UNIVERSIDADE FEDERAL DO CEARÁ
CENTRO DE CIÊNCIAS
DEPARTAMENTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

RAIANA LIRA CABRAL

ECOLOGICAL RELATIONS IN HYPERSALINE TIDAL FLATS (APICUM): A STUDY BASED IN CEARÁ STATE ESTUARIES

FORTALEZA

2015

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Tese submetida à Coordenação do Programa de Pós-Graduação em Ecologia e Recursos Naturais, da Universidade Federal do Ceará, como parte dos requisitos para a obtenção do título de Doutora em Ecologia e Recursos Naturais.

Orientador: Prof. Dr. Tiago Osório Ferreira (ESALQ/USP)

FORTALEZA

2015

Dados Internacionais de Catalogação na Publicação
Universidade Federal do Ceará
Biblioteca de Ciências e Tecnologia

C117e Cabral, Raiana Lira.
Ecological relations in hypersaline tidal flats (Apicum): a study based in Ceará state estuaries. / Raiana Lira Cabral. – 2015.
102f. : il., enc. color.

Tese (Doutorado) – Universidade Federal do Ceará, Centro de Ciências, Departamento de Biologia, Programa de Pós-Graduação em Ecologia e Recursos Naturais, Fortaleza, 2015.
Área de Concentração: Ecologia e Recursos Naturais.
Orientação: Prof. Dr. Tiago Osório Ferreira.

1. Planícies. 2. Rizosfera. 3. Solos - Salinidade. I. Título.

CDD 577

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Aprovada em 14/12/2015.

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AGRADECIMENTOS

A Universidade Federal do Ceará e ao Programa de Pós-graduação em Ecologia e Recursos Naturais pelo espaço e condições oferecidas para minha formação acadêmica e pessoal.

A Capes pela concessão da bolsa de doutorado e doutorado-sanduíche (PDSE), que permitiram a execução de todas as etapas de formação com tranquilidade e qualidade.

Ao meu orientador, prof. Dr. Tiago Ferreira pela abertura ao diálogo, paciência, incentivos, ensinamentos e reconhecimento. Mas, sobretudo pela relação de parceria e confiança que permitiram meu crescimento profissional, superação pessoal, vivência de experiências únicas e produção de bons resultados.

Ao prof. Dr. Xosé Luis Otero (Jordi) pelo espaço aberto na Universidade de Santiago de Compostela. Agradeço a dedicação, ensinamentos e confiança que permitiram o desenvolvimento e produção de resultados aqui apresentados. Grata pelo acolhimento e providências para que eu fizesse de Santiago e da USC minhas casas.

Ao prof. Dr. Tjisse van der Heide pelo espaço a mim oferecido na Radboad University of Nijmegen, minha gratidão pela dedicação e ensinamentos sobre ecologia de ecossistemas, estatística e modelagem ecológica.

A Ronaldo Gonzaga da Silva, pescador artesanal do Sitio Cumbe, cuja assistência foi essencial no trabalho de campo e cuja luta pela forma tradicional de vida mudaram minha percepção sobre “direitos ambientais”.

Ao prof. Dr. Ricardo Romero da UFC, pelo suporte e confiança na minha chegada a Fortaleza, pela disponibilidade e contribuições para a construção do meu trabalho.

A prof. Dra. Carla Resende da UFC, pelas importantes trocas de ideias, conselhos, incentivos e parceria ao longo desses anos de trabalho e formação.

Ao Dr. Michael Hutchings professor emérito da University of Sussex, pelos valorosos conselhos, troca de ideias e encaminhamentos durante os anos de produção da tese.

Aos profs. Dr. Itayguara, Dr. Christiano da UFC e todos amigos do laboratório de citogenética e evolução de plantas pelo carinho, amizade e trocas de ideias sobre ecologia e sobre a vida.

Aos profs. Dr.Valdomiro Souza-Junior e Dr. Angelo Alves da UFRPE, duas grandes referênias pofissionais, pelo incentivo e carinho que sempre dispensam a mim e ao meu trabalho.

Aos professores e pesquisadores ligados ao PPGERN que ao longo desses anos contribuíram de alguma maneira para minha formação e sempre que foi necessário dedicaram um pouco do seu tempo para de alguma maneira contribuir para produção dessa tese: Profs. Paulo, Roberto, Drude, Parentoni, Ligia e o Dr. Marcos Miranda.

Aos colegas da turma de 2011, por todo carinho e por tornarem o tempo de vivência no Ceará leve e produtivo. Sobretudo a Sanna, Dalva, Márcia, Luciana e Janaina Cruz cuja amizade extrapola os muros da universidade.

Aos colegas do Núcleo de Pedologia Aplicada (e associados), que de auxiliaram nos trabalhos de campo e de laboratório, na introdução à geoquímica e geoestatística. Sobretudo a Hermano, Gabriel, Daniel, Moacir, Isabel e Armando. A Gislaine, Adriana, Thales e Nuto faltarão sempre palavras para agradecer à altura a paciência, ensinamentos, carinho, dedicação e força que dispensaram ao meu trabalho.

A Larissa e Thyara pela valorosa ajuda nos trabalhos de campo.

A Vanessa Dina, por todo auxílio com a preparação e análise de amostras, mas sobretudo pela amizade e companherismo.

Aos técnicos da Funceme que sempre me receberam, auxiliaram e trocaram ideias sobre os processos analíticos. Ao Sr. Antônio José, muito grata pelo tempo dispensado e disponibilidade com que sempre me recebeu.

Aos técnicos do Laboratório de biogeoquímica e edafoloxia da Universidade de Santiago de Compostela, pelo acolhimento, disponibilidade e confiança. Sobretudo a María Santiso, cujos ensinamentos, auxílios com as análises laboratoriais e amizade são inestimáveis.

Aos "compis" da USC por tantas ideias trocadas e força com processos analíticos. Mas, sobretudo pelos infinitos cafés, pelos almoços, *pinchos* e boas conversas. A Adriana, Teresa, Maria, Maria Santiso, Maca, Andres, Pedro, Darío, Ruth, Elena, Saúl e Diego cuja companhia e amizade aqueceram meu coração e deixaram Saudades.

Aos "compis" John, Tita, Tommy, Oly, Yesy, Juan e Blanca por serem o sol de Santiago, o abraço amigo e a garantia de muitos sorrisos depois dos dias de trabalho duro. A Adri, infinita gratidão pela companhia e força dentro e fora da universidade!

As "meninas" com as quais dividi apartamento em Fortaleza ao longo desses anos: Dani, Rafa, Ayrles, Nivea, Bia e Marcia, por tudo!!

Aos amigos da "Netherlândia", essenciais na minha estada ali e que tanto me ensinam sobre a vida: Lidi, Luana, Ana, Cintia, Klívia, Milton, Natalia, Dudu, Patricia e Nico. Meu carinho pra sempre!

Aos amigos da vida: Dani, Gafan, Dina Aninha, Josy, Léo, Lilo, Andreza, Déa, Ana Rê, Sarinha, Talitha, Rildo, Naíza, Sorele, Erika, Ties, Gigio, Ana Lucía, Verena, Ideal, Judith, Sara, Fernanda, John e Julie pela presença, exemplo, palavras e abraços fundamentais nesses anos.

A minha mãe, Izabel Lira que além de todo amor, suporte afetivo e prático, dos incentivos para realizar meus sonhos, foi nesse período, conselheira, auxiliar de campo e laboratório. Para você o meu melhor!

Ao meu pai, Radjalma Cabral por todo incentivo e amor. Por ter me contribuído para o valor da responsabilidade e fé que carrego comigo.

RESUMO

ESTUDO DAS RELAÇÕES ECOLÓGICAS EM PLANÍCIES HIPERSALINAS (APICUM) NO ESTADO DO CEARÁ

Esse estudo teve como objetivo geral investigar processos ecológicos e a dinâmica do apicum. Esses sistemas se caracterizam por serem planícies hipersalinas que ocorrem em zonas costeiras de regiões áridas onde podem ser identificadas dentro de bosques de mangue ou entre o manguezal e ecossistemas de terra seca, como mata seca ou restinga. Os apicuns são áreas estratégicas para recuo das florestas de mangue em caso de aumento do nível do mar. Além disso, possuem grande importância econômica, visto que são áreas preferenciais para instalação de empreendimentos de aquicultura e salinas e por que representam zonas de segurança para populações tradicionais. Entretanto, muito pouco se sabe sobre os processos ecológicos que regulam a dinâmica do sistema. Os estudos compilados nessa tese visam de algum modo suprir lacunas sobre os processos ecológicos que regem a dinâmica desse sistema. No capítulo 1 foram avaliados possíveis mecanismos utilizados pelas plantas para sobreviverem ao ambiente limitante através do estudo dos solos rizosféricos e comparação com solos não colonizados por plantas. No capítulo 2, através de um estudo experimental de campo foram avaliados os efeitos da bioturbação de duas espécies de caranguejos nos solos de apicum e seus possíveis efeitos sobre as condições edáficas. O capítulo 3 aprofunda-se na avaliação das interações ecológicas que ocorrem entre o solo, microrelevo e a biota do sistema (plantas e animais). Nesse sentido, um modelo ecológico estrutural foi construído utilizando variações na elevação do relevo, propriedades do solo, biomassa das plantas e área de cobertura de caranguejos. Com base nos resultados, concluiu-se que o sistema apicum possui dinâmica ecológica muito própria e possui uma relação com os bosques de mangue graças ao compartilhamento de fluxos de matéria, nutrientes e populações de animais. A comunidade de plantas do apicum é composta, sobretudo por espécies clonais halófitas pioneiras e que parecem possuir estratégias diferenciadas para lidar com o estresse salino, fator limitante do seu crescimento e distribuição. O efeito da sazonalidade é notável, sobretudo nas áreas não colonizadas por plantas, indicando que possivelmente as plantas estabilizam o sistema solo em seu beneficio. Diferentes espécies de caranguejos são capazes de afetar a dinâmica biogeoquímica do solo. A bioturbação do solo pelas espécies estudadas provocou diferentes efeitos nas propriedades do solo, os quais parecem estar intimamente ligados as hábitos das espécies. Entretanto, as seus efeitos nos apicuns, embora importantes, são menos intensos que em áreas de manguezais. Processos ambientais ligados à salinidade do solo e à disponibilidade de nutrientes estão entre os principais fatores que regem a distribuição de caranguejos e crescimento das plantas nos apicuns. Esses processos são intimamente dependentes das variações do microrelevo. Uma combinação entre fatores abióticos (elevação do relevo e propiedades do solo) e relações positivas entre espécies de plantas parecem se os princiapis agentes na dinâmica ecológica dos apicuns. Estratégias de conservação de sistemas costeiros devem incluir a proteção dos apicuns visto seu importante papel ecológico no cenário de mudanças climáticas e importância para economia local, sobretudo por conta suas características ecológicas únicas.

Palavras Chave: planícies hipersalinas costeiras, áreas úmidas costeiras, rizosfera, bioturbação, solos salinos, facilitação e modelagem ecológica.

ABSTRACT

This study investigates ecological process and dynamic of the hypersaline tidal flats (HTF, locally knowns as “apicum”). The HTF systems are characterized by flat landscape and hypersaline soil conditions that may occour in arid and semiarid regions of the world. Usually HTF can be found inside mangrove forest or as a transitional system between mangrove and dry land ecosystem. These areas are highly important for advances of mangrove forest in case of sea level increase. Besides, HTF have great economic value, as prioritarian areas to install aquaculture or saline ponds. Also it represents security zones for traditional populations, as artisanal fishermen. However, the ecological process which drives the HTFs systems remain poorly knew. The studies presented in this doctoral dissertation aim to fulfill some lacks of knowledge about ecological process that could drive the HTF dynamic. On chapter 1 were evaluated possibles mechanisms used by plants in order to improve their survival in such stressed environment through the study of rhizosphere soils and comparison with bulk soils. On chapter 2, through an experimental study in the field, the possible effect of two crab species bioturbation on HTFs soils and it possible effects on soil properties were evaluated. The chapter 3 registered the evaluation of ecological interactions among biotic and abiotic fractions of the system using ecological modeling tools. In this sense, a structural ecological model was designed using microrelief elevation, soil properties, two plant species biomass and the covering areas of two crab species. Based on results obtained in these studies, it was possible to conclude that HTFs have a particular ecological dynamic and have close relation with mangrove forests due the nutrients, material and animal population flux shared by them. The plant community of HTFs areas is componed mainly by pioneers’ clonal halophytes species. These species seemed to have different strategies to deal with saline stress, an important limitant factor for their growing and distribution. The seasonal effects were noteworthy mainly in bulk soils. In this sense, it is possible that plant estabilize the environment in their benefit. The crabs were able to affect biogeochemical dynamic in HTF soils. However, the burrouing effects of crab species on soil properties were different and seemed reflect the species habit. Although bioturbation effects were important, the modifications on HTF soil properties were less evident than in mangrove forests. Environmental process related to salinity and nutrients availability are among the main factors to drive crabs distribution and plant growth in HTFs. These processes were dependent of microrelief variation. A combination of abiotic factors (microrelief elevation and soil properties) and positive relations among plant species seems to guide the ecological dynamics in HTFs systems. Conservation strategies of coastal environments areas must include the HTF protection due their importance for coastal environments on climate change scenario and economic importance, but mainly because their unique ecological characteristics.

Key words: hypersaline tidal flats, coastal wetlands, rhizosphere,bioturbation, soil salinity, facilitation, ecological modeling.

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INTRODUCTION

Mangroves are among the most important wetlands ecosystems in the world's subtropics and tropics (Alongi 2002). The ecosystem characteristics include food webs containing a mixture of marine and terrestrial species, nursery ground, breeding sites for different species, accumulation and transformation sites for sediments, nutrients and contaminants (Lee 1995, Alongi 2002, Jennerjahn and Ittekkot 2002, Schaeffer-Novelli 2002).

The Brazilian coast is under different environmental conditions what reflects on their ecological dynamic and formation of different associated ecological systems. In Ceará, 230 km^2 are covered by mangroves ecosystems (Menezes, 2005). In this region, mangrove forests are poorly developed due a low input of continental waters and long dry periods, which result in higher salt concentrations and limited growth of plant species (Schaeffer-Novelli et al.1990). Such arid and semiarid conditions favor the formation of hypersaline tidal flats (Ridd and Stieglitz 2002) in different phisiographical settings (Lebigre 2007).

Hypersaline tidal flats (HTFs) are locally known as "apicum" or "salgado". The word "apicum" (pl. apicuns) comes from indigenous language Tupi, "apecu" meaning saltwater marsh (Cunha 1999). These areas are characterized by high salinity concentrations (Ridd and Sam 1996, Sam and Ridd 1998, Albuquerque et al 2014) and connections with mangrove forests (Lebigre 2007, Meireles et al 2007, Albuquerque et al 2014a) (Figure 1).

Figure 1. Panoramic view of a HTF placed between a mangrove forest (on the left) and the coastal tableland (on the right).

Equivalent HTF environments in other semiarid regions of the world were named “tanne” (mostly in Africa and Oceania; Lebigre 2007) and share similar genetic and ecosystemic charctheristics (Bigarella 1947, 2001; Lana 2003; Conesa et al. 2011). However, the apicum differs from salt and tidal marshes mainly by the characteristics expressed plant composition (Table 1) and soil physicochemical characteristics in response to daily flooding duration and climate characteristics (Traut 2005; Albuquerque et al. 2014a). HTFs generally have low water inputs and are under high evapotranspiration rates, the soil presents high saline rates in comparison to others similar ecological systems (Albuquerque et al 2014b). In this sense, the HTFs are primarily vegetated by halophytes (Table 1; Marques 2010; Lebigre 2007), mostly clonal herbaceous succulents and grasses or, in some cases, are totally devoid of any vegetation cover (Hadlich et al. 2008).

Table 1. Floral composition of “apicum” and “tannes”.

Family	Species	Reference
Aizoaceae	*Sesuvium portulacastrum* (L.) L.	Marius (1981); Marius et al. (1987); Lebigre (2007)
Chenopodiaceae	*Arthrocnemum indicum*(Wild.)Moq.	Lebigre (2007)
Chenopodiaceae	*Atriplex spp.* (L.)	Lebigre (2007)
Chenopodiaceae	*Halosarcia indica subsp. leiostachya* (Benth.) Paul G.Wilson	Lebigre (2007)
Chenopodiaceae	*Salicornia spp.*(L.)	Lebigre (2007)
Chenopodiaceae	*Salsola littoralis* Moq.	Lebigre (2007)
Chenopodiaceae	*Sarcocornia* sp. (A.J. Scott)	Lebigre (2007)
Chenopodiaceae	*Suaeda spp.* Scop.	Lebigre (2007)
Poaceae	*Aeluropus lagopoides* (L.)	Lebigre (2007)
Poaceae	*Cynodon dactylon* (L.) Pers.	Lebigre (2007)
Poaceae	*Paspalum vaginatum* Sw.	Marius (1981)
Poaceae	*Sclerodactylon macrostachyum* (Benth.) A. Camus	Lebigre (2007)
Poaceae	*Sporobolus robustus* Kunth	Lebigre (2007)
Poaceae	*Sporobolus virginicus* (L.) Kunth	Lebigre (2007); R.L. Cabral (p.c., 2013)

Convolvulacae	*Cressa australis* R. Br.	Lebigre (2007)
Cyperaceae	*Cyperus laevigatus* (L.)	Lebigre (2007)
Cyperaceae	*Eleocharis caribaea* (Rottb. Blake)	Marius (1981); Marius et al. (1987)
Cyperaceae	*Eleocharis mutata* (L.)	Marius (1981)
Cyperaceae	*Fimbristylis sp.* Vahl	Lebigre (2007)
Amarantaceae	*Blutaparon portulacoides* (A. St.-Hil.) Mears	R.L. Cabral (p.c., 2013)
Amarantaceae	*Philoxerus vermicularis* (Linn.) P. Beauv	Marius (1981); Marius et al. (1987); Lebigre (2007)
Bataceae	*Batis marítima* (L.)	R.L. Cabral (p.c., 2013)

p.c. personal communication. Table extracted from Albuquerque et al. 2014.

Regarding the association of HTFs with mangroves, HTFs can be found inside mangrove forests (Maciel 1991; Schmidt 2006; Hadlich et al. 2008) or between mangrove forests and dry lands i.e., coastal tablelands in Brazil (Hadlich et al. 2008; Ucha et al. 2008; Marques 2010; Albuquerque et al 2014b). Therefore, it is suggested that the connection ‘mangrove forest-Hypersaline tidal flat’ is a necessary condition for the characterization of this ecosystem (Lebigre 2007; Hadlich et al. 2010). Mangrove forests are usually connected to adjacent systems by fluxes/exchanges of sediments, nutrients, organic matter, and also by animals which moves between these ecosystems (Tomlinson, 1986; Kjerfve, 1990).

From a geomorphological point of view, the HTFs are considered active areas which constantly receive sediments delivered via wind action, waves and by the river system which transports sediments from inland areas and deposits them along the coastal plains (Meireles et al. 2007). With respect to the edaphic perspective, these HTFs may act as a nutrient reservoir to the surrounding ecosystems providing organic matter, nutrients, and ions (Nascimento 1999; Marques 2010). Moreover, HTFs seem to represent a strategic site for protecting mangrove species fromthe rising of the sea level (Portugal 2002) as well as from other natural and (or) anthropogenic disturbances.

The most accepted hypothesis for the HTFs formation is related to less frequent tide flooding, low precipitation rates and long dry seasons which usually promote sharp increases in salinities, the disappearance of mangroves and the colonization of soils by halophytes (Marius, 1985). So, all processes are mostly driven by the water regime (Sadio, 1989), which also help to set the HTFs limits and size (Maciel 1991; Pellegrini 2000).

Hypersaline tidal flats also provide different resources for animal species, primarily decapod crustaceans (Nascimento 1993; Schmidt 2006). Crab species as *Ucides cordatus* (Linnaeus, 1763) and Uca spp. (Schmidt 2006), *Cardisoma ganhumi* (Latreille 1828) (Firmo et al. 2012) (Figure 2), Gecarcinidae and juvenile Callinectes are also found in HTFs (Normann and Pennings 1998). Most of these species play important role modifying and mantaining the system (Jones et al. 1994) and most of them are important fishery resources for local communities (Pinto et al. 2010). However a limited number of studies explain the ecological relations of these species in HTF.

Figure 2. Some crab species found in HTFs. (A) *Uca rapax*; (B) *Ucides cordatus*(C) *Cardisoma ganhumi*

Although mangroves and apicuns perform a great number of similar social and ecological functions, the latter are still subjected to a great variety of human pressures, especially in northeastern Brazil (Meireles et al. 2007).These ecosystems have declined over the centuries mainly due to anthropogenic activities (Schaeffer- and Citrón-Molero, 1999) and are among the most vulnerable areas in a climate change scenario (Erwin 2009). The construction of dams in semiarid inland river basins would reduce freshwater delivery to estuaries, therefore increasing the salt intrusion into freshwater regions (Knoppers et al. 2006; Hadlich and Ucha 2009). Similarly, shrimp farming activity and marine salt exploration in the salterns could also contribute to the development of HTFs due to the fact that both activities promote changes in water flow in mangroves because of pond construction. After abandonment, the sites previously affected by ponds construction may develop hypersaline soils (Meireles et al. 2010).

These ecosystems have been inadequately described by the environmental laws (Schaeffer-Novelli 2002, Ucha et al. 2008, Hadlich et al. 2008) such as the Brazilian Forest Code (Brazil 1965) and the Brazilian National Council of the Environment (CONAMA; Brazil 2002). In part, this lack on legal interpretation is related to a great knowledge gap that still exists, specifically with regard to these ecosystem formation and ecological functions (Hadlich et al. 2010). Determining how these ecosystems function is crucial to understanding their role on an ecosystemic level.

The studies developed during the last four years tried to improve the understanding of HTFs ecological components, their functions and possible connections with the mangrove ecosystem. In this sense, the following hypothesis were tested: (i) In HTFs systems the soil act as a limiting factor for plant growth and crab distribution; (ii) Plants and crabs can change soil properties in their benefit; (iii) Soil properties are good proxies to assess the connections between mangrove and HTFs. To test these hypotheses two different estuaries at the Ceará state were chosen (Pacoti river estuary and Jaguaribe river estuary). The selection of areas was based in two criteria: conservation of natural features and reduced anthropogenic activities (in the surroundings or inside the area).

Each of the following chapter results from basic questions and objectives to test the proposed hypothesis: Manuscript 1 – Are soil characteristics (mainly high salinity) able to control plant distribution or the native plants change HTF soil properties on their benefit? Considering that most times HTF plants present patch distribution, rizospheric soils of three species were evaluated and compared to bulk soils in order to verify the predominant process; Manuscript 2- Is bioturbation by crabs able to change soil properties? And what could be the consequences of these changes? Evaluation of the bioturbation effects of two HTF crabs in soil properties was conducted by comparing experimental plots where crabs were excluded with bioturbated areas. Manuscript 3- Are soil properties the main factor that drives plants and crabs distribution in HTF systems? Some interactions that could happen in HTF, both in the abiotic and biotic levels, were tested using ecological modeling tools in order to determinate the power of these interactions on the distribution of these biological components.

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CHAPTER 1

How plants change soil properties in a hypersaline tidal flat in their benefit?

(Como as plantas modificam propriedades do solo numa planície hipersalina costeira em seu benefício?)

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Resumo: As planícies hipersalinas são uma das areas úmidas costeiras localizadas nas regiões semiáridas mais pressionadas. Através da comparação de solos rizosféricos e não rizosféricos, nós investigamos as possíveis modificações geoquímicas mediadas por plantas para colonizar essas áreas. O solo rizosférico de três espécies e os solos de áreas próximas não colonizadas foram amostrados numa profundidade de 0-20cm nas duas estações mais marcantes para ambientes semiáridos. Nós analisamos propriedades físicas (composição granulométrica) e químicas (pH; potencial redutor; complexo de cátions trocáveis; condutividade elétrica; total C, N, S; NH4+ e NO3- trocáveis; além do fracionamento das fases sólidas do Fe). Os resultados foram submetidos a um teste ANOVA e Análise Discriminante. A maior parte dos solos estudados apresentou textura arenosa, baixo conteúdo de matéria orgânica e condições hipersalinas. Algumas propriedades químicas dos solos rizosféricos foram notavelmente diferentes ($p<0.05$) quando comparados com seus respectivos solos não rizosféricos. As diferenças entre as propriedades do solo evidenciaram as planícies hipersalinas como um ambiente heterogêneo. Nesse sentido, as plantas modificaram o ambiente para manter o solo com condições adequadas ao seu desenvolvimento. A comparação entre solos não rizosférico e rizosférico nos permitem concluir que as plantas modificam a sua rizosfera para criar um acumulo de nutrientes e assim aumentar as possibilidades de sobrevivência sob as condições ambientais existentes. As mudanças sazonais afetaram notadamente os processos biogeoquímicos solos das planícies hipersalinas, afetando principalmente os solos não rizosféricos através da modificação da disponibilidade de água no sistema.

Keywords: Solos rizosféricos, áreas úmidas costeiras, salinidade no solo, interação solo-planta, plantas nativas

Abstract: Hipersaline Tidal Flats are one of the most under pressured areas of semi-arid coastal wetlands. However, biogeochemical process related to this environment still rarely studied. Through a comparison of rizospheric soil and bulk, we investigated possible biogeochemical changes mediated by plants to colonize these areas. The rhizospheric soil of three plant species and an associated bulk soil were sampled from 0-20 cm depth, during the two remarkable seasons of semi-arid environments. Were analyzed the physical (grain size composition) and chemical properties (pH; redox potential; exchangeable complex; electrical conductivity; total C, N, S; exchangeable NH4+, NO3-; and partitioning of solid-phase Fe). The results were submitted to ANOVA tests and Discriminant Analysis (DA). Most of the studied soils presented sandy texture, low organic matter contents, and hypersaline conditions. Some chemical properties of rhizospheric soils were remarkably different ($p<0.05$) when compared with it respective associated bulk soil and among species. At the rhizosphere soils, some properties were influenced by seasons, but less when compared to bulk soils. The differences in soil properties evidence HTFs as heterogeneous environments. In this sense, the plants change their environment to keep the soil conditions adequate to their development. The comparison between bulk and rhizospheric soils allow us to conclude that plants change their rhizosphere by creating nutrient pools to improve the survival under the existent environmental conditions. Seasonal effects are crucial to understand soil biogeochemical processes in HTF, affecting mainly to bulk soils by changing water availability on the soil system.

Keywords: Soil rhizosphere, Coastal wetland, Soil salinity, Soil-plant interaction, Native plants

1.1. Introduction

Hypersaline tidal flats (HTF) are considered strategic areas for mangrove expansion in response to regional environmental changes (i.e. global climate change and sea level rise scenarios; Lacerda el al. 2007) in tropical parts of the globe. HTFs seem to be formed from a combination between hydric deficit and limited tidal flooding in an evaporative environment (see Albuquerque et al. 2014a) backing mangrove forest ecosystems. Mangrove and associated areas are interdependent, but connected by water, sediments, nutrients and organic matter fluxes, and also by animal populations that move between the different eco-components (Tomlinson 1986; Kjerfve 1990).

HTFs are found in Oceania (New Caledonia; Lebigre 2007, Marchand et al. 2011), Africa (Gabon, Madagascar; Lebigre et al. 1990) and Latin America (Brazil; Hadlich et al. 2008; Firmo et al. 2012; Albuquerque et al. 2014a). Although it seems to cover large areas, these ecosystems are subjected to increasing rates of anthropogenic disturbances; mainly related to economic activities, such as aquaculture (e.g. shrimp farms) and salt producing ponds (Lebigre et al. 1990; Ucha et al. 2008; Hadlich et al. 2008; Albuquerque et al. 2014b).

HTFs are characterized by its highly saline soils and, thus, by the predominance of grass and herbaceous halophytes species, which are distributed in a patchy pattern (Lebigre 2007; Hadlich et al. 2008; Albuquerque et al. 2014b). *Sporobolus virginicus* (C. Linnaeus) K. Kunth, *Batis maritma* (C. Linnaeus) and *Blutaparon portulacoides* (St. Hil.) are clonal plants typically present in stressful areas, and normally considered as pioneer species able to colonize and stabilize sites previously occupied by mangrove, flats and dunes (Medina et al. 1989; Cordazzo and Seeliger 2003; Bell and O'Leary 2003; Lonard et al. 2011; Lonard et al. 2013).

In additon to environment stabilization, these species play an important role in arid and semi arid wetlands because they offer refuge and protection to different species of decapoda crustaceans, mainly Uca gender, *Ucides cordatus* and *Cadisoma ganhumi*, which lives in HTFs (Nascimento 1993; Schmidt 2006; Firmo et al 2012). The plant species contribute to the nutrient flux from the HTF to the surrounding mangrove forests. Moreover, these plants species have also being studied for medicinal purposes

(Pereira et al. 2009; Lonard et al. 2013), for animal/human consumption and also for the environmental restoration of unproductive saline agricultural lands (Marcone 2003).

Some adaptive strategies developed by plants to colonize saline environments are related with the "plant-rhizosphere-soil" system (Liangpeng et al. 2007). The term “rhizosphere” is applied to the soil that interacts intimately with plant roots, in which the type, number, and activities of the microorganisms are different to the bulk soil (Gregorich et al. 2001; Richter et al. 2007; Herlihy 2008). High rates of chemical and biological activity are concentrated in this region and its effects may control nutrient biogeochemical cycles, greenhouse-gases emissions and the dynamics of pollutants (Liangpeng et al. 2007; Dantas et al. 2009). Thus, studies comparing the rhizospheric and non-rhizospheric soils may not only increase the knowledge on plants effects on natural occurring soil processes, but also their ability to change the soil environment, and the mechanisms for ecological succession (Rozema et al. 1985; Caçador et al. 2010).

Our study hypothesizes that plants may colonize hypersaline tidal flats by modifying soil biogeochemical conditions mainly in their rhizospheres. Thus, physical and chemical soil properties (grain size composition, Eh, pH, exchangeable and soluble cations, total C,N, S, salinity, exchangeable NH_4^+, NO_3^- and partitioning of solid-phase Fe) were analyzed in rhizospheric and non-rhizospheric (bulk) soils under three dominant plant species in hypersaline tidal flats in the semiarid Brazilian Coast (Ceará state) in two seasons (dry and wet). We include these two seasons in the study in order to compare the effects of different plants species on HTF soils characteristics through the year, and test the season effect in the system. We aim to increase the understanding on the effects and adaptation of HTF plants, which have high ecological importance for coastal ecosystems and economic interest. Besides, providing more information on plant-soil relations through biogeochemical processes, this study may contribute to understand the ecological processes as a whole and give key information to design appropriate strategies for conservation or environmental restoration.

1.2. Materials and methods

1.2.1. Study site description

The study area is located in an Environmental Protection Area (APA) at the Pacoti River estuary (3°49’48.91¨ S - 38°25’11.04¨ W), Aquiraz city, Ceará state, Northeastern Brazil (Figure 1A). The Pacoti River extends along 150 km and its stream flow regulates different reservoirs (Pacoti and Gavião), built to supply freshwater for human consumption.These reservoirs play an important role in the reduction of the water volume transferred to the estuary (Lacerda el al. 2007). In this sense, the decrease of river flow resulted in a greater influence of the marine influence, such as a greater salinity intrusion and sediment transportation (Melo et al. 2014).

The establishment of the Pacoti River APA on the estuary allowed a better conservation of the area due to their ecological importance in the controlling of the impacts that result from human activities on the estuary (Nascimento and Carvalho 2003).

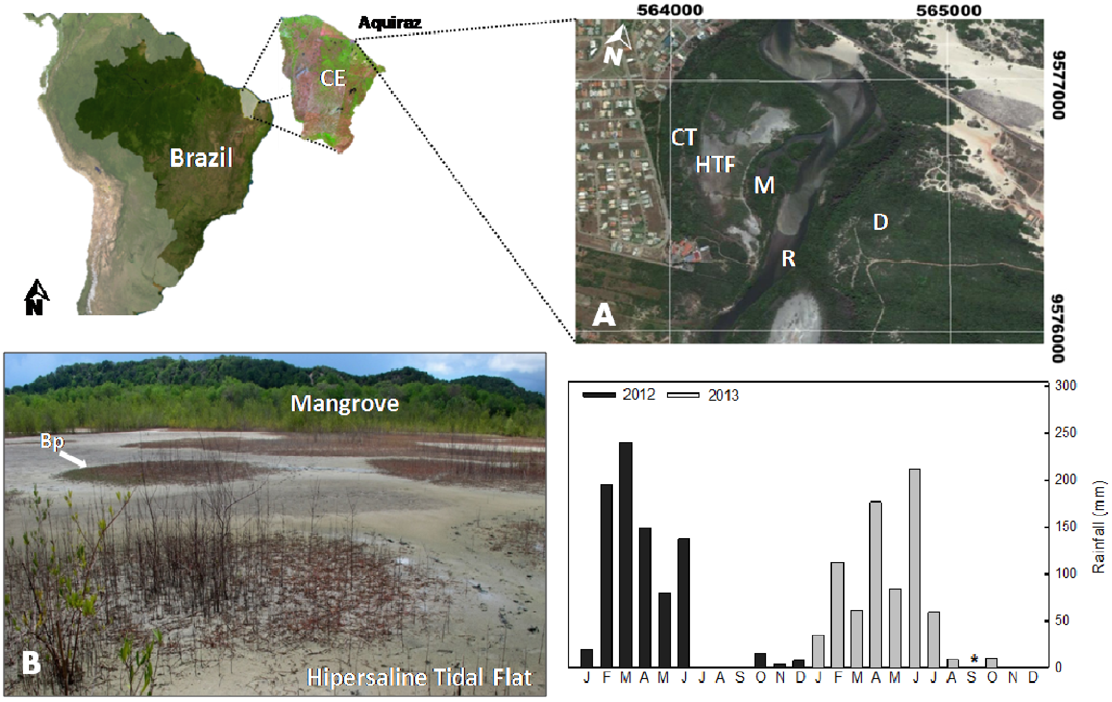

Figure 1. Study site location map (Pacoti River estuary, Aquiraz, Ceará state, Brazil). (A) Aerial photography of Pacoti estuary, where is possible to distinguish the coastal tableland (CT), the studied hypersaline tidal flat (HTF), the mangrove (M), Pacoti river (R) and costal dunes (D); (B) Landscape photography of studied area, showing the patch distribution of *Blutaparon portulacoides* (Bp) and mangrove forest on the background; Graph: Pacoti estuary monthly precipitation for 2012 and 2013 (studied years). Data from FUNCEME database of historical precipitation records. (*) Missing data

The studied area is a HTF with approximately 3.8 ha which is under a tropical semiarid climate, with mean annual temperatures ranging from 26 to 28°C (FUNCEME/IPECE 2012). The rainfall is distributed in two seasons: a rainy summer (from February to June) and a long dry season (from July to January) with mean annual rainfall of up to 1,200 mm. The tides on the estuary are semidiurnal, with maximum tidal amplitudes of about 3.1 m and minimum of 0.9 m (Freire 1989 *apud* Bezerra and Mattews-Cascon 2006).

The native vegetation of the studied HTF (Figure 2) consists of *Batis maritma* (C. Linnaeus) and *Blutaparon portulacoides* (St. Hil.), with the less abundant *Sporobolus virginicus* (C. Linnaeus) K. Kunth and some isolated young individuals of *Avicennia sp.* These species are often patchy distributed through the system (Figure 1B).

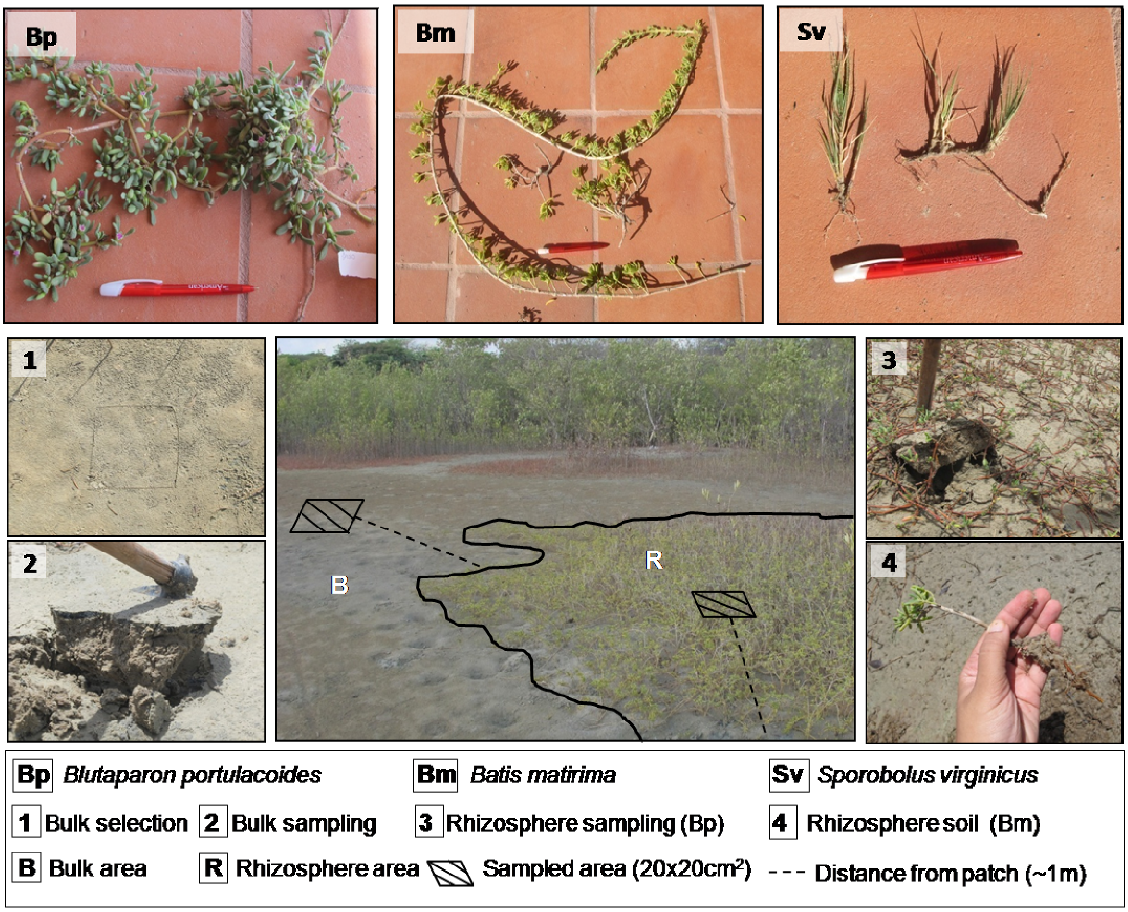

Figure 2. Studied plant species of Pacoti estuary and illustrated representation of soil sampling.

1.2.2. Soil sampling and sample preparation

The rhizospheric and bulk soil samples were collected in November 2012 (dry season) and April 2013 (wet season) (Figure 1). The rhizospheric soil (composed of particles directly attached to the roots) were collected in triplicates and were carefully separated from plant roots (*B. maritima, S. virginicus* and *B. portulacoides*) in the laboratory by shaking and brushing (for more details see Alvarez et al. 2011). The bulk soil samples were separately collected for each species outside the patches within one meter from board of the vegetation patch (Figure 2), accounting a total of 18 sampling points in each season, according with the number of species and their respective bulk soils (Figure 2). Samples were collected from 0-20 cm of depth, than were individually stored, placed into a portable cooler at low temperatures (approximately 4˚C) and transported to the laboratory.

Each sampling site was georeferenced using a portable GPS and the coordinates of each site were used for the measurement of the distance to the river using geoprocessing techniques.

During the sample collection, the redox potential (Eh) values of all samples were measured using portable platinum electrode. The probes were inserted in the centre of each sample to avoid contact with the atmosphere. The Eh values (mV) were obtained after equilibrating the electrodes for 2 minutes and the final readings were corrected by adding the potential (+244 mV) of a calomel reference electrode.

At the laboratory, the soil loosely adhered to the rhizhosphere (external rhizoshere) was removed by gently shaken (Chung and Zazoski 1994) and the particles that remained attached to the roots (internal rhizosphere) were separated using vigorous shaking and a toothbrush to remove the strongly adhered particles (Alvarez et al. 2011). Subsequently, the samples of bulk and rhizospheric soil (separated from roots) were air dried, crushed and sieved through a 2 mm sieve. Subsamples were frozen for posterior analysis and determination of iron forms by the sequential extraction method.

1.2.3. Analytical procedures

In the laboratory, the air-dried subsamples were used for the determination of grain size composition; pH; exchangeable and soluble cations; cations exchange capacity (CEC); electrical conductivity (EC); total C, N,S; available P; NH_4^+ and NO_3^-.

The pH (in water; 1:2.5 solid: liquid ratio) was measured with a glass electrode calibrated using pH 4.0 and 7.0 standards. A saturated extract using dried samples (Rhoades 1996) was prepared to measure EC, with a conductivity meter, and soluble cations and anions (Na^+, Ca^{2+}, Mg^{2+} and K^+) which were quantified by atomic absorption spectrophotometry. Total C, N, and S were determined with a LECO CNS-2000 auto-analyzer (LECO Corp.,St. Joseph, MI, USA).

The air-dried samples from HTF were washed with 60% (v/v) aqueous ethanol to remove soluble salts (Bower et al. 1952; Sumner and Miller 1996) until the silver nitrate test ($AgNO_3$ 0.05N) indicated absence of chloride before chemical and physical analyses. The grain size was determined by pipette method (Gee and Bauder 1986), with the samples submitted to previous oxidation of organic matter with H_2O_2 (30%) by using a combination of physical (overnight shaking) and chemical (0.015 M $(NaPO_3)_6$ + 1.0 M NaOH) dispersal methods.

Exchangeable K^+ and Na^+ were extracted with HCl 0.05 (EMBRPA 1997) and determined by and flame photometry, while exchangeable Ca^{2+} and Mg^{2+} were extracted with KCl 1 M (1:5, soil/solution) and determined by atomic absorption spectrophotometry. Cation exchange capacity (CEC) was calculated as the sum of exchangeable cations (Na^+, Ca^{2+}, Mg^{2+} and K^+; Sumner and Miller 1996). The equivalent sodium percentage (ESP) was calculated as percentage of exchangeable sodium divided by the cation exchange capacity. The calcium carbonate equivalent (CCE) was obtained by the AOAC method (AOAC 1970; Metson 1956). Available P was extracted with Mehlich 3 (Mehlich 1984; Hanlon and Johnson 1984), whereas NH_4^+ and nitrate were extracted with KCl 2 M and determinated by colorimetry (Kempers 1974).

Additionally, a partitioning of the solid-phase Fe was performed using fresh samples based on a combination of methods (Tessier et al. 1979; Huerta-Díaz and Morse 1990; Fortín et al. 1993), which enables the identification of six operationally distinct fractions, defined as follow:

(F1) *Exchangeable and soluble Fe*, extracted with $MgCl_2$ 1M (pH 7; 30 min. agitation);

(F2) *Iron associated to carbonate* extracted with NaOAc 1M (pH 5; 5 hours agitation);

(F3) *Iron associated to poorly crystalline Fe* (Ferrihydrite) extracted with hydroxilamine 0.04M + acetic acid 25% (6 h agitation at 30 ºC);

(F4) *Iron associated to poorly crystalline Fe* (Lepidocrocite) extracted with hydroxilamine 0.04M + acetic acid 25% (6 h agitation at 96 ºC);

(F5) *Iron associated to crystaline oxyhydroxide* extracted with sodium citrate 0.25 M + 0,25M + sodium bicarbonate 0.11M + Sodium dithionite(30 min. agitation at 75 ºC);

(F6) *Iron associated to Pyrite* (pre-treatment with 10 M HF and H_2SO_4 concentrated) extracted with HNO_3.

The degree of iron piritization (DOP) was calculated as follows: DOP (%) = F6*100 /[(∑F1..F5) +F6]; and determines the percentage of Fe which is combined into the pyritic fraction, allowing the comparison of pyrite content in soils with different reactive iron contents (Berner 1970). For further details, please see: Albuquerque et al. (2014); Nóbrega et al. (2014); Otero et al. (2009).

1.2.4. Statistical data analysis

Analyses were performed with the software SPSS version 21 (SPSS Inc. Chicago, IL). Non-normal data were log-transformed to meet conditions of normality and homogeneity of variance. To test the effects of rhizosphere on soils and to compare with bulk soils were used one-way analysis of variance (one-way ANOVA). A two-way ANOVA was used to assess the main effects of seasons, three plant species and their interaction on soil parameters. Two-way ANOVA were followed by Bonferroni´s post hoc comparison tests. A maximum probability level of $\alpha = 0.05$ was used throughout to determine statistical significances.

Furthermore, a discriminant analysis (DA) was performed in order to develop a function that results in an optimal differentiation (maximize the variance) among the plant species; among rhizosphere and bulk soil; and the seasons, identifying the most important variables for the groups distinction.

1.3. Results

1.3.1. General characteristics of bulk soils

Regarding the physical properties, the soil samples presented a prevalence of sand in the grain size composition. In this sense, sand contents ranged from 79% to of 93%, while silt ranged from 3% to 15% and clay from 2% to 6% (minimum and maximum values).

In general, regardless of the seasonal effects, the bulk soils presented alkaline conditions (pHs from 8±0.4 to 8.2±0.2; mean values) and suboxic to oxic conditions (Ehs from 189±68 to 260±43mV; mean values) (Figure 4). Some chemical properties of the bulk soils (e.g. organic matter, CCE, N compounds) were significantly different ($p<0.05$) from the rhizosphere soils. These soil properties were also more stable through season changes, since no significant differences were observed (Figure 3).

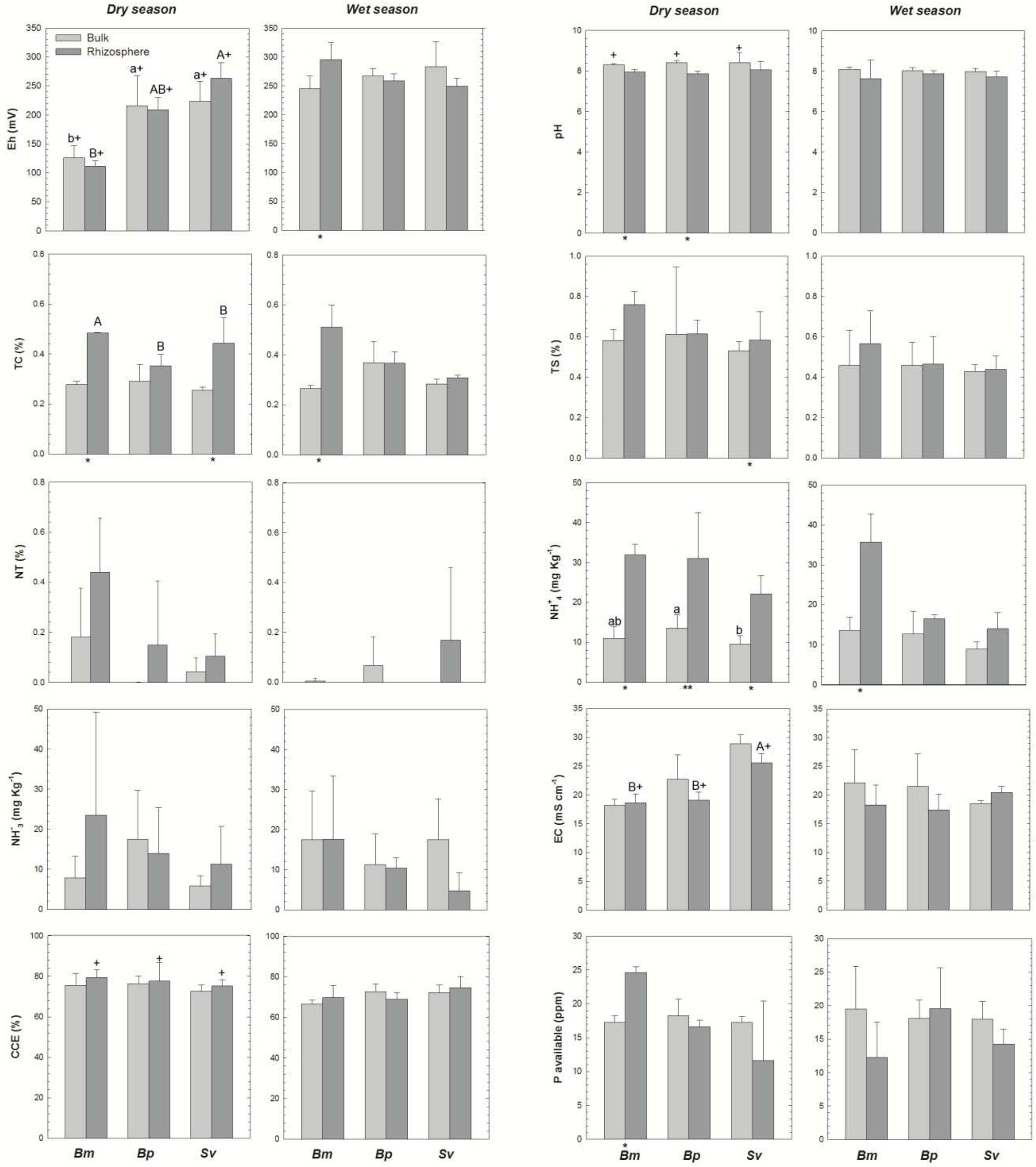

Figure 3. Soil properties of rhizosphere soil of *Batis maritima* (Bm), *Blutaparon portulacoides* (Bp) and *Sporobolus virginicus* (Sv) and it related bulk soils in two seasons. TOC: Total Organic Carbon, EC: Electric Conductivity; ESP: Excheageble Sodium Potential; TS: Total Sulfur. Equal small letters means there is no difference ($p<0.05$) for the same variable in bulk soils; Equal capital letters means there is no difference ($p<0.05$) for the same variable in rhizosphere soils; (+) seasonal variation ($p<0.05$); (*) significant difference ($p<0.05$) between bulk and rhizosphere.

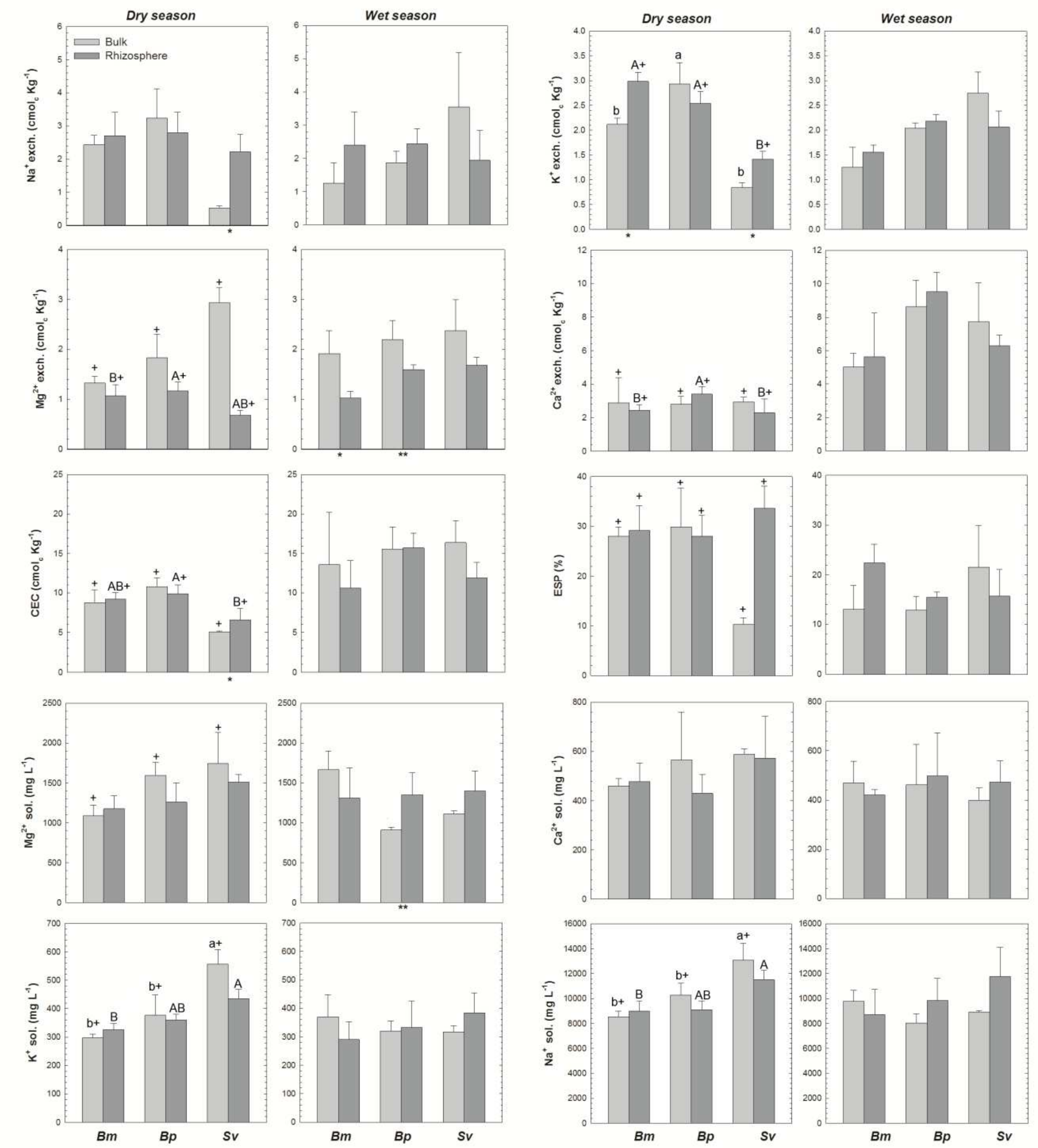

Figure 4. Soil properties of rhizosphere soil of *Batis maritima* (Bm), *Blutaparon portulacoides* (Bp) and *Sporobolus virginicus* (Sv) and it related bulk soils in two seasons. CEC: Cations exchangeable capacity; exch.: exchangeable; sol.: soluble. Equal small letters means there is no difference ($p<0.05$) for the same variable in bulk soils; Equal capital letters means there is no difference ($p<0.05$) for the same variable in rhizosphere soils; (+) seasonal variation ($p<0.05$); (*) significant difference ($p<0.05$) between bulk and rhizosphere.

Soil variables related with organic matter in the bulk soils hardly exceed 0.5% (Figure 3). Total Carbon (TC) ranged from 0.2% to 0.4%; total Sulfur (TS) from 0.2% to 0.9%, while total Nitrogen (TN) for most samples remained under the detection limit, reaching the maximum of 0.3%. However, the N compounds were among most abundant ions on the studied soils. In this sense, NH_4^+ varied from 7.57 to 23.68 mg Kg^{-1} and NO_3^- ranged between 7.57 and 29.88 mg Kg^{-1} (Figure 3). The calcium carbonate equivalent (CCE) also presented high values on the studied soils, ranging from the minimum of 68.1 to 81.3%.

Regarding the iron species (Figure 5), the Fe oxy-hydroxides, both poorly (F3 and F4) and well crystalline forms (F5) predominated (F3: from 2.01 to 16.23 µmol g^{-1}; F4: from 5.21 to 24.61 µmol g^{-1}; and F5 0.75 to 1.77µmol g^{-1}; minimum and maximum values among samples). The mean values of all other determined fractions (F1, F2 and F6) were under 1 µmol g^{-1} and the DOP always remained <1%.

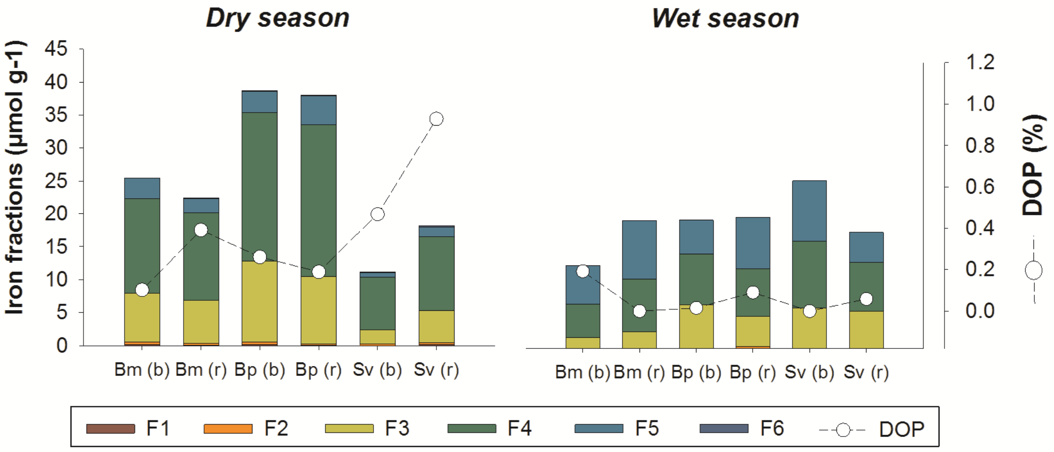

Figure 5. Iron fractions obtained in sequential extraction for bulk and rhizospheric soils in three plant species and two seasons. (F1) Exchangeable and soluble Fe; (F2) Iron associated to carbonate; (F3) Iron associated to poorly crystalline Fe (Ferrihydrite); (F4) Iron associated to poorly crystalline Fe (Lepidocrocite); (F5) Iron associated to crystaline oxyhydroxide; (F6) Iron associated to Pyrite;(DOP)degree of iron piritization. Bm: *Batis maritima*; Bp: *Blutaparon portulacoides*; Sv: *Sporobolus virginicus*; d: dry season; w: wet season.

1.3.2. Rhizospheric soils vs bulk soils characteristics

Some chemical properties of rhizospheric soils were remarkably different ($p<0.05$) when compared with it respective associated bulk soil (Figure 3). The mean value of pH (regardless of season differences) for bulk soils were 8.2±0.1 (BmB), 8.2±0.2 (BpB) and 7.8±0.3 (SvB) decreasing for 7.7±0.6 (BmR), 7.8±0.1 (BpR) and 7.8±0.3 (SvR) on plants rhizospheres. The opposite tendency was observed for TC and NH_4^+ contents, which increased in the rhizosphere soils. Total Carbon (mean values) in bulk soils were 0.27±0.01% (BmB), 0.32±0.08% (BpB) and 0.26±0.02% (SvB), while rhizosphere soils presented 0.48±0.05% (BmR), 0.34±0.04% (BpR) and 0.34±0.09% (SvR). The contents of NH_4^+ presented the most considerable differences. While bulk soils related to Bm, Bp and Sv presented, respectively, the mean of 11.8±3.1, 17±4.5, 8.3±1.8 mg Kg^{-1}, their correspondent rhizosphere soils presented 100% or more NH_4^+: 32.8±5.1 (BmR), 24.9±53.8 (BpR) and 18.3±5.9 mg Kg^{-1} (SvR) (Figure 3).

Chemical characteristics associated to rhizosphere soils were different among species and from its respective bulk soil (Figure 6B). Based on the total variance of 84.14% it could be assumed that the rhizosphere of the three species (BmR, BpR and SvR) were different between them. In contrast, Sv and Bp bulk soils presented a slight difference since the Factor 2 represented just 9.16% (Figure 6B).

The Bm and Bp rhizospheric soil samples (BmR and BpR, respectively) are associated with higher contents of NH_4^+, exchangeable K^+, crystalline Fe oxides (F5) and available P (Figure 6B). On the other hand, the rhizospheric soil from Sv (SvR) is associated to salinity related properties (EC, ESP and soluble Na^+), and all soluble cations (Figure 6B).

The consequences of these differences can be observed in the species distribution in response to soil properties (Figure 6A). In this sense, the Bp individuals are associated to sites where higher values of exchangeable cations (mainly Ca^{2+}, Mg^{2+} and K^+) and, also, poorly crystalline Fe oxyhydroxides (F3 and F4) were found. On the other hand, the Sv plants are located further away from the river and associated with variables related to higher salt content (e.g., EC and soluble cations; Figure 6A). The occurrence of Bm is associated to sites with higher contents of TC and TN and lower Eh values, when compared to the other species (Figure 6A).

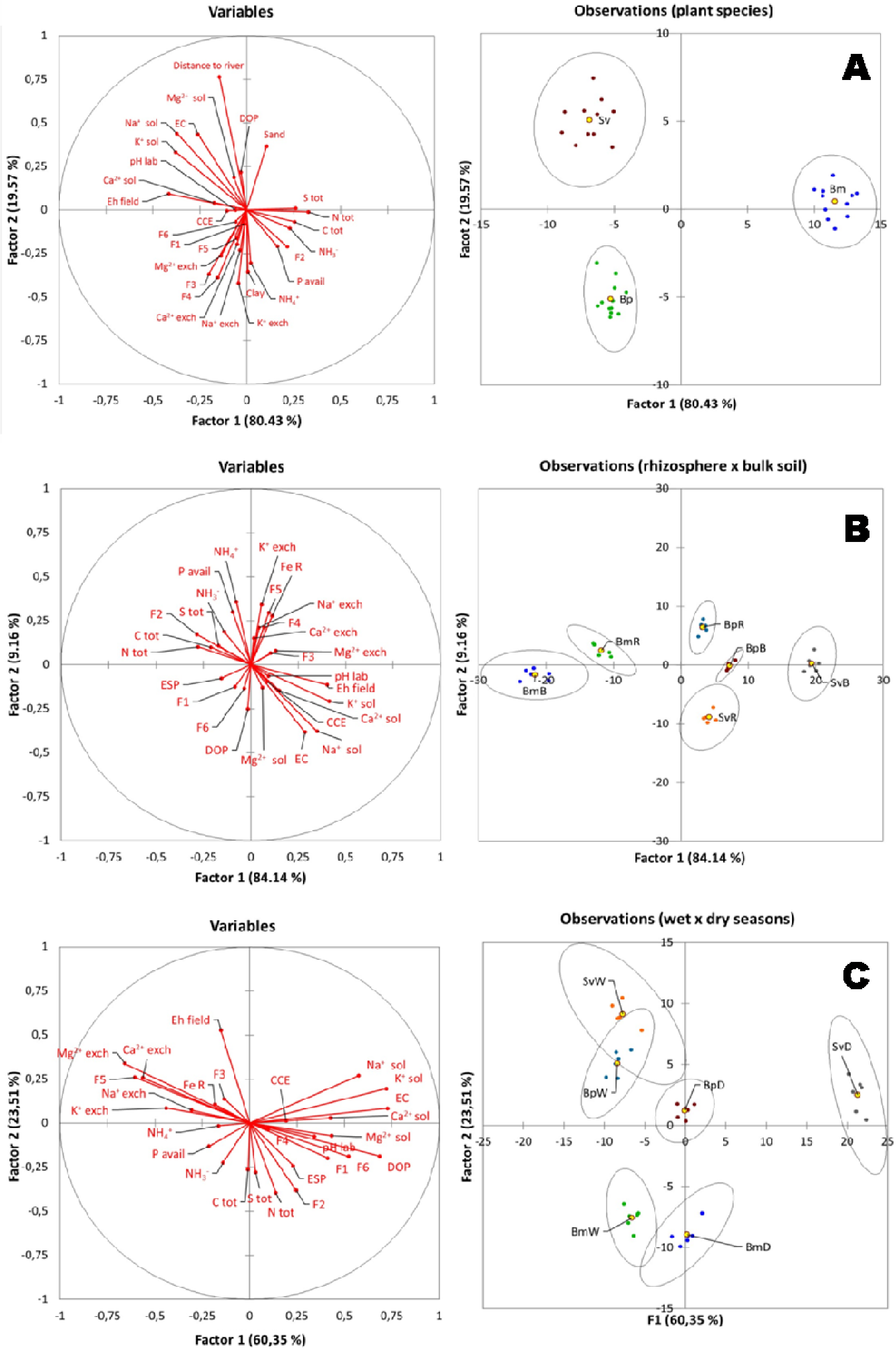

Figure 6. (A) Discriminant analysis of plant species distribution and soil properties in HTF. (B) Observation of rhizosphere and bulk soils properties. (C) Observation of rhizosphere and bulk soils properties during dry and wet season Sv: *Sporobolus virginicus*; Bm: *Batis maritma*; Bp: *Blutaparon portulacoides*. Exch.: exchangeable cation (Na^+ exch; K^+ exch; Ca^{2+} exch; Mg^{2+}

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exch); Sol.: soluble cation (Na^+ sol; K^+ sol; Ca^{2+} sol; Mg^{2+} sol); Tot: total (C tot; N tot; S tot); CEC: cations exchangeable capacity; ESP: exchangeable sodium percentage; EC: electrical conductivity; CCE: Calcium Cabonate Equivalent; F1: Exchangeable Fe; F2: Fe bound to Carbonate; F3: ferrihydrite Fe; F4: lepidocrocite Fe; F5: Crystalline Fe; F6: Pyritic Fe; DOP: Degree of Pyritization.

1.3.3. Seasonal patterns

Soil chemical properties in HTF seemed to be strongly affected by seasonal changes (Figure 3, 4 and 6C). Most studied properties, mainly on bulk soils, presented significant changes ($p<0.05$) in response to seasonal variation.

The changes in pH and cations dynamics on bulk soils between seasons were noteworthy. With regards to pH, the bulk soils presented alkaline conditions, but a significant decrease from dry (BmB: 8.2±0.07; BpB: 8.4±0.1; SvB: 8.4±0.5; mean values) to wet season (BmB: 8.09±0.1; BpB: 8.01±0.1; SvB: 7.9±0.1; mean values) was observed. The EC in bulk soils ranged from 17.6 mS cm^{-1} to 29.9 mS cm^{-1} (minimum and maximum observed values) but higher EC were registered in the dry season (Bm: 22.1±5.7; Bp: 22.7±1.4; Sv: 28.9±1.5 mS cm^{-1}; mean values) when compared to the wet season (Bm: 18.1±1.8; Bp: 17.1±1.4; Sv: 18.9±0.5 mS cm^{-1}; mean values).

At the rhizosphere soils, in lower dimension, some properties were influenced by seasons. A similar tendency of bulk soils was registered, mainly related to the redox potential and EC values (Figure 3). In this sense, the suboxic conditions prevailed both in the dry (BmR: 111±9.8; BpR: 208±21.5; SvR: 263±26.8mS cm^{-1}) and the wet season (BmR: 2965±28.5; BpR: 258±12.7; SvR: 249.6±13.4mS cm^{-1}; mean values). On the other hand, the salinity conditions were significantly higher during the dry season (BmR: 18.5±1.6; BpR: 22.7±1.4; SvR: 25.6±1.5 mS cm^{-1}; mean values) when compared to those in the wet season (BmR: 18.2±3.4; BpR: 17.4±2.6; SvR: 20.4±1.04mS cm^{-1}; mean values).

Regarding cations, season changes mostly affected ($p<0.05$) the soluble contents (K^+, Na^+, Mg^{2+}) on bulk soils (Figure 4). On bulk soils associated to Bm species, the contents of soluble K^+, Na^+ and Mg^{2+} decreased respectively from 370±78, 9783±860 and 1666±232 mg L^{-1} (mean values) to 297±12, 85454±449 and 1088±133mg L^{-1} (mean values) during the dry season. On the other hand, the bulk soils related to Bp and Sv presented the opposite trend. Higher contents of K^+ (Bp: 377±20mg L^{-1}; Sv: 556±51mg L^{-1}; mean values), Na^+ (Bp: 9783±860mg L^{-1}; Sv: 13083±1342mg L^{-1}; mean values) and Mg^{2+} (Bp: 1593±165mg L^{-1}; Sv: 1741±388mg L^{-1}) were registered during the dry season (Figure 4).

Moreover, species seemed to be associated with different soil properties in each season (Figure 6C). Samples from the dry period (BpD; SvD and BmD) were associated to the variables correlated to soluble cations, higher salt content (e.g., soluble cations, EC) and some iron forms (e.g F1, F2 and F4). On the other hand, samples from the wet period (BpW; BmW; SvW) were mostly associated to high Eh values, exchangeable cations and more stable iron forms (F5).

Furthermore, the soil properties that favored the grouping of Bm species through seasons were always related to available P and organic matter (Figure 6A). While the Sv and Bp was more related to soluble cations in the dry season, in the wet season the specie was related to exchangeable cations and more oxidizing conditions.

1.4. Discussion

1.4.1. HTF Bulk heterogeneity

Soil characteristics of the studied bulk soils were consistent with the typical characteristics expected for HTF soils (i.e. neutral-basic, hypersaline and with sandy texture soils; for more details see: Albuquerque et al. 2014a).

The predominance of sandy textures found in this study (Hadlich et al. 2008; Conesa et al. 2011; Albuquerque et al. 2014a) could be related to transportation of sandy material by wind, tide and transportation from inland (terrestrial) areas (Meireles et al. 2007).

Previous studies reported that soil processes involved in the formation of HTFs can explain some bulk soils characteristics. For example, the high contents of CCE registered in the studied soils (Figure 3) are probably related to the fact that $CaCO_3$ is a less soluble salt that precipitates at surface (Langmuir 1997; van Breeman and Buurman 2002). This process is important in order to buffer the pH on surface layers in HTF areas (Albuquerque et al. 2014a), being related to the basic conditions found on the studied areas.

Based on previous studies that evaluated the rates of total organic carbon in soils, it is possible to reinforce the heterogeneity of HTF system. In the analyzed soils, carbon and nitrogen contents rarely ranged over 0.5%, a tendency also observed by Albuquerque et al. (2014a) in superficial layers of HTF soil profiles. The bulk soil area is completely devoid of vegetation (Figure 1 and 2) and do not receive any other input of plant material, what can contribute to the low carbon contents.

The prevalence of iron oxyhydoxides (F3 to F5) and low DOP (<1%) in HTF soils (Figure 5) reflect the suboxic conditions in response to a low flood frequency. In fact, Albuquerque et al. (2014a) also found a dominance of iron oxyhydroxides (which ranged between 79 to 143µmolg^{-1} in the first 15 cm of soil profiles), and DOP values that did not reach 1%.

However the significant effects of season and rhizosphere in most chemical soil properties evidence that HTFs are heterogeneous environments, highly susceptible to changes, both spatially and temporally and must not be evaluated without taking into account these changes.

1.4.2. Plant effects on biogeochemical soil properties

Soil processes in HTF system, mainly on superficial layers, are incipient and normally highly influenced by seasonal changes, but our results allowed us to identify remarkable edaphic process ruled by plants which indicate changes from bulk and rhizospheric soils.

The first notable process by root action is the increase in the capacity of storage and retention of nutrients, reflected by an increase of total pool of nutrients (Weidenhamer and Callaway 2010) in the rhizosphere. The clear decrease in pH values on rhizosphere is a well-documented chemical process occurring at the soil-root interface (Chung and Zasoski 1994, Caçador et al. 2000, Hinsinger et al. 2003; Hinsinger et al. 2009). Moreover, all species were found in hypersaline conditions surviving where, according to Sylla et al. (1995), the development of plants should be limmited when EC is greater than 10 mS cm^{-1}.

The descrease in pH on rhizosphere soils when compared to bulk soils is mainly originated by H^{+} release by roots, organic acids release, root exudation, respiration (by roots and microorganisms) and redox-coupled processes, but also by environmental constraints (Hinsinger et al. 2003, Hinsinger et al. 2009). It is important to note that the large range of pH where Bm and Sv can grow (pH 5.2 to 8.8) (Lonard et al. 2011; Lonard et al. 2013) can facilitate the colonization of the areas by this species and indicates the ability of these plants to alter soil conditions to improve their surviving.

The organic matter incorporation and bioavailability on rhizosphere are also remarkable (Figure 2). These processes were specific to each species and reflected on the TC and NH_4^+ differences in rhizosphere when compared to bulk soils. The strong association of Bm with organic matter (Figure 6A) in opposite to Sv and Bp suggested that not only Bm is the specie that most contributed to organic matter contents, but also indicates the heterogeneity in the distribution of soil resources (mainly C, N, S) on the system.

The contents in inorganic nitrogen forms (NH_4^+ and NO_3^-) are usually greater in rhizospheric soils (Yin et al. 2012) and could be also related to the ability of clonal and halophytes plants to use these compounds to overcome high salinities. In our study, the NH_4^+ contents in rhizosphere soils were up to three times greater than those in the bulk soil, while NO_3^- did not present significant differences between areas (Figure 3). It is possible that NH_4^+ content was related to rhizosphere activity as a result of organic matter incorporation, which corresponds to the tendency observed mainly in Bm associated soils, where the highest values of TC and NH_4^+ among species were observed (Figure 3).

While changing soil conditions by increasing the NH_4^+ contents, it is possible for the plants to create a pool of nutrients (Weidenhamer and Callaway 2010) favouring the conditions for plant growth in a hypersaline habitat. The benefits are mainly related to a decrease in water consumption by using NH_4^+ rather than NO_3^- as the main nitrogen form on water transport (Høgh-Jensen and Schjoerring 1997; Yin and Raven 1998; Guo et al. 2007) in plants under the water stress. A recent study demonstrated that when clonal plants are experimentally supplied with NH_4^+ they were able to reduce water consumption, buffering the negative effect of water deprivation and causing an increase in clones performance (Roiloa et al. 2014). So, the selective use of high NH_4^+ by the studied species can ameliorate the water use-efficiency and mitigate the negative effect of hypersaline conditions. Besides, despite the increase of NH_4^+ on rhizospheric soils, no differences between rhizospheric soils between species (Figure 3) was observed, suggesting that NH_4^+ is not only an important resource for HTF plants, but also that plants can use it in similar ways.

The Sv species (rhizosphere soils) were mainly related to salinity properties and to soluble cations (Figure 6). This condition could be related to the fact that this species was found in areas far from the river and, due to the microrelief variations, less inundated by flooding tides. Recent studies suggested that Sv plants under controlled experiments have great development in higher concentrations of Na^+ and Mg^+ (in scale of 125 to 450mmol L^{-1}) at the same time they were able to absorve and selectvily retain K^+ (Bell and O'Leary 2003) thus, both fenomena may be related. The accumulation and compartmentation of ions and essential nutrients (particularly K) in plants in the presence of high concentrations of salinity-related ions (i.e. Na) are among the main physiological strategy of salt tolerance in halophytes (Flowers and Colmer 2008; Flowers et al. 2010; Soriano et al. 2014). This suggests that the great development of Sv in more saline areas may be related to the use of the available K to improve the growing in HTF conditions. The results of analysis which indicated a significant difference of K contents among Sv species and between its respective bulk soils, reinforce this idea.

It is noteworthy that, despite bulk soils of Bp and Sv being related to similar conditions (figure 6B), presenting low variance between them, their rhizosphere soils were strongly separated based on the discriminant analysis. In this sense, Bp samples were much more related to NH_4^+ availability and exchangeable K^+, while Sv more related to soluble K^+ (Figure 6B). This behavior indicates that, despite the fact that both species presented similar conditions on bulk soils, they probably use different strategies to survive in HTF, which could be related to a facilitation process, since Bp could help to mobilize the exchangeable K, while Sv would consume it. This hypothesis should be tested in further studies and could represent important advances to understand the mechanisms of colonization of HTF and an increase on success of environmental restoration practices of highly saline areas.

The ability to buffer the negative conditions by developing nutrient pools to overcame the salinity (as K^+ and NH_4^+), associated to the capacity of allocating resources by physiological integration, probably are the two main factors that explain success of these species on HTF system. The physiological integration means that stolon and rhizome connections allow translocation of resources and other substances between connected ramets growing in soil patches differing in quality (e.g. Hartnett and Bazzaz 1983; Slade and Hutchings 1987; Alpert 1999; Saitoh et al. 2002). The connection of ramets has been suggested as a mechanism of toxic dilution by the redistribution throughout the clonal system, with the consequent reduction of toxicity (Roiloa and Retuerto 2006b). This mechanism has also been suggested as a component of the resistance of halophytes to salt stress (Larcher 1995), and could also contribute to explain the growth of clonal plants in the hypersaline conditions of our study.

1.4.3. Seasonal effects on soil properties

The water regime condition and flooding events are highly important in the formation of HTFs and its soils (Marius, 1985 and Sadio 1989).The heterogeneity of the climatic system and physical settings in arid tropical environments produce a vegetation pattern more variable and less predictable (Bridgewater and Cresswell 1999).

The typical concentration of rainfall rates during a limited number of months (Figure 1) and the low frequency of tidal flooding (only twice a month during the spring tides; Albuquerque et al. 2014a) directly affects the dinamic of soil properties and plant-soil interactions (figure 6C).

Soil parameters such as pH, Eh, EC and amount of cations were significantly ($p<0.05$) affected (Figure 3, 4 and 6C) by these changes in the freshwater influx during the wet season.The long period without fresh water input by rainfall associated with the to the high evapotranspiration during the dry season (Medina et al. 1989; Hadlich et al. 2008; Albuquerque et al. 2014b) and topographic position (which rule the tidal flooding frequency) are related to the modification of soil properties and mainly to the intense salinization the environment .

The increase of saline conditions, high availability of soluble cations and more label iron forms (F1, F2 and F4) during the dry season (Figure 5 and 6) are caused because they are not efficiently removed from the system. The water input on the system during the wet season decreases the salinity condition, as reflected by the lower EC values and mobilizes more exchangeable cations from soils (Figure 6).

One interesting tendency noted in our results was that HTF plants not only are capable of significatly decreasing pH, but they also keep it stable through the seasons (Figure 3). So, despite the significant changes in the pH of bulk soils between seasons (Figure 3), on rizosphere, the environment is kept more stable by roots, even with the changes on water avalability in the system. In this sense, the pH dynamics in the studied bulk soils seems more related to seasonal effects. On the other hand, on rhizospheres, our study points to a combined effect of cations-anions exchange (mainly related to nitrogen abundance and its dynimcs) and redox-coupled process (mainly related to flooding events). But futher research should evaluate other possible processes gcoverning acid-base conditions in these environments; like respiration rates of roots and microorganims.

The oxidation-reduction potential can be easily affected by the dynamics of water in wetland systems and by root respiration (Chung and Zasoski 1994). The water input in HTF is very low compared to other coastal wetlands because normally is only related to spring tides, drainage of adjacent continental areas (Albuquerque et al. 2014a) and rainfall increase during wet seasons. At the studied area the oxidation-reduction potentials were always positive (around +200mV), indicating that HTF are under a suboxic to oxic condition. The changes in the redox conditions, were not striking but enough to result in the prevalence of the amorphous forms of iron formed by the oxidation of Fe^{2+} (figure 5), also registered by Albuquerque *et al*. (2014a) in other HTFs on Ceará state. It is important to highlight that these processes are incipient, but indicates the importance of season effects, mainly related to water avalability and iron dynamics. The significant difference of iron content between seasons probably indicates a redistribution of iron in the system, with losses during the wet season and increasing oxidation during dry season.

1.5. Conclusions

Almost all studied chemical soil properties of HTF were affected by seasonal changes or by plant influence. This characterizes the HTF as a heterogeneous system highly influenced by water availability and by plants that are able to survive under the existent hypersaline conditions.

Comparing bulk and rhizosphere soils it is possible to conclude that plants were able to modify the rhizosphere soil in their benefit. Through pH and redox mediated process, plants increase the contents of some nutrients that could be related to their survival under hypersaline conditions. Each plant is associated to a different soil resource, which is probably related to their physiological requirements and metabolism. For example, Bm and Bp where related to NH_4^+, but Bm even more to organic matter, while Sv highly related to soluble cations (such as K^+ and salinity). NH_4^+ and K^+ are ions that have been indicated as facilitators for clonal plants in these highly saline environments. However, due to the limited availability of studies on the nutritional and physiological needs of the studied plants, these ideas are hypothesis that can be tested in the future and that would also improve the success of environmental restoration activities in salt affected soils.

Season effects are extremely important to soil dynamics in HTF, mainly because it rules the fresh water input and thus affects the dynamics of cations, EC, pH and Eh. Despite the fact that rhizosphere soils were more affected by these seasonal changes, the plant action tended to keep the rhizospheric environment less variable trough seasons. This result suggests that the combined action of seasonal changes and plant action rule most of the biogeochemical processes in HTF, but also that plants had the capacity to change the soil conditions to improve their development.

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CHAPTER 2

Bioturbation effects of two species of land crabs on soil properties of hypersaline tidal flats

(Efeitos da bioturbação em duas espécies de caranguejos nas propriedades dos solos de apicum)

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Resumo. Crustáceos decápodas estão entre as mais importantes espécies do manguezal e sistemas ecológicos associados como o apicum. Nos apicuns brasileiros *Ucides cordatus* e *Cardisoma guanhumi* são facilmente encontrados. Essas duas espécies de caranguejos representam um importante recurso pesqueiro e são consideradas espécies-chaves no manguezal. Considerando a importância ecológica do *U. cordatus* e do *C. guanhumi,* tomou-se como hipótese que essas espécies coideriam afetar as condições biogeoquímicas nos solos de apicum. Para testar essa hipótese, um experimento de campo foi instalado nas áreas de prdominância de cada espécie. Nessas áreas, uma zona de exclusão foi montada e mantida por 9 meses. Posteriormente, as amostras de solos foram coletaas numa profundidade de 0-60cm e avaliadas para for Eh, pH, CE, conteúdo de C, N and S totais e ferro livre utilizado-se métodos padrões. Todas as amostras de solo apresentaram textura fina, condições hipersalinas e pouco conteúdo de matéria orgânica. Os dados resultam que ambos os caranguejos afetam significaivamente ($p<0.05$) a maioria das propiedades de solo avaliadas nessse estudo.Entretanto, cada caranguejo foi asociado a diferentes propriedades de solo e seu comportamnento de escavação afetou o solo de maneiras distintas. Esses refeitos refletem seu comportamento e história de vida.

Palavras-chave: escavação por caranguejos, biogeoquímica, engenheiros de ecossistema, *Cardisoma guanhumi*, *Ucides cordatus*

Abstract Decapods crustaceous are among the most important fauna to mangroves and associated ecological units, as hypersaline tidal flats (HTF). At the Brazilian HTF, the crabs genders *Uca*, *Ucides* and *Cardisoma*, these last two are critical fishery resource and key species to mangrove ecosystem. Considering *U. cordatus* and *C. guanhumi* ecological relevance, we hypothesized that their bioturbation could affect the biogeochemical conditions of HTF soils. To test this hypothesis, a crab exclusion experiment was conducted during eitght months and, then, the soil samples were collected at three different sites: a control site without crabs influence and sites occupied by *U. cordatus and C. guanhumi*. The soil samples were collected from 0 to 60cm and were evaluated for Eh, pH, EC, total C, N and S contents and iron content using standard methods. All soils presented fine texture prevalence (silt and clay) with hypersaline and oxic conditions, and low content of organic matter. Data show that both *U. cordatus and C. guanhumi* significantly ($p<0.05$) affect most studied soil properties (mainly pH, Eh, total N, total C and some iron fractions). However, the studied crabs were not associated with the same soil properties neither their behavior affected the soil in the same way, as a reflect of their behavior and life history.

Key words: burrowing crabs, biogeochemistry, ecosystem engineering, *Cardisoma guanhumi*, *Ucides cordatus*

2.1. Introduction

Hypersaline tidal flats (HTFs), locally known as “apicum”, are tropical ecological systems characterized by highly saline soils, connections with mangrove ecosystem and, sometimes, with dryland areas (Lebigre 2007; Albuquerque et al. 2014b). Those connections between adjacent ecosystems can happen through water, sediments, nutrients and organic matter fluxes, and also by animal population movements (Tomlinson 1986; Kjerfve 1990).

The HTFs offer habitat for different fauna and flora species (Albuquerque et al. 2014a) and represent strategic areas for mangrove expansion in case of environmental changes or sea level rise (Lacerda et al. 2007). Crabs as *Uca spp*., *Ucides cordatus* (Linnaeus, 1763) and *Cardisoma ganhumi* (Latreille 1828) uses areas for refuge, protection, and food resources. Additionally, birds and mammals are regular visitors of the HTFs.

C. guanhumi is one of dominant species (Firmo et al. 2012) in the HTFs and the presence of *Ucides cordatus* is mainly related to shaded areas by mangrove trees (Nascimento, 1993; Schmidt 2006). The role of *U. cordatus* and *C. ganhumi* activity and ecological importance for mangrove ecosystems have been extensively reported (Smith et al. 1991; Thongtham and Kristensen, 2003, Ferreira et al., 2007, Araújo-Júnior, 2010). However the importance of HTF areas to development of *C. guanhumi* and *U. cordatus* effects on HTF systems and the strategic importance of these areas for the species development remain poorly known.

C. guanhumi and *U. cordatus* have demonstrated great ecological and economic importance as fish resource. However, the combination of indiscriminate capture of crabs for food markets (Govender et al. 2008, Rodríguez-Fourquet and Sabat 2009; Pinto et al. 2010; Shinozaki-Mendes et al. 2013) and loss of habitat (mostly to aquaculture; i.e. shrimp farming, Pinto et al. 2010) included these species on the overexploited species list (Brasil, 2004). Based on the status of the species, decrease of natural habitats over the years and in a scenario of climate changing and increasing of sea level, a better understanding of ecological functions of crabs in different coastal lands can offer an improvement of conservation policies.

Most crabs have been considerate as “ecosystem engineers”. They are among species that modulate the availability of resources by promoting physical changes on the soil system, modifying, maintaining and/or creating habitats, changing the quality, quantity and distribution of resources utilized by other species (Jones et al. 1994, 1997; Kristsen 2008). The burrowing crabs can promote a biological reworking of soil and sediments (e.g. by ingestion, locomotion, transportation) causing significant implications on soil and landscape formation, and biogeochemical processes (Meysman et al. 2006). These modifications can include the nutrients dynamic, mineralization of organic matter and fluxes of water and oxygen (Jones et al. 2006; Maire et al. 2008).

We hypothesized that, being the HTFs soils naturally stressful environment, the effect of burrowing crabs can change the biogeochemical conditions of soils. So, we aimed to verify the possible changes that largest crabs found in HTFs (*Ucides cordatus* and *Cardisoma guanhumi*) can promote on soils. If it happens, evaluate if these modifications are similar comparing the two crabs effects. In these sense, there were selected different sites with and without crabs (isolated experimentally) where soil samples were collected and evaluated for pH, Eh, EC, Total C, Total N, Total S and free iron fractions.

2.2. Material and Methods

2.2.1. Study site description

The study area is located at the Jaguaribe River estuary (4°28’44’’ S - 37°46’44’’ W, Ceará State, NE-Brazil). The area is inserted at semiarid Northeast coast, where mean temperatures vary between 26 and 28^{o}C during the year (FUNCEME/IPECE 2012). The rainfall is distributed in two distinct seasons: wet from January to May (mean maximum of 237.8mm) and dry from June to December (mean maximum 47.7mm) (Leite et al. 2013). The tidal regime ranges between 1.4 and 2.6m (Tanaka and Maia, 2006).

Hypersaline tidal flats can be easily detected at the Jaguaribe estuary (Figure 1). However many of them were converted in aquaculture tanks (Araujo et al. 2012) or are often used as pasture for cows and goats (Albuquerque et al. 2014). To minimize external influences, the study was performed in a 1.4 hectare HTF surrounded by mangrove (consisting in an internal HTF, according to Lebigre 2007) and at the most isolated and well-conserved area (Figure 1).

The native vegetation of the studied HTF consists of clonal halophytes plants (e.g. *Batis maritma*, *Blutaparon portulacoides* and *Sporobolus virginicus*) and some isolated young individuals of *Avicennia sp.* and *Conocarpus erectus.* The plant density in the area varies according to the season and rainfall input, covering the area during the rainy seasons or presenting the typical patch distribution found in HTFs.

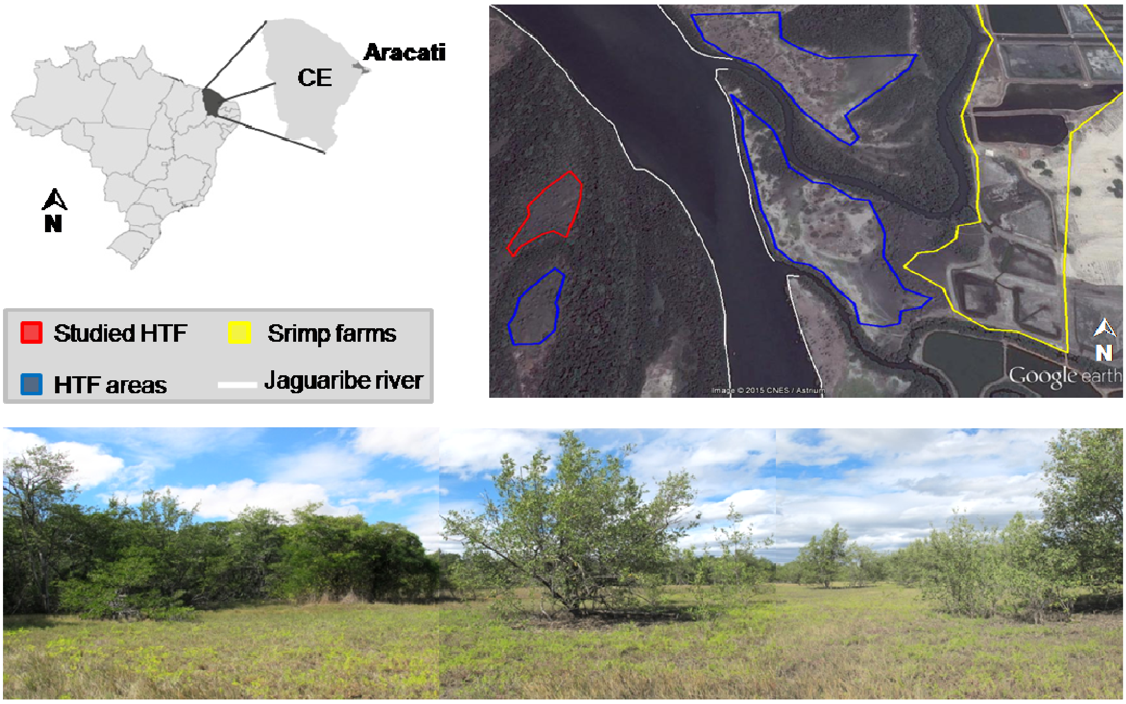

Figure 1. Study site location map (Jaguaribe River estuary, Aracati, Ceará state, Brazil). Aerial photography of Jaguaribe estuary, where is possible to distinguish the Studied area (red); other HTF in the surroundings (blue); shrimp farms (yellow); the mangrove forests and dunes. Bellow a panoramic view of the sampling area during the rainy season.

2.2.2. Studied crab species

Ucides cordatus (figure 2A) is a semi-terrestrial crab, considered one of the most abundant species found in the American mangroves, regarding biomass and diversity (Smith and Diele 2008, Oliveira et al. 2013). An individual of *U. cordatus* is considered a sexually mature adult when it presents a carapace width of 60 mm or more (Pinheiro and Fiscarelli, 2001; Leite et al., 2006). Males may reach carapace width up to 80 mm (Leite et al. 2013). Both in mangrove and HTF environments *U. cordatus* is a sympatric species of *Uca* spp. and other crabs (Smith and Diele, 2008), but a co-occurrence with *Cardisoma guanhumi* is only reported in the HTF areas (Schimidt, 2006).

The *Cardisoma guanhumi* (Latreille 1828) or “land crab” (figure 2B) is usually associated with different environments in estuaries: mangroves, muddy shores, brackish low-lying areas (Govender et al. 2008), dry forests commonly found near to estuaries (Firmo et al. 2012, Oliveira-Neto et al. 2014) and HTF (Firmo et al. 2012) and other flat areas (Oliveira-Neto et al. 2014). The adults males are larger than females and can weigh 500 grams, with maximum carapace widths around 49 to 100 mm (Gifford, 1962; Silva and Oshiro, 2000; Shinozaki-Medes et al. 2013). Usually, the species is indicated as sympatric of several *Uca* species (Gifford, 1962) and has mammals of *Procyon* genus as a natural predator (Gifford, 1962; Firmo et al. 2012).

2.2.3. Sampling procedures

Sampling sites were located in areas predominantly occupied by a single crab species (UC: *Ucides cordatus* or CG: *Cardisoma guanhumi*). The populations of crabs were concentrated in different physiographic positions: UC located at the limit between mangrove and HTF areas, and CG at an innermost, higher and dryer site (figure 2).

One exclusion zone was constructed in each area of crab dominance. This area was called as “control site” and was established in areas selected to avoid interference from plant activity (absence of pneumatophores, prop roots, grass, and halophytes). An area of $0.5 m^2$ was fenced off from the surroundings and covered on top with nylon nets (1 cm mesh, 1 m in height, and buried to a depth of 1.2 m) to eliminate crab burrowing activity (figure 3 A to C) (similar as done by Araujo et al. 2012). The control site were installed during the dry season (December 2012) and sampled after wet season (August 2013) (Figure 3 D and E) when both crab species are more active (Firmo et al. 2012). The soil sampled from the control site was used to compare with those sampled at “bioturbated sites” (natural HTF areas where crabs freely burrow and moves).

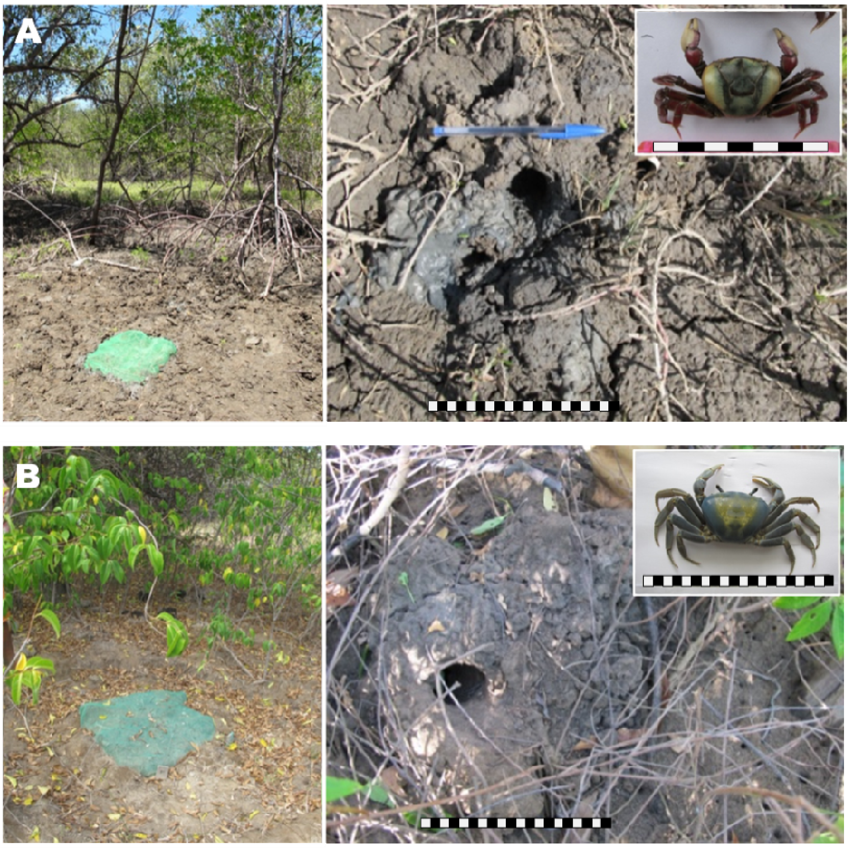

Figure 2. Both crab species and their respective bioturbated and control site. (A) *Ucides cordatus*; (B) *Cardisoma guanhumi*. Black and white stripes with 1 cm each.

After an isolation period of eight months, what included dry and wet seasons, the soil samples of control and bioturbated sites were collected. When the soil humidity was high enough to allow the insertion soil auger, the soil were collected with PVC tubes (50 mm in diameter and 50 cm in length). At dryer lands only soil inox auger (figure 3 F) was used.

Six cores were collected within each plot in four depths (0-10; 10-20; 20-40; 40-60 cm), three inside the control site and three surrounding the control site, with a minimum distance of 50 cm between the sampled point and the control. The tubes were hermetically sealed, and the augered samples were individually stored, placed into a portable cooler at ~5˚C and transported to the laboratory.

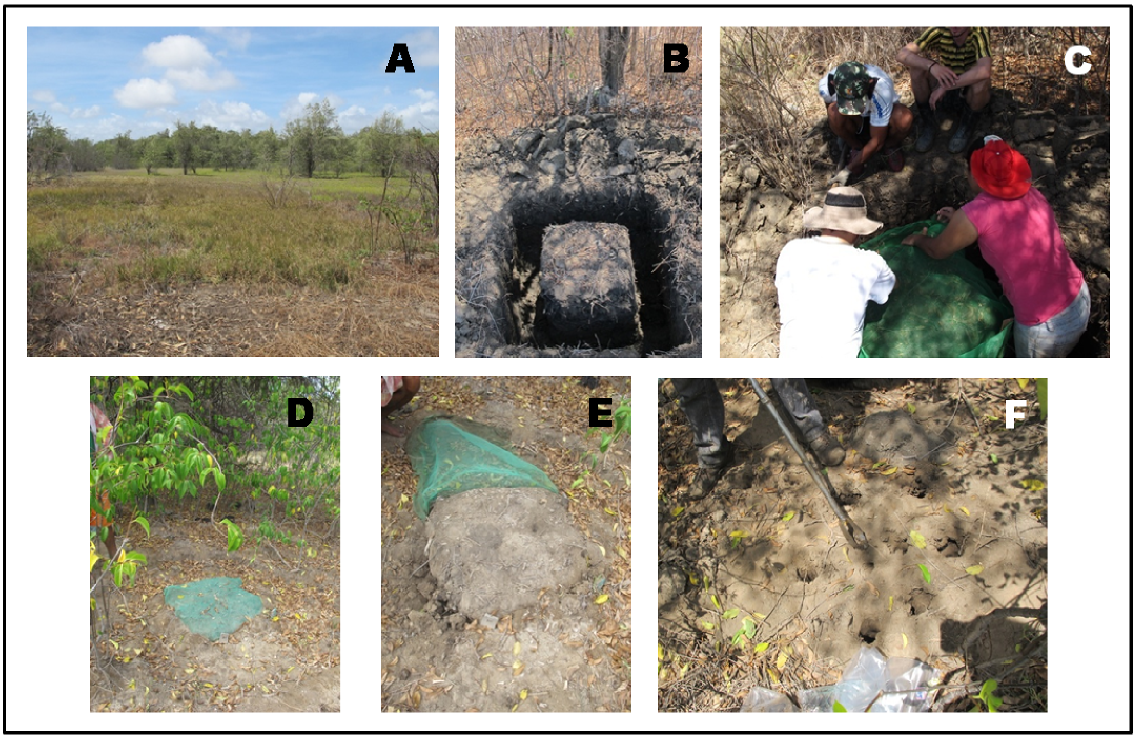

Figure 3. (A) General view of CG bioturbated site were sampled; (B) and (C) burrow and fencing off the CG; (D) Experiment after eight months of exclusion; (E) opening the exclusion area (control site); (F) soil sampling using a inox auger. Only three of those holes in the picture represent the soil sampling points, the others two represent failed attempt.

The redox potential (Eh) values of soil samples were measured using portable electrodes, after equilibrating for ~2 min, during the sample collection or immediately arrived in laboratory (PVC sampler samples). Probes were inserted in the center of each core to avoid contact with the atmosphere. The Eh was measured in the field using a platinum electrode and the final readings were corrected by adding the potential (+244 mV) of a calomel reference electrode.

2.2.4. Analytical procedures

In the laboratory, dried sub-samples were used for the determination of pH, EC and total C, total N and total S, whereas sub-samples were frozen for posterior analysis (see bellow). The pH (in water; 1 solid: 2.5 liquid ratio) was measured with a glass electrode calibrated using pH 4.0 and 7.0 standards. The electrical conductivity, used to characterize the salinity condition, was obtained using 10 g dried samples were taken in a 1:5 suspension (soil: liquid) (Sylla et al. 1995). Total C, N, and S were determined with an auto-analyzer (LECO CNS-2000 Corp., St. Joseph, MI, USA).

The grain size composition was determined by pipette method using a combination of physical (overnight shaking) and chemical (0.015 M $(NaPO_3)_6$ + 1.0 M NaOH) dispersal methods (Gee and Bauder 1986). Before the dispersion, the samples were pretreated with H_2O_2 (30%) to promote the oxidation of organic matter with and soluble salts were removed (with 60% aqueous ethanol) until the silver nitrate test indicates the absence of chlorides.

Additionally, a partitioning of solid-phase Fe was performed using fresh samples based on a combination of methods (Tessier et al.1979; Huerta-Díaz e Morse 1990; Fortín et al. 1993), which enables the identification of six operationally distinct iron fractions, defined as follow:

(F1) *Exchangeable and soluble Fe*, extracted with $MgCl_2$ 1M (pH 7; 30 min. agitation);

(F2) *Iron associated to carbonate* extracted with NaOAc 1M (pH 5; 5 hours agitation);

(F3) *Iron associated to ferrihydrite* extracted with hydroxylamine 0.04M + acetic acid 25% (6 h agitation at 30 ºC);

(F4) *Iron associated to lepidocrocite* extracted with hydroxylamine 0.04M + acetic acid 25% (6 h agitation at 96 ºC);

(F5) *Iron associated to crystalline oxyhydroxides* extracted with sodium citrate 0.25 M + 0,25M + sodium bicarbonate 0.11M + Sodium dithionite (30 min. agitation at 75 ºC);

(F6) *Iron associated to Pyrite* (pre-treatment with 10 M HF and concentrated H_2SO_4) extracted with $HNO_{3.}$

For further details, please see Albuquerque et al. (2014b); Nóbrega et al. (2014); Otero et al. (2009).

The reactive iron (FeR), which represents the Fe that can be reduced and incorporated into pyrite, can be assessed as the sum of the fractions 1 to 5 (i.e., $\sum F1 \rightarrow F5$). Additionally, the degree of piritization (DOP) was calculated as: DOP (%) = F6 / (FeR + F6), which determines the percentage Fe incorporated into the pyritic fraction, allowing the comparison of pyrite content in soils with different FeR contents (Berner 1970).

2.2.5. Statistical data analysis

Analyzes were performed with the software SPSS version 21 (SPSS Inc. Chicago, IL). Non-normal data were log-transformed to fit conditions of normality and homogeneity of variance. To test the effects of bioturbation on soils and compare the depth and areas (control and bioturbated) a two-way analysis of variance (two-way ANOVA) was performed. To compare the possible differences between crabs effects on soil we use a one-way ANOVA was performed.

Moreover, a discriminant analysis (DA) was performed in order to develop a function that results in an optimal differentiation (maximize the variance) among the crab species; among control and bioturbated site; and layers (0-10; 10-20; 20-40; 40-60 cm), identifying the most relevant variables for the groups distinction.

2.3. Results

A general evaluation of data, it was observed that environmental conditions (Eh and pH) of bioturbated areas related to *Ucides cordatus* (UC) were significant different from bioturbarted areas of *Cadisoma guanhumi* (CG) (ANOVA 1-way; $p<0.05$) (Figure 4; table 1). These differences were also registered for iron oxyhydroxic fractions (F4 and F5). However, neither nutrient content nor saline conditions were registered differences among areas.

The comparison between control areas of UC and CG crabs indicated that, besides the difference in environmental conditions (Eh and pH) and iron forms (F4 and F5), total C and total S were significant different among areas (ANOVA 1-way; $p<0.05$) (Figure 4; table 1).

Table 1. Differences between crabs effects on soil properties of control and bioturbated sites. Samples were evaluated by one-way ANOVA. SS, sum of squares; DF, degrees of freedom; F, F-distribution value; *P*, *P* value.

	Control site (UC x CG)				**Bioturbated site (UC*CG)**			
	DF	SS	F	P	DF	SS	F	P
pH	1	16.54	249.7	**<0.001**	1	13.37	4.85	**0.036**
Eh	1	83677.89	66.1	**<0.001**	1	10250.67	8.53	**0.008**
EC dS/m	1	0.00	0.0	0.999	1	1.42	0.04	0.839
N%	1	0.00	3.2	0.087	1	0.00	0.23	0.64
C%	1	1.50	9.2	**0.006**	1	0.05	0.06	0.803
S%	1	0.002	11.1	**0.003**	1	0.00	2.95	0.098
F2 (µmol g-1)	1	0.04	0.3	0.575	1	0.08	0.84	0.391
F3 (µmol g-1)	1	14.32	2.6	0.119	1	0.19	0.33	0.568
F4 (µmol g-1)	1	628.59	4.0	**0.049**	1	4939.94	14.27	**<0.001**
F5 (µmol g-1)	1	1171.30	8.7	**0.007**	1	1256.56	9.79	**0.005**
F6 (µmol g-1)	1	5.94	2.4	0.133	1	60.18	1.67	0.21
Dop (%)	1	9.51	3.0	0.095	1	3.07	0.58	0.456

2.3.1. Soil properties of *Ucides cordatus* sites and bioturbation effects

The areas where *Ucides cordatus* (UC) were distributed (bioturbated areas) presented fine texture, with predominance of silt (45%± 2.8), pH values near to neutral (~7.0), suboxic conditions throughout the soil profile and salinity rates (based on EC) around 26.2±5.4dS m^{-1} (figure 4). Total N, total C and total S presented very low contents and did not range 1% (figure 4). The dominant iron forms in UC areas were poorly crystalline Fe (F4) and crystalline Fe forms (F5) (respectively 61.2±15.6µmol g^{-1} and 43.9±10µmol g^{-1}, mean values; figure 5). The iron associate to pyrite was very low and rarely get over 1µmol g^{-1} (0.46±0.43µmol g^{-1}, mean values).

UC crabs control and bioturbated sites showed a strong overlap by discriminant analysis (DA; figure 6). These areas were mostly related to crystalline iron forms (F3, F4 and F5), pH and total S. Besides, except for total N and pyrite iron any significant difference among soil sampled from control and bioturbated site were registered

(ANOVA 2-way; $p<0.05$) (figure 4 and 5; table 2). The rates of total nitrogen and pyritization are very low still (rarely over 1%) in both areas (figure 4 and 5). However, the differences observed in F6 fractions among studied areas signalize a almost complete pyrite iron on soil in absence of crab burrowing.

In depth, the pH of control site presented no clear pattern, while in bioturbated site the condition seemed to become slightly acid and regular. The total N and total C presented significant variation among soil layers (ANOVA 2-way; $p<0.05$) (figure 4; table 2). However, it was not possible to assume these changes are only related to crab burrowing due the strong significance of interaction observed on ANOVA 2-way test (table 2).

2.3.2. Soil properties of *Cardisoma ganhumi* sites and bioturbation effects

The areas where *Cardisoma ganhumi* (CG) were found soils were oxic, slightly acid (pH of 6.4±0.2, mean values) and hypersaline 28.7±6.1dS m^{-1} (EC mean values) conditions (Figure 4). The soil presented fine texture with similar amount of silt (38%±3) and clay (37%±1). Total N and S, presented low contents and did not range 1% (figure 4).

The bioturbated site samples were clearly separated from control site by discriminant analysis (DA, Figure 6). At the control site (figure 4), pH, Eh, total C, total N and some iron fractions (F3, F4 and F5) were significant different (ANOVA 2-way; $p<0.05$) (table 2) from bioturbated site. The pH values decreased up to 5.6±0.2 (mean values), becoming more acid than the bioturbated sites. Total C and total N values were higher in bioturbated sites.

Most iron fractions were significantly different from another, and it is clearly observed when free iron values (the sum of all studied fractions) are compared among areas (figure 5). A predominance of iron oxyhydroxides (F4 and F5 fractions, mainly) were registered in both areas, but on the control site, F5 fraction were two times higher than the values obtained for the bioturbated site.

In both studied areas was observed the higher content of C, N and S in superficial layers (0-20 cm) which decrease in depth (figure 4). Despite a low pyritic iron (F6) and DOP values in both areas, a tendency of this fraction iron distribution through the soil profile were different in the presence of crabs.

Table 2. Effects of bioturbation on soils in depth. Samples were evaluated by two-way ANOVA. SS, sum of squares; DF, degrees of freedom; F, F-distribution value; *P*, *P* value. D*S: Depth*Site.

		Ucides cordatus (sites * depth)				*Cardisoma guanhumi* (sites * depth)			
	Source of Variation	DF	SS	F	P	DF	SS	F	P
pH	Site	1	0.0002	1.3	0.271	1	3.48	46.3	**<0.001**
	Depth	3	0.0014	3.6	**0.041**	3	0.26	1.2	0.36
	Site x Depth	3	0.0002	0.5	0.665	3	0.15	0.7	0.586
Eh	Site	1	2542.4	3.1	0.099	1	7383.8	8.6	**0.011**
	Depth	3	6264.4	2.6	0.096	3	697.4	0.3	0.845
	Site x Depth	3	2362.1	1.0	0.436	3	4624.2	1.8	0.193
EC dS/m	Site	1	11.7	0.3	0.599	1	33.1	0.6	0.437
	Depth	3	98.9	0.8	0.506	3	211.5	1.4	0.293
	Site x Depth	3	89.5	0.8	0.545	3	75.7	0.5	0.698
N%	Site	1	0.1	8.9	**0.011**	1	0.001	4.9	**0.047**
	Depth	3	0.4	11.6	**<0.001**	3	0.03	33.2	**<0.001**
	Site x Depth	3	0.1	4.1	**0.031**	3	0.004	5.5	**0.013**
C%	Site	1	0.02	3.6	0.083	1	0.01	0.7	**0.41**
	Depth	3	0.1	5.1	**0.016**	3	0.854	17.4	**<0.001**
	Site x Depth	3	0.1	4.2	**0.031**	3	0.06	1.3	0.325
S%	Site	1	0.004	0.4	0.546	1	0.0009	7.2	**0.02**
	Depth	3	0.03	1.0	0.45	3	0.003	7.1	**0.005**
	Site x Depth	3	0.02	0.6	0.627	3	0.001	2.9	**0.08**
F3 (µmol g-1)	Site	1	11.5	2.6	0.13	1	3105.6	32.0	**<0.001**
	Depth	3	29.8	2.3	0.131	3	1113.2	3.8	**0.034**
	Site x Depth	3	29.8	2.3	0.13	3	946.1	3.2	**0.054**
F4 (µmol g-1)	Site	1	62.5	0.3	0.572	1	3105.6	32.0	**<0.001**
	Depth	3	777.4	1.4	0.288	3	1113.2	3.8	**0.034**
	Site x Depth	3	104.1	0.2	0.904	3	946.1	3.2	**0.054**
F5 (µmol g-1)	Site	1	59.8	0.7	0.424	1	203.5	3.4	**0.088**
	Depth	3	144.2	0.6	0.656	3	292.1	1.6	0.23
	Site x Depth	3	336.4	1.3	0.325	3	105.4	0.6	0.63
F6 (µmol g-1)	Site	1	14.2	10.0	**0.01**	1	9.3	1.4	0.264
	Depth	3	3.5	0.8	0.515	3	10.6	0.5	0.674
	Site x Depth	3	8.2	1.9	0.188	3	5.7	0.3	0.838
DOP	Site	1	9.1	5.2	**0.046**	1	163.7	7.649	**0.02**
	Depth	3	1.4	0.3	0.845	3	89.9	1.406	0.298
	Site x Depth	3	13.0	2.4	0.124	3	46.1	0.72	0.562

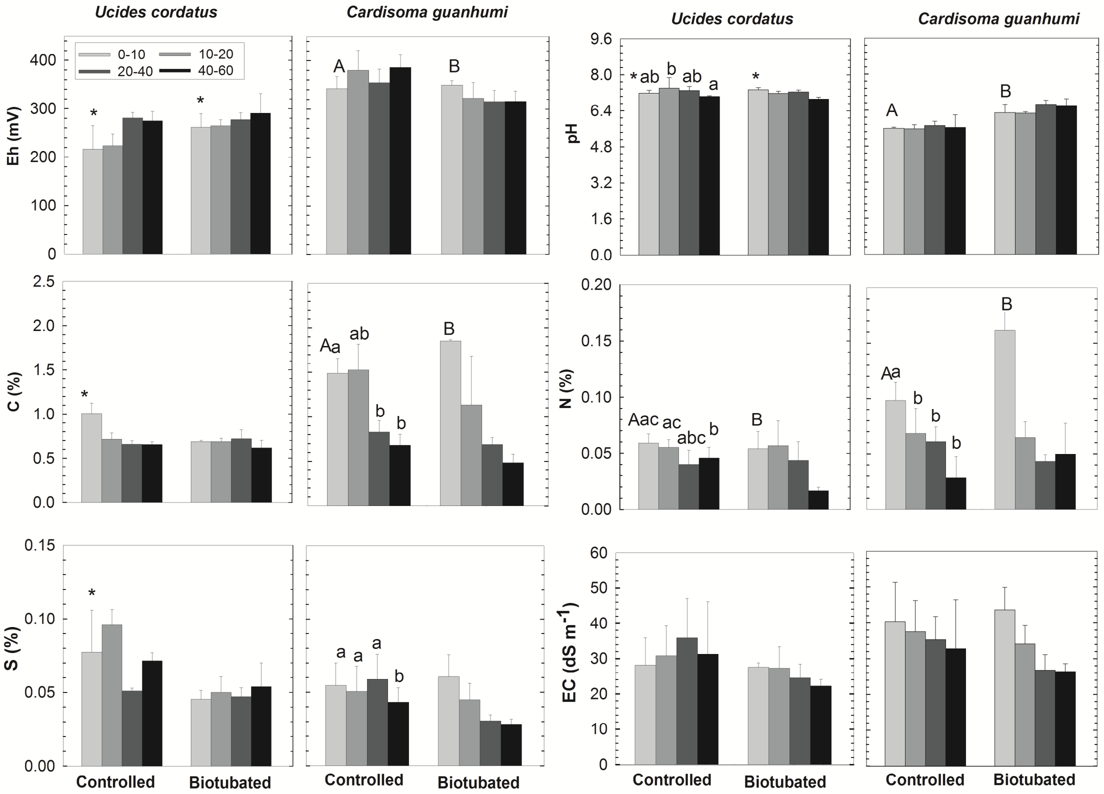

Figure 4. Soil properties from bioturbated and control site under action of *Ucides cordatus* and *Cardisoma ganhumi*. Different letters indicates significant differences (n=4; $p<0.05$) between layers and (*) significant differences between sites (bioturbated and control).

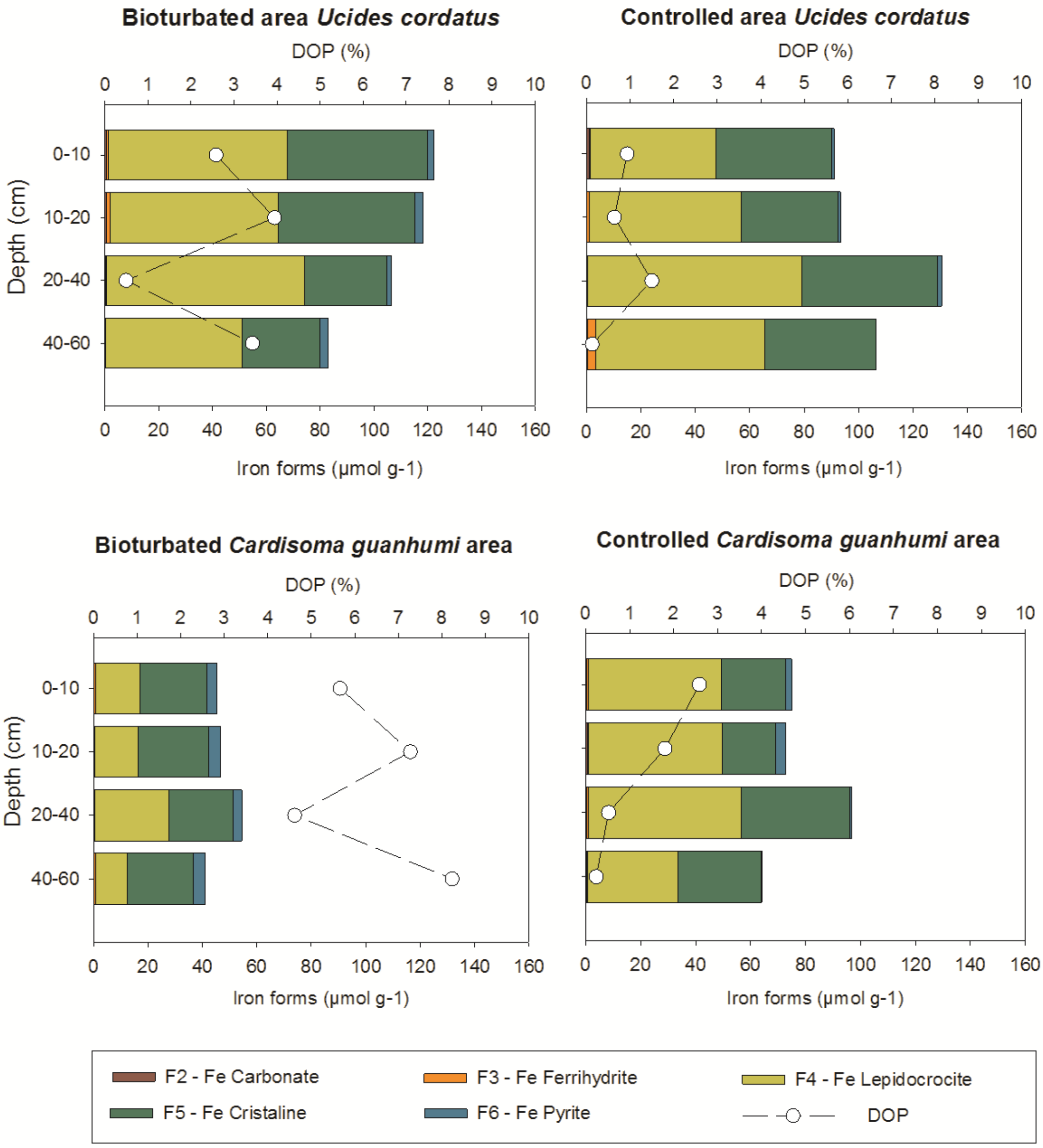

Figure 5. Iron fractions obtained in sequential extraction for the control and bioturbated site under the action of two crab species. The fraction F1 did not range the minimum detection limit.

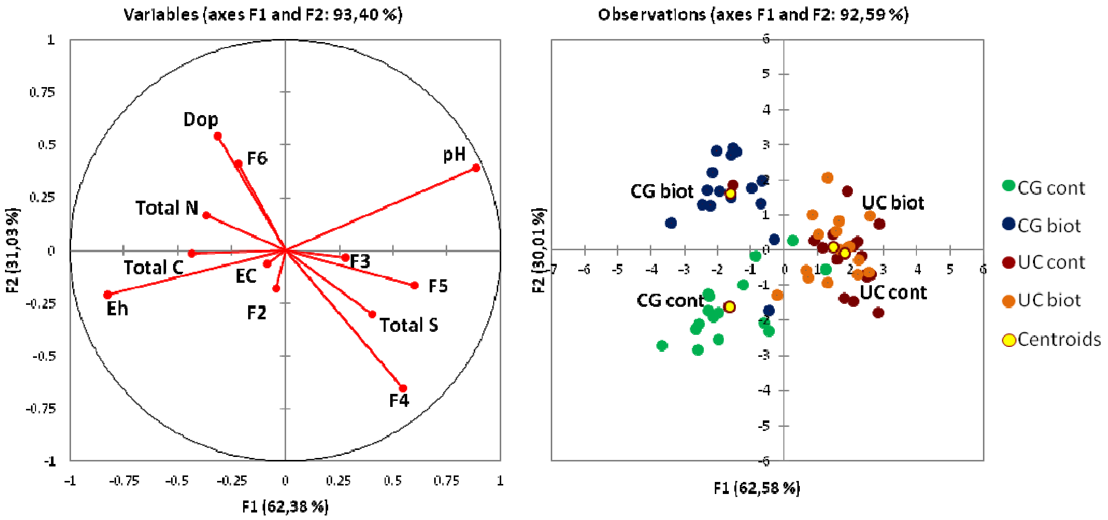

Figure 6. Discriminant analysis to compare soil properties of UC and CG bioturbated (UC biot and CG biot) and control site (UC cont and CG cont). EC: electrical conductivity; C, N and S (%): total contents; F2: Fe bound to Carbonate; F3: ferrihydrite Fe; F4: lepidocrocite Fe; F5: Crystalline Fe; F6: Pyritic Fe; DOP: Degree of Pyritization.

2.4. Discussion

2.4.1. *Ucides cordatus* bioturbation effects

There were not registered great differences among UC crabs control and bioturbated sites, what suggest that slight modifications done by the crabs could be enough to change the system. The modifications on pH, total N, total C and iron fractions (Figure 4 and 5; table 2) on these soils could be influenced by bioturbation activity but also as result of the environment heterogeneity.

The densities of UC individuals in mangrove forests have been associated with water level, drainage conditions (Alves and Nishida, 2004; Hattori 2006) and soil humidity/salinity (Alves and Nishida, 2004; Hattori 2006; Nordhaus et al. 2009). Temperature, vegetal covering, rooting, tidal flooding, interstitial water (Goes et al. 2010), soil particles size (Goes et al 2010; Gomes et al. 2013) and litter availability (Nordhaus et al 2009) also seem to have influence on population densities.

UC crabs were found in areas with a prevalence of fine textured soils, dominated by clay and silt-sized particles (clay/silt/sand proportion of 42.8%, 44%, and 13.2%; mean values trough soil profile). According to Goes et al. (2010) soils with low texture are preferably colonized by crabs since are easier to dig, although it provide less stable galleries. UC burrows are usually found near to the vegetation what can improve the construction stability. In mangroves, it is known that is a strong correlation between UC distribution with sediments fractions, once crabs were more abundant where there was a prevalence of silt fraction (Gomes et al. 2013) and seems the same to HTF areas inhabited by them. This behavior could be part of an ecological strategy to select low energy environments to construct their burrows, even if favors the accumulation of fine particles inside the burrow (Botto and Iribarne 2000).

The strong relation of *Ucides cordatus* with iron fractions associated to oxy-hydroxides (Figure 6) suggests the importance of oxic conditions to this species. It is knonw that UC crabs create an oxic environment in mangroves due to colonizing the soils, which are normally anoxic and reduced environment (Araújo et al. 2012). The aeration (Nordhaus et al 2009) and increased oxygenation on sub-superficial layers of mangrove soils related to crabs burrowing activity was already reported for mangrove (Jones, 1984; Ferreira et al 2007; Kristensen, 2008; Gutiérrez, 2008) and salt marsh (Montague, 1982; Bertness, 1985; Nomann and Pennings, 1998), and are mainly related to the opening of channels. HTFs are naturally oxic environment than mangroves and at the transitional point between these two systems the crabs can find good conditions to start their development. In these boarders they are not so exposed to high temperatures as central sites and, where maybe, they find less competition for resources than mangrove forests.

Besides no significant difference in F4 and F5 fractions among control and bioturbated sites were observed, their prevalence on soils colonized by UC could indicate water flux and redox changing conditions. When comparing the control site with the bioturbated site, it was noteworthy the prevalence of iron associated to oxyhydroxides and the decrease of reduces iron (F6 fraction or pyrite iron) through the soil profile (figure 5). The crab presence seems to affect the humidity condition through the soil profile, allowing the presence of reduced iron even at smaller depth.

The hydromorphism could be accentuated because of burrowing habits and the form of the burrow. It is known that UC adults can construct burrows with 0.6 to 2.0m deep (Costa, 1979; Nascimento, 1993; Nordhaus et al. 2009) where day spend about 52% of their time during the day (Nordhaus et al. 2009). During the other part of the day, these crabs are feeding or maintaining burrows (Nordhaus et al. 2009), since they have to remove part of sediments transported by the tide into the interior of the burrow (Botto and Iribarne 2000). By doing so, they probably bring along, in a bottom-up movement, humidity and reduced soil materials from deeper layers, where is possible for them to find buried mangrove soils (Albuquerque et al. 2014), which are more humid and/or the water table itself.

2.4.2. *Cardisoma ganhumi* bioturbation effects

There are several types of HTFs (Lebigre 2007), but in Brazil these areas are mostly located between coastal tablelands and mangroves (Albuquerque et al. 2014). Considering the ecological need of CG individuals to build their burrows and this intermediate configuration, the crabs transit and colonize the best spots in both areas, at the limits of the tableland and HTF, amplifying their possibilities of territory.

At the studied HTF most CG burrows were found near to trees and lianas and rarely in grass and halophytes areas (Figure 1). Oliveira-Neto et al. (2014) comparing forest and grassy areas found most of the CG population in a rain forest fragment near to one of water channels, among many species of trees and lianas. According to their study, the population in the forested site had a higher density and high average size of burrows compared with grasslands, mainly because at grassy areas the temperature could be higher and more variable, but also due to the restricted access to ground water (Govender et al., 2008).

The development of CG and its sexual maturation seems to be related to some environmental parameters such as air temperature, relative humidity, luminosity, and rainfall, but also to groundwater (depth and salinity) and some soil properties as humidity and salinity (Govender et al. 2008; Shinozaki-Mendes et al. 2013). In Brazilian semi-arid HTF in there are low variability of temperature through the year, and also a groundwater with a certain distance from terrain surface (personal observation).

The area of CG presented a slightly acid pH, mainly at the control site. This difference could indicate that the crab constant closing/opening channels and it a constant reworking of sediments can allow the bioirrigation of the area. As consequence increase the oxidation of soil and Fe and S forms, what reflect on pH decrease. The association of CG crabs to pyrite iron in DA (figure 6) and clear Fe lost (figure 5) could support this hypothesis, even though it seems a very insipient process.

Normally this crab specie is associated to sandy soils (Diele et al. 2010), as typically is found in HTFs (Albuquerque et al 2014). However, despite the studied soils presented higher percentage of sand fraction when compared to other studied areas, there were a prevalence of fine particles (clay/silt/sand proportion of 38%, 37% and 25%; mean values trough soil profile). But this difference could be a reflection of geomorphologic condition of the studied area as previously discussed.

CG was associated, among the studied soil properties, with organic matter and low iron contents (Figure 6). This relation reinforce is based on the fact that land crabs can be important litter consumers which affects litter standing biomass and nutrient cycling (Green et al. 1999; Twilley et al. 1997) because their generalist leaf litter consumption (Rodriguez-Fourquet and Sabat 2009).

However, the effects of bioturbation on the incorporation of this organic matter were not so effective when compared with those observed in mangroves (e.g. Araújo-Junior et al. 2012). Mainly because in the HTFs there are naturally low contents of total C, N, S (Albuquerque et al. 2014) and fast mineralization due to the climate restrictions. In this sense, the slight difference observed in total organic matter content from the surface to sub superficial layers (figure 4) could be more related to the accumulation of plant material from trees, lianas, and grasses that colonize the area.

It was observed a significant difference between the iron content of different studied fractions between the control and bioturbated areas (Table 2). The CG action seemed to promote a slight increase in iron associated with pyrite (formation or accumulation) mainly in two layers, 10-20cm and 40-60cm. This process could be related to the habits of the crabs. Normally CG spends most time out of water (Gifford, 1962), but their burrows are frequently made in a way to the keep contact with underground water (Pinder and Smits1993; Govender et al., 2008). To deal with high temperatures, these crabs developed nocturnal habits, normally dwell in burrows for a long time (Pinder and Smits1993; Govender et al., 2008) and so they can constantly move to deeper layers to maintain temperature, humidity of the burrow to avoid desiccation. However, also be inside the burrow allow them be protected against high temperatures, low humidity, wind action and avoid predators (Bliss 1979; Greenaway 1988). The movement bottom-up could bring more reduced soil material (i.e., reduced iron forms) causing the observed patterns. However, the heterogeneous distribution of iron forms in soil layers are common in hydromorfic environments and the vertical distribution and movement patterns of crabs in their burrows are poorly known. So, more tests should be done to confirm this hypothesis.

When compared to isolated soils (Figure 5) it is evident not only the increase of iron associated to oxy-hydroxides (almost two times higher than in bioturbated sites) but the decreasing to almost zero the pyrite formation through the profile. Tendency normally observed in HTF soils (Albuquerque et al. 2014) This result reinforces the importance of crabs as key agents on sulfur and iron cycling (Gribsholt et al. 2003; Nielsen et al. 2003) in HTF as mangroves. Probably longer studies and evaluation of deeper soil layers, measurement of temperature and humidity of soil through the profile and burrows can offer more information to clarify this process in HTF.

Our results indicated that HTF system can be affected by CG bioturbation, mainly influencing pH and redox conditions on soils. It is noteworthy that despite CG was classified as resilient to changes in land use and land cover by Govender et al. (2008), the species cannot survive to the and change of territory of HTF and the weak management of fishery resources of the Brazilian coast. In this sense not only the species can be pressed but the whole environment, representing an un-esteemed loss.

The crabs behaviors can affect the establishment of species, that are not necessarily related to their population (Fanjul et al. 2007; Ciechanowski et al. 2011), by controlling the availability of food resources and creation of new niches, for example. So, further studies could the effect of UC and CG bioturbation on native plants of HTF

2.5. Conclusions

Our results indicated that the bioturbation by *Ucides cordatus* and *Cardisoma guanhumi* do not affect soil properties at the same way. Their feeding habits and their movement and maintenance of burrow seems to affect differently the studied soil properties. Bioturbation in HTF, as in mangroves, had notable effects on water and oxygen fluxes trough the soil profile as the iron geochemistry signalizes. However, these changes are less striking than those previously reported in mangrove forests probably because biogeochemical process at HTF is less pronounced, particularly in respect to iron.

Besides, it is important to highlight the importance of HTF as habitat for the life story of two remarkable and overexploited crab species, becoming evident the importance of conservation of these areas, not only as an area of possible expansion for mangroves forests but as areas with well defined ecosystemic function. More studies, which evaluate more environmental variables (e.g. temperature) and soil conditions (e.g. humidity) and others soil properties (e.g. cations as Ca and Mg that are important to crab physiology and fractions of C, N, and S) in order to improve the comprehension about the effects of soil on crabs development and the result of bioturbation on this ecosystem.

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CHAPTER 3

Abiotic factors and facilitation as the main drivers of community composition on a Brazilian hypersaline tidal flat

(Fatores abióticos e processos de facilitação como as principais influências na composição da comundade em um apicum brasileiro)

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Resumo. O paradigma para a estrutura de comunidades de plantas nas planícies hipersalinas é completamente baseada na influência abiótica como topografia, frequência de inundação e propriedades do solo. Entretanto, interações positivas como a facilitação pode ter um importante efeito em diferentes níveis biológicos. Esse estudo testou a hipótese de que fatores abióticos têm papel chave na distribuição de espécies em apicuns. Uma área de apicum foi selecionada e dividida num grid de 38 parcelas para que elevação do microrelevo fosse medidade e, amostras de solo e informações sobre abundância de plantas e distribuição de caranguejos fossem coltadas. Foram realizadas análises laboratoriais para análise de pH, Eh, CE, matéria orgânica, total S, total C and Total N. Além disso, a biomassa das plantas e medição das tocas dos caranguejos e sua área de cobertura foram utilizados na contrução do modelo. Utilizou-se a modelagem de equação estrutural (SEM) para testar essa hipótese e verificar se plantas e animais podem atuar para aumentar sua adaptação através da modificação de condições de solo e de interações intra ou interespecíficas. Os resultados do modelo ecológico final indicam que condições abióticas e interações positivas atuaram no controle da comunidade vegetal. A biomassa da espécie de planta mais dominante na área estudada, *Sporobolus virginicus,* foi diretamente afetada pela elevação do terreno, teor de matéria orgânica e conteúdo total de enxofre no solo. Em contraste, *Blutaparon portulacoides* não foi afetada por nenhum fator incluído na análise, mas parece ter facilitado o crescimento da espécie *S. virginicus.* A comunidade de caranguejos aparentemente é exclusivamente controlada pelas condições abióticas e nenhuma interação biótica positiva ou negativa foi observada.

Palavras-chave: salinidade do solo, áreas úmidas costeiras, facilitação, *Sporobolus virginicus, Blutaparon portulacoides, Ucides cordatus, Uca rapax*

Abstract The paradigm for plant communities structure in tidal flats is completely based on the abiotic influence, such as topography, inundation frequency and soil characteristics. However, positive interactions, like facilitation, may have a strong effect in different biological levels. This study tested the hypotheses that abiotic factors are the main drivers of the biotic distribution in hypersaline tidal flats. One HTF area was selected and a sample grid with 38 ponts was used to measue the elevation, to collect soil sample, to evaluate plant abundance and crabs distribution. Laboratorial analysuis were conduced to evaluate pH, Eh, EC, organic matter, total S, total N and total C. Besisdes of that, plants biomass and crabs holes measures were used to buid a ecological model. The authors used Structural Equation Modeling (SEM) to test the hypotheses and to check if both plant and crab species could improve their adaptation by changing soil conditions or by establishing plant-plant or plant-animal interactions. Results suggest that the interplay between abiotic conditions and facilitative interactions may have controlled the plant distribution. The most dominant plant species, the grass *Sporobolus virginicus* was strongly affected by elevation, soil organic matter contents, and total sulfur contents in soils. In contrast, the succulent species *Blutaparon portulacoides* was not affected by any factor included in our analysis, but seemed to strongly facilitated the growth of *S. virginicus*. The crab community appeared exclusively controlled by abiotic factors (soil properties and microrelief) without any significant positive or negative biotic interactions.

Key words: soil salinity, coastal wetlands, facilitation, *Sporobolus virginicus, Blutaparon portulacoides, Ucides cordatus, Uca rapax*

3.1 Introduction

Hypersaline tidal flats (HTFs) form the key geomorphological and ecological link between mangrove forests and the dry upland, especially in (semi-)arid coastal regions. HTFs can be found in different tropical parts of globe like Brazil (Lebigre 1999; Albuquerque, 2014), Gabon and Madagascar (Africa; Lebigre 2007) and New Caledonia (Oceania; Lebigre 2007) and despite their prevalence, ecological functions and socioeconomic importance, these systems are poorly understood and are increasingly subjected to anthropogenic disturbance.

These areas are normally devoid of vegetation or mostly colonized by halophytes or saline tolerant herbaceous species (Marius, 1981; Marius et al., 1987; Lebigre, 2007; Albuquerque et al., 2014) normally distributed in patches. In Brazil, the most common plant species are *Blutaparon portulacoides*, *Batis maritima*, *Philoxerus vermicularis*, *Eleocharis caribaea*, *Sesuvium portulacastrum* and *Sporobolus virginicus* (Marius et al., 1987; Albuquerque et al., 2014). Some mangrove tree species, typical from transition areas can be found inside the system or its outer limits, mainly *Avicennia shaueriana*, *A. germinans* and *Conocarpus erectus*. Hypersaline tidal flats provide resources for different animal species. Birds and mammals (Lacerda, 2001) can be found as visitors, but some decapods crustaceans, like the crabs *Uca* spp, *Ucides cordatus* and *Cardisoma guanhumi* can colonize the HTF (Nascimento 1993; Schmidt 2006; Firmo et al. 2012; Albuquerque 2014).

Drivers of spatial variation in plant species composition and functional structure need to be understood for an improvement of wetlands ecosystems restoration and biodiversity conservation (Andrew et al. 2012). However, even if small-scale soil spatial heterogeneity is recognized as important drivers for plant communities, the understanding of the process remains limited (Laliberté et al. 2013). Normally, in arid and semi-arid ecosystem, where patch distribution occurs, abiotic factors are thought to affect the redistribution of resources and nutrients to vegetation, mostly by water fluxes (Pueyo et al., 2013). In estuarine environments He et al. (2011) related plant distribution with geomorphological conditions, nutrients distribution, oxygen availability and salinity. Topography, tide frequency and its duration, physical and chemical soil characteristics are also suggested as determinant to vegetal communities in coastal wetlands (Lefeuvre et al., 2003).

Despite abiotic influence, biological components can interact and promote important modification on their own dynamics. For a long time, ecological theories emphasized the negative interaction, as competition and predation, as strong drivers of diversity (Bruno et al. 2003; Laliberté et al. 2014). Bertness and Shumway (1993) suggested that ecologists concentrated efforts to understand competitive process and the habitats in which they are more important. However, positive interactions between neighboring organisms are now considered fundamental and, in some cases, deeply affect the abiotic environment to determine the communities structure (Bruno et al 2003). Positive interactions are characterized when, through intraspecific or interspecific interactions one organism make the local environment more favorable for another organisms, either directly or indirectly (Stachowicz 2001) . The identification of positive interactions and their influence in biological dynamics and abiotic modification have been described with great contributions to coastal ecosystems (Brooker and Callaghan 1998; van der Heide et al 2007, Nomann and Pening 2008; van der Heide et al 2011, Monge and Gornish 2015).

Soil-based resources can affect the performance of plants in different levels (Wijesinghe et al 2005). Some studies demonstrated that heterogeneity in resource supply affected directly the relations among plant communities, often resulting in competition (Filtter 1982, Fransen et al 2009, Wijeinghe et al 2005). However, the relative importance of positive interactions in environmental modifications seems to increase if plant communities are submitted to abiotic stress (Brooker and Callaghan 1998; Brooker et al 2005; Dohn et al 2013; Castellanos et al. 2014). In these cases, the relative importance of competition decreases (Bertness and Callaway 1994). The positive interactions in hypersaline coastal environments are also expected to be found between crabs and plants in order to ameliorate the system and improve their adaptation (Mikoff et al 2006).

Thus, an integrated approach can skip an individualistic perspective (Chooler et al, 2001). Several studies demonstrated that better a understanding of terrestrial plant diversity and ecological relations could be achieved if researches tested the interaction of biotic and abiotic factors (Bertness and Shumway 1993; Laliberté et al 2013; Laliberté et al. 2014). Considering that HTF systems conditions are harsh, sometimes even to halophytes species (Sylla et al 1995), an attention to positive interactions can change basic predictions and improve the understanding of natural communities (Bruno et al, 2003; Dohn et al 2013). Evaluating abiotic conditions, soil properties and ecological interactions (animals and plants) may further explain the regulatory mechanisms of these systems.

We based our study on the hypotheses that abiotic factors in small scale are key factors driving the biotic distribution in hypersaline tidal flats (HTF). Therefore, plants and animals may change soil conditions and interact between them to improve their fitness and ability to cope with HTF conditions. To achieve the proposed objectives we used a Structural Equation Modeling (SEM) to examine the relation between soil components, microrelief, plant biomass and crab cover per area in this ecological system and to quantify the importance of these relations.

3.2. Material and methods

The study area is located in Jaguaribe River estuary (4°28’44’’ S - 37°46’44’’ W) in the municipality of Aracati, Ceará state, Northeastern Brazil. The area is located at the semiarid Northeast coast, where mean temperatures vary between 26 and 28^{o}C (FUNCEME/IPECE 2012). Rainfall is distributed in two distinct seasons: a wet season; from January to May (mean maximum of 237.8mm) and a dry season from June to December (mean maximum 47.7mm) (Leite et al. 2013). The tidal regime is characterized by ranging between 1.4 and 2.6m (Tanaka; Maia, 2006).

Data were collected using a grid which covered 1.4 ha of the HTF area in Jaguaribe estuary (Figure 1). The grid was established with a regular spacing between points of 20 m x 20m. Every each 20m, after verifying the elevation, a square with 0.50 x 0.50 cm was randomly placed. Inside the square measurements of species composition were performed and soil samples were collected. A total of 38 points were surveyed and sampled.

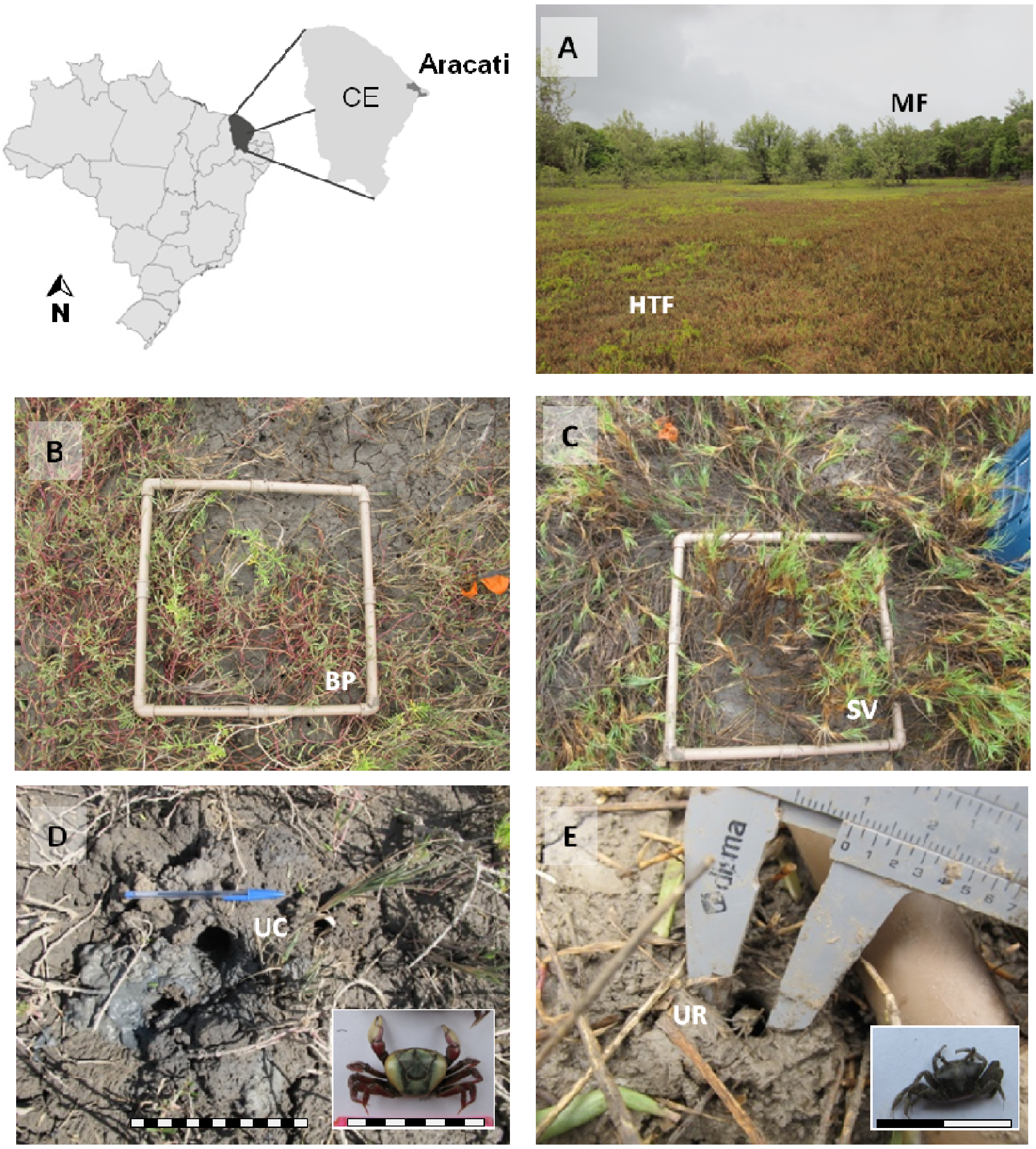

Figure 1. Map of the study site location (Jaguaribe River estuary, Aracati, Ceará state, Brazil). (A) HTF landscape during the rainy season (HTF) and surrounding mangrove forest (MF). (B) Sampling of *Blutaparon portulacoides*. (C) Sampling of *Sporobolus virginicus*. (D) *Ucides cordatus* and burrow entrance (UC); (E) *Uca rapax* and burrow entrance. Black and white stripes are equivalente to one centimiter. Strips black and white have=1cm.

The Elevation was measured with a DGPS (Differential Global Positioning System) in which a moving station (GPS) is connected with a fixed station (Artur et al. 2014). In each plot, all plants species were cut in the ground level and separated in paper bags (per specie, per plot) to determinate its biomass. The crab burrows were counted and identified by their shape and slop to the ground (Wunderlich; Pinheiro; Rodrigues 2008). The burrows opening were measured to estimate crab size and sexual maturity (Pinheiro; Fiscarelli 2001) and counted to calculate their coverage area per plot

($\sum(pi*r^2)$). Additionally soil samples were collected (0-10 cm). Samples were air dried and analyzed to determine physical and chemical attributes: total Carbon, total Nitrogen and total Sulfur, total organic matter, electrical conductivity, pH and Eh.

We used Structural Equation Modeling (SEM) (Amos v20) to test the hypothesis by analyzing the relations between the abiotic and biotic factors. The parameters utilized to build the model were plant biomass of the two most abundant plants in the area (*Sporobolus virginicus* and *Blutaparon portulacoides*), coverage of crab holes in the area (*Ucides cordatus* and *Uca rapax*), total Nitrogen (Nt) and Sulfur (St), Organic Matter (OM), Electrical conductivity (EC) and Elevation (E). To approach a normal distribution for the analyzed variables Nt, St, OM and EC were log transformed ($y=\log_{10}(x+1)$) and all others variables were square root transformed ($y=\sqrt{x}$); all transformations performed in the SPSS software (version 21).

The elevation had significant correlation with all variables tested in this study, so was chosen to be the independent variable to built the model. The aim was to test how elevation affects the spatial distribution of soil characteristics and the measured biotic parameters, and also other direct and indirect effects on its distribution. In summary, the models included four steps (Figure 2): (1) test the relation between abiotic factors; (2) test the effect of all abiotic factors on biotic factors; (3) test the possible effects of elevation and biotic factors on soil characteristics; (4) test the effects of relation between biotic factors themselves.

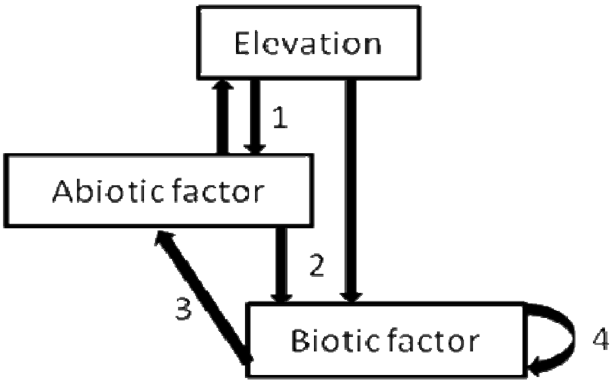

Figure 2. The conceptual path analysis model. Arrows represents direct effects of one variable (boxes) on another. Numbers represent four steps described in “materials and methods”.

To estimate the casual relationships in the environment we analyzed each model twice, one with all data and possible effects and, in a second analysis, with the best models choose using Akaike´s Information Criteria (AIC). All models were than analyzed with a stepwise backward elimination of relations included the default model based on significance of the relation $p<0.05$ and X^2 test (probability level >0.05).

3.3. Results

3.3.1. General soil properties and species distribution

The evaluated soil properties presented heterogeneity and most biogeochemical processes seemed to be incipient. The area presented netural-basic pH, oxic conditions and hypersaline conditions and very low content of total C, total N, total S and organic matter (OM).

The studied HTF is colonized mainly by herbaceous halophytes plants *Sporobolus virginicus* and *Blutaparon portulacoides*, with rare spots of *Sesuvium portulacastrum, Batis maritma* and *Conocarpus erectus* abundance. No patchy distribution was found at the studied site, but a clear zonation between *Sporobolus virginicus* and *Blutaparon portulacoides* areas was observed.

Three species of crab where identified colonizing the studied area; *Cardisoma guanhumi*, *Ucides cordatus* and *Uca rapax*. But only these last two were studied due the randomly collection of points. The galleries related to *U. cordatus* where found at plots nearest to the mangrove outer limits and all holes had an opening with Gallery Opening Diameter (GOD) less than 51 mm and were distinguished as belonging to young and sexual immature individuals (Leite 2013). In the other hand *U. rapax* were found in almost all area with no clear distribution pattern and with great variety of burrow entrance sizes.

The combination of correlation and structural equation modeling allowed identifying elevation, total S and OM. as most explanatory properties for plant and animal distributions in HTF (Figure 3).

3.3.2. HTF’s ecological interaction

SEM models are constructed to determine dominant mechanisms, the effects between variables or processes, considering the goals of the analysis (Laliberté et al. 2013). Using Akaike´s Information Criteria (AIC) the best model, build as a flowchart, was chosen after the stepwise and backward tests (Figure 3). According to the tests, plant community was controlled by interplay between the abiotic conditions and facilitative interactions (Figure 3B). Total Nitrogen, electrical conductivity, pH and Eh had no significant importance to explain the community dynamics. On the other hand, the most dominant plant species, the grass *Sporobolus virginicus,* was strongly affected by elevation, organic matter content, and total S content in the soil (p values = 0.001, 0.035, 0.033, respectively) (Figure 3B) . The explanation of *S. virginicus* by soil properties (OM and S) was also affected when OM was left out of model. It means, when OM is left ou the model (Figure 3A), total S effect became more predictor (p value 0.035 to 0.022) (Figure 3B).

Total S content was also the soil variable which had more effects over all tested biotic parameters, except in the biomass of *Blutaparon portulacoides* which was not affected by any factor included in our analysis. However, *B. portulacoides* seemed to strongly facilitate the growth of *S. virginicus* due the strong correlation (significance of 0.003) highlighted by the model (Figure 3B). The positive interaction seems to improve the adaptation of *Sporobolus virginicus,* because when the model was tested without the plant interactions it became 10% weaker (R^2= 0.501 to R^2=0.403) (Figure 3).

The crabs community, in the other hand, seemed to be exclusively controlled by the abiotic conditions; with no significant positive or negative biotic interactions. More than 48% of *Uca rapax* and 51% of *Ucides cordatus* distribution were explained by the model (Figure 3). But elevation, total S and total OM as abiotic variables seemed to affect the crabs species in a different way. Total S content had larger explanation power for both crab species (p < 0.001). However elevation strongly affected *U. rapax* (0.047), while OM was useful to explain *U. cordatus* distribution (p<0.001).

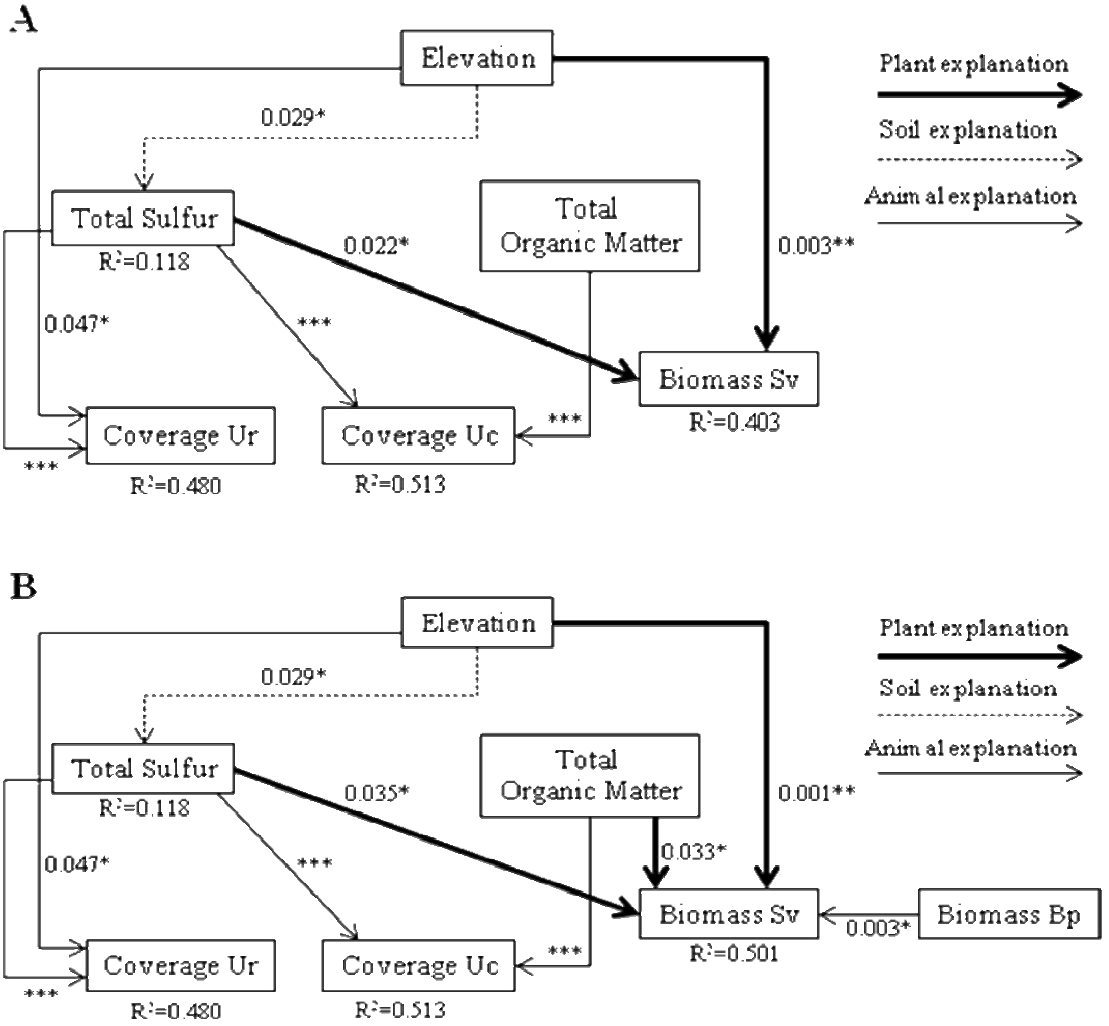

Figure 3. Models for ecological relations based on SEM analysis. Arrows indicate significant direct effects. The R^2 values represent the total variance explained by all significant predictors (*p < 0.05; **p < 0.01; ***p < 0.001). (A) Model without positive interaction between plant species and OM interaction in plants; (B) Final model with best explanations to abiotic and biotic variables values.

3.4. Discussion

Environment heterogeneity and incipient biogeochemical processes, mainly in surface layers are among common characteristics of HTF (Albuquerque et al 2014a; Albuquerque et al, 2014b). Thus, identifying patterns and the relative importance of the relations among ecosystem components becomes especially difficult.

It was noteworth that a combination of microrelief and soil properties (reflectd on total S and OM content) explained most ecological distribution of crabs and plants on the studied HTF. However, the way this combination affected the plants and crabs seemed different. The elevation changes and total S seemed responsible to the explain

48% of *Uca rapax* distribution, while total S and OM explained 51% of *Ucides cordatus* distribution (Figure 3). In the other hand, according with the testes total S, OM and elevation explained 40% of *Sporbolus virginicus* biomass (Figure 3A).

It was expected that microrelief changes could promote localized changes of soil properties (Crawford and Abbott 1994). However, among studied soil properties, only total S content variation was related to elevation changes (Figue 3). This relation could be a proxy for environmental processes related to microrelief variation and it effect on water flux. The salt water incoming during the tide flood could lead to sulfate accumulation in downstream positions. The significant relation of total S with most plant and animals tested in the model could reinforce its conection to salt water influx.

The OM content could be also related to tide flood. The organic material from mangrove forests areas and dry land vegetation could be carried and sttled at the intern portions of the HTF system. According with the tests used in the model, the OM could not be related to a production and storage by native plants from HTF. If so, positive and significant relations (arrow from plants to OM content) would have appeard on the model (Figure 3).

It would be possible that bioturbation effects (feeding and burrowing activities) close to plants could generate changes in the soil structure and properties which could facilitate plant growth (Mikoff et al 2006) and production (Nomann and Penning 1998) by buffering environmental stress conditions (Bortolus et al. 2002, Escapa et al. 2007). On the other hand, plants colonization could, due to shadowing and decreasing soil temperatures (Bortulus et al 2002) facilitate crab colonization by reducing chances of crab dissection. However, according to our model the relation between crabs and plants in HTF could be classified as neutral. So the plant productivity in hypersaline coastal lands seems to be more affected by salinity and soil stability for roots than by aeration or decomposition caused by crabs (Nommand and Penning 1998).

3.4.1. The implications of positive interaction in HTF plants community

This study has documented a highly significant effect of facilitative interaction between two different plant species in HTF. Both species present a clonal growth pattern and are among the natural species found in this habitat (Lebigre 2007, Albuquerque et al 2014a).

It was noteworthy the impact of the positive relation of *Blutaparon portulacoides* on *Sporobolus virginicus* biomass. The inclusion of *B. portulacoides* biomass on the model improved the explanation of *S. virginicus* biomass in 10% (Figure 3B) compared to the scenario without the positive interaction (Figure 3A).

Clonal vegetation normally allows plants to obtain optimum use of heterogenous environments (Chapin et al. 1994; Jódnsdóttir and Callaghan 1988). It is possible that a number of positive interactions between plants can occur through physiological connections, for example, via the connections between their ramets (Brooker and Callaghan 1998). The exact mechanism by which *S. virginicus* was facilitated by their neighbors is unknown. However, one possible explanation is the release and sharing of nutrients in order to buffer the negative conditions and improving water consumption.

In fact, some studies indicated that clonal plants tend to use N compounds as NH_4^+ and NH_3^- (Høgh-Jensen and Schjoerring 1997; Yin and Raven 1998; Guo et al. 2007; Roiloa et al. 2014) or other ions, such as $K^{+,}$ (Flowers and Colmer 2008; Flowers et al. 2010; Soriano et al. 2014) to improve their ability to colonize saline soils. Previous studies related *Blutaparon portulacoides* rhizosphere soil with strong relation to NH_4^+ availability and exchangeable K^+, while *Sporobolus virginicus* rhizosphere soil more related to soluble K^+ (Bell and O'Leary 2003). So, both species could face similar environmental conditions on bulk soils using different strategies and through positive interactions, plants could ameliorate saline stress and improve their growth (Bertness and Hacker, 1994). In this sense it is possible that a facilitation process, in which *B. portulacoides* could mobilize NH_4^+ and exchangeable K, enlarging the nutrient pool of these ions, while *S. virginicus* would consume only K^+.

Further studies using controlled experimental studies combined to field sampling could provide important information to clarify ecological process in HTFs and suggest what other factors may explain the *S. virginicus* and *B. portulacoides* distribution.

Our model suggests that abiotic conditions, microrelief and soil properties have different roles in HTFs. Although the microrelief seems to rule spatial distribution of species (plants and crabs) along a heterogeneous gradient, a wide perspective whitch include biotic interations should be observed in order to understand the plant community. Positive interactions may help species to broaden its distribution along environmental gradient (Choler et al. 2001) and it hypotheis could be much more observed by avoiding of individualistic perspectives of plant communities.

3.5. Conclusions

Our results demonstrate that, SEM is useful tool to verify ecological interactions even in highly heterogeneous and dynamic ecosystems. Dispite abiotic factors seemed driving mechanisms in the structuring of plant and crabs communities in HTFs, facilitation may be an important factor to plant community organization. So, plant-plant interactions should, therefore, be included in future system analyses and management policies.

We suggest that the study of plants and crabs distribution and abundance at HTF, should investigate not only soil properties as abiotic conditions. Others environmental characteristics such, soil humidity, water infiltration rate and temperature should give more answers about plants and crabs distribution.

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