 0, 5, 15, and 30 by extracting with 2 N KCl and performing a standard colorimetric procedure on a Scientific Instruments Auto Analyzer. The ^{15}N content of the combined NH_4^+ and NO_3^- was determined on day 5, 15, and 30.

KCl extracts and the total nitrogen digestates were analyzed for ^{15}N content throughout the experiment. Ammonium and nitrate (reduced to NH_4) from KCl extracts were diffused to tubes of 1 N HCl using a procedure modified from Adamsen & Reeder (1983) by Vitousek & Matson (1985), with the diffusion extended to 14 days. Standards containing both NO_3 and NH_4 were run, with all recoveries over 96%, averaging 99.7%. Samples were always run with Devarda's alloy since NH_4^+ levels were generally too low for mass spectrometry, requiring 20–100 μg N. Digestates were diffused in the same way.

Tubes containing HCl and the ^{15}N were dried and sent to Isotope Services in Los Alamos, New Mexico for ^{15}N determination. Natural abundance of ^{15}N was previously determined on our soils (0.3689%; Fry, pers. comm.).

Net N mineralization was calculated as the difference between final and initial contents of inorganic nitrogen for each incubation. Gross N mineralization and immobilization were calculated using the ^{15}N pool dilution equations of Kirkham & Bartholomew (1954). The equations assume that the inorganic nitrogen pools are small relative to the mineralization rates, that both rates are constant throughout the incubation period, and that no ^{15}N is immobilized and remineralized during the course of the incubation. The first assumption holds true under laboratory incubation conditions such as these, where mineralization rates were relatively high. The assumption of constant mineralization rates throughout an incubation is not strictly true, since mineralization rates commonly decline throughout an incubation. Last, the assumption of no remineralization of ^{15}N is probably only true for short incubation periods, and so gross mineralization and immobilization rates were not calculated for day 30.

Indices of soil N turnover rates for each incubation period were calculated following Schimel (1986):

$$\text{N turnover (\%/day)} = \frac{\text{gross N mineralization} \times 100\%}{\text{total N}}$$

Microbial biomass C, N and P

Microbial biomass C and N were measured simultaneously on days 5, 15, and 30 using chloroform fumigation methods originally described by Jenkinson & Powlson (1976), and modified by Voroney & Paul (1984). Samples were fumigated with ethanol-free chloroform for 24 hours, evacuated, reinoculated, and incubated in a major jar with a base trap and deionized water as described above for 10 days at 20 °C. After the incubation, the soils were extracted with KCl for nitrate and ammonium determinations, and the base trap titrated for CO_2 as described above.

Microbial biomass C was calculated using an equation provided by Voroney and Paul (1984), using a K_c of 0.41:

$$\text{microbial biomass C (mg/kg)} = CO_2 \text{ produced}/K_c$$

Microbial biomass N was calculated using equations empirically derived by Voroney (1983):

$$K_n = [1.86 \times (CO_2 \text{ produced/Ni flush})^{-0.879}], \text{ and}$$

$$\text{microbial biomass N (mg/kg)} = \text{Ni flush}/K_n.$$

^{15}N content of the chloroform labile fraction was determined using the diffusion procedure described above. Microbial biomass ^{15}N was calculated as the excess ^{15}N of the flush divided by K_n.

In addition, data from the experiment were used to calculate microbial growth and growth efficiency to index microbial growth per unit respiration cost. The equations used are as follows (Schimel 1988):

$$\begin{matrix}\text{microbial growth} \\ (\text{mg C/kg/day})\end{matrix} = \begin{matrix}\text{gross} \\ \text{immobilization}\end{matrix} \times \begin{matrix}\text{C/N} \\ \text{(new biomass)}\end{matrix}$$

$$\text{growth efficiency (\%)} = \frac{\text{microbial growth} \times 100\%}{(\text{microbial growth} + CO_2 \text{ evolution})}$$

The value we used for the C/N ratio of the new biomass was 6, approximating literature values for mixed soil populations (Hunt et al. 1987).

Microbial biomass P was measured on day 30 using methods of Brookes et al. (1982, 1985). Samples were fumigated with chloroform, extracted with $NaHCO_3$, and the extractant was analyzed for Pi using the ammonium-molybdate assay described by Olsen & Sommers (1982). We corrected the Pi

flush by a K_p of 0.4 (Brookes et al. 1982), with no correction for fixed P because of the extremely low carbonate and clay contents of the soils (Burke et al. 1987; Burke 1989).

Statistical tests

All data were tested for the main effects of vegetation type, shrub position, and depth as well as all possible interactions using an analysis of variance. The data were analyzed using the ANOVA subprogram of SPSS/PC (SPSS/PC 1986). Significance levels for all tests were $p < 0.05$. Very few interactions were significant for any of the analyses; only main effect significances are presented from the results of the full models.

Results

Total carbon, nitrogen, and phosphorus

Total soil carbon concentrations (C_t) were significantly different among vegetation types, with the *A. tridentata* ssp. *vaseyana* soils having the highest C_t (Fig. 1a). Soil depth and shrub-intershrub position did not have a significant ($p = 0.05$) effect on C_t, but C_t was generally higher under shrubs than between, and in the ssp. *vaseyana* vegetation type, was significantly higher at the surface (0–5 cm) than the subsurface (5–15 cm).

Total soil nitrogen concentrations (N_t) varied significantly with vegetation type, shrub-intershrub position, and depth (Fig. 1b). N_t was highest in the ssp. *vaseyana* vegetation type. In both the ssp. *vaseyana* and the ssp. *wyomingensis* vegetation types, N_t was higher under shrubs than between, and higher in surface soils than in subsurface soils.

Total soil phosphorus concentration (P_t) in these soils was not significantly different among vegetation types, soil depths, or shrub-intershrub positions. P_t ranged from 0.2 to 0.35 mg/g, with consistently lower P_t in the *nova* vegetation. The C/N and C/P ratios of these soils were not significantly affected by vegetation type, shrub-intershrub position, or depth.

Microbial biomass C, N, and P

Soil microbial biomass C and N both varied significantly with vegetation type, shrub-intershrub position, and depth. Microbial biomass C and N were higher in the ssp. *vaseyana* vegetation type than the other two types,

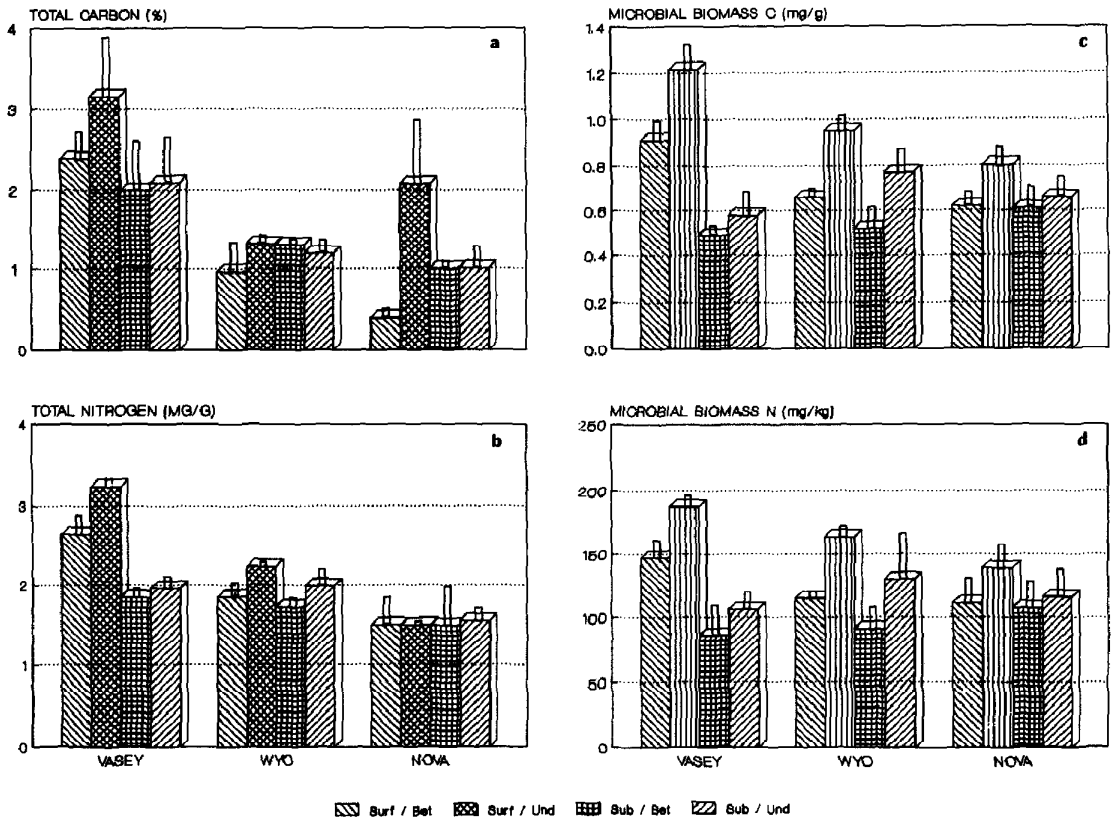

Fig. 1a–d. Total soil C and N and microbial N and C (after 30-day incubations) in 3 sagebrush vegetation types, stratified by shrub-intershrub position and by depth. VASEY = *A. tridentata* spp. *vaseyana*; WYO = *A. tridentata* ssp. *wyomingensis*; NOVA = *A. nova*. Surf/Bet = surface (0–5 cm), between shrub; Surf/Und = surface, under shrubs; Sub/Bet = subsurface (5–15 cm), between shrubs; Sub/Und = subsurface, under shrubs. Error bars represent standard error of the mean.

Table 2. Carbon and nitrogen turnover and the ratio of C mineralized to N mineralized (net) in soils incubated for 5, 15 and 30 days in the laboratory. Soils were collected from 3 sagebrush vegetation types, and were stratified by depth and by shrub-intershrub position. Significance levels are *p* values from ANOVA's testing for the effects of the 3 treatments and their interactions. No interactions were significant. Values in parentheses are standard errors of the means

Vegetation type	Shrub-intershrub position	Depth (cm)	Carbon turnover (% per day)			Nitrogen turnover (% per day)		C mineralized:N mineralized		
			Day 5	Day 15	Day 30	Day 5	Day 15	Day 5	Day 15	Day 30
A. tridentata ssp. *vaseyana*	Between shrubs	0–5	0.27 (0.06)	0.22 (0.05)	0.18 (0.04)	0.14 (0.01)	0.09 (0.01)	102.3 (46.3)	47.9 (7.6)	33.6 (3.2)
		5–15	0.22 (0.11)	0.14 (0.07)	0.10 (0.05)	0.12 (0.02)	0.06 (0.00)	100.7 (–)	101.2 (38.9)	44.0 (9.6)
	Under shrubs	0–5	0.44 (0.17)	0.21 (0.04)	0.16 (0.03)	0.17 (0.04)	0.09 (0.02)	92.5 (41.3)	45.8 (5.2)	30.8 (7.3)
		5–15	0.24 (0.13)	0.23 (0.16)	0.20 (0.11)	0.16 (0.02)	0.08 (0.01)	41.9 (11.7)	55.7 (2.2)	28.8 (4.6)
A. tridentata ssp. *wyomingensis*	Between shrubs	0–5	0.44 (0.25)	0.34 (0.15)	0.26 (0.13)	0.17 (0.02)	0.10 (0.02)	38.2 (7.9)	28.7 (3.0)	18.1 (0.3)
		5–15	0.12 (0.01)	0.08 (0.04)	0.05 (0.02)	0.12 (0.02)	0.05 (0.01)	168.0 (51.4)	78.9 (7.8)	27.6 (1.9)
	Under shrubs	0–5	0.39 (0.02)	0.35 (0.01)	0.29 (0.00)	0.16 (0.02)	0.09 (0.01)	65.2 (9.0)	60.5 (1.3)	48.4 (15.6)
		5–15	0.40 (0.02)	0.26 (0.04)	0.20 (0.04)	0.14 (–)	0.06 (0.01)	143.0 (–)	127.6 (45.6)	57.9 (10.0)
A. nova	Between shrubs	0–5	0.50 (0.47)	0.42 (0.37)	0.35 (0.33)	0.19 (0.03)	0.10 (0.01)	71.1 (6.2)	38.5 (4.6)	16.7 (4.2)
		5–15	0.44 (0.04)	0.19 (0.07)	0.14 (0.07)	0.12 (0.05)	0.08 (0.01)	174.1 (8.9)	67.9 (4.2)	65.2 (16.9)
	Under shrubs	0–5	0.22 (0.08)	0.16 (0.02)	0.15 (0.06)	0.23 (0.02)	0.13 (0.00)	143.4 (96.2)	57.1 (18.8)	36.4 (9.8)
		5–15	0.44 (0.22)	0.31 (0.15)	0.24 (0.12)	0.16 (0.01)	0.08 (0.00)	133.1 (35.2)	91.7 (0.9)	58.1 (10.1)
Significance levels:	vegetation type		0.81	0.54	0.52	0.24	0.17	0.81	0.87	0.02
	depth		0.67	0.48	0.40	0.01	0.001	0.59	0.0001	0.02
	shrub-intershrub		0.49	0.83	0.82	0.19	0.23	0.74	0.03	0.007

higher under shrubs were than between, and higher in surface soils than subsurface soils (Fig. 1c–d). Microbial biomass C and N did not change significantly during the experiment. K_n values ranged from 0.30 to 0.42 and were significantly higher in the ssp. *vaseyana* soils than the other vegetation types, in surface soils than subsurface, and under shrubs than between shrubs. This trend suggests that the actual C/N biomass ratios differ, and probably the microbial communities of the various treatments as well.

Microbial biomass P data were highly variable, ranging from 5 to 35 mg/kg, with no significant main effects. The same trends occurred for microbial P as for microbial N and C, with highest biomass P in surface ssp. *vaseyana* soils. Sodium bicarbonate-extractable P (available P, or Pa) ranged from 4.8 to 18.4 mg/kg, with highest values in the surface soils and in the ssp. *vaseyana* vegetation.

Carbon turnover

Carbon mineralization rates (respiration) decreased during the incubation, with highest daily rates occurring during the first 5 days of incubation (Fig. 2a–c). C mineralization rates for all 3 periods (5, 15, and 30 days) were significantly different among vegetation types, with ssp. *vaseyana* soils having the highest rates. Shrub-intershrub position also had a significant effect, with rates higher under shrubs for all vegetation types and depths. Finally, rates were significantly higher in the surface soils (0–5 cm) than in the subsurface soils (5–15 cm).

Carbon turnover rates (Table 2) were not significantly different among treatments for any effect. Turnover decreased from 0.20–0.44% per day in the first 5 days to 0.10–0.35% per day in the 30 day incubation.

Nitrogen turnover

Net potential N mineralization rates were determined from the laboratory incubations (Fig. 2d–f). More than 85% of the N mineralized (net) was present as NO_3. Daily net mineralization rates neither increased nor decreased through the incubation period from day 5 to day 15 and 30. Depth was the only significant effect on mineralization rates for 5- and 15-day incubations, although rates were consistently higher in the ssp. *vaseyana* soils than the other two types, and were generally higher under sagebrush shrubs than between, as shown previously by Charley & West (1977). The 30-day incubation rates showed the same pattern, but both vegetation type and depth were significant effects.

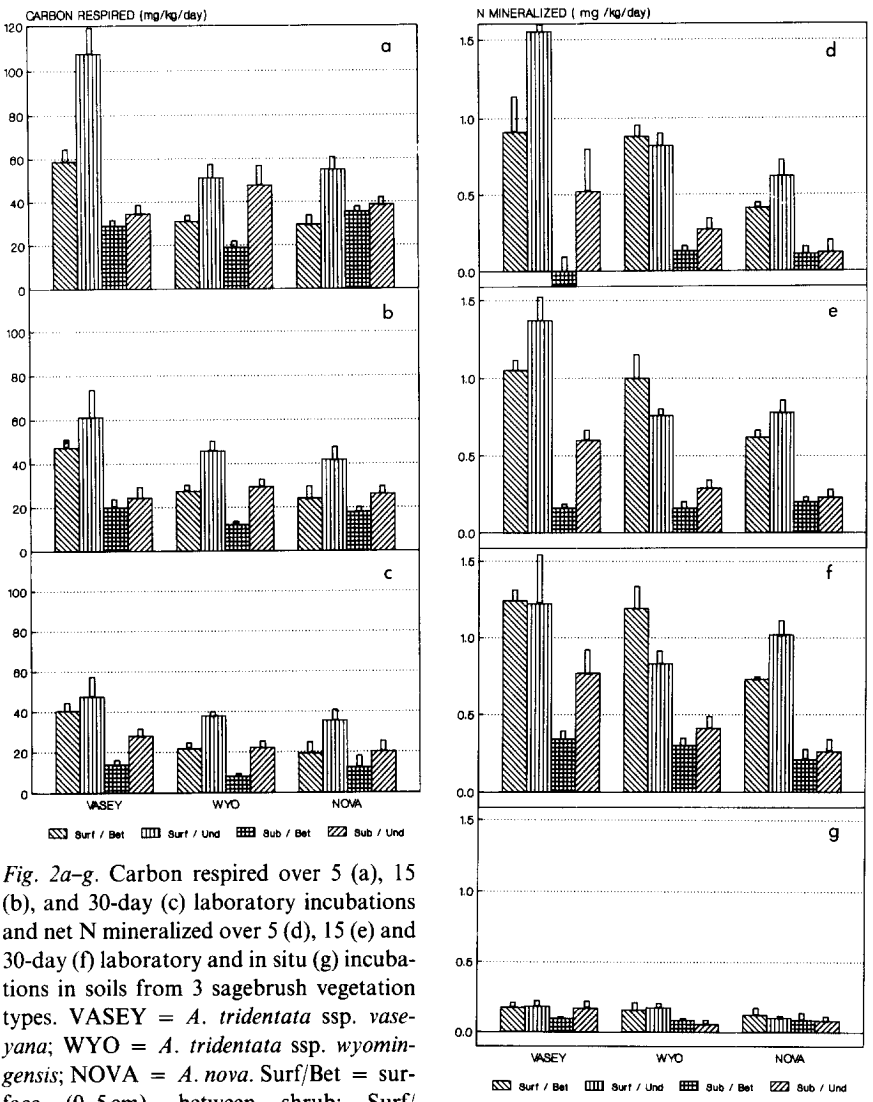

Fig. 2a–g. Carbon respired over 5 (a), 15 (b), and 30-day (c) laboratory incubations and net N mineralized over 5 (d), 15 (e) and 30-day (f) laboratory and in situ (g) incubations in soils from 3 sagebrush vegetation types. VASEY = *A. tridentata* ssp. *vaseyana*; WYO = *A. tridentata* ssp. *wyomingensis*; NOVA = *A. nova*. Surf/Bet = surface (0–5 cm), between shrub; Surf/Und = surface, under shrubs; Sub/Bet = subsurface (5–15 cm), between shrubs; Sub/Und = subsurface, under shrubs. Error bars represent standard error of the mean.

In situ net N mineralization rates over a 30-day field incubation were 1/5 to 1.10 the potential mineralization rates (Fig. 2g). Soil moisture in these field incubations ranged from 4 to 6% in the surface soils and from 6 to 7% in the subsurface soils, as compared with 13–22% (field capacity) in the

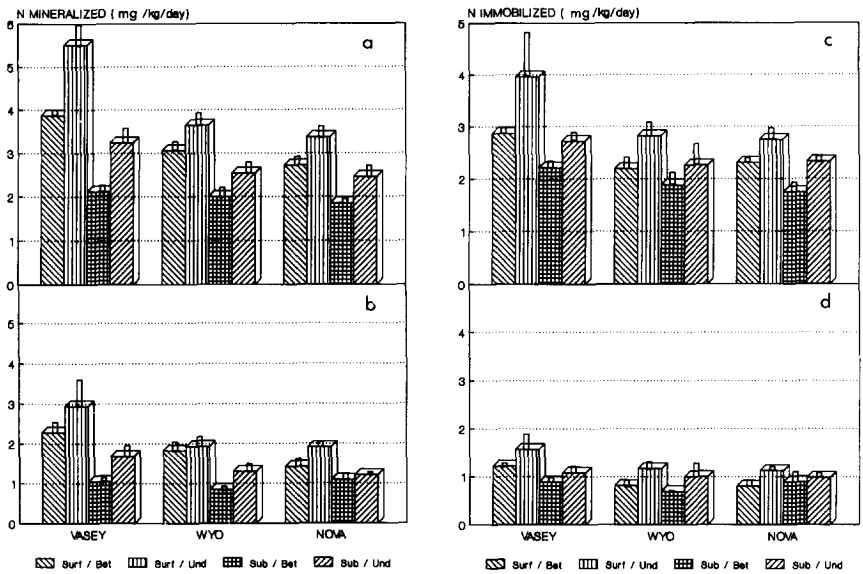

Fig. 3a–d. Gross N mineralization measured in 5 (a) and 15-day (b) laboratory incubations, and gross N immobilization measured in 5 (c) and 15-day (d) lab incubations of soils from 3 sagebrush types amended with ^{15}N. VASEY = *A. tridentata* ssp. *vaseyana*, WYO = *A. tridentata* ssp. *wyomingensis*, NOVA = *A. nova*. Surf/Bet = surface (0–5 cm), between shrub; Surf/Und = surface, under shrubs; Sub/Bet = subsurface (5–15 cm), between shrubs; Sub/Und = subsurface, under shrubs. Error bars represent one standard error of the mean.

laboratory incubations. There were no differences in mineralization rates among vegetation types of shrub-intershrub positions during this period. Results from other studies (Burke 1989) show that differences among vegetation types in in situ net N mineralization rates only occur during spring and early summer periods, when soil moisture is high but variable across the landscape. Surface soils had significantly higher mineralization rates than the subsurface soils, despite lower soil moisture.

Gross N mineralization rates calculated from the isotope pool dilution data showed a large decrease between the 0–5 day incubation and the 0–15 day incubation (Fig. 3a–b). For both incubation periods, mineralization rates were significantly highest in soils from the ssp. *vaseyana* vegetation type, significantly higher in the under-shrub positions than the between-shrub positions, and signfiicantly higher in the surface than the subsurface soils. Gross N immobilization rates showed the same patterns and significances (Fig. 3c–d), and were generally lower than the gross mineralization rates, resulting in positive net N mineralization rates.

The relationship between microbial biomass N and gross N mineralization was linear for all soils for both the 5- and 15-day incubations (Fig. 4a).

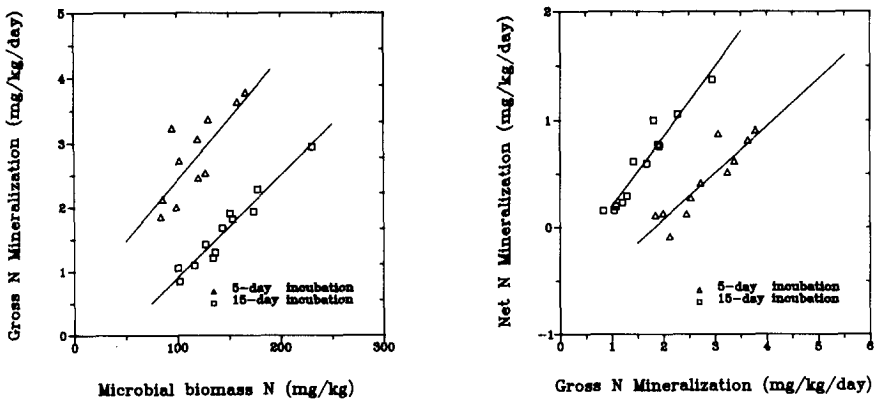

Fig. 4a–b. The relationship between gross N mineralization and soil microbial biomass N (a) and between goes and net N mineralization (b) in 5 and 15-day incubations of sagebrush soils amended with ^{15}N. Each point represents the mean of 3 samples from a specific vegetation type, shrub-intershrub position, and depth. R^2 values for a) are 0.62 (5-day) and 0.94 (15-day), and for b) are 0.90 (5-day) and 0.92 (15-day), all significant at $p < 0.05$.

The amount mineralized per day per unit of microbial biomass N was lower for the 15-day incubation than 5-day incubation. Similarly, the relationship between net and gross N mineralization was linear for all soils for both 5- and 15-day incubations (Fig. 4b). Net mineralization became a more significant proportion of gross N mineralization from day 5 to day 15 for all soils.

Nitrogen turnover rates were significantly lower in the subsurface soils than in the surface soils (Table 2). Although the trend was not statistically significant, N turnover was generally highest in *nova* soils for all depths and shrub-intershrub comparisons. Turnover rates decreased from the 5-day incubation to the 15-day incubation.

Ratios of C mineralization to net N mineralization (C/N_{min}), representing a quality of substrate use, are presented in Table 2. C/N_{min} decreased for all treatments through the course of the incubations. Vegetation type and shrub-intershrub position did not affect C/N_{min} significantly for any of the incubations. In the 15- and 30-day incubations, C/N_{min} was significantly higher in the subsurface soils than in the surface soils.

Microbial biomass growth and growth efficiency

Estimates of microbial growth (Table 3) show the same trends as the gross N immobilized rates from which they were derived. Microbial growth efficiency estimates, expressing growth relative to respiration cost, ranged from 22–37% during the first 5 days of the incubation, and decreased to 13–26% during the 15-day incubation (Table 3). These values are at the low

Table 3. Microbial growth and growth efficiency (after Schimel, 1988) for soils incubated for 5 and 15 days in the laboratory. Soils were collected from 3 sagebrush vegetation types, stratified by shrub-intershrub position and by 2 depths. Values in parentheses are standard errors of the means. Significance levels are *p* values from ANOVA's testing for main effects and interactions. No interactions were significant.

Vegetation type	Shrub-intershrub position	Depth (cm)	Microbial growth (mg C/kg/day)		Growth efficiency (%)	
			Day 5	Day 15	Day 5	Day 15
A. tridentata ssp. *vaseyana*	Between shrubs	0–5	17.2 (0.6)	7.3 (0.2)	23.1 (2.3)	13.6 (0.9)
		5–15	13.2 (0.9)	5.4 (0.3)	31.6 (0.9)	21.3 (0.9)
	Under shrubs	0–5	28.8 (9.1)	9.4 (2.3)	22.2 (1.2)	13.6 (1.2)
		5–15	16.3 (1.7)	5.6 (0.3)	32.5 (1.3)	19.9 (4.2)
A. tridentata ssp. *wyomingensis*	Between shrubs	0–5	13.1 (1.3)	4.9 (0.3)	29.8 (2.6)	15.5 (1.6)
		5–15	11.2 (1.3)	4.1 (0.1)	37.2 (1.1)	25.6 (0.9)
	Under shrubs	0–5	16.9 (1.4)	7.0 (1.1)	25.2 (1.8)	13.2 (0.3)
		5–15	13.5 (–)	6.0 (0.7)	25.6 (–)	16.9 (0.5)
A. nova	Between shrubs	0–5	13.8 (0.8)	4.8 (0.4)	32.6 (3.2)	17.2 (1.5)
		5–15	10.4 (1.2)	5.4 (0.7)	22.9 (3.5)	14.2 (1.1)
	Under shrubs	0–5	16.4 (3.3)	6.8 (0.2)	22.9 (0.6)	23.1 (1.6)
		5–15	13.9 (0.9)	5.9 (0.4)	22.8 (1.2)	18.4 (2.5)
Significance of vegetation type			0.020	0.039	0.078	0.428
depth			0.007	0.022	0.005	0.000
shrub-intershrub position			0.007	0.014	0.014	0.002

Table 4. 15-N budget (excess 15-N in μg/g) for inorganic nitrogen (N_i) and microbial biomass nitrogen (MBN) through the course of soil incubations for 5, 15, and 30 days. Soils were collected from 3 sagebrush vegetation types and were stratified by shrub-intershrub position and by two depths. Values in parentheses are standard errors of the means. Significance levels reported are *p* values from ANOVA's testing for the main effects and their interactions. Only main effects are reported, as all interactions were nonsignificant.

Vegetation type	Position	Depth (cm)	Day of incubation								
			0		5		15		30		
			N_i	MBN	N_i	MBN	N_i	MBN	N_i	MBN	% recovery
A. tridentata ssp. *vaseyana*	Between	0–5	5	0	1.3 (0.25)	0.7 (0.19)	1.5 (0.14)	0.1 (0.05)	1.7 (0.20)	0.1 (0.06)	71.4 (4.5)
		5–15	5	0	1.0 (0.17)	0.6 (0.24)	1.0 (0.18)	0.7 (0.17)	1.2 (0.23)	0.6 (0.09)	70.0 (0.3)
	Under	0–5	5	0	1.5 (0.13)	0.3 (0.16)	1.6 (0.06)	0.7 (0.11)	1.8 (0.08)	0.4 (0.19)	94.8 (4.7)
		5–15	5	0	1.2 (0.28)	0.7 (0.06)	1.4 (0.07)	2.0 (0.24)	1.7 (0.15)	2.1 (0.22)	61.9 (1.3)
A. tridentata ssp. *wyomingensis*	Between	0–5	5	0	1.8 (0.28)	0.5 (0.08)	2.1 (0.12)	0.1 (0.14)	2.3 (0.05)	0.0 (0.00)	66.8 (12.5)
		5–15	5	0	1.4 (0.13)	0.5 (0.12)	1.4 (0.09)	0.7 (0.15)	1.7 (0.19)	0.3 (0.18)	69.7 (10.6)
	Under	0–5	5	0	1.4 (0.01)	0.4 (0.05)	1.5 (0.12)	0.7 (0.22)	1.5 (0.28)	0.9 (0.36)	57.2 (6.8)
		5–15	5	0	1.2 (–)	0.6 (–)	1.3 (0.16)	1.0 (0.13)	1.4 (0.16)	1.2 (0.28)	68.4 (7.7)
A. nova	Between	0–5	5	0	1.4 (0.11)	0.8 (0.14)	1.9 (0.09)	0.5 (0.08)	2.1 (0.09)	0.1 (0.02)	63.7 (6.0)
		5–15	5	0	1.8 (0.47)	1.0 (–)	1.2 (0.12)	1.1 (0.16)	1.3 (0.04)	0.7 (0.10)	69.5 (6.6)
	Under	0–5	5	0	1.3 (0.50)	1.1 (0.32)	1.4 (0.17)	0.8 (0.07)	1.7 (0.32)	0.8 (0.13)	77.5 (5.1)
		5–15	5	0	1.2 (0.17)	1.0 (0.11)	1.1 (0.15)	1.3 (0.14)	1.2 (0.21)	1.2 (0.36)	71.9 (6.4)
Significance of vegetation type					0.380	0.005	0.035	0.502	0.339	0.230	0.955
depth					0.438	0.385	0.0001	0.0001	0.001	0.0001	0.284
shrub-intershrub position					0.680	0.509	0.224	0.0001	0.116	0.0001	0.090

end of ranges reviewed by Payne & Wiebe (1978) and reported by Schimel (1988), and most closely correspond with bacterial rather than fungal carbon assimilation efficiencies reviewed by Holland & Coleman (1987). Soils from under-shrub positions had significantly lower microbial growth efficiencies than soils from between-shrub positions, and surface soils generally had lower efficiencies than the subsurface soils.

^{15}N Budget

Using the ^{15}N data from the KCl extractions of both fumigated and unfumigated samples, we constructed a ^{15}N budget for the inorganic and microbial nitrogen during the experiment (Table 4). By day 5 of the incubation, most of the tracer ^{15}N was gone from the inorganic fraction, resulting in only 1 to 1.8 μg tracer ^{15}N per gram of soil in the ammonium + nitrate fraction. The ^{15}N content of the inorganic pool decreased from day 5 to day 15, and from day 15 to day 30, indicating remineralization of tracer ^{15}N into the inorganic pool. In the first 5 days 20% of the original ^{15}N was immobilized into the microbial biomass. No clear trend in ^{15}N content of the microbial biomass from day 5 to day 30 was evident. The remineralization of ^{15}N suggests that gross mineralization rates, microbial growth, and microbial growth efficiency calculated for day 15 using the mineral N pool dilution equations are overestimated to some extent; gross immobilization rates are underestimated.

Recovery of ^{15}N from digestions at the end of the experiment (Table 4) ranged from 57.2 to 94.8%. The ^{15}N recovered on day 5 and day 15 in the Ni and microbial biomass fractions was generally lower than the final ^{15}N recovered, which suggests sequestering of ^{15}N in organic matter other than living microbial biomass.

Discussion

Variation among vegetation types

Vegetation type exerted a clear control over nutrient turnover and nutrient availability. Nearly all fractions measured (Ct, Nt, Pt, Pa, microbial biomass C and N) were either significantly or consistently higher in soils from the ssp. *vaseyana* vegetation type than the ssp. *wyomingensis* and *nova* types. Little difference was found between these two latter types. All mineralization, immobilization, and microbial growth rates varied concomitantly with the pools, showing highest rates in the ssp. *vaseyana* types. These results alone might suggest a simple landscape fertility gradient among vegetation types.

Examination of turnover indices, however, indicates that "active" material (Parton et al. 1987) in the ssp. *vaseyana* soils is more limiting than that in the two other vegetation types. Surface soils of the ssp. *vaseyana* type had consistently lower N turnover rates than the other vegetation types, both for the 5-day and the 15-day incubations, showing that gross N mineralization rates per unit of soil N are not as high in this type. Microbial growth efficiencies in the first 5 days were consistently lower in the ssp. *vaseyana* type. These two trends indicate that soil microbial biomass in the ssp. *vaseyana* type is closer to steady-state. Although gross N immobilization and microbial growth are higher in the ssp. *vaseyana* soils, suggesting higher total active material, the lower C and N turnover rates and microbial efficiency suggest that microbial activity in the "richer" (higher C_t, N_t, and P_t) landscape positions is more limited by labile material.

Differences in microbial efficiency among vegetation types, as described above, dampen after the first 5 days of the experiment. All soils had undergone rapid mineralization and immobilization of labile material by this time, and efficiencies in general were declining as labile material became more limiting (Dommergues et al. 1978). Similar results have been documented in the laboratory by Shen et al. (1984), who found that respiration rates decreased during his 10- and 20-day incubations, and by Schimel (1986), who found decreased rates of C and N mineralization during incubations. Increased labile substrate limitation through the incubation period is also evident in the decrease in C/N_{min} and the increase in net relative to gross mineralization, indicating maintenance-level substrate use. Under field conditions, rapid decline of labile materials across the entire landscape probably does not occur, since optimal soil moisture and temperature conditions will only rarely persist for long periods of time across the entire landscape. Because of higher relative availability of labile material, soils from *nova* sites may be more likely than ssp. *vaseyana* soils to be able to respond rapidly to pulses of increased moisture. Thus, microflora in the *nova* soils may be primarily water limited over the short term, while microflora of ssp. *vaseyana* soils are more limited by substrate.

Variation between shrub-intershrub positions

At a smaller spatial scale, shrub-intershrub variability, vegetation exerted a similar effect. Total and available nutrient pools were generally higher under than between shrubs, as has been previously documented in arid and semi-arid shrublands (Charley & West 1977; Lajtha & Schlesinger 1986; Klopatek 1987). In this study, we also found microbial biomass pools to be generally higher under shrubs than between shrubs, as were all mineralization, immobilization, and microbial growth rates. Microbial efficiency, however, was

significantly lower under shrubs than between for both the 5- and 15-day incubations, suggesting again the possibilty of limitation by labile material. C/N_{min} and C and N turnover showed no trends with shrub-intershrub position. This contrast between shrub and intershrub positions mirrors the comparison described above for between vegetation types.

Variation with depth

Trends with depth correspond with those across vegetation types and shrub-intershrub positions: as total nutrient pools increase, turnover, microbial efficiency, and the fraction of labile material apparently decrease. Results of the study indicate that surface soils are richer than subsurface soils in total organic matter, but have a lower fraction of active material. All total and available nutrient pools and mineralization rates were higher in the surface soil (0–5 cm) than in the subsurface (5–15 cm) soils, as one might expect from the results of Fyles & McGill (1987). We also found that immobilization, and microbial growth rates were higher in the surface soils, but that N turnover, C/N_{min}, microbial efficiency, and active/total biomass were significantly lower in the surface soils, however, and as we have suggested above, these trends imply microbial growth limitation by labile material.

Nitrogen loss

The recovery of ^{15}N after 30 days indicates that losses of N were occurring. Very high net nitrification rates were observed in this experiment, as were high nitrate concentrations (6–50 ppm as N). Under high soil moisture and soil temperature conditions in the field, we have observed relatively high N_2O production rates as Stratton (Matson, unpubl. data). In the field, N_2O production may be associated with nitrification (Bowden 1986; Parton et al. 1988), although denitrification may also occur in saturated soil micropores, especially during snowmelt periods. In this experiment, high N_2O losses from nitrification rates could account for much of the ^{15}N not recovered on day 30.

Conclusions

Laboratory incubations of ^{15}N-amended soils from the mountain big sagebrush system at Stratton, Wyoming, indicate that nutrient turnover and availability have complex responses to landscape and microsite variations. Soils from areas of greater organic matter accumulation – at any spatial

scale – have a greater potential for high mineralization and respiration rates. However, data from laboratory incubations indicate that soil microbes at sites rich in organic matter tend to be relatively more substrate limited than soils with less organic matter.

In the field, soils of the richer, higher productivity sites (*vaseyana* sites) are generally more subject to favorable microclimatic conditions than soils from lower organic matter accumulation areas. As a result, microbial activity probably occurs over a longer time span in the spring and early summer, perhaps reducing the proportion of labile organic matter relative to the total organic matter pool. Responses to improved soil microclimate conditions are limited by this pool of active material, as was evident in the relatively lower microbial efficiencies of "richer" sites in the first 5 days than in soils from "poorer" sites. Soils from areas with lower organic matter accumulations (e.g., *nova* sites), however, have shown an ability to have relatively higher microbial efficiencies during the first 5 days of incubation. In the field, these "poorer" soils are probably limited initially by soil microclimate, and only after a relatively prolonged period of activity will they experience limitation by soil organic matter pools.

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