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15. The 1-μl injections were made into animals that had been tested with the 0.5-μl dose 1 week previously. The animals received different drugs on the first and second trials.
16. It is interesting that the combination of DDA and apomorphine caused little or no rotation. This supports growing evidence that the rotational response to dopamine agonists is mediated by dopamine receptors that are not coupled to adenylate cyclase [P. Seeman, *Pharmacol. Rev.* **32**, 229 (1980)]. The DDA and apomorphine combination should have caused rotation if the dopamine receptor coupled to adenylate cyclase was involved because the adenylate cyclase on the side injected with DDA would have been inhibited, leaving the effect of apomorphine on the contralateral side unopposed. This line of reasoning is not incompatible with our conclusion that the intracaudate injection of NECA stimulated adenosine-sensitive adenylate cyclase and caused apomorphine to produce rotation toward that side. In the case of DDA the effect of the nucleotide would be to inhibit dopamine-sensitive adenylate cyclase by an action at P sites on the same cells, while in the case of NECA and apomorphine NECA need not necessarily act on the same cells as apomorphine.
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Relation of Soil Water Movement and Sulfide Concentration to *Spartina alterniflora* Production in a Georgia Salt Marsh

Abstract. *It is proposed that differences in plant height and productivity of the salt-marsh cordgrass* Spartina alterniflora *are the result of a dynamic interaction among tidal water movement, dissolved iron and sulfide concentrations in marsh soils, and bacterial sulfate reduction. Tidal water movement regulates the input of iron into marsh soils and the drainage of sulfide-containing interstitial water, and thereby controls the concentration of dissolved sulfide formed as a result of bacterial sulfate reduction. Near tidal creeks, where water movement and plant height and production are greatest, sulfide concentrations are lowest; in more elevated regions of marsh, where water movement and plant production are least, sulfide concentrations are highest. Plant height and productivity may be limited by the effects of sulfide on nutrient uptake.*

Local gradients in production of the halophyte *Spartina alterniflora* are a distinctive feature of Atlantic and Gulf coast salt marshes. The height and biomass of *S. alterniflora* are greater on the banks of tidal rivers and creeks than they are in the more elevated, landward regions of marsh (*1*). Annual net production of the tall growth form is three to five times that of the short form (*2–4*) and, although the tall form occupies only about 10 percent of a marsh surface area, it accounts for 30 to 50 percent of total marsh production (*3, 4*). Plant production (per square meter) along tidal creeks is among the highest of any terrestrial habitat (*5*) and has a significant impact on carbon cycling in estuaries.

The differences in growth of the plants have been explained by salinity stresses (*4, 6*), nitrogen limitation (*7–11*), and iron limitation (*12–14*), but these explanations have proved to be unsatisfactory or have been found inapplicable to a wide range of habitats (*15*). The most consistent current hypotheses suggest that production is regulated by oxygen transport within plants and by the sulfide concentration and oxidation-reduction (redox) status of the growth substrate (*16*). Mendelssohn *et al.* (*17*) have shown that the availability of O_2 within *S. alterniflora* roots is related to physiological differences in energy production or catabolism in the tall and short forms of the plants. Although the observed physiological differences are responsible for differences in the production of plants, the mechanisms resulting in gradients of oxygen availability within marshes have not been clearly delineated. Sulfide may directly affect *S. alterniflora* production as a result of increased mortality (*9*) and inhibition of the transport system involved in nitrogen uptake (*10, 11, 16*); sulfide may also lower oxygen availability, thereby changing patterns of catabolism (*17*). However, controls of sulfide concentration have not been determined nor adequately related to the differences in productivity within marshes. Redox profiles have been positively correlated with productivity and soil water movement in a New England marsh (*16*) and with plant height in a Louisiana marsh (*17*), but the controls of redox status or the mechanisms resulting in gradients within marshes of the southeast United States or Gulf Coasts are unclear.

We propose that the gradients in the edaphic factors that regulate *S. alterniflora* production are controlled by a dynamic relation among tidal water movement, interstitial sulfide and iron concentrations, and bacterial sulfate reduction.

Data supporting the hypothesis were obtained by G.M.K. and M.J.K. from soils of Sapelo Island, Georgia, which contained tall (TS), intermediate (IS), or short (SS) growth forms of *S. alterniflora*. Natural soil water movement is much greater in TS than in SS marshes, as documented by several studies that reveal significant vertical and lateral movement in the TS, but virtually no movement in the SS (*6, 18, 19*). Data were also obtained from two other intermediate marsh sites on Sapelo Island in which soil water flow had been experimentally altered by R.G.W. and A.G.C. Soil in one of the regions (ISD) contained drainage pipe (outer diameter, 15 cm), which had been placed below ground in trenches. The other region (ISR), adjacent to the first, was trenched to simulate disturbances created by laying the pipe, but no pipe was left in place (*20*). Studies of infiltration rates in the experimental sites showed increased movement in the ISD site and restricted movement in the ISR site with respect to the control IS site. Infiltration rates were 2.95, 0.55, and 0.29 liter/min-m^2 in ISD, IS, and ISR plots, respectively. The slowness of the movement in ISR was probably due to packing of soil and decreased capillary space (*20*). In soils where water movement was increased, plant growth was stimulated twofold; where movement was restricted, plant growth was inhibited by a factor of 2 (*20*). Other physical and biological characteristics of these marsh sites have been described (*21, 22*). Interstitial water was collected from all sites during October in both 1980 and 1981, and from TS and SS sites in August 1981, for analyses of dissolved sulfide, sulfate, and iron (*23, 24*). Rates of bacterial sulfate reduction were also determined by a direct injection technique (*25*) on soil cores from the same areas during October in both 1980 and 1981.

Sulfide concentrations vary markedly [Fig. 1A and (*26*)] across Sapelo Island marshes and are inversely correlated with soil water flow and plant production (*3, 4, 6, 18*). The lowest concentration of sulfide (< 90 μmole per liter of interstitial water) is observed in the TS and experimental ISD sites where water flow is relatively high; in the SS and experi-

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Table 1. Distribution of sulfate reduction and iron in salt-marsh soils. Sulfate reduction rates are given as means ± standard error (S.E.) for five depths with the 0- to 10-cm interval sampled during October 1980. The means ± S.E. for dissolved interstitial iron (Fe_{diss}) are given for ten depths within the 0- to 30-cm interval sampled during October 1980. Values for iron soluble in 6*N* HCl (Fe_{HCl}) are the means ± S.E. of nine cores (six from July 1981 and three from October 1981), sampled at six depths; the values are expressed as micromoles per cubic centimeter of soil. Values for iron digestible in aqua regia (Fe_{pyr}) are the means ± S.E. of nine cores for the 0- to 24-cm interval, with sampling and replication as for Fe_{HCl}. The pyritization index (PI) is given by PI = $Fe_{pyr}/(Fe_{HCl} + Fe_{pyr})$ (*36*).

Site	Sulfate reduction (mmole/ m^2-day)	Fe_{diss} (mmole/ liter)	Fe_{HCl} (μmole/cm^3)	Fe_{pyr} (μmole/cm^3)	PI
TS	40.0 ± 10.8	980 ± 214	287.2 ± 14.0	52.7 ± 22.8	0.16
SS	25.7 ± 8.1	23 ± 5.4	105.9 ± 34.0	91.4 ± 32.6	0.46

mental ISR site, sulfide concentrations are 1 to 3 mmole per liter of interstitial water. Although these variations in dissolved sulfide are related to soil water flow, they are not correlated with rates of bacterial sulfate reduction, which is the major source of sulfide in marsh soils (*27, 28*). The rates of sulfate reduction measured during October 1980 ranged from 25 to 45 mmole of SO_4 reduced per square meter per day for the 0- to 10-cm increment of soil at all marsh sites (Table 1); the rates are within ranges reported by others for salt-marsh soils (*27, 28*). No significant differences among sites were observed, an indication that sulfate reduction in itself does not account for the distinct patterns of dissolved sulfide at the various marsh sites.

The distribution of dissolved sulfide can, however, be accounted for by examining dissolved iron concentrations (Fig. 1B). Pools of dissolved iron are inversely related to those of dissolved sulfide; the highest concentrations of dissolved iron are found in the TS and ISD sites, and the lowest concentrations are observed in the SS and ISR sites. The patterns of sulfide thus appear to be the result of differential precipitation of iron sulfides at the various sites. Although iron sulfides such as mackinawite and pyrite are formed at all sites, the potential for precipitation of sulfide is much less in SS than in TS sites because of the smaller pools of dissolved interstitial iron and reactive particulate iron (soluble in 6*N* HCl) in the SS soils [Table 1, (*29*), and (*30*)]. In addition, the diagenesis of iron minerals is much more complete in SS than in TS as indicated by the pyritization index (PI) (Table 1). Jørgenson (*29*) has suggested that the reactive iron pool and formation of dissolved ferrous iron from reactive iron are the most important steps limiting pyrite formation in coastal sediments. In addition, Jørgenson (*29*) notes that at PI ≥ 0.50, reactive iron pools are relatively unavailable for continued precipitation of iron sulfides. Thus, the high PI in SS soils (Table 1) is consistent with a lack of available iron for sulfide precipitation and the consequent accumulation of high concentrations of dissolved sulfide. The low pools of dissolved sulfide in TS soils are maintained by the equilibrium of sulfide with high concentrations of dissolved and reactive iron available for precipitation, as indicated by a low PI.

Differences among sites in PI and the availability of iron for sulfide precipitation could be affected by pyrite oxidation, which has been observed for soils of Great Sippewissett Marsh (*28*). Greater pyrite oxidation in TS soils, for example, could result in a lower PI and increased iron availability. However, since soil *p*H data do not support increased pyrite oxidation from SS to TS soils (*31*), the role of differential pyrite oxidation as a determinant of PI and reactive iron in Sapelo Island soils is equivocal and should be the subject of further study.

Sulfide concentrations might also be regulated to some extent by plant-mediated uptake and oxidation (*32*). Carlson and Forrest (*32*) have shown that significant quantities of sulfide enter *S. alterniflora* roots exposed to high sulfide concentrations. However, it is not certain whether sulfide uptake is active or passive and simply a function of pore water concentrations. Additional work is therefore necessary to quantitate the impact of plant metabolism on pore water chemistry.

The differences in sulfide and iron distributions among the various marsh sites might be due in part to differential input of iron into the marsh soil and soil water flow. Iron is transported into salt marshes in both particulate and colloidal forms that precipitate from the water column. The particulate and colloidal matter in Sapelo Island tidal water contains a high concentration of reactive iron [~ 417 μmole per gram (dry weight)] (*33*); virtually all of this iron is found in particles > 8 μm in diameter. Iron input is not uniform across the marsh surface, however, since sedimentation of particulate and colloidal matter is much greater in TS than in SS regions (1 to 2 cm as contrasted with < 1 mm per year) (*34*). Erosion, slumping, and decapod burrowing (*33*) may also lead to greater reworking of the TS than the SS soils. This reworking could lead to the burial of iron

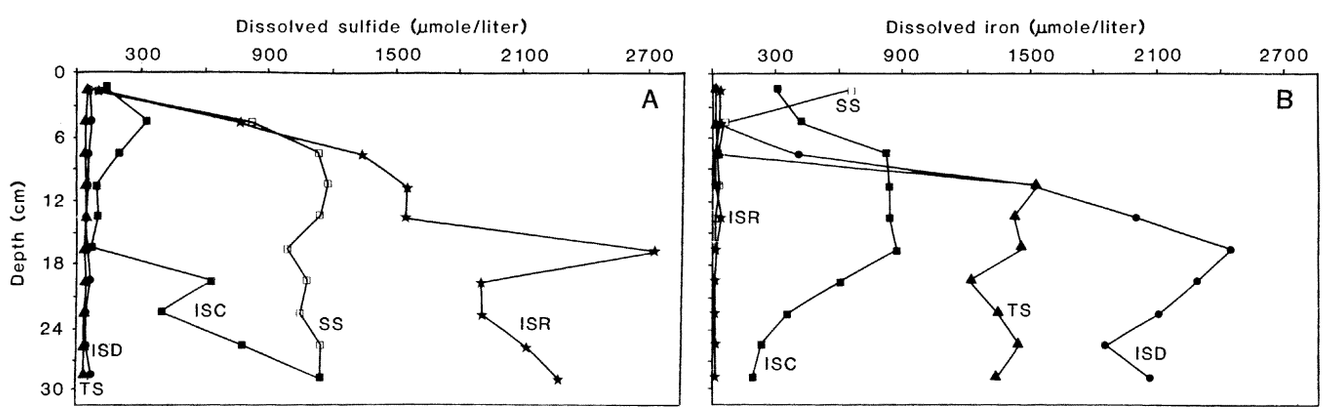

Fig. 1. (A) Dissolved sulfide and (B) total dissolved iron in the interstitial waters of various marsh soils sampled in October 1980; similar results were obtained on other sampling dates. *SS*, short *S. alterniflora*; *TS*, tall *S. alterniflora*; *ISC*, intermediate *S. alterniflora* (control); *ISD*, intermediate site with increased (drained) soil water movement. *ISR*, intermediate site with decreased soil water movement. Each point represents the mean of triplicate samples with a coefficient of variation ≤ 20 percent.

deposited at the TS soil surface and facilitate oxidation of iron sulfide minerals formed at depth by raising them to the surface layer of the soil. Soil water movement can affect sulfide concentration by draining pore water containing sulfide. Sulfide formation in excess of iron inputs may be removed by soil water drainage in regions such as the TS and ISD. Drainage of pore waters would have minimal impact on sulfide concentrations in areas of low water movement such as the SS and ISR. Thus, the combination of the differences in iron input and the known differences in soil water movement result in the observed patterns of dissolved iron and sulfide distribution within the various marsh sites.

Although dissolved iron concentrations vary directly with plant production, iron availability in itself does not appear to limit production, since iron plays only a secondary role in nutrition even at the levels commonly found in the relatively unproductive SS marsh soils (*14*). Consequently, we propose that sulfide is the major factor limiting *S. alterniflora* production at the level of the plant itself. At the level of the ecosystem, however, the major limiting factor is the interaction among soil water movement and iron and sulfide concentrations. Although sulfide is produced at similar rates in the marsh sites with relatively high production and those with low production, greater iron input and soil water movement result in very low sulfide concentrations in the TS region. Low iron input combined with little water flow results in the accumulation of high concentrations of dissolved sulfide in the SS regions, which causes decreased plant production. The relatively high concentrations of sulfide found in all but the TS regions may directly inhibit active transport of nitrogen by the roots, but also may elicit shifts from an oxidative to a fermentative metabolism in the root tissue because of lowered soil redox potential (*16, 17*). Such a shift results in decreased energy for nutrient uptake and growth and is analogous to the effect of sulfide on rice (*35*).

The role of water movement in controlling both iron and sulfide concentrations is shown in data from the two experimental sites where water flow was altered. Increased water movement in the ISD compared to the control IS site yielded concentrations of iron and sulfide similar to those in the TS (Fig. 1, A and B). In addition, the increase in water flow resulted in increased plant production (*20*). Diminished water flow in the ISR resulted in decreased plant production and changes in iron and sulfide concentrations to values similar to those in the SS.

We conclude that the gradient in plant production within salt marshes of the southeastern Atlantic and Gulf coasts and the plastic physiological response of *S. alterniflora* to its environment appear to be a function of soil water movement and iron input. Both water movement and iron input decrease from the productive, creekbank regions to the less productive, more landward regions. Decreases in water movement and iron input result in a gradient of increasing sulfide that decreases plant production. Changes in plant production may be a response to sulfide toxicity or to changes in redox caused by the sulfide gradient (*16, 17*). The relative effect of water movement on *Spartina* production among different marshes is believed to be a function of tidal amplitude, particulate and colloidal iron concentrations in tidal water, rates of sulfate reduction, and soil hydrology.

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