

## Bacterial communities and biogeochemical transformations of iron and sulfur in a high saltmarsh soil profile

Marcio R. Lambais<sup>a,\*</sup>, Xosé Luis Otero<sup>b</sup>, Juliano C. Cury<sup>a</sup>

<sup>a</sup>Departamento de Ciência do Solo, Universidade de São Paulo, 13418-900 Piracicaba, SP, Brazil

<sup>b</sup>Departamento de Edafología e Química Agrícola, Facultad de Biología, Universidad de Santiago de Compostela 15782, Spain

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### ABSTRACT

Microbial community structure in saltmarsh soils is stratified by depth and availability of electron acceptors for respiration. However, the majority of the microbial species that are involved in the biogeochemical transformations of iron (Fe) and sulfur (S) in such environments are not known. Here we examined the structure of bacterial communities in a high saltmarsh soil profile and discuss their potential relationship with the geochemistry of Fe and S. Our data showed that the soil horizons Ag (oxic–suboxic), Bg (suboxic), Cr<sub>1</sub> (anoxic with low concentration of pyrite Fe) and Cr<sub>2</sub> (anoxic with high concentrations of pyrite Fe) have distinct geochemical and microbiological characteristics. In general, total S concentration increased with depth and was correlated with the presence of pyrite Fe. Soluble + exchangeable-Fe, pyrite Fe and acid volatile sulfide Fe concentrations also increased with depth, whereas ascorbate extractable-Fe concentrations decreased. The occurrence of reduced forms of Fe in the horizon Ag and oxidized Fe in horizon Cr<sub>2</sub> suggests that the typical redox zonation, common to several marine sediments, does not occur in the saltmarsh soil profile studied. Overall, the bacterial community structure in the horizon Ag and Cr<sub>2</sub> shared low levels of similarity, as compared to their adjacent horizons, Bg and Cr<sub>1</sub>, respectively. The phylogenetic analyses of bacterial 16S rRNA gene sequences from clone libraries showed that the predominant phylotypes in horizon Ag were related to *Alphaproteobacteria* and *Bacteroidetes*. In contrast, the most abundant phylotypes in horizon Cr<sub>2</sub> were related to *Deltaproteobacteria*, *Chloroflexi*, *Deferribacteres* and *Nitrospira*. The high frequency of sequences with low levels of similarity to known bacterial species in horizons Ag and Cr<sub>2</sub> indicates that the bacterial communities in both horizons are dominated by novel bacterial species.

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### 1. Introduction

Saltmarshes are among the most valuable and vulnerable environments of coastal areas and have key roles in maintaining ecosystem functionality. In general, saltmarsh soils and sediments are highly affected by the tidal water dynamics and are redox-stratified (i.e. oxic, suboxic and anoxic zones) with increasing depth. In such environments, changes in redox conditions are associated with shifts in microbial respiratory pathways that couple organic matter oxidation to terminal electron acceptors with decreasing free energy yield, including Fe(III) and sulfate (Froelich et al., 1979). It has been shown that sulfate reduction can account for more than 50% of the total carbon oxidation rates in

saltmarsh soils (Howarth and Merkel, 1984; King, 1988). In addition, carbon oxidation coupled to Fe(III) reduction may also have an important contribution to the total carbon oxidation rates under certain environmental conditions (Lowe et al., 2000; Kostka et al., 2002a,b). Together, these data indicate that in such environments the iron (Fe) and sulfur (S) cycles are driven essentially by organic matter oxidation.

At least four main reactions have been proposed for the redox cycle of Fe: 1) Fe(III) solubilization by organic ligands, 2) reduction of Fe(III) to Fe(II) by organic ligands, soluble reduced S or solid phase reduced S, 3) oxidation of Fe(II) by Fe(III) minerals, and 4) formation of Fe-sulfide minerals such as pyrite when excess of sulfide is available (Luther et al., 1992). In the presence of oxygen, Fe(II) can be oxidized, forming Fe-oxyhydroxide minerals. Many Fe(III) minerals of varying stabilities are found in sediments and soils, including goethite, hematite, magnetite, ferrihydrite, lepidocrocite and maghemite (Cornell and Schwertmann, 1996). The reactivity of Fe-oxyhydroxides depends on their mineralogy, crystallinity and grain size, and in general less stable minerals (i.e.

\* Corresponding author. Departamento de Ciência do Solo, ESALQ, USP, Av. Pádua Dias, 11, 13418-900 Piracicaba, SP, Brazil. Tel.: +55 19 3417 2107; fax: +55 19 3417 2110.

E-mail address: [mlambais@esalq.usp.br](mailto:mlambais@esalq.usp.br) (M.R. Lambais).

ferrihydrate) should react more promptly than more stable minerals (i.e. goethite and hematite) (Cornell and Schwertmann, 1996). Even though there is no selective chemical extractor for specific Fe(III) forms, differential extraction techniques have been extensively used to study Fe-oxyhydroxides in soils and sediments (Chao and Zhou, 1983; Fortín et al., 1993; Raiswell et al., 1994; Kostka and Luther, 1994; Haese, 2000; Roden, 2003, 2004). However, the association of specific reactions with members of the microbial community has been hampered by the difficulty in cultivating the majority of the microbial species inhabiting saltmarsh soils and sediments.

Culture-independent molecular techniques have been widely used to study microbial communities involved in the geochemical transformations of Fe and S, however most studies rely on culture-dependent methods (Lowe et al., 2000; Koretsky et al., 2003, 2005). Molecular methods show that most of the microorganisms in saltmarsh soils cannot yet be assigned to known phylogenetic groups, suggesting that the central geochemical processes in such environments are carried out by unknown microbial species (Devereux et al., 1996; Lydell et al., 2004). This poses a considerable challenge in identifying the particular bacterial species that carry out the oxidation/reduction of Fe and S in saltmarsh soils. The first step in identifying the functional groups that carry out redox transformations is to characterize the phylogenetic relationships between the species that occur in different redox zones in the soils, and the second step would be linking microbial taxa to the specific biogeochemical processes.

The establishment of a clear relationship between phylogeny based on the 16S rRNA gene and metabolic function in the environment, however, is not a trivial task as bacteria may gain different functions by horizontal gene transfer and acquisition of mobile genetic elements that confer various traits. In cases where central electron transport pathways are widely shared within a phylogenetic group, the use of 16S rRNA based methods can provide an indication that certain bacterial species may carry out a specific geochemical process. For example, using sequencing of the 16S rRNA gene to evaluate the community of sulfate-reducing bacteria (SRB) in saltmarsh environments, it has been shown that SRB rRNA comprised approximately 5% of the total rRNA extracted from the sediments in a site with low rates of sulfate reduction. In contrast, SRB rRNA accounted for up to 30% of the total rRNA in a site with higher rates of sulfate reduction, suggesting that some microbial populations can be associated with specific geochemical processes (Devereux et al., 1996).

In this study we used polymerase chain reaction-denaturing gradient gel electrophoresis (PCR-DGGE) of the 16S rRNA gene to determine whether the structures of bacterial communities were stratified along a high saltmarsh soil profile exhibiting redox zonation. In addition, we used partial sequencing of 16S rRNA gene clone libraries to estimate the diversity of bacteria in the oxic-suboxic and anoxic soil horizons, as well as to characterize the most abundant phylogenetic groups potentially associated with the occurrence of different forms of Fe and S in the solid phase. We hypothesized that the redox stratification in high saltmarsh soils is associated with the selection of specific dominant phylogenetic groups of bacteria, which might be involved in oxidation/reduction of the most available forms of Fe and S in the soil.

## 2. Materials and methods

### 2.1. Localization and site description

This study was conducted at Mera high saltmarsh (43°40'40"N, 7°53'13"W), in the Ría of Ortigueira, one of the most preserved saltmarshes in the Iberian Peninsula protected by the Natura 2000 network of the European Union. Soil sampling was carried out in

July 2004, at low tide on the edge of a canal colonized by *Halimione portulacoides*. The dicotyledonous *H. portulacoides* colonizes well-aerated saltmarsh soils, since it is a poor competitor in flooded soils (Armstrong et al., 1985). The vegetation at the sampling location has been described in detail by Sánchez et al. (1998). The sampling location is only completely flooded in the spring tide, and the entire soil profile remains above water table during low tide. Soil samples were collected during low tide. According to the pedological characteristics, the soil profile contained four horizons: Ag (0–38 cm), Bg (38–78 cm), Cr<sub>1</sub> (78–108 cm) and Cr<sub>2</sub> (108–130+ cm), representing, respectively, an oxic/suboxic zone, a sub-oxic zone, a suboxic zone with color indicating the presence of reduced Fe and an anoxic zone (Fig. 1). The upper two horizons (Ag and Bg) were characterized by light colors with red mottles and intense biological activity with high amounts of fine roots and pedotubules (Fig. 1; Table 1). The deeper horizons, Cr<sub>1</sub> and Cr<sub>2</sub>, did not contain plant roots and were gray and black in color, respectively. Sand content was <10% and there were no significant changes in texture along the soil profile (clay loam) (Table 1). Soil samples were collected in triplicate from the horizons after removing approximately 10 cm from the creek bank. Samples were stored in plastic bags at 4 °C for chemical and physical-chemical analyses and at –80 °C prior to DNA analyses.

### 2.2. Chemical and physical-chemical analyses

Physical-chemical analyses were conducted to ascertain soil pH and electrical conductivity (Crinson CM2201, Crinson Instruments SA, Barcelona, Spain). Soil color was determined using wet samples and a Munsell Soil Color Chart. Redox potential (Eh) was determined *in situ* with a platinum electrode previously tested using a standard redox solution (Crinson, Eh: 468 ± 5 mV at 25 °C). The value obtained was then corrected by adding the potential of a calomel reference electrode (244 mV). Total sulfur (total S) and organic carbon (TOC) concentrations were determined using an elemental analyzer (CNS-1000, LECO), after removing carbonates with 6 N HCl (Huerta-Díaz and Morse, 1992). The concentration of

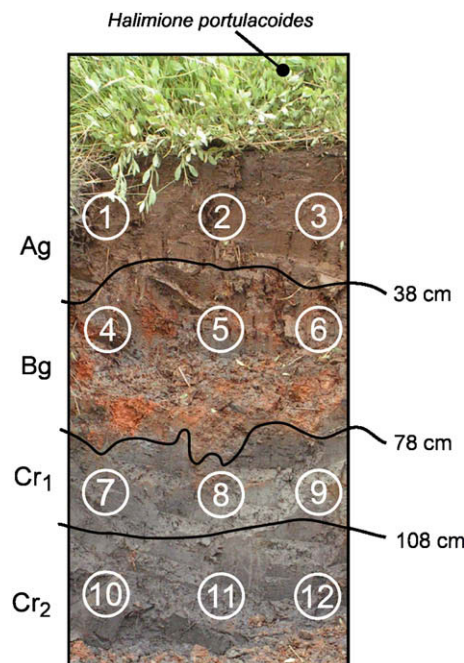


Fig. 1. Mera saltmarsh soil profile studied. Ag, Bg, Cr<sub>1</sub> and Cr<sub>2</sub> represent the horizons defined and the numbers represent the positions from where soil was sampled.

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