ochemistry 1: 79–93 (1984)
tinus Nijhoff/Dr W. Junk Publishers, Dordrecht. Printed in the Netherlands.

nation and mineralization of organic sulfur in forest soils*

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words: Organic sulfur formation, organic sulfur turnover, forest floor and soil ons, regulation, energy availability

ract. The incorporation of sulfur from inorganic sulfate into organic matter was ined using ^{35}S for O1, O2 and A-horizon samples from two hardwood forests ed at the Coweeta hydrologic laboratory, near Franklin, NC. This temperature- ndent transformation was stimulated by increased availability of sulfate or energy he process was inhibited by sodium azide, erythromycin and candicidin. These data st that bacteria and fungi mediate sulfur incorporation via the formation of the lent linkages. The latter possibility was confirmed by characterization of the organic r fraction after isolation and partial purification from O2 layer material. Evidence esented which indicates that the sulfur of this fraction is subject to mineralization depolymerization of the carbon matrix and methods are given for the direct and ect assessment of potential turnover rates. The availability of sulfate from ralization appears to depend upon the rate of incorporation of sulfur into organic er. Thus, substantially higher levels of extractable sulfate were detected when over of the isolated organosulfur fraction was assayed for in the presence of azide, an itor of sulfate incoporation. However, the reverse was true when turnover was itored in the presence of glucose and succinate which stimulate sulfate incorporation.

oduction

ious studies of the fate of ^{35}S-labelled sulfate in forest soils indicate that sulfur of this anion is rapidly incorporated into a non-salt extractable tion believed to consist of organic matter (Fitzgerald et al., 1982; Strick l., 1982). This organic fraction appears to be metabolically active since lies monitoring the level of ^{35}S associated with this fraction indicate stantial decreases of sulfur within 48 h. In A-horizon soils from four erent watersheds located in the Coweeta basin of Western North Carolina, decrease was associated with a concomitant increase in inorganic sulfate ickland and Fitzgerald, 1983). The existing data, although limited and rect, suggest that sulfate-sulfur can be incorporated into organic matter ch in turn is subject to reconversion to inorganic sulfate.

ntribution from a symposium on the role of sulfur in ecosystem processes held ust 10, 1983, at the annual meeting of the A.I.B.S., Grand Forks, ND; Myron hell, convenor.

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In this paper, we review methods for determining sulfur incorporation into organic matter and turnover potentials for the incorporated sulfur by direct and indirect means. We also report the isolation and partial characterization of the organic fraction which becomes labelled with ^{35}S during exposure to sulfate. Finally, through the use of compounds which stimulate or inhibit the incorporation process, we attempt to explain how the processes of incorporation and turnover may be regulated in soils and forest floor layers of the Coweeta basin. The term 'turnover' is used here to describe the depolymerization and mineralization of a non-salt extractable sulfur fraction which results in the partial solubilization of this fraction.

Site description and sampling

Samples were collected from two watersheds (WS 2 and WS 18) at the Coweeta Hydrologic Laboratory in the Southern Applachian mountains. These watersheds are covered by mature mixed hardwood forests. Detailed site descriptions may be found in Swank and Douglass (1977). Several soil types occur in the watersheds, but sampling was restricted to the sandy loam, Ashe Series on each watershed. This series is a member of the Typic Dystrochrept family. Samples from the O1 and O2 layers were collected by hand; whereas, soil from the A1 (0–5 cm) horizon was collected by hand spade. All samples were kept in sealed plastic bags and maintained at 4 °C between collection and experimentation. Sampling on WS 18 was carried out in August 1982 for all experiments except organic sulfur isolation. Samples for this work were taken in March 1983. All sampling on WS 2 occurred during September of 1980.

Formation of organic sulfur

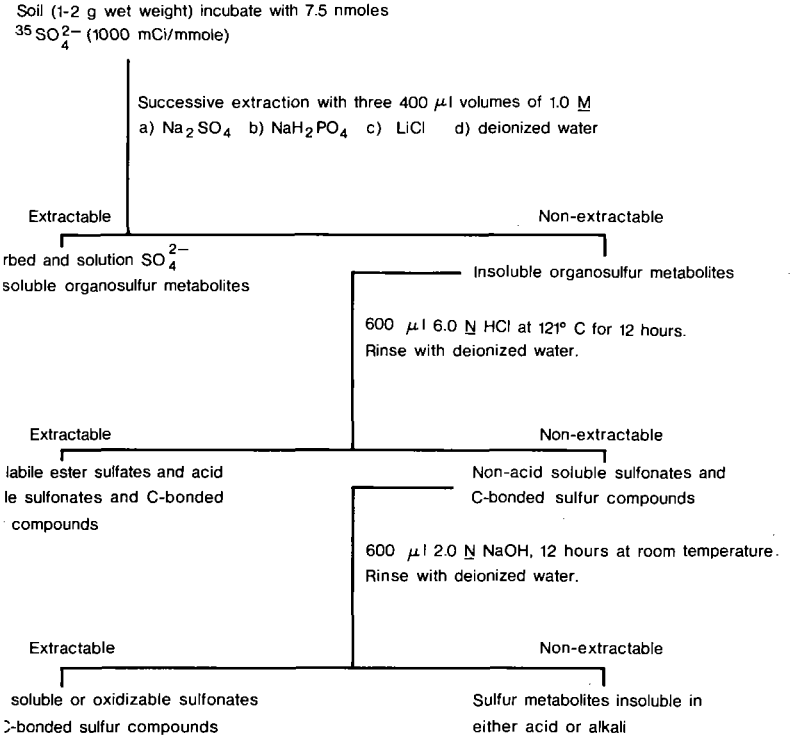
Method

Samples (1–2 g wet wgt.) were incubated at 5°, 10°, 15° or 20 °C for 48 h with 7.5 nmoles $^{35}SO_4^{2-}$ (1 Ci nmole^{-1}, 3.7×10^{10} Bq nmole^{-1}). A detailed description of apparatus may be found in Fitzgerald et al. (1982). After incubation, samples were extracted with three successive 400 µl volumes of 1.0 *M* Na_2SO_4, NaH_2PO_4 and LiCl followed by three volumes of deionized water. This procedure was shown by Fitzgerald et al. (1982) to quantitatively remove adsorbed inorganic sulfate and soluble organosulfur metabolites from the sample. The remaining residue, containing ^{35}S incorporated into non-salt extractable organic sulfur, was then treated with 600 µl of 6.0 *N* HCl for 12 h at 121 °C. The hydrolyzate was collected by centrifugation and the residue was washed with water. Acid treatment causes hydrolysis of ester sulfate (Fitzgerald, 1976) and solubilization of low molecular weight fulvic acid containing carbon bonded sulfur and sulfonate sulfur.

ese latter linkages are not ruptured in boiling acid (Figzgerald, 1976; nitzer and Khan, 1972; Schnitzer and Skinner, 1968). The remaining due, containing sulfur as sulfonate and/or carbon bonded sulfur in large lecular weight components, was then treated with 600 μl of 2.0 N NaOH 12 h at room temperature and washed with deionized water. The raction procedures are summarized in Figure 1. The recovery of ^{35}S was asured with a Beckman LS 9000 liquid scintillation counting system with rgy windows set at 0–655 meV. The entire procedure consistently ioved 95–100% of the added ^{35}S. The total amount of sulfur incoporated o organic matter was calculated as the sum of the amounts extracted by acid and alkali treatments.

mples of results obtained

ious parameters influencing the capacity of these soils to incoporate ate into organic sulfur were examined. The ^{35}S inorganic sulfate was led to samples (1.0 g wet wgt.) at concentrations from 2.0 to 16.0 nmoles ate per gram of sample and the capacity of soils to incorporate sulfate at



ure 1. Procedure for measuring the incorporation of ^{35}S-labelled sulfate (SO_4^{2-}) into anic matter.

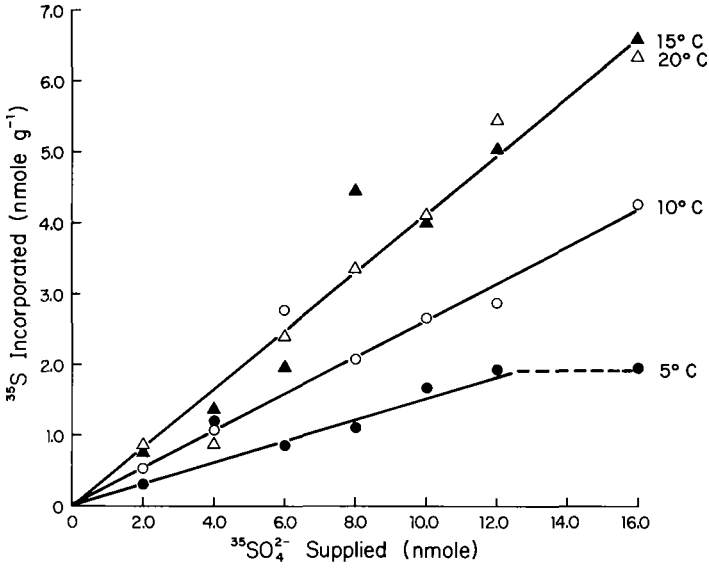


Figure 2. Relationship between organic sulfur formation in O2 layer samples from watershed 18 and the amount of added inorganic sulfate.

5°, 10°, 15°, and 20°C was determined. An example of the results obtained with O2 layer samples is shown in Figure 2. The capacity of this layer to incorporate inorganic sulfate into organic matter after 48 h increased linearly up to 16 nmoles of added sulfate at 10°, 15° and 20°C and up to 12 nmoles per gram at 5°C. Correlation coefficients at 5°, 10°, 15° and 20°C were 0.937, 0.950, 0.978 and 0.988, respectively; slopes were 0.151, 0.250, 0.425 and 0.424. The capacity of these samples to incoporate sulfate into organic matter does therefore appear to be dependent upon incubation temperature. These results also suggest a capacity to respond to elevated sulfate inputs. Similar results were obtained with O1 and A1 horizon samples although at respectively higher and lower incorporation capacities. Although we realize that disturbance of the samples may certainly change the importance of processes from the in situ levels, there is no reason to believe that the processes themselves will be altered. Since sulfate input exceeds sulfate export in these watersheds as much as seven fold (Swank and Douglass, 1977), it seems plausible to suggest that these watersheds have a large reserve buffering capacity against increasing sulfate ion inputs from acidic precipitation.

When samples were treated prior to incubation with compounds which stimulate or inhibit microbial metabolism, it was found that the incorporation of sulfate into organic matter was microbially mediated (Table 1). At two sampling sites within watershed 18, increasing the concentrations of glucose amendments to A1 horizon samples resulted in an increase in the levels of

ble 1. Influence of various compounds on the incorporation of sulfate into the non-
extractable organic sulfur fraction of the forest floor and A1 horizon of Watershed
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ditions	Incorporation (nmoles $^{35}S\,g^{-1}$ dry wgt.)				
	Plot 9			Plot 1	Plot 5
	O1	O2	A1	A1	A1
ne	26.3	4.0	1.8	0.37	0.85
ythromycin[b]	19.2	1.0	0.7	–	–
ndicidin[c]	4.2	2.6	1.7	–	–
dium Azide[d]	1.0	0.6	0.4	–	–
ucose[e]					
0.6	–	–	–	0.80	1.48
1.2	–	–	–	0.76	1.64
4.8	–	–	–	1.38	1.62

ll samples were incubated for 48 h at 20 °C.
inal concentration, 0.5 mg g^{-1} dry wgt. of sample.
nal concentration, 10.66 mg g^{-1} dry wgt. of sample.
inal concentration, 128 mg g^{-1} dry wgt. of sample.
nal concentration, mmoles g^{-1} dry wgt. of sample.

fate incorporated into non-salt extractable organic sulfur. Treatment of mples with the antibacterial antibiotic erythromycin or the antifungal-tialgal antibiotic, candicidin (Lampen, 1969), indicated predominantly cterial involvement in incoporation in the O2 layer and the A1 horizon ile process was dominated by eukaryotes in the O1 layer. The high level inhibition of incoporation caused by sodium azide (an inhibitor of tochrome oxidase) suggests that the incorporation process is carried out by robically respiring organisms (Table 1).

rnover of organic sulfur (Indirect measurement)

thod

e septs in this procedure are summarized in a flow diagram (Figure 3). ganic sulfur was generated in samples (1–2 g wet wgt.) by incubation for h with 7.5 nmoles of $^{35}SO_4^{2-}$ (1.0 Ci $nmole^{-1}$; 3.7×10^{10} Bq $nmole^{-1}$). llowing this incorporation period, samples were extracted with four 0 µl solutions of 1.0 *M* NaH_2PO_4 followed by five 600 µl volumes of ionized water. The P: ^{35}S ratio of the extractant is $3 \times 10^5 : 1$, and it ould therefore quantitatively remove adsorbed inorganic sulfate from the mple since on a molar basis the phosphate anion desorbs even specifically sorbed sulfate (Johnson and Cole, 1980; Chao et al., 1962). The ^{35}S ich remained in the sample was present as non-salt extractable organic fur. The samples were then extracted with two 400 µl volumes of a super-tant obtained by mixing water with a subsample of unlabelled forest floor soil tested (sample : water = 1 : 5). The addition of the supernatant obtained

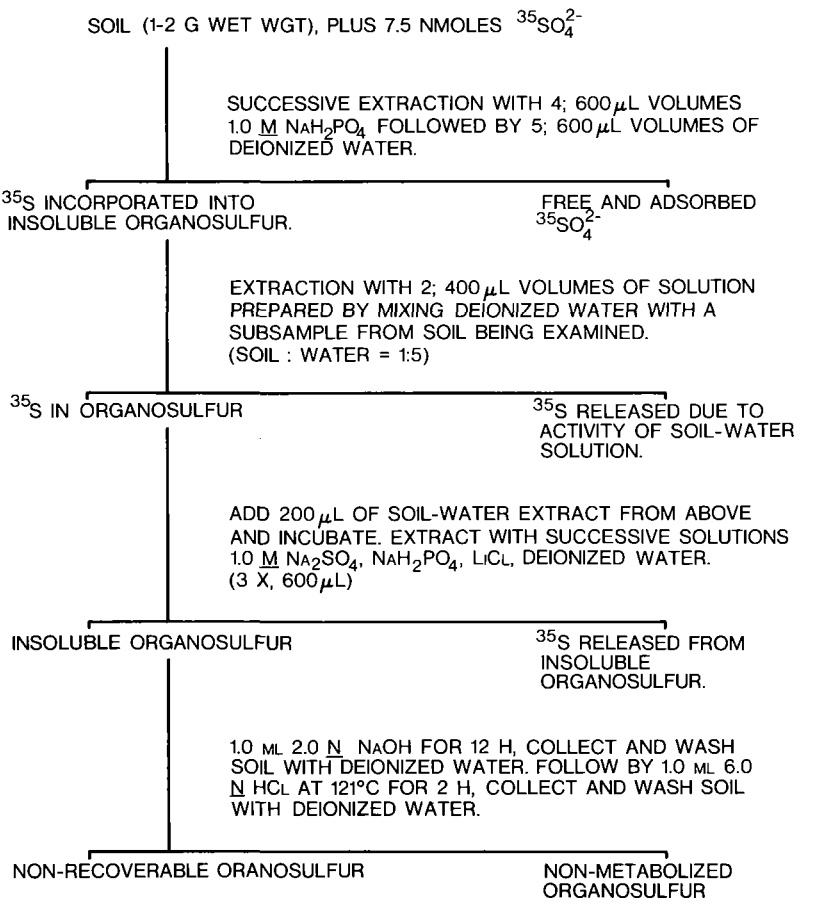


Figure 3. Procedure for the indirect determination of organic sulfur turnover.

from this mixture served to replace any microflora or soil constituents lost during the initial extraction procedure. A 200 μl aliquot of the supernatant was then added to each sample. After incubation for 48 h, the samples were extracted with 600 μl volumes of the salt solutions employed in Figure 1. Sulfure released during the second incubation period must necessarily be released from a form which was previously non-salt extractable, i.e. not adsorbed, but covalently linked sulfur. Aliquots (80 μl) of extracts collected during the reconstitution process and after the turnover incubation period were applied to Whatman no. 1 paper strips and subjected to electrophoresis for 2 h at 250 V in either 0.1 *M* sodium acetate-acetic acid or 0.1 *M* barium acetate-acetic acid buffers, pH 4.5. The paper strips were then dried at 35 °C and ^{35}S-labelled components were located by scanning in a Packard

0/21 radiochromatogram scanner. Inorganic sulfate was identified by d movement in soidum acetate-acetic acid (~ 14 cm) and by pre- tation as barium sulfate in the barium acetate-acetic acid buffer (move- t = 0 cm). Any component migrating at a slower rate than this anion ne sodium acetate-acetic acid buffer contains sulfur in a covalent linkage. samples were then treated with 1.0 ml of 2.0 *N* NaOH for 12 h at room perature, and the residue was washed with water. This was followed 1.0 ml of 6.0 *N* HCl at 121 °C for 2 h and the residue was again washed water. Turnover capacity (%) was determined as the nanomoles of lled sulfur released during reconstitution and turnover incubation divided he sum of the nanomoles of labelled sulfur released and nanomoles of lled sulfur extracted by alkali and acid (X 100).

mples of results obtained

trophoresis of extracts obtained from reconstitution washes and after over incubation showed that, in addition to inorganic sulfate, there was ed a covalently linked organosulfur component released from a previously -salt extractable fraction of the samples examined. A component biting an electrophoretic mobility of zero in the sodium acetate-acetic buffer was present in all samples but was only extracted after recon- tion and turnover incubation. This component was never detected in the sphate and water extracts used to remove non-metabolized inorganic ite from the samples prior to reconstitution and turnover incubation.

he capacity of samples to release inorganic sulfate and the organosulfur ponent increased with increasing incubation temperature from 5–30 °C ckland et al., 1984). In addition, treatment of samples immediately prior urnover incubation with glucose, methionine, cysteine, or ammonium ite (all 5 mmole g^{-1}) also exerted no influence on the process. These pounds might be expected to influence turnover if the process was ted by carbon, sulfur and/or nitrogen availability. Moreover, treatment amples with erythromycin, candicidin or sodium azide also failed to t any influence on turnover capacity. Since the sulfur is present in lent linkage, and since the turnover process was not influenced by bitors of microbial growth or by nutrients which commonly regulate wth and metabolism in terrestrial systems, it seems likely that, at least he short-term studies, temperature is a controller of organic sulfur eralization rates. This may reflect differences in temperature activity ma of extracellular enzymes in the soil. The involvement of such enzymes ne degradation of soil organics has been suggested elsewhere (Dodgson Rose, 1970; Bettany et al., 1980).

urnover of organic sulfur appears to occur at the highest rate in the ayer. The mineral horizons are, however, of the greater relative importance ne recycling of sulfur at Coweeta. Although the rate of sulfur turnover in O2 layer was greater than twice that observed in the A1 horizon, when

the mass of the total standing stock on a given watershed is taken into consideration, the potential turnover rate in the top five centimeters of the A1 horizon is more than 180 time that of both and O1 and O2 layers combined (data not shown).

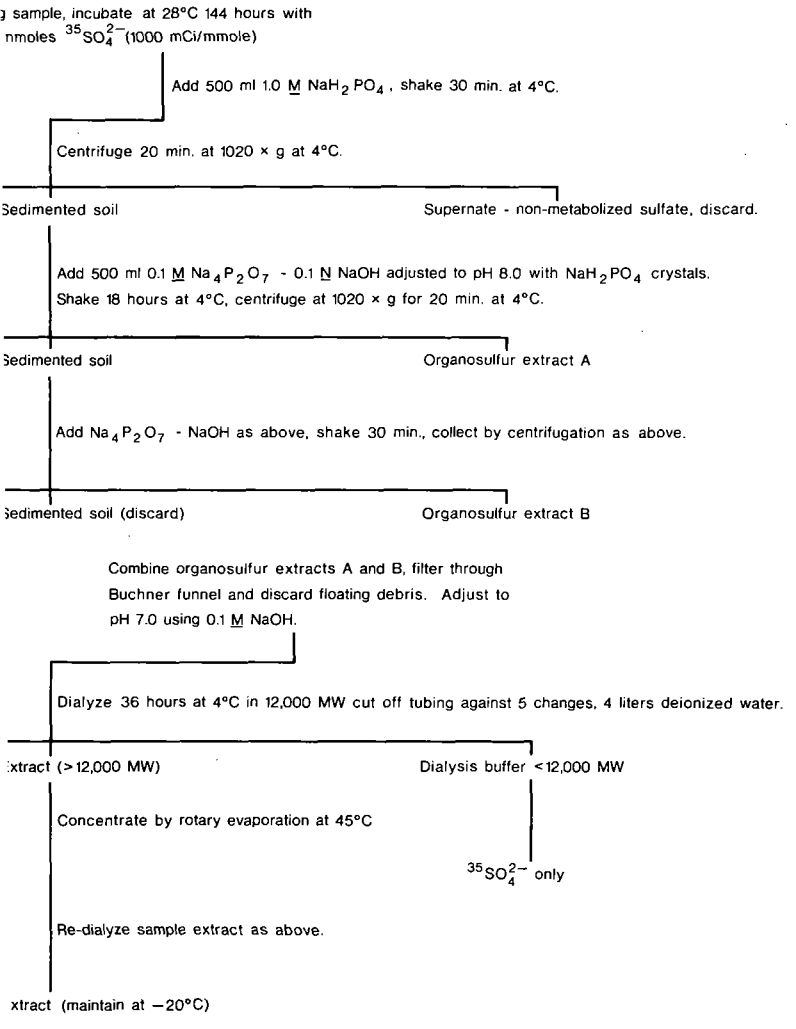
Isolation of organic sulfur

Method

Wet O2 layer (100 g) collected from watershed 18 was incubated at 28 °C for 144 h with approximately 570 nmoles of $^{35}SO_4^{2-}$ (1 Ci mmole^{-1}, 3.7 x 10^{10} Bq mmole^{-1}). The sample was then shaken with 500 ml of 1.0 *M* NaH_2PO_4 for 30 min at 4 °C, and the residue was collected by centrifugation. The supernatant, containing non-metabolized sulfate, was discarded. The residue was then treated with 500 ml of a 0.1 *M* $Na_4P_2O_7$ – 0.1 *M* NaOH solution which had been adjusted to pH 8.0 with NaH_2PO_4 crystals. After shaking for 18 h at 4 °C, the supernatant was collected by centrifugation and retained. The residue was again treated with pyrophosphate for 30 min at 4 °C. After centrifugation, the combined supernatants were filtered to remove floating debris. The filtered supernatant was adjusted to pH 7.0 with 0.1 *N* NaOH and dialyzed for 36 h at 4 °C 12 000 molecular weight cut off dialysis tubing against 5 changes, 41 each of deionized water. The dialyzed extract was then concentrated by rotary evaporation at 45 °C and redialyzed as above. Extracts were maintained at – 20 °C subsequent to analysis to electrophoresis on paper for 2 h at 200 V in 0.1 M KH_2PO_4–K_2HPO_4 buffer, pH 7. The extraction procedure is outlined in Figure 4.

Results

In an attempt to achieve higher yields, pyrophosphate extraction at pH 9.0, 10.0 and 13.0 was attempted. However, the more alkaline conditions caused oxidation of the organic material extracted and this resulted in significant release of inorganic sulfate. Due to the low levels of oxidation and consequent sulfate release at pH 8.0, we feel that this extraction procedure caused little alteration of the organosulfur extracted. An electrophoretogram of the final extract from the O2 layer is shown in Figure 51. Since this extract contained both particulate as well as soluble ^{35}S, the component exhibiting zero electrophoretic mobility actually consists of two organosulfur components, one which is soluble in water and one which is insoluble. We believe that the former is a depolymerization product of the insoluble component and dialysis indicates that both components are greater than 12 000 in molecular weight. The mobile component apparent in this electrophoretogram was identified as inorganic sulfate. Recent analyses (Fitzgerald, unpublished) suggest that this sulfate results from the hydrolysis of labile ester linkages during the phosphate extraction step.



ıre 4. Procedure for isolation of organosulfur from litter and soil.

nover of isolated organosulfur (Direct measurement)

hod

: dialyzed organosulfur extract from the O2 layer (approx. 5.0×10^6 cpm) added to 2.0 g of O2 layer material or A1 horizon soil. The samples were ıbated at 30 °C for various time intervals and extracted using 600 µl ımes of the salt solutions described in Figure 1. Each extract (80 µl) subjected to electrophoresis for 2 h at 200 V in 0.1 *M* $KH_2PO_4 - K_2HPO_4$ fer pH 7.0, and the level of ^{35}S associated with each component separated

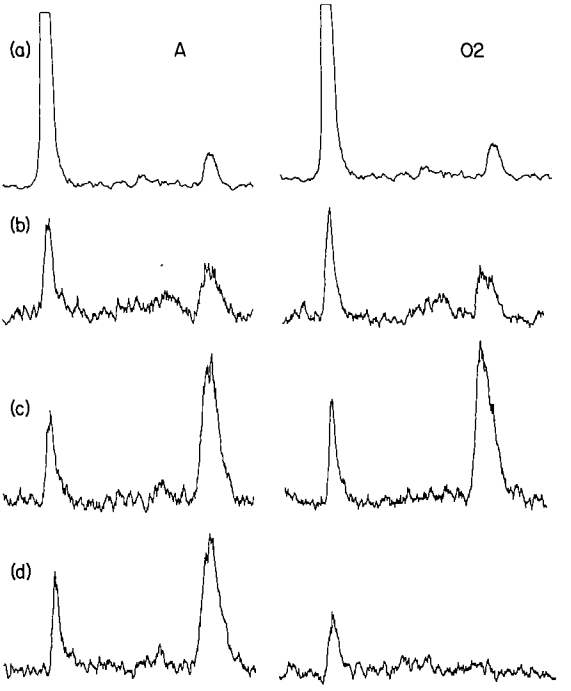


Figure 5. Electrophoretic analysis of organic sulfur extracted from the O2 layer of watershed 18. (a), Electrophoretogram scans of the dialyzed-pyrophosphate extract before incubation with A-horizon and parent O2 layer samples; (b, c, d), electrophoretogram scans of salt extracts of incubation mixtures after 0, 24 and 132 h at 30 °C, respectively. First peak; organosulfur, second peak; inorganic sulfate.

by electrophoresis was calculated by triangulation after radiochromatogram scanning;

$$\frac{\text{peak hgt.} \times \text{peak width at } \frac{1}{2} \text{ hgt.} \times \text{sensitivity (CPM)}}{6.3}$$

where 6.3 is a constant based on scanning speed and collimator width (Packard Instrument Company, 1978).

Sets of samples from the O2 layer and the A1 horizon containing the organosulfur extract were also treated with sodium azide (128 mg g^{-1} sample) or with glucose and succinate (5 mmole each g^{-1} sample) and levels of ^{35}S as soluble organosulfur, insoluble organosulfur or inorganic sulfate were determined. Soluble organosulfur and inorganic sulfate were determined by triangulation after electrophoresis of salt extracts as above; whereas, insoluble organosulfur is the amount of ^{35}S which remained non-salt extractable after incubation.

sults

ter addition of the isolated organosulfur extract to samples from the A1 rizon or the O2 layer, most of the ^{35}S was found to be in a form not ractable by salt solutions (Figure 5b). For the sulfur in this non-salt ractable organosulfur form to be mobilized (i.e. solubilized), it must ner be mineralized to inorganic sulfate or converted to a more soluble, ver molecular weight organosulfur form. After incubation at 30 °C for 24 h 132 h (Figure 5c and 5d, respectively), distinct differences in the distri- tion of ^{35}S activity in the two sulfur fractions (soluble organosulfur and rganic sulfate) of A1 soils and O2 material were observed. In the A1 rizon, there was a substantial increase in extractable inorganic sulfate er 24 h. The levels of soluble organosulfur extracted did not alter after ner 24 or 132 h of incubation, and the level of extractable inorganic fate after 132 h did not appear to differ substantially from the level served after 24 h. However, after the initial increase in sulfate observed er 24 h of incubation with the O2 layer samples (Figure 5c), there was no ger any extractable sulfate present in the sample after 132 h of incubation gure 5d). Also, the levels of extractable organosulfur diminished after 24 l 132 h. These data suggest that inorganic sulfate and soluble organosulfur eased during initial incubation of O2 layer material may be re-incorporated o an insoluble non-salt extractable organosulfur form after prolonged ubation.

Since the levels of inorganic sulfate and soluble organosulfur appeared to ctuate considerably during incubation of A1 horizon and O2 layer samples, levels of sulfate, soluble organosulfur, and insoluble organosulfur were nitored every 12 h for 144 h. The results indicated that transformation sulfur among these pools is a dynamic process in both the A1 horizon gure 6a) and in the O2 layer (Figure 7a). Samples from both horizons ibited substantial changes in the levels of inorganic sulfate present within rt time intervals. While mineralization does occur in the A1 horizon, it y appears to occur at a slightly higher rate than reincorporation. In the O2 er, however, there was an initial increase in sulfate followed by reincor- ation of sulfate at a much higher rate than mineralization.

The influence of sodium azide (an inhibitor of sulfate incorporation by obes), or glucose and succinate (stimulators of sulfate incorporation) was monitered every 12 h for 144 h. When incorporation activities were ibited by treatment with sodium azide, the levels of extractable inorganic fate increased in both the A1 and O2 samples (Figures 6b and 7b) above se of the controls (Figures 6a and 7a). Treatment of samples with a cture of glucose and succinate exerted no net effect in the A1 horizon gure 6c) but stimulated incorporation to such an extent in the O2 layer t there was no extractable sulfate present after 72 h of incubation (Figure . Although the lack of effect by glucose in the A1 horizon appears at first

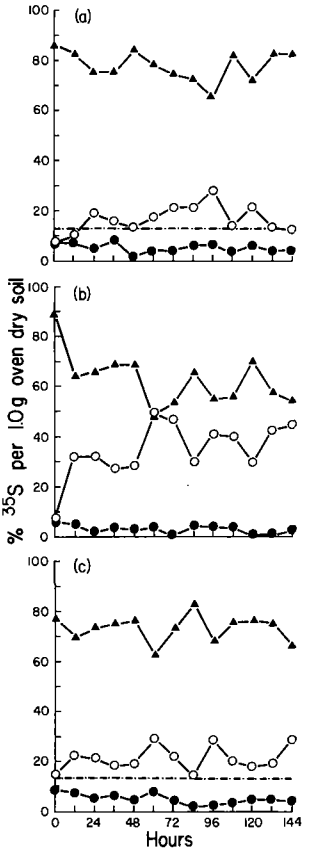
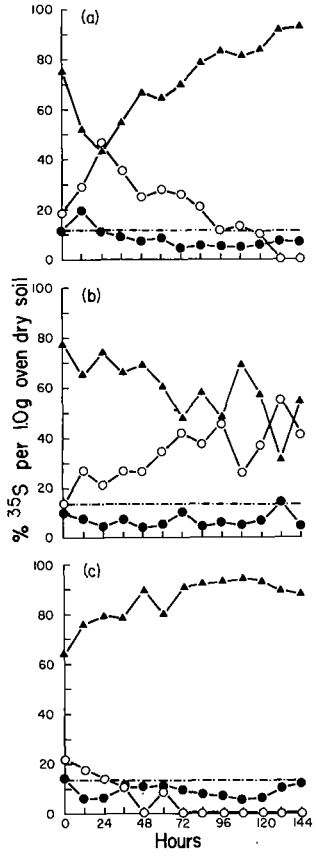


Figure 6. Metabolic fate of sulfur after incubation at 30 °C of isolated O2 layer organosulfur with A-horizon soil from watershed 18 in absence (a) and presence of sodium azide (b) or a mixture of glucose and succinate (c). •, Salt extractable organosulfur; ○, salt extractable sulfate; ▲, non-salt extractable sulfur. Broken line indicates the level of sulfate initially present in the organosulfur preparation.

to contrast with the results reported in the section 'Formation of Organosulfur' and in Table 1, it must be noted that the formation experiments concerned only the conversion of sulfate to organic sulfur. However, the results reported here involve the addition of an organosulfur extract to a sample and monitoring levels of soluble and insoluble organosulfur present in the sample as well as sulfate. The addition of a readily available carbon source therefore influences primary incorporation of sulfate into organic matter but has little or no influence upon the dynamics of incoporation versus mineralization in the A1 horizon. This may reflect differences in the flora of the differing horizons. The A1 populations may be dominated by organisms utilizing more recalcitrant forms of organic matter while the O2



re 7. Metabolic fate of sulfur after incubation at 30 °C of isolated O2 layer organo- r with parent O2 layer material from watershed 18. See legend to Figure 4 for ination of symbols.

ulations have more readily available carbon sources and thus more rously growing populations. If this were true, one would expect a greater onse in the O2 layer.

Results suggest that sulfate may be generated from soluble as well as luble organic sulfur. The inverse relationship observed between levels of ganic sulfate and insoluble organic sulfur (Figures 6 and 7) suggests that insoluble form may be desulfated directly. Alternatively, it may first onverted to a lower molecular weight form which is then desulfated. e the addition of sodium azide prevents reincoporation by microflora of ite or soluble organosulfur into a more insoluble form and results in a ease of the average soluble organosulfur levels in the A1 and O2 horizons and 44% respectively, data not shown), soluble organosulfur seems to be

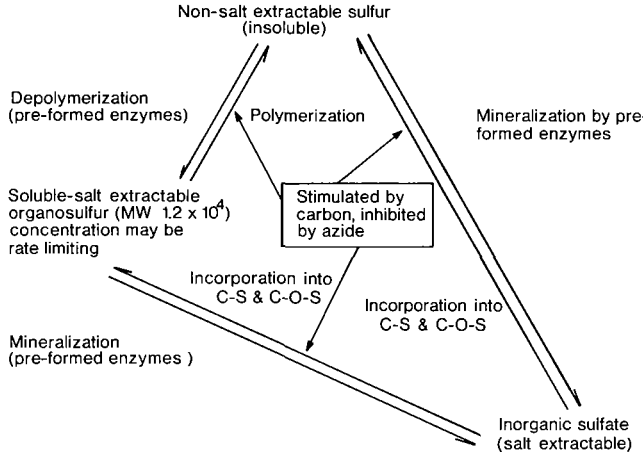
desulfated directly. The possibility that sulfate is produced directly from both soluble and insoluble organosulfur and not completely by a process where soluble organosulfur is an intermediate cannot be excluded since soluble organosulfur levels do not diminish in the absence of azide (i.e. it may be regenerated through depolymerization of the insoluble component).

Discussion

Investigation of pathways for the generally of organic sulfur from sulfate and data relating to the sulfur turnover potential of this fraction may have far reaching implications in terms of our understanding of ecosystem processes associated with this element. With a few exceptions (Likens et al., 1977; Cole and Johnson, 1977), the quantity of sulfate entering forest ecosystems in acidic precipitation is in excess of that leaving in stream flow. Thus, most forested watersheds accumulate sulfur from this anion (see e.g., Johnson et al., 1982), and forests of the Coweeta basin are no exception (Swank and Douglass, 1977). The incorporation of sulfur into organic matter together with sulfate adsorption (Johnson et al., 1980, 1982; Swank et al., 1984) may account for this apparent accumulation.

The process whereby sulfate is incorporated into organic matter also immobilizes the anion and may thus lessen the adverse effect of acidic precipitation by retarding nutrient loss from these forests. As Johnson and Cole (1980) pointed out, any process which reduces sulfate mobility will also reduce cation leaching from forest ecosystems. A detailed understanding of the sulfate incorporation process is therefore a major prerequisite in the assessment of the effects of atmospheric deposition on forest ecosystems. In contrast to agricultural systems in which this process and the associated levels of organic sulfur are reasonably well documented, it should be clear from this paper and other recent work (Mitchell et al., 1984) that forested systems have been neglected (see also Tabatabai and Bremner, 1972; Bettany et al., 1973, 1979; Fitzgerald, 1976; Freney, 1979; David et al., 1982).

The potential for organic sulfur turnover must have equal importance in explanations of watershed sulfur budgets and assessments of atmospheric deposition impacts. Clearly, if the tendency for this fraction once formed to generate sulfate is great, then the contribution of organic formation to sulfur accumulation will be slight. Moreover, the buffering effect that this process has on cation leaching will also be transitory. Thus, increased knowledge of factors which regulate the rates of organic sulfur formation and mineralization is critical to our understanding of the environmental significance of these processes. Data presented here suggest that sulfur incorporation depends primarily upon the level of available sulfate and energy; no compound has yet been found which directly influences the turnover process. Because the formation of a covalent sulfur linkage, e.g. an ester linkage, requires the expenditure of energy (2 moles ATP per ester linkage formed; see Dodgson



ıre 8. Postulated conversions between non-salt extractable organic sulfur, salt actable organic sulfur and inorganic sulfate in soils and forest floor layers of the 'eeta basin. COS, ester sulfate; C–S, carbon bonded sulfur.

l., 1982), it was not surprising to find that energy sources such as glucose ıulated the formation of organic sulfur at least in the O2 layer. The use of le in this work shows that when the rate of organic sulfur formation is ıced, the level of available sulfate from mineralization is increased. ɜrnatively, when the rate of organic sulfur formation is stimulated by ːose little sulfate is made available. These data suggest that the energy ply to this system indirectly controls the level of sulfate from organic ur minerization by exerting a direct control over the rate of organic ur formation.

On the above basis, it might be predicted that sulfur incorporation is a re relevant ecosystem process in mesic-energy rich forest sites whereas ieralization may dominate energy deficient-more xeric sites. Alternatively, interconversion between organic and inorganic sulfur occurring in either may be in equilibrium; the direction of which is determined by carbon ut and hence by energy availability. Thus, even in a forest site which is icient in available carbon, some organic sulfur will be formed to an extent endent upon the degree of carbon deficiency which exists at any given e. Moreover, mineralization under these conditions should continue until energy level falls below a threshold which makes organic sulfur formation ossible. Presumably, this threshold level is determined by the importance the latter process in relation to other energy-requiring process taking ːe simultaneously in the forest site under consideration. In conclusion, it uld be emphasized that these predictions are based upon laboratory ived data and as such are subject to influences associated with sampling

which may not exist in the field. A further verification of these predictions will entail not only laboratory analysis of samples taken from a variety of forest ecosystems but will also depend upon detailed study of these processes, in situ.

Current concepts relating to the formation and mineralization at forest soil organic sulfur are summarized in Figure 8.

Acknowledgements

The research upon which this symposium presentation is based was supported by NSF grants, DEB-8009066 and BSR-8215259. We thank Jaru T. Ash for expert technical assistance and W. T. Swank for advice on sampling. We also acknowledge the USDA for providing a dissertation grant for TCS. TCS is grateful to the Graduate School of the University of Georgia and to the Coweeta LTER group for providing funds to attend this symposium.

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