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Nutrient and microbiological characteristics of fine benthic organic matter in mountain streams

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Abstract. Fine benthic organic matter (FBOM) was collected over a 10-mo period from 14 1st-order streams in the Cascade Mountains of western Oregon to investigate 1) relationships between FBOM substrate quality and microbial activity, 2) links between organic matter sources and FBOM substrate quality, and 3) how FBOM is influenced by riparian vegetation, elevation, and season. Streams drained forests in 3 successional age classes: old-growth forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), and young regenerating stands, either 10 y old with a large riparian herbaceous component, or 30 y old and surrounded by deciduous trees such as red alder (*Alnus rubra*).

Seasonal trends showed a major autumn depression in carbon:nitrogen ratios (C:N) and an increase in microbial activities, a likely result of increased leaf inputs after an early fall storm. Decreases in C:N, total C, total N, and organic P were correlated with reciprocal increases in respiration, β–glucosidase and phosphatase activities, and acetylene reduction, all of which are relative indicators of microbial activity. Lower C:N and higher denitrification potentials, respiration rates, β–glucosidase and phosphatase activities, and mineralizable N were observed in young stands compared to old growth, suggesting higher quality FBOM and faster decomposition rates in young stands. An exception to this trend was acetylene reduction, which was greater in FBOM from old-growth streams. Significantly lower C:N at high elevations (1220–1280 m) versus low elevations (580–800 m) suggested the presence of more herbaceous vegetation and alder in high-elevation riparian zones. Lower total N and total C, and elevated denitrification potentials, acetylene reduction, respiration rates, and phosphatase activity at low elevations (580–800 m) suggested greater decomposition rates at low elevations. Organic P was 3.6 and 2.2 mg P / g organic matter at high and low elevations, respectively, a significant difference probably resulting from the young geologic age of parent material at high elevations. Data from this study suggest a potential link, mediated by shifts in FBOM, between headwater forest management and dynamics of stream food webs.

Key words: fine benthic organic matter, mountain streams, microbial indicators, tree harvest effects, elevation effects, Douglas-fir, red alder.

Fine benthic organic matter (FBOM) is a potentially important link between the management of riparian forests and stream productivity. In forested headwater streams, often <1% of total solar radiation reaches the stream, severely limiting in-stream primary production (Gregory et al. 1987). Thus, allochthonously derived FBOM is an important nutritional source for microorganisms and invertebrates (Vannote et al. 1980, Cummins et al. 1989, Schlosser 1991). Variation in invertebrate abundance has been linked to autumn leaf inputs, winter and spring leaf processing, summer reduced organic inputs, and summer transport of FBOM (Schlosser 1991, Wallace et al. 1991, 1993). Because invertebrates serve as food for vertebrate predators such as fish and salamanders, forest management practices that influence the type and amount of FBOM in streams will influence productivity at higher trophic levels.

Qualitative shifts in leaf litter composition in the early-to-middle stages of decomposition in streams have been examined in numerous studies (Petersen and Cummins 1974, Suberkropp et al. 1976, Findlay and Arsuffi 1989). These investigations have shown that changes in leaf species and composition lead to marked differences in microbial processing rates (Suberkropp and Klug 1976). Decomposition rates of leaf and woody debris are also related to both initial litter carbon:nitrogen ratios (C:N) and activities of extracellular enzymes (Taylor et al. 1989, Sinsabaugh et al. 1992, Sinsabaugh and Linkins 1993). Low initial C:N typically is associated with high litter decomposition and mass loss rates. Vari-

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ous extracellular enzymes directly involved in the decomposition process exhibit different rates of activity over time, which suggests successional change in the microbial community and in sources of C and/or N (Sinsabaugh and Linkins 1990, 1993, Sinsabaugh et al. 1992).

The decomposition of allochthonous leaf litter and woody debris is also a major source of fine particulate organic matter (FPOM) (Ward 1986). Because most transported organic matter moves through streams as FPOM or dissolved organic matter (Benke et al. 1988), FPOM is a potentially important link between terrestrial and aquatic environments. Interest in understanding FPOM is increasing, but few studies consider the effects of harvesting riparian forests on the chemical or microbial characteristics of stream sediment or FPOM.

Fine benthic organic matter varies in chemical composition by source and decay state (Ward et al. 1994), which may be reflected in changes in the C:N of FBOM. For example, C:N may be lower in material from a herbaceous and/or highly processed source than in material from a woody source and/or during the initial stages of processing. However, there is little difference in the microbial activity of FBOM from streams running through different forest types, which suggests that headwater and riparian vegetation may have little influence on the chemical composition of FBOM (Hargrave 1972, Ward 1986, Sinsabaugh and Linkins 1990, Sinsabaugh et al. 1992). In these cited studies, chemical differences attributable to differences in sources of streamside vegetation may have been swamped by inputs of FBOM generated from readily degradable stream algae, herbaceous plants, or alder leaves during litter processing (Suberkropp and Klug 1980, Ward 1984).

In this study we 1) examine the relationship between FBOM nutrient composition, or substrate quality, and microbial activity, 2) investigate seasonal trends in FBOM characteristics, and 3) compare the qualitative characteristics of FBOM from streams flowing through stands with riparian zones dominated by coniferous, deciduous, or herbaceous vegetation at 2 elevations for 1 y.

Methods

Site description

Fine benthic organic matter samples were collected from 14 1st-order streams flowing through forest in 3 successional age classes: 3 Douglas-fir (*Pseudotsuga menziesii*) stands ~10 y old (10YS), 5 Douglas-fir stands 30 y old (30YS), and 6 old-growth forest (OG) stands dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*) in the H. J. Andrews Experimental Forest (HJA) in the western Cascade Mountains of Oregon. Riparian vegetation of the 8 young stands was dominated by herbaceous plants (10YS) or deciduous trees (30YS), primarily red alder (*Alnus rubra*) and maple (*Acer macrophyllum, A. circinatum*). On 10YS and 30YS, no riparian vegetation buffers were left during cutting, and stands were replanted with Douglas-fir seedlings. Streams at high (1220–1280 m) and low (580–800 m) elevations were selected. An effort was made to keep similar stand age × elevation plots on the same slope and aspect.

Sample collection, preparation, and storage

Streams were sampled for FBOM on 8 occasions: 9 August 1995, 14 October 1995, 28 October 1995, 4 November 1995, 18 November 1995, 9 December 1995, 6 April 1996, and 12 May 1996 (Sampling 1 through Sampling 8, respectively). Surficial FBOM was collected from streambeds with a hand-held vacuum pump into a 2-L collecting jar. The intake line was fitted with a 1-mm stainless steel screen, thus allowing benthic material to be wet-sieved during sampling. Samples were transferred to polystyrene jars (500 mL) and stored during field sampling in an insulated chest with stream water and ice. In the laboratory, a slurry was prepared by decanting excess stream water from the jars, and subsequent mixing to keep FBOM suspended while subsamples were taken. Subsamples were taken with 1-, 3-, or 5-mL plastic syringes with enlarged openings. All laboratory analyses involving slurry began immediately upon return from FBOM collection, i.e., within 8–12 h. Temperatures used in the biochemical assays were not chosen to mimic in situ temperatures because we wanted to measure potential microbial rates under standardized conditions.

Microbial activity

Denitrification potential (DNIT) was determined as N_2O emission during anaerobic incubation of FBOM supplemented with glucose and $NaNO_3$ (Martin et al. 1988). Duplicate 5-mL

FBOM slurry samples in 25-mL Erlenmeyer flasks were capped with rubber stoppers and purged for 3 min with argon at 120 cc/min. Flasks were shaken gently during the purging to ensure that entrapped air bubbles were removed. The flasks were incubated for 1 h at 24°C. Two mL of sterile solution of 1 mM glucose and 1 mM $NaNO_3$ were then injected through the stopper. Afterwards, 2 mL of headspace gas were removed with the same syringe, and the incubation was continued. After 1 h and 3 h, a gas chromatograph (GC) equipped with an electron capture detector was used to assay 0.5 mL of headspace gas for N_2O.

Respiration (RESP) was measured on duplicate 5-mL FBOM slurry samples in 25-mL Erlenmeyer flasks capped with rubber stoppers. Headspace gas samples (0.5 mL) were collected after 1 h preincubation at 24°C, and again 2 h later. They were analyzed for CO_2 on a GC fitted with a thermal conductivity conductor.

Putative N-fixation rates (NFIX) were determined by the acetylene reduction method (Weaver and Danso 1994). Samples were prepared as for DNIT analysis, except that the headspace gas was replaced with 1.5% O_2, 12.5% acetylene, and 86% argon. After 24 h of incubation, 0.5 mL of headspace gas was removed and analyzed for ethylene on a GC fitted with a flame ionization detector. A control without acetylene was analyzed for endogenous ethylene production.

Phosphatase activity (PHOS) was determined by the spectrophotometric assay of Tabatabai and Bremmer (1969), as modified by Zou et al. (1992). One mL of 50 mM *p*–nitrophenyl phosphate substrate was added to duplicate 1-mL subsamples containing suspended FBOM. The tubes were shaken and then placed with duplicate controls without phosphatase substrate in a 30°C water bath for 1 h. After incubating, 1 mL of 50 mM *p*–nitrophenyl phosphate was added to the controls, and all reactions were immediately stopped by the addition of 0.5 mL of 0.5 M $CaCl_2$ and 2 mL of 0.5 M NaOH. The mixtures were centrifuged for 5 min at 500 × the force of gravity. From the supernatant, 0.2 mL of solution was diluted with 2.0 mL deionized water. The optical density was measured at 410 nm, and a standard curve was prepared from 0.02 to 1.0 μmol/mL *p*–nitrophenol (pNP). The same general procedure used for PHOS was followed to measure β–glucosidase (BGLC), except that 1 mL of 10 mM *p*–nitrophenyl β–D glucopyranoside was used as the substrate, the incubation period was 2 h, and 2 mL of 0.1 M tris[hydroxymethyl]aminomethane at pH 12.0, instead of 0.5 M NaOH, were added to terminate the reaction.

Nutrient characteristics

Mineralizable N (NMIN) was measured by the 7-d anaerobic incubation method (Keeney 1982). Duplicate 10-mL FBOM subsamples were placed in 50-mL screw-top test tubes, which were filled to the top edge with deionized water (53 mL), capped, and incubated at 40°C for 7 d. After incubation, 53 mL of 4 M KCl were added. The test tubes were shaken for 1 h in the presence of 0.4 mL 10 M NaOH, and analyzed for NH_4-N with a selective ion electrode (Corning, Medford, Massachusetts).

Extractable ammonium (EA) was determined by adding 50 mL of 2 M KCl to duplicate 10-mL samples in 250-mL Erlenmeyer flasks. Flasks were capped, shaken while incubating for 1 h in the presence of 0.4 mL 10 M NaOH, and analyzed with a selective ion electrode to determine KCl-extractable ammonium concentration. Net mineralization was calculated as NMIN − EA.

Noncellulose polysaccharide content (PSAC) of air-dried FBOM was estimated by colorimetric determination of total sugars (Lowe 1993). Total C and total N (CTOT and NTOT) were determined by dry combustion with a Carlo-Erba NA 1500 Series II high-temperature combustion furnace on oven-dried subsamples ground to pass through a 250-μm sieve. Total and inorganic P (PTOT and PINORG) were estimated colorimetrically in 1 N H_2SO_4 extracts from dry samples ignited at 550°C and unignited samples, respectively (Olsen and Sommers 1982). Organic P (PORG) was calculated by the difference, PTOT − PINORG.

Statistical analyses

Analysis of variance.—Analysis of variance (ANOVA, SAS 6.11 for Windows, SAS Institute Inc., Cary, North Carolina) was used to test for differences between riparian successional stage or treatment means and elevation means for each date. Correlations between microbial activity and nutrient availability were determined by

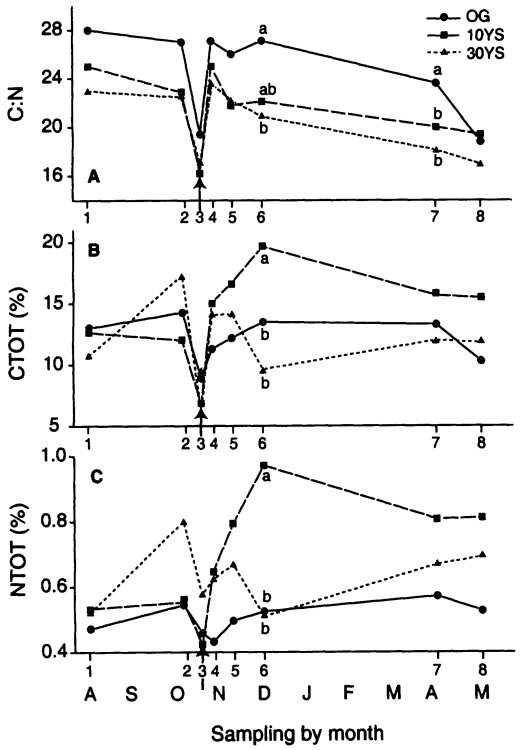


FIG. 1. Mean (A) C:N, (B) total C (CTOT), and (C) total N (NTOT) of fine benthic organic matter collected from headwater streams in old growth (OG), 10-y-old stands (10YS), and 30-y-old stands (30YS) in the Oregon Cascades. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) among treatments. Arrow indicates timing of storm event.

the nonparametric Spearman Rank method of analysis.

Multivariate ANOVAs (MANOVAs) were used in conjunction with univariate analyses as an additional explanatory tool to detect overall patterns over time, e.g., whether or not treatment or elevation differences in FBOM were significant over the entire sampling period, and whether or not these differences were influenced by season. The SAS procedure "proc mixed" and the variance/covariance matrix resulting in the largest value for Akaike's Information Criterion for each variable were used for repeated measures MANOVAs. Repeated measures analyses were used where sampling date (TIME) and either treatment (TRT) or elevation (ELEV) were explanatory variables. There were 3 TRT levels: OG, 30YS, and 10YS, and 2 ELEV levels: HIGH (1220–1280 m) and LOW (580–800 m). Only OG and 30YS were included in repeated measures analyses for elevation effects; LOW 10YS were excluded because they had no high-elevation counterpart. Only Samplings 1–5 were included in the MANOVAs. Samplings 6–8 were excluded because the assumptions of repeated measures were violated by nonrandom missing data; snowpack prohibited sampling of high-elevation sites on these dates. Some variables were missing on additional dates because of equipment failure.

Principal components analysis.—A matrix of 112 sample units (streams × dates) by 10 biochemical/activity variables and 5 environmental variables and site characteristics was analyzed by principal components analysis, with Euclidean distance measures and correlation on PC-ORD software. Missing data were replaced according to recommendations by Tabachnik and Fidell (1989). Incomplete data collection led to the deletion of 30 samples and 3 variables: DNIT, EA, and PTOT. Five outliers were deleted. One outlier had an unusually high rate of N-fixation for both duplicates in Sampling 1; field notes indicated that this site had deep, slow-moving pools, which suggested that reduced oxygen concentrations could have stimulated N-fixation. Four outliers were deleted from the same 10YS, which had consistently higher CTOT and NTOT than other 10YS, and which was the only site to have abundant devil's club (*Oplopanax horridum*).

Results

Seasonal effects

One pattern showed high C:N in August and early October, with a rapid, significant drop in late October (Sampling 3), and a recovery in early November (Fig. 1A). Similar patterns were observed for CTOT, NTOT, DNIT, and PORG (Figs 1B, 1C, 2A, 3A).

A 2nd pattern, reciprocal to the 1st, was found for NFIX, PTOT, PINORG, RESP, BGLC, PHOS, and PSAC (Figs 2B, 3B, 3C, 4A–D). Instead of decreases in late October (Sampling 3) and mid-November (Sampling 5), these variables pulsed upward, returned to prepulse levels, and then generally remained steady until spring, when there was an upswing.

Although missing data made patterns difficult to discern, EA and NMIN followed similar

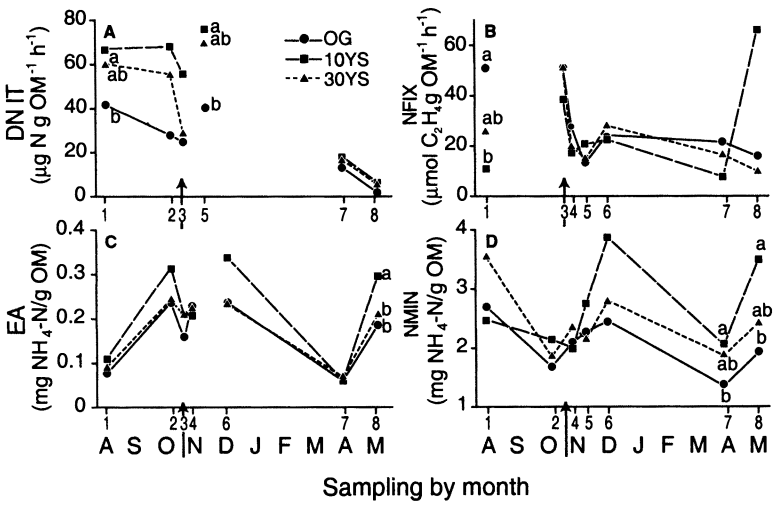


FIG. 2. Mean (A) denitrification potential (DNIT), (B) acetylene reduction (NFIX), (C) extractable ammonium (EA), and (D) mineralizable N (NMIN) of fine benthic organic matter collected from headwater streams in old growth (OG), 10-y-old stands (10YS), and 30-y-old stands (30YS) in the Oregon Cascades. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) among treatments. OM = organic matter. Arrow indicates timing of storm event.

trends from November through May. They reached some of their lowest values in April, increased in May (Figs 2C, 2D), and differed most in early October, when concentrations of EA increased and NMIN decreased. The seasonal patterns were similar when EA and NMIN were normalized to total N instead of organic matter (OM).

Treatment effects

Microbial activity.—Respiration rates, PHOS, and DNIT were lowest for FBOM in OG and highest in 10YS, with mean rates in 30YS falling between 10YS and OG rates (Table 1). Both BGLC and PHOS exhibited significant treatment effects (MANOVA, $p = 0.02$), but BGLC did not show significant seasonal differences between 10YS and 30YS (Table 1). Differences in DNIT between OG and 10YS were large at the beginning of the study, and minimal by spring.

Acetylene reduction followed a trend opposite to the other activity assays. Rates in FBOM from OG were significantly higher than rates in FBOM from younger stands at Sampling 1 and, overall, NFIX averaged 38, 27, and 22 μmol C_2H_4 g OM^{-1} h^{-1} in OG, 30YS, and 10YS, respectively.

Nutrient characteristics.—Treatment effects were not as strong for FBOM nutrient characteristics as they were for FBOM microbial activity. No overall treatment effect was found for FBOM C:N; however, mean ratios were highest in OG, a pattern repeated for 7 of the 8 sampling dates (Fig. 1A). In contrast, the mean averages for CTOT, NTOT, and PTOT were lowest in OG (Table 1); however, seasonal CTOT values in OG were frequently intermediate relative to 10YS and 30YS (Fig. 1B). Differences between OG and young stands were significant for some sample dates (Figs 1B, 1C, 3B). The labile components EA, NMIN, PINORG, and PORG (Figs 2C, 2D, 3A, 3C) followed trends similar to those for nutrient totals, which were typically lowest in OG. An exception was PSAC, with mean concentrations in OG and 10YS similar to and greater than those in 30YS; no consistent treatment effect was evident (Fig. 4D).

Elevation effects

Microbial activity.—Average rates were higher at low elevation versus high elevation for DNIT, NFIX, RESP, and PHOS (Table 1, Figs 5A, 5B, 6A, 6C). Denitrification potentials were significantly higher at low elevations (MANOVA, $p = 0.05$ for ELEV), with mean values at low elevations nearly double those at high elevations (53

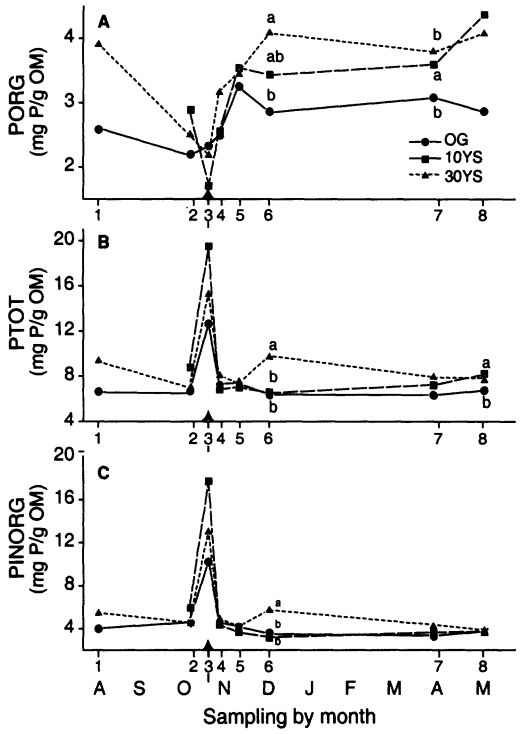


FIG. 3. Mean (A) organic P (PORG), (B) total P (PTOT), and (C) inorganic P (PINORG) of fine benthic organic matter collected from headwater streams in old growth (OG), 10-y-old stands (10YS), and 30-y-old stands (30YS) in the Oregon Cascades. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) among treatments. OM = organic matter. Arrow indicates timing of storm event.

and 29 mg N g OM^{-1} h^{-1}, respectively). Although not significant, BGLC at high-elevation sites was typically greater than at low elevations (Fig. 6B). Respiration, PHOS, and BGLC had elevated rates in late October (Sampling 3). Missing data made seasonal trends in NFIX and DNIT difficult to discern.

Nutrient characteristics.—Carbon:nitrogen ratios were significantly higher in FBOM at low-elevation sites than at high elevations (MANOVA for ELEV effect, $p = 0.05$, Table 1). Total C and NTOT were significantly lower at low-elevation sites than at high elevations (MANOVA for ELEV effect, $p = 0.03$ and 0.02, respectively). Aside from a dip in values for C:N, CTOT, and NTOT in late October (Sampling 3), average values remained relatively stable at both elevations (Fig. 7A–C). Total P followed a trend opposite to C:N, CTOT, and NTOT (Fig. 8B), rising rather than falling in late October. In addition, PTOT was typically higher at high-elevation sites than at low elevations. Organic P and PINORG were significantly higher at high-elevation sites than at low elevations (MANOVA, $p = 0.01$ for ELEV effect); however, PORG showed the same decline during Sampling 3 as did C:N, CTOT, and NTOT (Fig. 8A, 8C). Mineralizable N and PSAC were also higher at low-elevation sites than at high-elevation sites (Figs 5C, 6D). In fact, PSAC was significantly higher at low elevations (MANOVA, $p = 0.01$ for ELEV effect). The largest disparity between low- and high-elevation concentrations of PSAC occurred during Sampling 3, when concentrations were depressed at high-elevation sites and rose at low elevations.

Principal components analysis

The first 3 dimensions explained 66.6% of the variation in the data set. Table 2 shows loadings for each variable for Axes 1–3. Axis 1 explained 31.2% of the variation and was primarily attributable to microbial activity, especially PHOS, BGLC, and RESP, as well as CTOT. Axis 2 explained 23.9% and was attributed to substrate quality, particularly C:N, CTOT, NTOT, and PORG. The 11.5% of variation explained by Axis 3 was attributable to N availability, as shown by NMIN and NFIX.

Examination of TRT, TIME, and ELEV in biochemical space elicited an interesting relationship among C, N, and microbial activity (Fig. 9). Most FBOM samples were located in an area that had low NTOT and high CTOT (high C:N), and low activity rates, PORG, and NMIN (Area I, Fig. 9A). This area included all OG, low-elevation sites, except for 2 sites in Area II, and most sampling dates (Fig. 9A–C). In contrast, Area II had low CTOT and NTOT (low C:N), and high activity rates and NMIN. Area II also contained high-elevation 10YS and 30YS sampled predominantly in late October (Sampling 3) (Fig. 9A–C). This date represented a change from high C:N and low activity (Sampling 2), to low C:N and high activity rates. Area III, which contained the smallest number of samples, had low C:N as well, but CTOT, NTOT, and NMIN were high, and activity rates, except BGLC, were generally low. Most notably, Area III had high PORG. All high-elevation sites had high concentrations of PORG, and this area con-

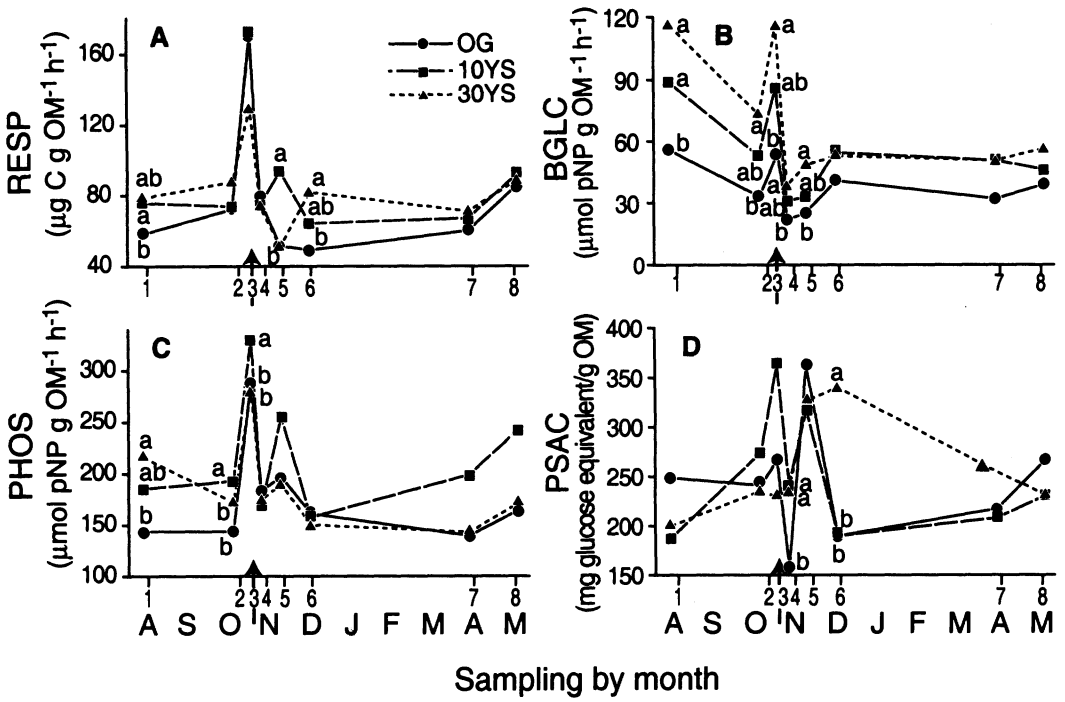


FIG. 4. Mean (A) respiration (RESP), (B) β−glucosidase activity (BGLC), (C) phosphatase activity (PHOS), and (D) labile polysaccharide concentration (PSAC) of fine benthic organic matter collected from headwater streams in old growth (OG), 10-y-old stands (10YS), and 30-y-old stands (30YS) in the Oregon Cascades. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) among treatments. OM = organic matter, pNP = *p*–nitrophenol. Arrow indicates timing of storm event.

tained 30YS, 10YS, and both high- and low-elevation sites.

Discussion

Seasonal effects

In general, seasonal shifts in FBOM substrate quality and microbial activities were greater than shifts related to treatment or elevation. The principal seasonal anomaly was closely associated with a storm event in October, documented by rain gauges at HJA. This storm likely delivered large quantities of litter, especially deciduous leaves and herbaceous plant material, to the streams immediately prior to sampling, and may have dislodged senescent algal detritus released by the rising flows (Cummins and Klug 1979). Introduction of this readily decomposable organic matter could have caused the dramatic shifts we measured in most FBOM characteristics.

A dramatic shift occurred in C:N. Shifts in C:N can reflect 2 main phenomena in natural detritus. First is the accumulation of N as C is lost during litter decay, reducing C:N. As litter or coarse woody debris decomposes, C is removed as CO_2, and N and P become sequestered within humic materials produced during decomposition (Suberkropp et al. 1976, Sinsabaugh et al. 1993). The 2nd phenomenon involves differences in litter quality or source. For example, fresh woody materials exhibit high C:N, whereas alder leaves, herbaceous vegetation, and algae exhibit much lower C:N. Which phenomenon caused the storm-induced reduction of C:N (Fig. 1A) is the main question of this study.

If the reduced C:N associated with the October pulse was caused by the introduction of highly decomposed litter, we would expect this pulse to be accompanied by a reduction in microbial activity. Yet, we observed a large increase in all variables associated with the activity of heterotrophic microorganisms: RESP, BGLC, and PHOS (Fig. 4A–C). Beta-glucosidase, which is usually associated with fungi and

TABLE 1. Least-squared means (* = medians for log-transformed values) for variables measured in 1st-order streams in old growth (OG), 30-y-old (30YS), and 10-y-old (10YS) stands, and at low (580–800 m) and high (1220–1280 m) elevations in the Oregon Cascades. OM = organic matter. pNP = *p*–nitrophenol, *n* = number of observations.

Variable	Units	Abbreviation	Treatment			Stream elevation		*n*
			OG	30YS	10YS	Low	High	
C:N	–	C:N	26	22	22	26	20	62
Total C	%	CTOT	12.0	13.1	12.7	10.9	15.1	62
Total N	%	NTOT	0.48	0.64	0.60	0.45	0.75	62
Denitrification potential*	$\mu g\ N\ g\ OM^{-1}\ h^{-1}$	DNIT	30	50	67	53	29	49
Mineralizable N*	mg NH_4-N/g OM	NMIN	2.1	2.4	2.3	2.4	2.0	48
Extractable ammonium	mg NH_4-N/g OM	EA	0.18	0.20	0.21	0.19	0.19	50
Acetylene reduction*	$\mu mol\ C_2H_4 g\ OM^{-1}\ h^{-1}$	NFIX	38	27	22	26	21	52
Respiration*	$\mu g\ C\ g\ OM^{-1}\ h^{-1}$	RESP	77	80	95	84	78	62
β–glucosidase*	$\mu mol\ pNP\ g\ OM^{-1}\ h^{-1}$	BGLC	35	71	53	46	56	62
Phosphatase*	$\mu mol\ pNP\ g\ OM^{-1}\ h^{-1}$	PHOS	176	203	219	214	166	62
Labile polysaccharides	mg glucose equivalent/g OM	PSAC	261	225	274	269	225	61
Total P	mg P/g OM	PTOT	8.4	9.4	10.4	8.8	10.0	51
Organic P	mg P/g OM	PORG	2.4	2.4	2.5	2.2	3.6	51

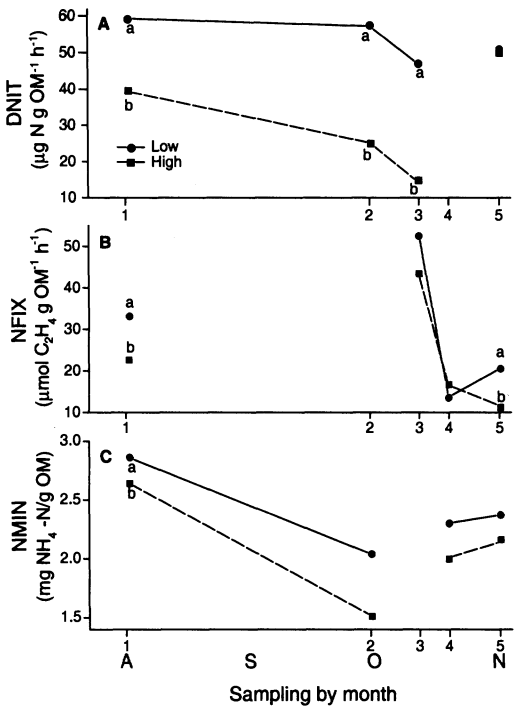


FIG. 5. Mean (A) denitrification potential (DNIT), (B) acetylene reduction (NFIX), and (C) mineralizable N (NMIN) of fine benthic organic matter collected from headwater streams in the Oregon Cascades at low (580–800 m) and high (1220–1280 m) elevations. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) between elevations. OM = organic matter.

bacteria, hydrolyzes cellobiose to low-molecular-weight glucose monomers that become available for microbial uptake (Overbeck 1991). Phosphatase hydrolyzes organic P esters to inorganic phosphate, and is produced by a wide range of organisms, including bacteria, algae, and fungi (Overbeck 1991). The increased microbial activity we measured suggests that the low C:N observed was caused by the input of high-quality litter with relatively high concentrations of organic N.

The link between substrate quality and decomposability has been observed in studies of heartwood (Baker et al. 1983) and litter decomposition (Suberkropp et al. 1976, Gregory 1978, Findlay and Arsuffi 1989). One variable monitored in these studies, noncellulose polysaccharides, directly addresses the question of FBOM quality. Noncellulose polysaccharides should be readily decomposed by microorganisms and, therefore, disappear from FBOM rapidly. Thus, elevated concentrations of PSAC in FBOM should be an indicator of the relative decomposability of FBOM. The increase in PSAC after the October pulse suggests that the reduction in C:N in October was the result of the input of litter of relatively recent origin.

In our study, storm-induced spikes in FBOM characteristics returned to prespike values rapidly. Other studies have shown that both the composition (Ittekkot et al. 1985) and the amount of FPOM in streams can change with flow rate (Cuffney and Wallace 1989), and suggest that the rapid return of C:N and PSAC to baseline levels after a storm may be caused by either rapid transport of FBOM or rapid decomposition (Figs 1A, 4D).

In addition to collecting FBOM from low-order streams, we conducted similar seasonal studies at HJA on FBOM taken from small watershed settling basins in which all sediments are trapped over time (H. L. Bonin and co-workers, unpublished data). These data suggest that at least some of the change in FBOM may be the result of rapid decomposition. If the short duration of the October spike were controlled primarily by rapid transport, we would predict that it would take longer for spikes in settling-basin FBOM to return to prespike levels because these basins retain sediments over time. Essentially the same spikes in activity and C:N were observed in these sediments as in stream FBOM, which suggests that the rapid return of values to prespike levels resulted, at least in part, from rapid decomposition. The apparent short residence time of readily decomposable organic matter in FBOM may explain seasonal variations in the qualitative characteristics of stream FBOM reported by Ward (1986), who found that FBOM lignin and cellulose concentrations remained relatively constant, despite qualitative differences in allochthonous inputs into streams.

We also observed decreased C:N in FBOM collected in the spring. At the same time as C:N was decreasing, PSAC, RESP, and PHOS were increasing, which suggests the presence of readily degradable organic C. These trends likely reflect an increase in the relative proportion of autochthonous algae incorporated into FBOM as a result of increased daylight. Increased algal influence may explain other seasonal patterns as well. Increases in NMIN would be expected

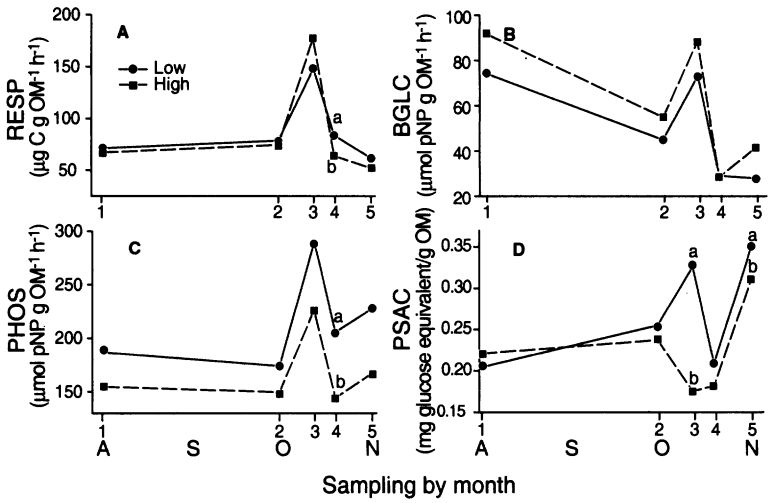


FIG. 6. Mean (A) respiration (RESP), (B) β−glucosidase activity (BGLC), (C) phosphatase activity (PHOS), and (D) labile polysaccharide concentration (PSAC) of fine benthic organic matter collected from headwater streams in the Oregon Cascades at low (580–800 m) and high (1220–1280 m) elevations. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) between elevations. OM = organic matter, pNP = *p*–nitrophenol.

with increases in organic N-rich algal biomass. In addition, algae are an important sink for stream nitrate, and reductions in DNIT would also be expected with increased algal activity. These trends support our contention that observed spring patterns were caused by increased stream algal activity (Fig. 2A, 2D).

As predicted, C:N was higher in OG reaches than in streams running through harvested riparian areas (Table 1). Woody debris is a major component of detrital inputs into low-order streams in old-growth forests (Triska and Cromack 1980), and would generate FBOM with high C:N. In contrast, FBOM from the harvested stands should exhibit low C:N, because alder, as well as herbaceous and algal inputs, are N-rich. With the exception of PHOS and BGLC, differences among treatments were relatively small, and were not statistically significant. However, the trends were the same as in the seasonal data, where differences over time were significantly different (all variables except DNIT were significantly different at $p \leq 0.0001$).

In the seasonal data, C:N was inversely related to measurements of microbial activity. The same relationship held in the comparisons of stream FBOM collected from OG and harvested forests. Respiration, PHOS, and BGLC were all lower in OG streams than in 10YS and 30YS (Table 1). Phosphatase activity and BGLC, the only variables that showed statistically significant treatment effects, were also higher in 10YS and 30YS.

Treatment effects

Based on the likely litter sources, we assumed that detritus would be higher in quality and thus more readily degradable in streams running through young stands than those in OG. For this reason, we predicted that the concentrations of both NMIN and PSAC would be higher in FBOM from young strands than in OG. This trend was observed for NMIN, but not for PSAC (Table 1). Labile polysaccharides may be degraded before reaching the FBOM pool, or residence time in the pool may be quite short as a result of decomposition soon after arrival.

Mineralizable N was lower in FBOM from streams running through OG than in FBOM from streams in younger stands, although the difference was not statistically significant (Table 1). The data also indicated other differences in N levels and dynamics of FBOM between OG and younger strands. The trends were consistent with the relationship seen in the seasonal data, but none of these differences was statistically significant. Extractable ammonium and DNIT were both greater in 10YS and 30YS than in OG FBOM. In past studies, denitrification po-

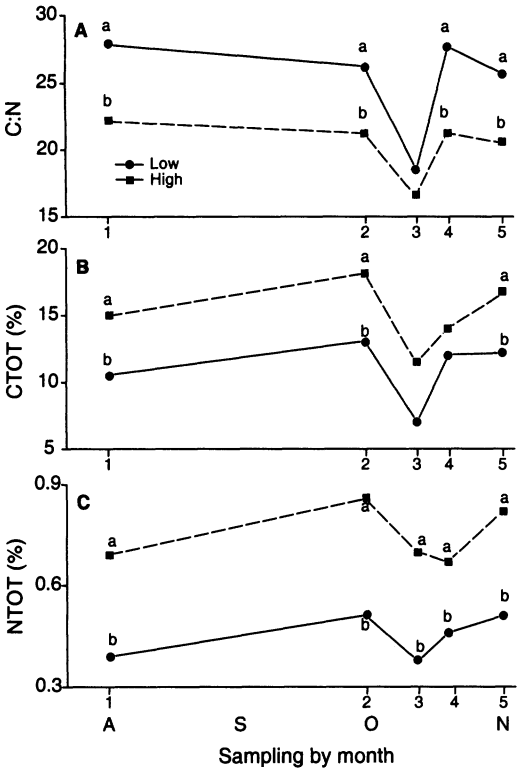


FIG. 7. Mean (A) C:N, (B) total C (CTOT), and (C) total N (NTOT) of fine benthic organic matter collected from headwater streams in the Oregon Cascades at low (580–800 m) and high (1220–1280 m) elevations. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) between elevations.

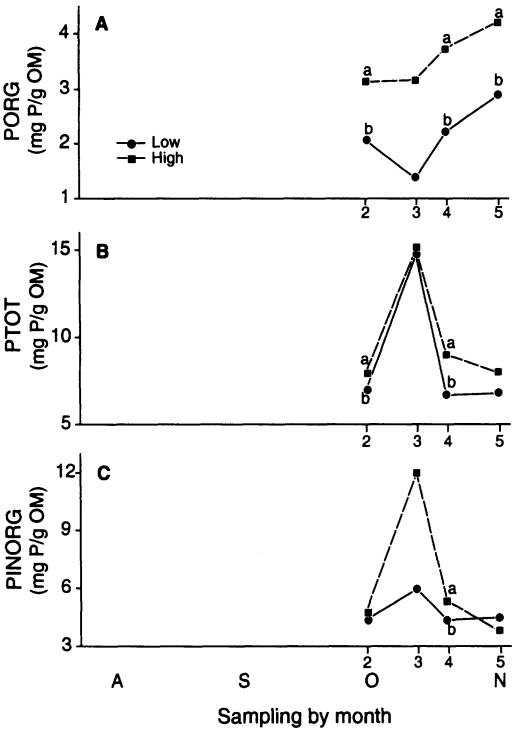
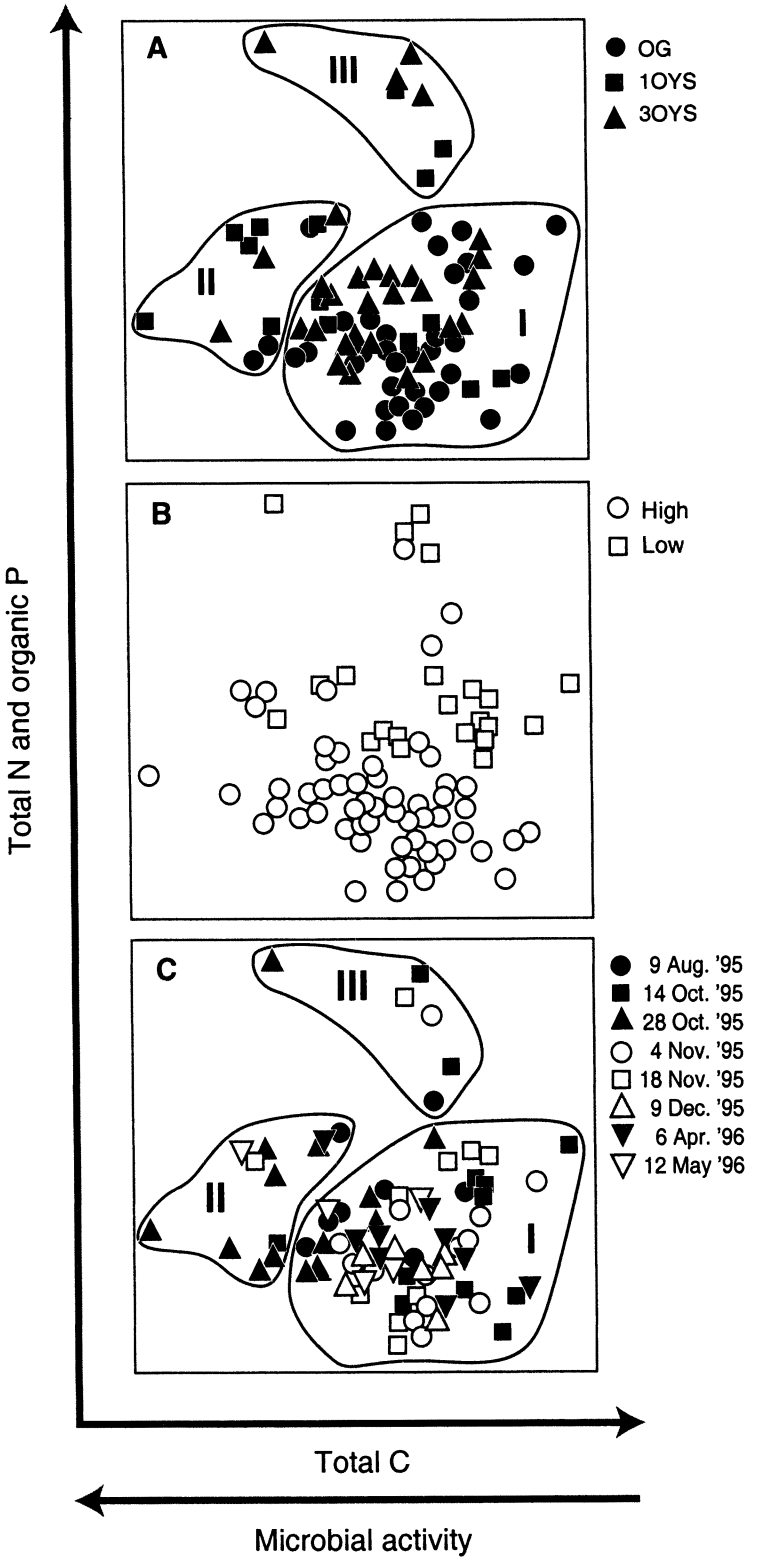


FIG. 8. Mean (A) organic P (PORG), (B) total P (PTOT), and (C) inorganic P (PINORG) of fine benthic organic matter collected from headwater streams in the Oregon Cascades at low (580–800 m) and high (1220–1280 m) elevations. Different letters for samples collected on the same date indicate significant difference (ANOVA, $p \leq 0.05$) between elevations. OM = organic matter.

TABLE 2. Pearson Kendall correlations of biochemical variables with ordination axes for principal components analysis of sample units (streams × sampling) in biochemical space.

		Correlation with ordination		
Variable	Abbreviation	Axis 1	Axis 2	Axis 3
C:N	C:N	0.545	−0.643	0.180
Total C	CTOT	0.697	0.555	−0.060
Total N	NTOT	0.333	0.895	−0.048
Mineralizable N	NMIN	−0.499	0.229	0.608
Acetylene reduction	NFIX	−0.376	−0.088	0.558
Respiration	RESP	−0.653	0.170	−0.526
β-glucosidase	BGLC	−0.642	0.518	−0.105
Phosphatase	PHOS	−0.864	0.062	0.004
Labile polysaccharides	PSAC	−0.482	−0.341	−0.039
Organic P	PORG	0.126	0.625	0.372


A
III
II
I
OG
1OYS
3OYS
B
High
Low
C
III
II
I
9 Aug. '95
14 Oct. '95
28 Oct. '95
4 Nov. '95
18 Nov. '95
9 Dec. '95
6 Apr. '96
12 May '96
Total N and organic P
Total C
Microbial activity

tential has been a good indicator of nitrate availability in soils (Griffiths et al. 1997). It should, therefore, be correlated with NMIN—the potential source of mineralized N. The correlation between DNIT and NMIN was $r = 0.45$ ($p \leq 0.05$). These data, along with C:N, enzyme activity, and respiration, suggest that both FBOM substrate quality and microbial activities are greater in 10YS and 30YS streams than in OG streams.

Elevational effects

We compared streams running through OG and 30YS stands at high and low elevations to examine effects of climate on FBOM characteristics. Our results suggest that qualitative elevational differences in riparian vegetation are reflected in differences in FBOM characteristics. Reduced DNIT, NFIX, RESP, and PHOS (Fig. 7, Table 1) reflect that microbial activity was generally lower in high-elevation than in low-elevation FBOM. In addition, C:N, NMIN, and PSAC were lower in high-elevation FBOM. These trends are best explained by shifts in qualitative characteristics of FBOM from older, more completely decomposed organic matter entering streams at high elevations in contrast to younger, more readily decomposed material entering at low elevations.

A surprising aspect of this study was the strong influence of elevation on PORG, which at high elevations was nearly double that at low elevations (Fig. 8A). High PORG concentrations are most likely the result of differences in parent material age. All of the streams sampled in this study run over andesitic and basaltic lava flows; however, high-elevation flows are as young as 4 million y, whereas flows at low elevations are much older geologically, i.e., from the upper Oligocene and lower Miocene (Swanson and James 1975). Younger volcanic soils are much richer in P.

The role of P in this study is complex. In most Pacific Northwest studies of stream litter decomposition, available N is assumed to limit microbial activity. If this were the case, we would predict that biologically active N (i.e., NMIN) would be correlated with measures of microbial activity such as RESP, PHOS, and BGLC; in fact, the r values for these correlations were 0.30, 0.56, and 0.49, respectively, and all correlations were statistically significant. We do not know the basis for these correlations. High levels of NMIN could serve as a source of energy or N, enhancing microbial growth and increasing microbial biomass. There were also significant correlations between PTOT (which was primarily inorganic P) and RESP, PHOS, and BGLC (r = 0.60, 0.48, and 0.46, respectively), when normalized to g organic matter (g OM). The r values become even larger (0.71, 0.70, and 0.65, respectively) when the data are normalized to g dry mass (g DM). These correlations suggest that P may be limiting to microbial activity in some way. Nitrogen and P may limit decomposition in streams (Triska et al. 1975). However, no stimulation in microbial activity was observed with the addition of inorganic N and P in a study of particulate organic matter in 4 southern Appalachian Mountain headwater streams (Peters et al. 1987).

This relationship could explain the seasonal similarities between PTOT and measures of microbial activity. It does not, however, explain the differences that occurred with elevation. If our hypotheses that P availability is greater at high elevations than at low, and that P may be limiting to microbial growth (and thus activity) are correct, we predict that microbial activities would be greater at high elevations, where P is more abundant. However, we observed the opposite. Thus, P may not be limiting at high elevations; rather, activity may be limited by substrate quality or temperature.

The higher correlations between PTOT and other variables with data normalized to g DM rather than to g OM was a suprise. We found this to be true of all correlations with variables associated with microbial activity. If the inorganic stream sediment component had no influence on microbial activity, we would expect that data normalized to g OM would result in higher correlations than data normalized to g DM because differences in the % OM in these sedi-

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FIG. 9. Overlays of principal component analysis ordination of 82 samples in biochemical space. Data are analyzed by (A) treatment (OG = old growth, 10YS = 10-y-old stands, 30YS = 30-y-old stands), (B) elevation (low = 580–800 m; high = 1220–1280 m), and (C) sampling date.

ments would dilute the more active organic fraction. Given the increased correlations in data normalized to g DM, we conclude that the inorganic fraction has a positive influence on microbial activity.

In conclusion, changes in FBOM substrate quality in small streams can affect microbial activity. The quality of FBOM, in turn, is linked to the quality of allochthonous litter inputs. Seasonal trends in FBOM suggest that recalcitrant FBOM from relatively poor-quality sources, such as woody debris, constitutes the bulk of FBOM residing in streams. This pool is supplemented seasonally by pulses of readily degradable FBOM from either autochthonous production or high-quality allochthonous inputs. In our study, stand vegetation and elevation effects on FBOM quality and activity persisted yearround, and were evident >30 y after clearcutting. Because FBOM provides an important link between terrestrial detritus and aquatic food chains, the changes in FBOM characteristics that we have documented suggest a strong causal link between forest management practices and stream productivity.

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