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Acetate concentrations and oxidation in salt marsh sediments

Abstract

Acetate concentrations and rates of acetate oxidation and sulfate reduction were measured in S. alterniflora sediments in New Hampshire and Massachusetts. Pore water extracted from cores by squeezing or centrifugation contained >0.1 mM acetate and, in some instances, >1.0 mM. Pore water sampled non destructively contained much less acetate, often less than 0.01 mM. Acetate was associated with roots, and concentrations varied with changes in plant physiology. Acetate turnover was very low whether whole core or slurry incubations were used. Radiotracers injected directly into soils yielded rates of sulfate reduction and acetate oxidation not significantly different from core incubation techniques. Regardless of incubation method, acetate oxidation did not account for a substantial percentage of sulfate reduction. These results differ markedly from data for unvegetated coastal sediments where acetate levels are low, oxidation rate constants are high and acetate oxidation rates greatly exceed rates of sulfate reduction. The discrepancy between rates of acetate oxidation and sulfate reduction in these marsh soils may be due either to the utilization of substrates other than acetate by sulfate reducers or artifacts associated with measurements of organic utilization by rhizosphere bacteria. Care must be taken when interpreting data from salt marsh sediments since the release

of material from roots during coring may affect the concentrations of certain compounds as well as influencing results obtained when sediment incubations are employed.

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Anaerobic decomposition is an important component of the cycling of carbon in sediments. Acetate is a significant intermediate in this decomposition, both as a fermentation product and a substrate (Lovley and Klug 1986). It is generally assumed that acetate is an important precursor for bacteria, such as sulfate-reducing and methane-producing bacteria, which are situated at the terminal step in the anaerobic decomposition pathway. In fact, acetate accumulates in sediments in which these processes have been inhibited (Smith and Klug 1981; Michelson et al. 1989). In subtidal marine sediments, the measured rate of acetate oxidation often exceeds the rate of sulfate reduction (Sansone 1986). However, it has been proposed that the discrepancy between these two rate measurements is due to the presence of an acetate pool that is not bioavailable (Christensen and Blackburn 1982; Novelli et al. 1988) leading to an overestimation of acetate oxidation.

Sulfate reduction accounts for more than half of the decomposition that occurs in salt marsh sediments and rates of sulfate reduction in marsh sediments are among the highest recorded (Howarth and Hobbie 1982). These high belowground rates are due to high rates of primary production in salt marshes and the fact that a large fraction of this productivity is allocated to growth belowground (Schubauer and Hopkinson 1984). Studies of the utilization of organic substrates in these sediments could potentially be hampered by the fact that common techniques such as coring, squeezing

and centrifugation of sediments destroy root and rhizome material. Howes et al. (1985) reported that dissolved organic carbon concentrations in Spartina alterniflora sediments were as much as 7 times higher in samples collected using destructive techniques than concentrations in pore waters obtained using non-destructive methods. Since the actual concentration of a substrate is multiplied by a rate constant (obtained using radiotracers) to obtain actual rates of bacterial utilization of a compound (Wright 1978), erroneously high natural concentrations due to destructive sampling should yield erroneous rates of organic uptake.

Although several previous studies have investigated acetate cycling in freshwater and marine sediments, sediments inhabited by vascular plants have not been examined similarly even though it has been shown that anaerobic bacterial metabolism is high in vegetated sediments relative to unvegetated habitats (Hines 1991). The present study was conducted to determine the potential role of acetate in salt marsh sediments. In particular, the objective was to examine the effects, if any, of the release of acetate during sediment processing on the use of acetate by microbes in vegetated sediments.

Samples were collected from two New England salt marshes from 1983 through 1988. The first was Chapman's Marsh in southern New Hampshire (Hines et al. 1989) where sediments were sampled in a creekside stand of tall S. alterniflora and in a stand of S. patens. Samples were also collected in

adjacent areas in which S. alterniflora had been recently killed by wrack. The second site was in a stand of short S. alterniflora in Great Sippewissett Marsh in Massachusetts (Howarth et al. 1983). Samples here were also collected in areas in which the S. alterniflora had been killed by covering grasses with wooden planks.

Sediment cores from Chapman's Marsh were collected and handled anoxically as described previously (Hines et al. 1989). Sediment samples from Sippewissett Marsh were obtained using a 6.4 cm diameter corer which was immediately capped.

Pore waters were collected anoxically by destructive and non-destructive methods. For destructive samples from Chapman's Marsh, core sections were centrifuged at 5,000 x g. Core material was chopped for placing into centrifuge tubes when necessary. In one set of Chapman's Marsh samples, cores were sliced vertically and one half was processed as described above. The other half was sectioned and the sediments separated from root and rhizomes by washing with seawater. The remaining plant material was chopped and placed into centrifuge bottles similarly to whole core material, mixed with artificial sea water and then centrifuged. The resulting water was then processed similarly to other pore-water samples. The non-destructive pore water samples from Chapman's Marsh were collected anoxically using in situ Teflon sippers (Hines et al. 1989) which were deployed several days prior to the first sampling.

For pore-water sampling in Sippewissett Marsh, cores were extruded, sections were immediately placed in a Reeburgh press (Reeburgh 1967) and pore water pressed out. For non-destructive sampling, core sections were placed within a Reeburgh press and pore water collected without applying pressure using a syringe with a 12-gauge needle inserted into the sediment.

Pore waters from Chapman's Marsh were filtered through 0.4-μm Nuclepore filters, the pH was adjusted with 2 N NaOH and they were stored frozen in acid-washed serum vials sealed with Teflon-lined septa. Samples from Sippewissett Marsh were filtered through 0.45-μm Millipore filters and the pH adjusted with 1 N NaOH.

Acetate was measured using gas chromatography (GC). For Chapman's Marsh, thawed pore water samples were concentrated by evaporation at 80° C, mixed with 100 μl of 10% H_3PO_4, and desalted using a microdistillation system (Christensen and Blackburn 1982). The efficiency of distillation was determined using standards and [^{14}C]acetate. Most samples collected by centrifugation contained sufficient acetate such that preconcentration by evaporation was not necessary. Desalted samples were immediately mixed with an equal volume of 1% formic acid in a microliter syringe and injected into a Perkin Elmer model Sigma 300 gas chromatograph equipped with a 1-m, 4-mm-diameter glass column packed with 0.3% Carbowax 20 M, 0.1% H_3PO_4 on 60/80 mesh Carbopack C (Supleco, Inc.) and a flame ionization detector. The injector was 200° C,

the oven was 120° C, the detector was 130° C and the N_2 flow rate was 80 ml min^{-1}. Standard mixtures of volatile fatty acids (Supleco, Inc.) were put through the entire procedure. The detection limit was ~10 μM. Sippewissett Marsh samples were analyzed similarly to those above and as described by Novelli et al. (1988).

Acetate oxidation rate constants were determined using ^{14}C. Anoxic subsamples (1.0 ml) from Chapman's Marsh cores were mixed with an equal volume of deoxygenated (N_2) artificial sea water in a serum vial and then sealed with a Teflon-lined septa. Slurries were injected with 0.1 or 1.0 μCi of uniformly labeled [^{14}C]acetate. After incubation for 2-24 h, bacterial activity was stopped by injection of 0.25 ml of 10% formaldehyde. Production of $^{14}CO_2$ from acetate oxidation was determined by acidifying killed slurries, stripping with N_2, and trapping CO_2 in vials containing a 1:1:2 mixture of methanol, phenethylamine and a scintillation cocktail, respectively. Replicate control samples were killed with foramldehyde prior to incubation with ^{14}C and were treated similarly. An insignificant quantity of [^{14}C] acetate was carried over from the slurry to the traps. The efficiency of recovery of CO_2 was determined by adding a solution of [^{14}C]bicarbonate to killed controls. Radioactivity was determined by scintillation counting. Rate constants were calculated using a linear equation. Because uptake was very slow in most instances, there was no significant difference between rate constants calculated this

way and constants calculated using natural log transformed data. Acetate oxidation rates were calculated as the product of the rate constants and the pore-water concentrations of acetate corrected for sediment porosity.

Acetate oxidation in Sippewissett samples was determined by injecting uniformly labeled [^{14}C]acetate directly into subcores held within syringes. Sample processing was similar to that described by Novelli et al. (1988). Briefly, after 2-3 h the incubation was terminated by extruding samples into jars containing formaldehyde and NaOH. After mixing, the jars were fitted with phenethylamine impregnated glass fiber filters, the samples were acidified with H_2SO_4, and the trapped $^{14}CO_2$ determined by scintillation counting.

Rates of sulfate reduction were determined using ^{35}S (Howarth and Merkel 1984; Hines et al. 1989). In all cases, except the in situ experiment described below, sediment cores were subcored and sections in syringes were injected with ^{35}S and incubated in the dark for 12-18 h at in situ temperatures. Reactions were stopped by either injection of 10% zinc acetate followed by freezing (Massachusetts samples) or by rapid freezing alone (all other samples). The incorporation of ^{35}S into the acid-volatile (HS^- and iron monosulfides) and chromium-reducible (S° and pyrite) phases were determined for all samples.

On one occasion, rates of sulfate reduction and acetate oxidation were measured in the field by injecting $^{35}SO_4$ or [^{14}C]acetate directly into undisturbed Sippewissett Marsh

sediments at depths of either 5 or 10 cm. The experiment was carried out at low tide and inside very large diameter core tubes which had been placed in the marsh a month previously. After incubation, cores containing the radioisotope were collected using 6.4-cm-diameter core tubes and sulfate reduction rates determined as described above. Cores for sulfate reduction were frozen using Dry Ice after injecting zinc acetate. Cores for acetate oxidation were immediately sectioned and placed in a solution of formaldehyde and NaOH. All the sediment within the tubes was removed from the field for disposal as radioactive waste. Parallel experiments were run on marsh samples collected near the experimental site but with the incubations conducted in situ in syringes as described above for acetate oxidation and sulfate reduction rates in Sippewissett Marsh.

Dissolved acetate concentrations were highest in samples collected using destructive techniques (Tables 1 and 2). The highest concentrations (>1.5 mM) were in the tall S. alterniflora in Chapman's Marsh during vegetative growth (i.e. June 1986) (Table 1). The disturbed (cored) samples yielded acetate levels that were greater than undisturbed samples by as much as 500-fold or more. When cores were washed free of sediment and the remaining root material was processed like an intact core, ~75% of the acetate found in intact cores was recovered (Table 1). In addition, acetate concentrations in squeezed Sippewissett samples collected

during summer were 5–10 fold higher than in pore-water samples removed using a syringe and needle (data not shown).

In most instances, acetate concentrations were much higher than other volatile fatty acids such as propionate and butyrate. The GC techniques used were not able to detect formate, but 67 μM formate, 245 μM acetate, and 27 μM propionate were found in Sippewissett pore waters in the summer using a derivatization GC method (D.G. Shaw pers. comm.). Subtidal unvegetated marine sediments generally contain low concentrations of acetate (14-70 μM) (Novelli et al. 1988; Michelson et al. 1989) compared to these vegetated sediments, even when destructive techniques are used to collect pore water.

Acetate concentrations using destructive techniques during the growing season were highest in the upper 5 and 15 cm in S. patens and S. alterniflora sediments, respectively (Table 1), corresponding to the depths where live roots and rhizomes generally existed. Below the live root zone, acetate concentrations decreased and were usually similar in samples collected by non-destructive or destructive techniques. These data indicated that acetate was associated with root and rhizome material and that ambient pore water acetate levels were low. Although samples from destructive techniques were collected rapidly, in many instances the acetate concentrations were very high. This result indicated that acetate was probably released directly from roots rather than from precursors released from roots during processing.

The latter could only occur if acetate production from a precursor was extremely fast.

Acetate concentrations in marsh sediments varied greatly throughout the year and these variations, in samples collected destructively, corresponded to major changes in the physiological state of marsh grasses (Table 1). Highest acetate concentrations were noted in S. alterniflora sediments when plants were growing rapidly aboveground, i.e., June 1986 when levels exceeded 1.5 mM (Table 1). After flowering in August, acetate levels were ~10 times less than during June. However, the June and August data are not directly comparable since samples were collected in different years. In September 1985 when plants were senescing, acetate concentrations increased in S. alterniflora sediments in New Hampshire, decreased by December, and were at the lowest recorded levels prior to the initiation of growth in May 1986. The only New Hampshire samples that contained significant concentrations of VFA other than acetate were those collected in September when S. alterniflora was senescing. The lowest acetate concentrations were in sipper samples collected during the summer.

Acetate oxidation rate constants in vegetated marsh sediments ranged from 0.002 to 1.8 d^{-1} (Table 3). The highest values were obtained in sediments in which S. alterniflora had been previously killed while the lowest values were in S. patens sediments. Rate constants did not vary consistently with depth. Triplicate subsamples

generally varied by less than 20%. The rate constants in these vegetated sediments were 5 to several thousand-fold lower than in unvegetated subtidal sediments studied by others (Table 3). The inverse of the rate constants yields turnover or residence times of acetate of 0.5–500 d in vegetated sediments. Because of the slow turnover in the marsh sediments, it was often difficult to obtain data which were linear over time. Some of the lower values in Table 3 were obtained using data from only the 0 and ~20 h time points.

Figure 1 depicts acetate oxidation as a function of sulfate reduction for the salt marsh sediments studied. The acetate oxidation rates (acetate concentration * rate constant) were calculated using acetate concentrations obtained from destructive techniques. The 1:1 line represents a situation where all of the sulfate reduction could be due to acetate utilization using the 1:1 stoichiometry of acetate oxidized to sulfate reduced. Values above this line indicate that processes other than sulfate reduction were responsible for acetate oxidation while values below this line indicate that sulfate-reducing bacteria were utilizing substrates other than acetate. Acetate did not appear to be an important substrate for sulfate reduction. This lack of imporatnce was most pronounced in the S. patens sediments where often less than 1% of the sulfate reduction was due to acetate oxidation. For comparison, the unvegetated Buzzards Bay data of Novelli et al. (1988) are

included in Fig. 1. These sediments are typical of unvegetated sediments in that they exhibited high rates of acetate oxidation compared to sulfate reduction activity.

There were no significant differences in rates of sulfate reduction and acetate oxidation when measured using either in situ or core incubation techniques (Table 4). Therefore, sediment disturbance during sampling did not affect these processes. Unfortunately, this experiment was conducted in October when plant and microbial metabolic activity and acetate concentrations in pore water were relatively low. Therefore, we did not anticipate a large stimulation of acetate uptake. However, despite the lack of difference in acetate concentrations using the two pore water collection methods, the large discrepancy between sulfate reduction and acetate oxidation persisted.

Acetate concentrations in marsh samples collected using destructive techniques were much higher than those reported for unvegetated coastal marine sediments (<70 μM) (Novelli et al. 1988; Michelson et al. 1989). The destructive techniques also yielded acetate concentrations that were much higher than those obtained using sippers in the marsh. We previously noted a 5-fold increase in acetate concentrations in centrifuged samples of unvegetated subtidal sediment compared to samples obtained using sippers (Hines and Tugel, unpublished). In addition, Shaw and McIntosh (1990), working in subtidal coastal sediments, reported that the first 5 ml of pore waters obtained from sediment squeezers was enriched

~10-fold in acetate compared to the remaining water obtained. However, this enrichment in acetate in unvegetated sediments was small relative to our marsh results. Obviously, the higher concentrations in vegetated sediments were due to the presence of roots.

Acetate concentrations in disturbed samples of marsh sediments were highest when plants were at their peak of physiological activity. In addition, acetate in S. alterniflora sediments was found closely associated with root material devoid of sediments. Since pore water samples were collected rapidly, these findings indicated that the bulk of the sedimentary acetate, or its precursor, was produced by roots. Acetate has been shown to be a fermentation end product of unicellular algae (Gfeller and Gibbs 1984) and certain lower animals (Crawford 1980). To our knowledge, the production of acetate by roots of marine vascular plants has not been previously determined, nor have data on the abundance of root-associated acetate been reported. It remains unclear how acetate is produced in the Spartina rhizosphere.

Acetate oxidation rate constants in the salt marsh sediments were often extremely low (Table 3) compared to constants reported for unvegetated coastal sediments (Novelli et al. 1988; Michelson et al. 1989). These low rate constants also persisted in samples that were not disturbed prior to or during incubation, including the experiment where radiotracers were injected directly into the sediment in the

field. Hence, the unusually slow acetate turnover in the marsh was not an artifact of acetate liberation from roots by coring and sample processing.

Sulfate reduction rates in salt marsh sediments greatly exceeded rates of acetate oxidation (Fig. 1). This result differed greatly from studies of unvegetated marine sediments where acetate oxidation rates exceeded rates of sulfate reduction in some cases by several-fold (Novelli et al. 1988; Michelson et al. 1989). We noted a few instances in the salt marsh sediments where rates of these processes approached the 1:1 stoichiometry expected if acetate were an important substrate for sulfate reduction. However, none of the rates in the marsh samples exhibited a ratio of acetate oxidation to sulfate reduction that was as high as in the majority of samples collected from unvegetated sediments (Fig. 1). Ratios were low in marsh samples regardless of the type of incubation used, be it sediment slurries or direct injection of tracer in the field. This discrepancy persisted even when incubations for measuring acetate oxidation were as long as those used for measuring sulfate reduction, i.e., overnight. If acetate was a significant substrate for sulfate reduction, then any effects of coring on the acetate pool would have affected sulfate reduction and acetate oxidation similarly. Therefore, the low ratio noted here was probably not due simply to the release of large quantities of acetate during sample handling.

It was unclear why there was such a large mismatch between acetate oxidation rates and sulfate reduction and why it was more pronounced in S. patens than in S. alterniflora. One explanation is that acetate was simply not a major substrate for sulfate reduction. Other compounds which are produced by Spartina roots, such as malate and ethanol, are known to be utilized directly by sulfate-reducing bacteria. Hines et al. (1989) suggested that seasonal changes in the allocation of carbon in S. alterniflora were responsible for much of the temporal variations in sulfate reduction activity. Aquatic vascular plants are known to excrete significant quantities of organic carbon from roots and this carbon can be utilized by the sediment microflora (Moriarty et al. 1986). However, it is not known whether these exudates from S. alterniflora are capable of replacing acetate as the primary substrate for sulfate-reducing bacteria in the marsh.

Another more likely explanation for the mismatch between acetate oxidation and sulfate reduction is the possibility that the radio-acetate used for measuring acetate oxidation did not thoroughly reach the microsites of active acetate oxidation. Roots and rhizomes supply acetate (or its precursor) to the sediments and provide three dimensional diffusional gradients. Therefore, it is unlikely that sediment incubations involving injections, cores or slurries could mimic the in situ chemical conditions and the physical juxtaposition of microorganisms and substrates. Our

inability to mimic natural rhizosphere conditions may be similar to problems encountered in studies of mycorrhizal nutrition in the rhizosphere of terrestrial plants (Coleman et al. 1978). One would not expect this type of artifact to affect measurements of sulfate reduction rates since sulfate is abundant and derived from overlying waters.

Another reason for the mismatch may be that during the slow utilization of tracer substrates by bacteria there is a delay in the release of terminal products (CO_2) because of differences in the relative turnover times of intracellular intermediates (King and Berman 1984). This artifact is severe for substrates like glucose which also yield extracellular fermentation products which must be further oxidized to CO_2 (King and Klug 1982). The artifact also should be most pronounced in environments exhibiting relatively slow rates of substrate turnover such as the marsh sites presented here. We measured only the production of CO_2 and did not include the uptake of acetate into intracellular pools or into biomass. It is conceivable that a significant percentage of ^{14}C had yet to be released as CO_2 when the incubations were terminated and that the actual rates of acetate consumption were substantially faster.

We still do not know whether to use acetate concentrations in cores or from sippers to calculate acetate oxidation rates; an uncertainty that complicates our interpretation. Since acetate oxidation rate constants were determined using cores, we chose to use acetate

concentrations from core samples for calculating acetate oxidation rates. If sipper data had been used, the difference between acetate oxidation and sulfate reduction would have been much larger. We believe that the sipper values are the true pore-water concentrations. However, regardless of the acetate concentrations used, the calculated acetate oxidation rates were a small percentage of sulfate reduction.

It has been proposed that a significant portion of the acetate in marine sediments is not bioavailable (Christensen and Blackburn 1982; Novelli et al. 1988). If a portion of the acetate extracted from the marsh samples was not bioavailable, then the acetate oxidation rates in the marsh sediments were even lower than those presented here, and the differences between the rates of acetate oxidation and sulfate reduction would be even larger. Therefore, the acetate bioavailability argument that has been used to explain the discrepancy in acetate oxidation and sulfate reduction in unvegetated sediments tends to widen the gap between these processes in these salt marsh sediments.

The release of acetate during coring may have stimulated sulfate reduction. Therefore, it is possible that previously reported rates of sulfate reduction in salt marshes, all of which have utilized coring techniques, may have been overestimated. This notion is counter to the sulfate reduction data obtained from the direct field injection experiment where undisturbed and disturbed samples yielded

similar rates of sulfate reduction. However, since acetate levels were low when this experiment was conducted, these data are probably not representative of what would occur in samples collected during the growing season when large quantities of acetate are present in the root zone. Hence, the experiments to verify whether coring yields erroneous sulfate reduction rate data in marshes remain to be conducted. However, when surficial unvegetated marine sediments were amended with acetate 5 to 50-fold over in situ concentrations, sulfate reduction activity increased ~2-fold (Hobbie et al. unpublished data). These results are not directly comparable to marsh sediments but they demonstrate the potential for stimulation of sulfate reduction during coring. This enhanced sulfate reduction phenomenon cannot be used to reduce the discrepancy between acetate oxidation and sulfate reduction since any stimulation of sulfate reduction by acetate release would also increase the rate of acetate oxidation. However, a 2 or even 5-fold change in sulfate reduction would not eliminate the majority of the difference between the rates of these processes.

In conclusion, acetate concentrations in salt marsh sediments are much higher than in unvegetated sediments. Acetate is released during coring and increases pore water acetate levels several fold. Acetate turnover and oxidation rates in salt marsh sediments are much lower than in unvegetated sediments. In addition, unlike unvegetated sediments, acetate oxidation in salt marsh sediments accounts

for only a small percentage of the sulfate reduction activity. The discrepancy between acetate oxidation and sulfate reduction in marsh sediments may be due to compounds other than acetate acting as major substrates for sulfate reduction, to artifacts from an inability to introduce radio-acetate into the appropriate bioactive pool, or to intracellular pool artifacts. Investigators studying salt marshes must be careful in interpreting results from samples obtained from destructive sampling techniques such as coring when compounds are released from roots.

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References

Christensen, D., and T. H. Blackburn. 1982. Turnover of C-14 labeled acetate in marine sediments. Mar. Biol. 7: 113-119.

Coleman, D. C., C. V. Cole, H. W. Hunt, and D. A. Klein. 1978. Trophic interactions in soils as they affect energy and nutrient dynamics. I. Introduction. Microb. Ecol. 4: 345-349.

Crawford, R. M. M. 1980. Metabolic adaptations to anoxia. p. 119-136. In D. D. Hook and R. M. M. Crawford (eds.), Plant life in anaerobic environments. Ann Arbor Science.

Gfeller, R. P., and M. Gibbs. 1984. Fermentative metabolism of *Chlamydomonas reinhardtii* I. Analysis of fermentation products from starch in dark and light. Plant Physiol. 75: 212-218.

Hines, M. E. 1991. The role of certain infauna and vascular plants in the mediation of redox reactions in marine sediments. p. 275-286. In J. Berthelin (ed.), Diversity of environmental biogeochemistry. vol 6. Elsevier.

Hines, M. E., S. L. Knollmeyer, and J. B. Tugel. 1989. Sulfate reduction and other sedimentary biogeochemistry in a northern New England salt marsh. Limnol. Oceanogr. 34: 578-590.

Howarth, R. W., A. E. Giblin, J. Gale, B. J. Peterson, and G. W. Luther III. 1983. Reduced sulfur compounds in the pore waters of a New England salt marsh. Ecol. Bull. 35: 135-152.

Howarth, R. W., and J. E. Hobbie. 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: A review. p. 103-127. In V. S. Kennedy (ed.), Estuarine comparisons. Academic.

Howarth, R. W., and S. Merkel. 1984. Pyrite formation and the measurement of sulfate reduction in salt marsh sediments. Limnol. Oceanogr. 29: 598-608.

Howes, B. L., J. W. H. Dacey, and S. G. Wakeham. 1985. Effects of sampling technique on measurements of porewater constituents in salt marsh sediments. Limnol. Oceanogr. 30: 221-227.

King, G. M., and T. Berman. 1984. Potential effects of isotopic dilution on apparent respiration in 14C heterotrophy experiments. Mar. Ecol. Prog. Ser. 19: 175-180.

King, G. M., and M. J. Klug. 1982. Glucose metabolism in sediments of a eutrophic lake: Tracer analysis of uptake and product formation. Appl. Environ. Microbiol. 44: 1308-1317.

Lovley, D. R., and M. J. Klug. 1986. Model for the distribution of sulfate reduction and methanogeneis in freshwater sediments. Geochim. Cosmochim. Acta 50: 11-18.

Michelson, A. R., M. E. Jacobson, M. I. Scranton, and J. E. Mackin. 1989. Modeling the distribution of acetate in anoxic estuarine sediments. Limnol. Oceanogr. 34: 747-757.

Moriarty, D. J. W., R. L. Iverson, and P. C. Pollard. 1986. Exudation of organic carbon by the seagrass *Halodule wrightii* Aschers. and its effect on bacterial growth in the sediment. J. Exp. Mar. Biol. Ecol. 96: 115-126.

Novelli, P. C., A. R. Michelson, M. I. Scranton, G. T. Banta, J. E. Hobbie, and R. W. Howarth. 1988. Hydrogen and acetate cycling in two sulfate-reducing sediments: Buzzards Bay and Town Cove, Mass. Geochim. Cosmochim. Acta 52: 2477-2486.

Reeburgh, W. S. 1967. An improved interstitial water sampler. Limnol. Oceanogr. 12: 163-165.

Sansone, F. J. 1986. Depth distribution of short-chain organic acid turnover in Cape Lookout Bight sediments. Geochim. Cosmochim. Acta 50: 99-105.

Schubauer, J. P., and C. S. Hopkinson. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. Limnol. Oceanogr. 29: 1052-1065.

Shaw, D. G., and D. J. McIntosh. 1990. Acetate in recent anoxic sediments: Direct and indirect measurments of concentration and turnover rates. Estuarine Coastal Shelf Sci. 31: 775-788.

Smith, R. L., and M. J. Klug. 1981. Electron donors utilized by sulfate-reducing bacteria in eutrophic lake sediments. Appl. Environ. Microbiol. 42: 116-121.

Wright, R. T. 1978. Measurement and significance of specific activity in the heterotrophic bacteria of natural waters. Appl. Environ. Microbiol. 36: 297-305.

Table 1. Acetate concentrations (μM) in sediments from Chapman's Marsh, New Hampshire on various dates using destructive (core) and non-destructive (sipper) sampling techniques.

Depth (cm)	Spartina alterniflora		Spartina patens		Dead S. alt.*	S. alt
	Core	Sipper	Core	Sipper	Core	Roots†
August 1985						
2	144	0.2	115	0.8		
5.5	147	0.7	9	5		
11.5	271	2	17	2		
17.5	25	11	22	1		
September 1985						
2	417	3	101	unsaturated‡		
5.5	338	<0.1	50	2		
11.5	159	1	7	3		
17.5	61	1	44	29		
December 1985						
2	115	14	4	7		
5.5	53	9	12	2		
11.5	8	59	9	3		
17.5	86	7	1	2		
May 1986						
2	115		8		18	
5.5	53		5		23	
11.5	8		6		18	
17.5	86		11		4	
June 1986						
2	1600		240			970
5.5	1500		160			
11.5	870		23			630
17.5	870		36			

S. alterniflora killed by wrack during previous summer.

†half of core washed free of sediment and roots processed like whole core (see text). 5.5 cm value = 0-8 cm, 17.5 cm value = 9-20 cm.

‡neap tide, upper few cm not saturated with water so unable to collect sipper sample.

Table 2. Acetate concentrations in short *Spartina alterniflora* soils in Sippewissett Marsh on various dates using destructive (core) techniques.

Date	Depth (cm)	Acetate (μM)
Jun 1983		
	1.2	290
	4	300
	7	170
	15	63
Oct 1983		
	1.2	390
	4	270
	7	250
	15	230
Oct 1983 (dead)*		
	1.2	250
	4	230
	7	130
	15	130
Aug 1984		
	2	77
	6	130
	10	52
	15	44
	20	18
	25	26
Aug 1984 (dead)*		
	2	35
	6	95
	10	23
	15	19
	20	15
	25	21

*Grass killed during summer of 1982 by covering with plywood.

Table 3. Acetate oxidation rate constants for salt marsh sediments. Data from unvegetated marine sediments included for comparison

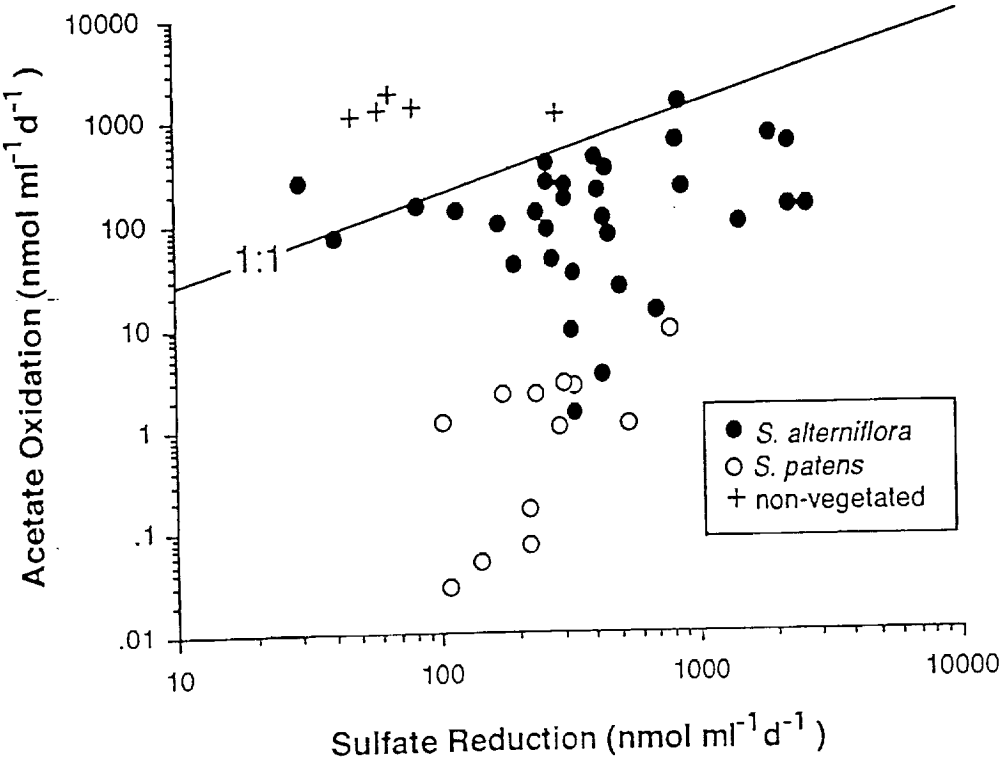
Site	Date	Depth (cm)	n	Rate constant (d^{-1})
Chapman's Marsh, NH				
Tall *S. alterniflora*	Jun-Aug	1.0-20	20	0.068 - 0.48
Spartina patens	Jun-Aug	1.0-20	12	0.002 - 0.12
Sippewissett Marsh				
Short *S. alterniflora*	Jun, Oct	1.2-15	8	0.31 - 2.9
Dead *S. alterniflora*	Oct	1.2-15	4	0.48 - 4.0
Unvegetated				
Novelli et al. 1988	Aug	0.0-16		12 - 48
Michelson et al. 1987	Apr	0.0-10		7.9 - 31

Table 4. Sulfate reduction and acetate oxidation in Sippewissett Marsh in samples incubated either by direct injection of radiotracers into sediments in the field (Field) or injection of tracers into previously retrieved cores (Laboratory). Included are acetate concentrations and rate constants. All acetate data are for 5 cm depth.

Parameter	Field	Laboratory
SO_4^{2-} reduction (nmol ml^{-1} d^{-1})		
5 cm	339 ± 112 (n=3)	200 ± 79 (n=3)
10 cm	118 ± 12 (n=2)	64 ± 64 (n=3)
Acetate (μM)	46*	23-75†
Acetate oxidation rate constant (d^{-1})	<0.144	<0.144
Acetate oxidation (nmol ml^{-1} d^{-1})	<5	<10
Acetate oxidation:SO_4^{2-} reduction ratio	<0.01	<0.01

*Pore water removed with syringe.

†Pore water removed by squeezing in Reeburgh press.


10000
1000
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1
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1000
10000
1:1
Acetate Oxidation (nmol ml^{-1} d^{-1})
Sulfate Reduction (nmol ml^{-1} d^{-1})
S. alterniflora
S. patens
non-vegetated

Figure Legend

Fig. 1. Acetate oxidation rates vs. sulfate reduction rates in sediment samples from various salt marsh sediments. The non-vegetated sediments are from Buzzards Bay, Massachusetts as reported in Novelli et al. (1988).

Abstracts of Manuscripts Submitted or in Preparation

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