TESE DE DOUTORAMENTO

BIOGEOCHEMISTRY OF MARINE PHANEROGAMS SOILS

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Biogeochemistry of marine phanerogams soils

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D. Antonio Martinez Cortizas

e

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This thesis is bases in the following manuscripts:

Manuscript 1: Piñeiro-Juncal, N., Leiva-Dueñas, C., Serrano, O., Mateo, M.A., Martinez Cortizas, A., 2020. Pedogenic processes in a *Posidonia* oceanica mat. *Soil Systems* 4,18, 1-15.

Contribution of the PhD student: Conceptualization, laboratory analysis, statistical analysis, data interpretation and manuscript writing.

Manuscript 2: Piñeiro-Juncal, N., Díaz-Almela, E., Leiva-Dueñas, Deulofeu, O., Frigola, J., Soler, M., Martinez Cortizas, A., Giralt, S., García-Orellana, J., Mateo, M.A., Processes driving seagrass soils composition along the western Mediterranean: the case of the southeast Iberian Peninsula. Under review at *Science of the Total Environment*.

Contribution of the PhD student: Conceptualization, statistical analysis, data interpretation and manuscript writing.

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Contribution of the PhD student: Laboratory analysis, statistical analysis, data interpretation and manuscript writing.

Manuscript 4: Piñeiro-Juncal, N., Leiva-Dueñas, C., Serrano, O., Mateo, M.A., Martinez Cortizas, A., 2020. Cover loss in a seagrass *Posidonia oceanica* meadow accelerates soil organic matter turnover and alters soil prokaryotic communities. *Organic Geochemistry*. **JCR IF (2019): 3.231, Q2 in Geochemistry and Geophysics**

Contribution of the PhD student: Part of the laboratory and statistical analysis, data interpretation and manuscript writing.

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RESUMO

As fanerógamas mariñas, ou herbas mariñas, forman parte dunha segunda colonización das augas costeiras pouco profundas por parte de plantas superiores. A recolonización levouse a cabo por tres camiños evolutivos diferentes, pero todas as herbas mariñas desenvolveron adaptacións semellantes á vida no mar, sinalando a presión ambiental como o principal factor de selección evolutiva. Como os cetáceos, volveron ao mar levando consigo características propias dos seus devanceiros terrestres. Algúns destes trazos morfolóxicos e fisiolóxicos, desenvolvidos para a súa adaptación á vida na terra, poden ter promovido a desenvolvemento de mecanismos diferentes a aqueles empregados polas algas para a adaptación a algúns dos retos da vida mariña. Por exemplo, o reforzo dos seus tecidos con lignina para manter a posición ergueita fóra da auga pode ter dado soporte ao desenvolvemento do sistema lacunar, o cal permite ás herbas mariñas bombear O_2 á súa rizosfera para reducir fitotoxinas como o Fe^{2+}, Mn^{2+} ou os sulfuros. O desenvolvemento de órganos soterrados é un dos principais trazos das plantas terrestres e o trazo máis salientable das herbas mariñas desde o punto de vista da interacción co substrato onde medran.

Os prados mariños están distribuídos nas áreas costeiras de todos os continentes agás da Antártida. As seus doseis promoven a deposición de sedimento e, tanto a dosel como os seus órganos subterráneos, reducen a resuspensión deste sedimento, promovendo a formación de solos ben estruturados seguindo una secuencia cronolóxica onde máis profundo é equivalente a máis vello. Os cambios promovidos pola planta no substrato ocorren na rizosfera e poden variar coa madurez da pradaría mariña. Os rizomas das herbas mariñas e as puntas das súas raíces liberan O_2 e compostos orgánicos cara ao substrato, promovendo a formación de micronichos bioxeoquímicos ao seu redor. As herbas

mariñas non son as únicas que promoven estes cambios no substrato baixo o prado; macro e microinvertebrados así como comunidades de microorganismos tamén xogan un papel na diaxénese destes solos. As herbas mariñas do xénero *Posidonaceae* desenvolven solos cunha alta carga orgánica, coñecidos como matas. O papel destas matas como reservas de carbono a longo prazo ten promovido un grande interese na comunidade científica sobre o destino da materia orgánica soterrada nos solos das herbas mariñas. A acumulación de materia orgánica nestes solos ten sido relacionada con (1) a promoción da retención de partículas debido ao dosel das herbas mariñas, (2) as condicións anóxicas que se acadan dentro do solo e (3) o carácter refractario dos tecidos das herbas mariñas, que poden ser preservados durante milleiros de anos.

Tradicionalmente, os substratos baixo os prados de herbas mariñas teñen sido considerados como sedimentos. Con todo, co paso do tempo, a presenzas das herbas mariñas transforma radicalmente estes substratos mediante adicións, subtraccións, transferencias e transformacións (i.e., procesos de formación de solo) dunha mera acumulación de sedimentos a un solo. A definición de solo do *Unite States Department of Agriculture Soil Taxonomy* recoñece a posibilidade da formación de solos baixo as herbas mariñas dende a súa primeira edición. Non obstante, os solos subacuáticos teñen sido ignorados en gran medida na investigación das ciencias do solo. Por outra banda, os solos subacuáticos son apenas recoñecidos baixo a *World Reference Base for Soil Resources* até os dous metros de profundidade de auga (medido en marea baixa con mareas vivas). Este límite arbitrario significa que o substrato baixo o mesmo prado de herbas mariñas, coa mesma idade e as mesmas características, pode ser considerada un solo ou non dependendo unicamente da profundidade da columna de auga baixo a que se atope, unha aproximación que non é compatible co *soil-continuum*. A intensidade das transformacións e o tipo de solo que resulte delas vai depender de varios factores, como o réxime climático de temperatura, os organismos que o transformen, a batimetría, o réxime hidrodinámico, a material de orixe, o tempo, as características da columna de auga máis eventos catastróficos. Aínda que os solos de herbas mariñas poden ser tan diversos como as súas contrapartes terrestres, estar continuamente baixo auga, medrar en grosor por acúmulo de sedimentos e desenvolver condicións favorables para a acumulación de materia orgánica son trazos comúns para a meirande parte deles. Estes trazos son compartidos en parte con solos subaéreos de turbeiras, marismas de marea ou auga doce máis solos de mangleiros. O recoñecemento completo dos substratos baixo prados de herbas mariñas como solos axudaría a esclarecer a natureza destes depósitos con maior eficiencia, e máis a reflectir os procesos nos cales aqueles servizos ecosistémicos relacionados co substrato teñen a súa orixe. Ademais, este recoñecemento deixaría patente que, aínda cando se perde a cobertura vexetal (i.e., o prado morreu), os servizos ecosistémicos seguen a ser fornecidos e o prado "morto" aínda é un ecosistema funcional, moi lonxe dun fondo desértico.

O obxectivo desta tese é estudar a bioxeoquímica dos solos formados baixo as herbas mariñas e, empregando a información edafolóxica dispoñible, establecer unha descrición e clasificación preliminar destes solos. Os solos das pradarías de *Posidonia oceanica* empréganse como modelo da bioxeoquímica dos solos de herbas mariñas debido ao alto impacto que estas teñen no seu substrato, así como a grande cantidade de información dispoñible sobre as súas interaccións planta-substrato. Os solos estúdanse empregando a profundidade como un indicador da idade do material; a máis profundo, máis antigo. Os prados mariños mostrados están distribuídas en dúas areas xeográficas: a baía de Portlligat no noroeste do Mar Mediterráneo, e a costa andaluza no suroeste do Mar Mediterráneo. A baía de Portlligat alberga unha densa e ben desenvolvida pradaría de *P.*

oceanica que se estableceu alí dende, polo menos, hai 6000 anos. A grande cantidade de información dispoñible sobre esta baía e o seu prado, xunto coa presenza dunha sección do prado que perdeu a súa cobertura vexetal ("morreu") fai de Portlligat un lugar ideal para o estudo da bioxeoquímica do solo e a súa resposta perante a perda da cobertura vexetal. A costa andaluza (sur da Península Ibérica, suroeste do Mar Mediterráneo) presenta unha grande heteroxeneidade ambiental que se pode dividir en tres áreas, dúas das cales foron mostradas. A primeira area mostrada mostra as características propias do Mar Mediterráneo, mentres que a segunda, o Mar de Alborán, mostra características intermedias entre o Mediterráneo e o Océano Atlántico. Esta gran variabilidade ambiental mais a extensa superficie ocupada por prados de herbas mariñas (>10,000 ha) ofrece un rango moi amplo de mostraxe, permitíndonos estudar os trazos bioxeoquímicos comúns a todos os solos das seus prados mariños e os principais factores controlando a formación e composición dos solos de herbas mariñas.

Para iniciar o estudo da bioxeoquímica dos solo desta tese, comezamos por una aproximación exploratoria xeral a través da composición elemental dos mesmos (fluorescencia de raios X), a súa distribución granulométrica e o contido en materia orgánica. A técnica de pirólise analítica foi empregada para estudar a composición molecular da materia orgánica e o seu cambio coa profundidade. As comunidades microbianas e a súa actividade foron estudadas mediante dúas técnicas distintas: as Ecoplates^{TM} (Biolog), que miden a actividade microbiana potencial de xeito semi-cuantitativo empregando incubación en diversas fontes de carbono; e a metaxenómica, que identifica especies mediante a secuenciación do ADN presente nunha mostra ambiental. Por último, fíxose unha revisión bibliográfica das publicación sobre substratos baixo prados de herbas mariñas buscando algúns dos principais descritores empregados en edafoloxía: cor, pH, porosidade, potencial redox, densidade, textura, contido en materia orgánica e contido en carbonatos, para tentar a descrición e clasificación preliminar de estes solos.

Os resultados desta tese están presentados en cinco manuscritos científicos, dous dos cales están publicados en revistas con revisión por pares, un terceiro ten aceptación definitiva, outro foi enviado a revista e atopase baixo revisión e o último esta sendo preparado para o seu envío a revista no momento de escritura desta tese.

O **manuscrito 1** presenta o estudo dunha testemuña de solo de 475 cm de longo tomada na baía de Portlligat, buscando atopar indicios de horizonación e estruturación vertical no solo. O obxectivo deste estudo é avanzar no coñecemento dos procesos a longo prazo de formación da mata de *P. oceanica*, xa que a meirande parte dos estudos realizados nela están centrados na rizosfera, estudando procesos a curto prazo. Para acadar este obxectivo, animalizouse a composición elemental, empregando fluorescencia de raios X, o contido de carbonatos e o contido de materia orgánica grosa e fina (por riba e por baixo de 2 mm de grosor). A covarianza entre as propiedades do solo foi explorada empregando unha análise de compoñentes principais. Atopáronse catro sinais bioxeoquímicos principais: a humificación da materia orgánica, a acumulación de carbonatos, a textura do solo e o decaemento do contido de materia orgánica coa profundidade. Os resultados revelan unha alta estruturación do depósito que sofre transformacións fisicoquímicas propias de procesos pedoxénicos en troques de procesos propios da simple acumulación de sedimentos. A mineralización da materia orgánica mostrou dúas fases, correspondéndose, moi probablemente, coa rizosfera e o solo baixo esta. Tentouse facer unha clasificación preliminar deste solo, clasificándoo como a *Fluvaquent Entisol*. Porén, é necesario afondar na investigación destes solos para describir e clasificar de xeito adecuado os substratos baixo os prados de herbas mariñas.

O **manuscrito 2** representa un escalado do primeiro manuscrito, empregando a mesma aproximación cunha colección de 15 testemuñas mostradas na costa andaluza. Trece delas en prados de *P. oceanica* e dúas en prados de *Cymodocea nodosa*. Este estudo pretende determinar cales son os factores que controlan a composición dos solos de herbas mariñas buscando procesos comúns nestes quince prados. As variables empregadas foron a composición elemental, a susceptibilidade magnética, o contido de carbono orgánico (carbono que fai parte de moléculas orgánicas) e a distribución granulométrica das mostras. A maiores, as testemuñas foron datadas empregando ^{210}Pb e AMS^{14}C para estimar a taxa de elevación dos prados. Empregouse unha análise de compoñentes principais global, coas quince testemuñas, para explorar os principais procesos bioxeoquimicos ligados á formación do solo. Os resultados mostran que a chegada de material terrestre xoga un papel chave no control da composición da pradaría. Ademais, a acumulación de carbono orgánico non segue ningún patrón coa profundidade no solo, suxerindo que a variación temporal nas entradas de carbono orgánico cara ao solo son un factor determinante na distribución desta variable coa profundidade. Os nosos resultados parecen indicar que o establecemento dun prado estable e ben desenvolvido de *C. nodosa* no Mar Mediterráneo pode estar promovido pola imposibilidade do establecemento dun prado de *P. oceanica* debido ás condicións ambientais adversas. O comportamento dos metais nos depósitos baixo estes prados e a súa interacción coa materia orgánica e máis cos carbonatos é incerto. En resumo, os resultados deste manuscrito remarcan a influencia dos procesos xeoquímicos da conca terrestre nas características do solo baixo os prados de herbas mariñas, con grande influencia no contido en carbono orgánico, así como a necesidade de afondar no coñecemento do comportamento de elementos metálicos para explorar todo o potencial destes solos para o seu uso como arquivos ambientais.

No **manuscrito 3**, as Ecoplates^{TM} de Biolog foron empregadas para estimar os patróns coa profundidade da actividade microbiana potencial na mata. As Ecoplates^{TM} son un método semi-cuantitativo de estimar a actividade funcional microbiana potencial medindo a respiración dunha mostra ambiental incubada en diferentes fontes de carbono. As fontes de carbono están divididas en seis grupos: carbohidratos, polímeros, ácidos carboxílicos, aminoácidos, aminas e compostos mixtos. A respiración da comunidade microbiana indicase pola redución de sales de tetrazolioque van incluídas no medio de cultivo xunto a fonte de carbono. Mostras dunha testemuña de solo de 130 cm de lonxitude tomada na mata de *P. oceanica* da baía de Portlligat foron incubadas baixo condicións aerobias e anaerobias. Tanto o metabolismo aerobio como o anaerobio mostrou actividade a tódalas profundidades incubadas. A redución da sal de tetrazolium indicou que os carbohidratos, aminoácidos e os polímeros foron os compostos máis consumidos, mentres que os ácidos carboxílicos, as aminas e os compostos mixtos presentaron baixo ou ningún consumo. Até onde sabemos, este é o primeiro traballo onde mostras de solo son incubadas en condicións anaerobias empregando Ecoplates^{TM}. Os nosos resultados suxiren una estratificación da actividade microbiana moi pronunciada controlada, con grande probabilidade, pola presenza de O_2 no solo. A pesar da alta actividade aerobia nos primeiros 40 cm do solo, a actividade anaerobia foi predominante, explicando a grande capacidade dos solos de *P. oceanica* para estabilizar a materia orgánica.

Mentres que os manuscritos anteriores permitiron observar e explorar a composición do solo e os seus cambios coa profundidade, para interpretar os seus procesos bioxeoquimicos, no **manuscrito 4** comparamos tres testemuñas de solo mostreadas no prado da baía de Portlligat en tres condicións distintas. A primeira testemuña foi recollida na mesma area onde foi tomada a testemuña empregada no primeiro e terceiro manuscrito, a segunda testemuña foi recollida nunha area de prado morto (onde a cobertura vexetal desapareceu) e a terceira testemuña foi tomada na area de prado vivo adxacente a area de prado morto. O obxectivo deste estudo foi entender como a perda da cobertura vexetal afecta ao ciclo do carbono no solo. Para isto varios indicadores foron analizados: 1) o contido de nitróxeno, carbono total, carbono orgánico e carbono inorgánico; 2) a composición molecular da materia orgánica na fracción inferior a 2 mm empregando pirólise analítica, e a súa relación coa profundidade como indicador de idade; e 3) cambios na diversidade das comunidades de bacterias e arqueas empregando *metabarcoding*. Os resultados mostraron unha mineralización preferencial de polisacáridos e *guaiacyl* e *syringyl* ligninas e un enriquecemento selectivo de produtos de ácidos *p*-hidroxibenzoicos e compostos de cadeas metiladas. Tanto a profundidade no solo como a cobertura vexetal mostraron efectos significativos sobre a riqueza e diversidade de bacterias e arqueas. As variacións espaciais dentro do prado nas entradas de materia orgánica cara o solo e as diferencias na composición das comunidades microbiolóxicas entre as testemuñas resaltaron a importancia da variabilidade interna no propio prado. A perda da cobertura vexetal promoveu a degradación da materia orgánica e a promoción da comunidade de arqueas na rizosfera, pero parece non ter afectado a capas máis profundas do solo. Este estudo mostra a importancia da protección dos solos de herbas mariñas contra a erosión para evitar a liberación dos depósitos de materia orgánica milenaria.

O **manuscrito 5** presenta a revisión bibliografía do grande esforzo científico feito para estudar os substratos das herbas mariñas co obxectivo de paliar a falta de estudos edafolóxicos en ambientes subacuáticos mariños. Para isto, algunhas das principais características empregadas no estudo dos solos foron recollidas e resumidas neste manuscrito. A revisión bibliográfica englobou publicacións científicas entre o ano 1980 e xuño do 2020, atopando máis de 3.800 publicacións nas cales figuraba información sobre a densidade do solo, a textura, o potencial redox, pH, contido de carbonatos ou carbono orgánico ou a porosidade. Atopáronse grandes faltas de información xeográfica e sobre grupos específicos de herbas mariñas, sendo as herbas adaptadas a áreas climáticas temperadas as máis estudadas, especialmente os xéneros *Posidonia* e *Zostera*. A pesar desta falta de información as seguintes conclusións puideron ser inferidas: (1) a meirande parte dos prados de herbas mariñas teñen texturas areosas, e o xénero *Posidonia* non pode medrar en texturas limosas. (2) Aínda que promoven a acumulación de materia orgánica, as herbas mariñas non adoitan formar solos orgánicos. A formación destes solos parece ser un feito anecdótico ligado a prados de *P. oceanica*. (3) A clasificación máis probable para estes solos e *Entisols* segundo a *Soil Taxonomy*, é como *Fluvisols* ou *Gleysols* segundo a *World Reference Base for Soil Resources*. Porén, é necesaria máis investigación para clasificalos adecuadamente.

O resultados en conxunto dos cinco manuscritos permitiron a discusión da estratificación dos procesos bioxeoquímicos destes solos entre a rizosfera e o subsolo. A rizosfera presenta procesos dirixidos tanto polas herbas mariñas como polas comunidades microbianas, sendo predominante a actividade potencial aerobia, e estando enriquecida en compostos orgánicos sinxelos de degradar en comparación co subsolo. No subsolo a actividade potencial predominante é a anaerobia e está enriquecido en compostos derivados de ácidos *p*-hidroxibenzoicos e compostos de cadeas metiladas. Os procesos bioxeoquímicos son dirixidos polas comunidades microbianas, non tendo efecto os cambios fisiolóxicos das herbas mariñas nestas capas de solo.

A degradación da materia orgánica no solo co tempo discútese empregando a testemuña de solo do primeiro manuscrito como referencia, xa que as características xeofísicas e a baixa chegada de sedimento terrestre á zona onde foi recollida aseguran unha entrada continua da mesma proporción de materiais orgánicos e inorgánicos. A degradación parece seguir tres fases: unha fase de degradación rápida, unha de degradación lenta e unha fase de estabilización. A morte do prado promove unha rápida degradación da materia orgánica fina debido a un efecto *priming* na rizosfera, pero semella non afectar a cotas máis profundas do solo.

O uso de solos de *P. oceanica* como modelo de bioxeoquímica de solos de herbas mariñas poder ter sobreestimado aqueles procesos ligados a materia orgánica, xa que estes solos acumulan moita máis materia orgánica que os solos doutras herbas. Ademais, *P. oceanica* forma prados persistentes, que aseguran unha constante transformación do substrato, que non se acada en prados de herbas mariñas transitorios, que teñen un efecto moito menor. Aqueles procesos ligados á fisioloxía da planta tamén poden ter sido sobreestimados, debido á alta produtividade de *P. oceanica*. Por ultimo as tipoloxías de substratos colonizados por esta herba son unha fracción dos que pode colonizar o total das herbas mariñas.

En resumo, os maiores achados desta tese son: (1) a existencia de dous compartimentos nos solos de herbas mariñas, a rizosfera e o subsolo; (2) que os principais procesos bioxeoquímicos están ligados á acumulación e mineralización da materia orgánica; (3) os cambios na fisioloxía da herba mariña so afectan á bioxeoquímica da rizosfera; e que (4) non todos os substratos baixo prados mariños poden ser considerados solos pero, dado tempo abondo, todos os substratos baixo prados mariños rematarán por se converter nun solo. Como se atopou no prado de Portlligat, é moi posible que tódolos prados mariños teñan unha alta heteroxeneidade nos seus trazos bioxeoquímicos e comunidades bacterianas. O exame da súa distribución espacial é recomendado cando se formula/planifica un experimento ou recollida de mostras. Sería de grande interese a análise de mostras de solos de herbas mariñas ás que se lles eliminase a fracción orgánica, para estudar os procesos inorgánicos, particularmente comparando prados con concas de diferentes litoloxías. Sería necesario o desenvolvemento de máis estudos centrados no comportamento dos elementos metálicos nestes solos para poder explorar todo o seu potencial como arquivos ambientais, xa que estes son variables chave para estudar a minaría, a metalurxia e o desenvolvemento industrial por parte de poboacións humanas.

RESUMO

SUMMARY

Marine phanerogams, known as seagrasses, represent a secondary colonization of marine shallow waters by terrestrial plants. Like cetaceans, they returned to the oceans carrying traits of their terrestrial ancestors. Some of the morphological and physiological traits developed to adapt to life in aerial environments have allowed seagrasses to overcome some marine life challenges by mechanisms different of those used by algae. For instance, the reinforcement of their tissues with lignin to maintain upright position out of the water may have supported the development of the lacunar system, which allows seagrasses to reduce phytotoxics such as Fe^{2+}, Mn^{2+} or sulfide in their rhizosphere. The development of belowground organs is one of the main characteristics of terrestrial plants and the most outstanding seagrass characteristic from the plant-substrate interaction point of view.

Seagrass meadows are distributed in coastal areas of all continents but the Antarctica. Their canopies promote sediment accretion and canopy structure and belowground organs reduce sediment resuspension, promoting the development of well-structured soils following a chronological sequence in which deeper equals older. Plant derived changes in the substrate take place in the rhizosphere and can vary with meadow maturity. Seagrass rhizomes and root tips release O$_2$ and organic compounds to the substrate promoting the formation of biogeochemical micro-niches in its rhizosphere. Seagrasses are not the sole organisms promoting physico-chemical changes in the meadow substrate, macro- and micro-invertebrates and the microbial communities have a role as well in the diagenesis of the substrates. Seagrass from the *Posidonaceae* genus develop high organic mater (OM) content soils, known as “mats”. The role of mats as long-term carbon reservoirs has boost the interest about the fate of the OM buried

in seagrass soils. The OM accumulation in the soil has been linked to (1) particle trapping and deposition favored by the seagrass canopy, (2) the anoxic conditions in the sediments and (3) the refractory character of the seagrass tissues, which can be preserved over millennia.

Traditionally, seagrass substrata have been considered sediments. However, given enough time, the seagrass presence would radically transform it -through additions, removals, transfers and transformations- from a mere accumulation of sediments into a soil. The Unite States Department of Agriculture Soil Taxonomy definition of soil recognizes the possibility of soil formation below seagrasses since its first edition. Nonetheless, subaqueous soils have been largely neglected in soil science research. On the other hand, subaqueous soils are only recognized by the World Reference Base for Soil Resources up to 2 m depth at low spring tide. This arbitrary limit implies that the seagrass substrate of the same meadow, with the same age, and same characteristics, could be considered or not a soil on the sole basis of the depth of the water column – approach not consistent with the soil-continuum. The intensity of transformation and the nature of the seagrass soil formed would be determined by several factors like climatic temperature regime, organisms, bathymetry, flow regime, parent material, time, water column attributes, and catastrophic events. Although seagrass soils can be as diverse as their terrestrial counterparts, being permanently water saturated, growing in thickness, and creating favorable conditions to accumulate OM, are traits common to most of them. These characteristics are partially fulfilled as well by subaerial soils from peatlands, tidal or freshwater marshes and mangroves. The full recognition of seagrass substrates as soils would help to clarify the nature of the deposit more efficiently and better reflect the processes through which ecosystem services related to the substrate are provided. Furthermore, it would highlight that even when the plant cover has disappeared (i.e., the meadow has died), ecosystem services will still be provided and the "dead" substrate will still be a functional ecosystem and not a barren bottom.

This thesis aimed to study the biogeochemistry of seagrass soils and, using the available pedological information, to establish a preliminary soil description and classification. *Posidonia oceanica* meadows are used as a model for seagrass soils biogeochemistry due to high impact of the plant over the substrate and the large quantity of available information about its interaction with the substrate. The soils are studied using depth as a proxy for time. The seagrass soils sampled for this study are distributed in the Portlligat bay (Northwest Mediterranean) and along the Andalusian coast (Southwest Mediterranean). The first approach used was a general exploration of the soil composition through grain size distribution, organic matter (OM) content and elemental composition (X-ray fluorescence, XRF). Analytical pyrolysis was used as well to study the molecular composition of the OM. The microbial communities structure and activity was explored using Biolog EcoPlates^{TM} and metabarcoding. Finally, a review of the main characteristics of seagrass meadows is presented in an attempt to preliminarily describe and classify them. The outcome of this approach is reported in five scientific manuscripts, three of which have been published in peer-reviewed journals, one has been submitted and is under revision while this thesis is being written and the last is being prepared for submission.

Manuscript 1 presents the study of a 475 cm-long core from Portlligat bay looking for evidence of horizonation or vertical stratification. This study aimed to better understand the long-term formation processes of a *Posidonia oceanica* mat, as most of the research performed in those soils are focused in the rhizosphere (short-term processes). To this end, we analyzed the elemental composition, using XRF, the carbonate content and the coarse and fine OM content (above and below 2 mm). The covariation between these soil properties were explored with principal component analysis. Four main physico-chemical signals were found: humification, accumulation of carbonates, texture and OM depletion. The results revealed a highly structured deposit undergoing pedogenetic processes. Organic matter mineralization showed two phases, very likely within and below the rhizosphere. A preliminary classification is attempted.

Manuscript 2 represents the upscaling of the first study. The same approach was used to analyze 15 cores along the Andalusian coast, 13 from *Posidonia oceanica* meadows and 2 from *Cymodocea nodosa* meadows, aiming to determine which factors drive the composition of these seagrass soils and looking for common processes. The proxies used were elemental composition (XRF core-scanning), magnetic susceptibility, C_{org} content and gran size distribution. Furthermore, the cores were dated using ^{210}Pb and AMS^{14}C techniques to estimate soil accretion. A principal component analysis was used to explore the main geochemical processes linked to soil formation. The results showed that terrestrial fluxes play a key role in meadow soil composition. Furthermore, C_{org} accumulation did not follow any general trend with depth, suggesting that temporal variation in C_{org} inputs is an important factor in determining carbon depth distribution within the soil. The results suggested that the establishment of well-developed, stable *C. nodosa* meadows in the Mediterranean may be promoted by environmental conditions that are not suitable for the settlement of *P. oceanica*. Metal's behavior within the meadow deposit and their interaction with OM and carbonates is unclear.

In **Manuscrit 3** Biolog EcoPlates^{TM} were used to assess the distribution patterns of potential microbial activity within the mat. EcoPlates^{TM} are a semi-quantitative method developed to characterize microbial functional activity by measuring the respiration of different carbon sources divided into six guilds: carbohydrates, polymers, carboxylic acids, amino acids, amines and miscellaneous compounds.

Respiration of the microbial community is revealed by the reduction of a tetrazolium dye that is included with the carbon source. Mat samples from a 130 cm-long core of *P. oceanica* were incubated, under anaerobic and aerobic conditions. To our knowledge, this represented the first attempt to incubate soil samples in Ecoplates under anaerobic condition. The results suggest a pronounced stratification of the microbial community controlled by oxygen availability. Despite the higher aerobic metabolism in the top 40 cm, the anaerobic metabolism was dominant in the overall core length, supporting the high capacity of *P. oceanica* soils for OM stabilization.

While the previous three manuscripts enabled to observe and explore the composition and change with depth of seagrass soils, to infer its biogeochemical process in **Manuscript 4** we compared three cores of the Portlligat meadow with different status: the first one is the same core studied in Manuscript 1 and Manuscript 3; a second core was taken in an area of death meadow (were the seagrass cover has been lost) and the third core was sampled in a living meadow next to the death meadow area. In this study we aimed to understand how seagrass cover losses affect the carbon cycle in the soil by analyzing i) total, inorganic and organic carbon and nitrogen contents; ii) using analytical pyrolysis to assess the molecular composition of the geochemically reactive OM (<2mm fraction) and its relation to depth from the soil surface, as a proxy for time; and iv) metabarcoding to infer bacterial and archaeal diversity changes. The results showed the preferential mineralization of polysaccharides and guaiacyl and syringyl lignin, and a selective preservation of *p*-hydroxybenzoic acid moieties and methylene chain compounds. Soil depth and plant cover showed significant effects on microbial richness and diversity. Spatial variations in SOM inputs and microbial differences in community composition between cores highlighted the importance of intra-meadow variability. Furthermore, this study showed that seagrass cover loss enhances OM mineralization and highlights the importance of soil stabilization against erosion to avoid the release of millenary organic carbon stocks.

Manuscript 5 presents a review of the large effort invested in seagrass substrates research to contribute to amend the lack of pedological studies in subaquatic marine environments, by summarizing the data typically used for soil description and classification. A literature review of papers published between 1980 and June 2020 yielded more than 3,800 references from which the available information about bulk density, grain size, redox, pH, carbonate content, organic carbon content and porosity was gathered. Large knowledge gaps were found geographically and in seagrass diversity, being the temperate meadows, especially those from *Posidonia* and *Zostera* genus, the ones more studied. Nonetheless, some conclusions could be inferred: (1) Most seagrass substrates have sandy textures, being the *Posidonia* genus not able to grow in muddy substrates. (2) Although they promote OM accumulation, seagrasses are unlikely to form organic soils. The formation of Histosols seems to be a rare event linked to the *Posidonia* genus. (3) The most likely classification of seagrass derived soil is as Entisols according to the ST-USDA, and as Fluvisols or Gleysols according to the WRB-FAO.

Summarizing, the major findings of this thesis are (1) that there are two distinct biogeochemical compartments in seagrass soils, the rhizosphere and the subsoil, (2) that the main processes found were somewhat related to OM accumulation and mineralization, (3) changes in plant physiology, or death, affect the rhizosphere biogeochemistry, but not the subsoil, and (4) that not all substrates below seagrass meadows meet the characteristics of a soil, but given enough time, all substrates below seagrass meadows are likely to be transformed into soils. The use of *P. oceanica* soils as a model may have overestimated the importance of OM geochemistry in seagrass soil, as those soils show higher OM concentrations than other seagrasses soils. As found in the Portlligat meadow, it is likely that seagrass meadows would have a high spatial diversity and the examination of their spatial distribution is recommended to select the area more suitable for an experiment or for samples retrieval. It would be particularly interesting to compare the inorganic chemistry of meadows with geologically contrasting adjacent watersheds. Metal behavior in the soil was unclear. Further research on the biogeochemistry of metallic elements in the soil would contribute to the efforts devoted to fully explore the potential of these soils as environmental archives of past human activities, as metal content is a key proxy for mining, metallurgy and industrial development.

GENERAL INTRODUCTION

1. Marine phanerogams: the seagrasses

Marine phanerogams, known as seagrasses, are a polyphyletic group of marine angiosperms from the superorder Alismatales (Hartog and Kuo 2006). They do not represent an intermediate state between algae and terrestrial plants, but a secondary colonization of marine shallow waters by terrestrial plants (Duarte 1991; Lambers et al. 2008). Phylogenetic analysis indicates that there were at least three independent lineages that returned to the sea by parallel evolution (Les et al. 1997)(Fig. 1). However, seagrasses have developed similar morphological and physiological adaptations to live in the sea, suggesting the habitat as the leading selection force for those adaptations (Wissler et al. 2011; Lee et al. 2018). Like cetaceans, they returned to the oceans carrying traits of their terrestrial ancestors (Lambers et al. 2008). However, molecular and morphological adaptations occurred as the mechanisms developed to live inland faced the challenges posed by the underwater realm. For example, several of their molecular developments can be linked to cope with the saline environment (Wissler et al. 2011), leaves sheath and blade morphology and physiology evolved to allow photosynthesis in sea water (Kuo and den Hartog 2006) and, in most cases, seagrasses developed submarine pollination (Ackerman 2006). On the other hand, some of the original terrestrial traits may have allowed seagrasses to overcome some marine life challenges. For instance, the reinforcement of their tissues with lignin to maintain upright position out of the water (Sarkanen and Ludwig 1971) may have supported the development of the lacunar system (Klap et al. 2000), which allows seagrasses to reduce phytotoxics such as Fe^{2+}, Mn^{2+} or sulfide in their rhizosphere (Borum et al. 2006).

The development of belowground organs is one of the outstanding characteristics of terrestrial plants. Similar to many seagrass adaptations to marine life, roots seem to have appeared in several independent evolutionary lineages, as a requirement of the terrestrial

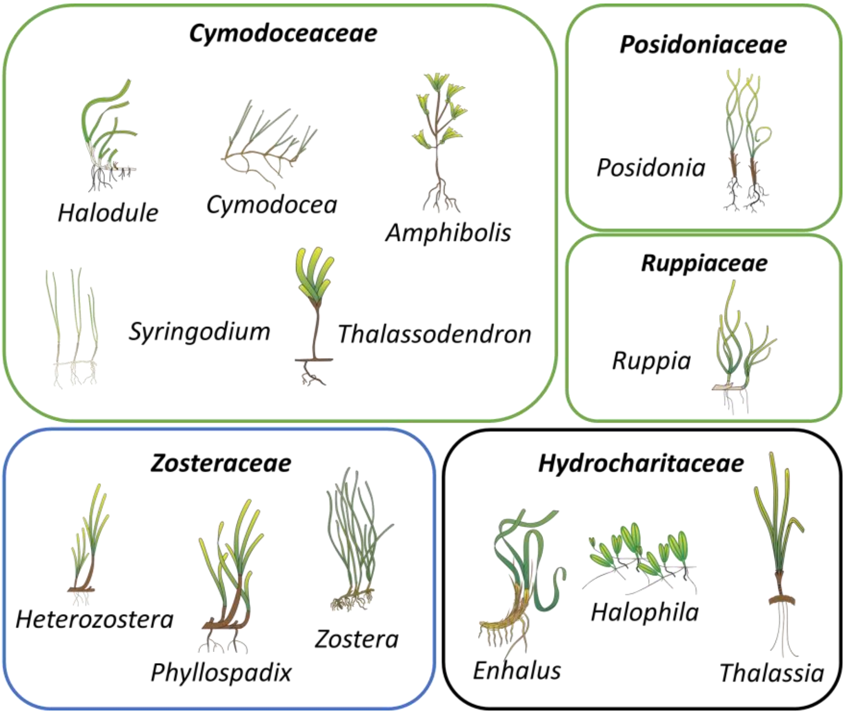

Figure 1: families and genera of seagrasses with an example of one of their species morphology (not scaled). The color of the boxes represent the sea colonization lineage they belong acording to Les et al. (1997). IAN Symbol Libraries is acknowledged for the seagrass symbols.

environment (Doyle 2017; Shekhar et al. 2019; Fujinami et al. 2020). The evolution of hypogenous rhizomes allows the formation of large storage and nutrient exchange networks (Jónsdóttir and Watson 1997; Janeček et al. 2008) that confer resistance to mild recurrent disturbance, as burial (Xue et al. 2016; Herben and Klimešová 2020). The main functions of rhizomes in seagrasses seem to be anchoring, mechanical support, storage, and regulation of vegetative growth (Kuo and den Hartog 2006).

2. Seagrass meadows and soil diagenesis

Seagrass meadows are distributed in coastal areas of all continents but the Antarctica, showing a higher seagrass diversity in the tropics than in temperate areas (Holmer 2018). They can be found upon hard and soft bottoms from clay/silty to coarse sediments (Koch 2001). Their water depth distribution is constrained by light penetration (Duarte 1991).

Their canopies promote sediment accretion by direct trapping of particles and by lowering the hydrodynamic force (Agawin and Duarte 2002; Hendriks et al. 2008; Gruber and Kemp 2010; Hansen and Reidenbach 2012). Furthermore, canopy structure and belowground organs reduce sediment resuspension (Ward et al. 1984; Terrados and Duarte 2000; Gacia and Duarte 2001; Widdows et al. 2008). Usually, this increased sedimentation and avoided resuspension lead to an increase of the fine fraction content in the deposit (Bos et al. 2007; Rueda et al. 2008). However, low canopy density in sheltered intertidal areas can cause turbidity and favor fine fraction loss (van Katwijk et al. 2010). The deposit grows in thickness forming, when undisturbed, well-structured soils following a chronological sequence in which deeper equals to older (Mateo et al. 2002). Together with inorganic particles, seagrass meadows bury organic matter (OM), both autochthonous and allochthonous. The anoxic conditions of their soils promote the conservation of this OM from decades to centuries (Mateo et al. 2006).

Plant derived changes in the substrate are held in the rhizosphere and can vary with meadow maturity (Holmer 2018). Rhizosphere depth differs largely between species but is usually restricted to the upper 40 cm. It has been reported to occupy from 3 to 80% of the substrate volume and has a total absorptive area often exceeding 1 m^2 m^{-2} (Duarte et al. 2005a). Seagrass rhizomes and roots release O_2 which avoids the formation of phytotoxics, generating oxic microenvironments (Borum et al. 2006; Jensen et al. 2007). Moreover, seagrass roots release dissolved OM promoting microbial activity. The roots uptake nutrients from the soil, however, is not the only path of nutrient uptake, as nutrients absorbed by the leaves can occasionally outmatch those absorbed through the roots (Holmer 2018). The seagrasses are not the sole organism promoting physico-chemical changes in the meadow substrate. Burrowing organisms directly affect diagenesis through oxygenation and mixing of the soil material (Kristensen 2000). Microbial communities intervene in OM mineralization and nutrient cycling (Marbà et al. 2006).

Figure 2: Bajos de Alquian *Cymodocea nodasa* meadow soil, East Andalusia, source GAME (left); Els Pujols *Posidonia oceanica* reef, Balearic Island, source Miguel Ángel Mateo (right).

Microbial communities in marine sediments are usually stratified following the exhaustion of electrons acceptors with depth. However, the oxic microzones formed around seagrass rhizomes and root tips allow the development of aerobic metabolisms throughout the length of the rhizosphere (Seymour et al. 2018). Kilminster and Garland (2009), working with *Halodule wrightii* and *Syringodium filiforme* meadows, found that distance from the roots, O_2 release and root structure affected the distribution of the microbial community. What has also been related to seasonality, root age or meadow health status (García-Martínez et al. 2005, 2009). Community composition is influenced by both environment factors and the seagrass species, but seems to be more dependent on the first (Cúcio et al. 2016).

Some seagrass species (e.g., *Posidonia oceanica* or *Posidonia australis*) develop high OM content soils, known as "mats" (Boudouresque and Meinesz 1982; Mateo et al. 2006). Mats can form shallow waters reefs creating shallow lagoons between them and the shore that host smaller seagrass and marine reef species (Boudouresque and Meinesz 1982; Serrano et al. 2017). The role of mats as long-term carbon reservoirs has boost the interest about the fate of the OM buried in seagrass soils. Although several soil carbon stocks and fluxes estimations in seagrass meadows have been published (e.g. Serrano et al. 2018, 2019; Kindeberg et al. 2019), information about physicochemical processes involved in OM degradation within the soil are scarcer. The OM accumulation in the soil has been linked to (1) particles trapping and deposition favored by the seagrass canopy, (2) the anoxic conditions in the sediments and (3) to the refractory character of the seagrass tissues, which can be preserved over millennia (Mateo et al., 1997; Lavery et al., 2013; Serrano et al., 2016b). Trevathan-Tackett et al. (2020) suggested that the decomposition of seagrass tissues in the soil is not a steady process but rather a multi-phase process, being the first and more intense a passive leaching phase. However, degradation dynamics would dependent on the type of seagrass tissue, leaves litter or belowground organs. Kaal et al. (2016), working over *P. oceanica* tissues preserved in the soil, found that carbohydrates, syringyl lignin, and C16-fatty acids were degraded while p-hydroxybenzoic acids were selectively preserved.

3. Seagrass substrates as soils

Traditionally, seagrass substrata have been considered sediments (Kristensen and Rabenhorst 2015). Soft marine bottoms are sedimentary deposits and, consequently, it is straight forward to state that seagrass colonize and live upon sediments. Sedimentary deposit can be also found inland (e.g. alluvial deposition), but the denomination of sediment or soil does not depend on the parent material, sediment or bedrock, but in the presence or absence of a transformation of these materials that would usually depend on whether they are colonized by plants or not (Soil Survey Staff 1999; IUSS Working Group 2015). Plant colonization would not necessarily result in the formation of a soil (e.g. intermittent dune plant colonization), as the parental material should necessarily undergo additions, removals, transfers and transformation (i.e. main soil processes) (Simonson 1959). On these grounds, it is not possible to argue that every substrate below seagrasses would be a soil, because the required physicochemical changes are not always present. However, the presence of the seagrass triggers changes in the substrate that, given enough time, would radically transform it from a mere accumulation of sediments, alike in terrestrial pedogenesis.

The Unite States Department of Agriculture Soil Taxonomy (ST-USDA) definition of soil recognizes the possibility of soil formation under seagrass since its first edition (Soil Survey Staff 1975). However, as pointed by Demas (1993), subaqueous soils were largely neglected in soil science research. After Demas' efforts, subaqueous soils were directly acknowledged in the ST-USDA second edition (Soil Survey Staff 1999). Also including the possibility of subaqueous soil being formed without plant presence, as long as pedogenesis was taking place, coinciding with a shift from a plant-substrate interaction to a process-based point of view (Ellis 2006). On the other hand, subaqueous soils are only recognized by the World Reference Base for Soil Resources (WRB-FAO) up to 2 m depth at low spring tide (IUSS Working Group 2015). This partial recognition allows substrata from meadows formed by intertidal or shallow waters seagrasses, as *Zostera spp.* (Moore and Short 2006), to be recognized as soils, but prevents substrates of meadows below 2 m depth from being considered soils, even if those meadows are composed by seagrasses with a higher impact over the substrate, such as *Posidonia spp.* (e.g. Fourqurean et al. 2012). Furthermore, this arbitrary limit implies that the seagrass substrate of the same meadow, with the same age, and same characteristics, could be considered or not a soil on the sole basis of depth – approach not consistent with the soil-continuum.

As discussed above, the development of a soil underneath seagrass meadows would require that soil processes (i.e additions, removals, transfers and transformation) have occurred. Material additions in seagrass substrate can be consider, for example, OM accumulation, which significantly increases compared to adjacent bare sediments due to the presence of belowground organs or to the trapping of allochthonous OM (Mateo et al. 2006); addition of nutrients (Marbà et al. 2006); or addition of biogenic carbonates (autochthonous or allochthonous) promoted by the plant presence (Mazarrasa et al. 2015; Saderne et al. 2019). Removal of material can happen trough CO_2 (Mateo et al. 2006) and CH_4 release (Al-Haj and Fulweiler 2020) or bioturbation (Thomson et al. 2019). Transfers of material can occur also by bioturbation (Thomson et al. 2020), by plant uptake (Marbà et al. 2006) and burial of plant tissues, or by dissolution and reprecipitation of carbonates (Hu and Burdige 2007). Last, examples of transformations are the microbial assimilation of OM (Mateo et al. 2006), the nutrient cycling (Marbà et al. 2006), or sulfide reduction (Holmer et al. 2003b).

The intensity and nature of these soil processes would be determined by several factors that would dictate the final characteristics of the soil formed. Looking to encompass factors with influence in soil formation, Henry Jenny (1941) proposed a factorial analysis model,

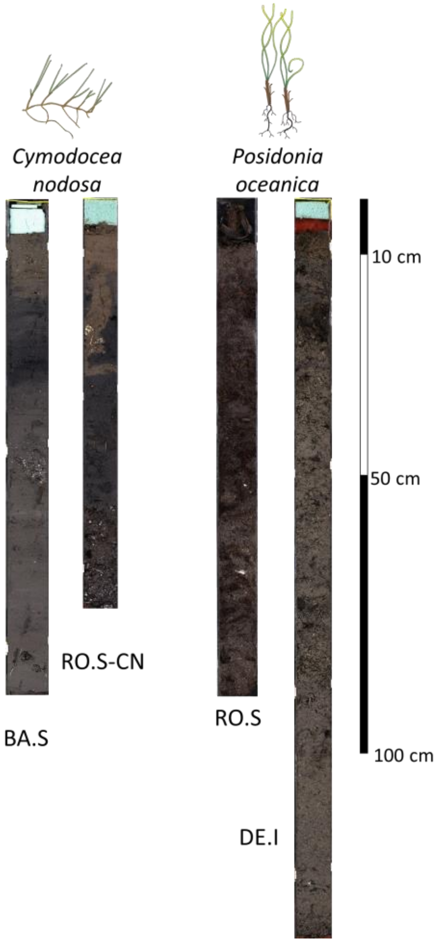

Figure 3: from right to left, cores from Bajos de Alquian (6.8 m depth) and Roquetas (1 m depth) *Cymodocea nodosa* meadows and Roquetas (1.5 m depth) and Villaricos (15.9 m depth) *Posidonia oceanica* meadows.

where the factors consider were: climate, organisms, relief (topography), parental material and time. These factors were later revised together with the genetic model for estuarine sediments – geology, bathymetry and hydrology condition (Folger 1972a,b) – for their adaptation to subaqueous soils by Demas and Rabenhorst (2001). The final model proposed included climatic temperature regime, organisms, bathymetry, flow regime, parent material, time, water column attributes, and catastrophic events. To which extent will water temperature influence the temperature of the soil below seagrass meadows is still uncertain, as temperature transmission with depth in seagrass soils has not been thoroughly assed. Salisbury and Stolt (2011) found a good correlation between water temperature and soil temperature at 25 and 50 cm depth in subaqueous soils, although water temperature influence decreases with depth. An indirect effect of climate temperature regime over soil formation would be which seagrass species is able to settle (Hartog and Kuo 2006). Seagrass species have different soil modification capacities, for example, to increase the content of OM and carbonates (Mazarrasa et al. 2015; Trevathan-Tackett et al. 2017). The seagrass itself plays key roles in the evolution of seagrass substrates (Marbà et al. 2006). Burrowing (Kristensen et al. 2013; Thomson et al. 2019) and calcifying organisms (Saderne et al. 2019), microbes (Marbà et al. 2006; Seymour et al. 2018) or humans (Serrano et al. 2011; Greiner et al. 2013), are also major exponents involved in soil transformation. Bathymetry would determine light availability, which would affect plant density (Pergent-Martini et al. 1994) and photosynthetic activity (Duarte 1991), affecting soil formation dynamics by, for instance, modulating the O_2 flow to the rhizosphere (Borum et al. 2006). The regime flow would refer to the local hydrodynamics affecting, among others, plant productivity (Fonseca and Kenworthy 1987), and the sedimentary balance of the meadow (Fonseca and Bell 1998; Schanz and Asmus 2003). The characteristics of the parental material, such as texture, mineralogy, nutrient load, etc..., will strongly determine which seagrass species will settle, its performance, and the chemical transformations that will take place (Koch 2001; Holmer et al. 2003b; Marbà et al. 2008). Time is a necessary factor in any soil formation, as the intensity of all pedogenic changes would be influenced by it. The water column attributes (light attenuation, resuspension potential, sediment particles travelling distance, among others) would control the amount and nature of what is deposited on the meadow, along with plant physiology (photosynthetic rate, compensation thresholds, etc.; Duarte 1991; Koch 2001; Leiva-Dueñas et al. 2020). Finally, catastrophic events (e.g. extreme storms or oil spills) may affect soil formation, for example, by increasing plant rate mortality, and thus decreasing its effect over the substrate (Gera et al. 2014). Although seagrass soils can be as diverse as their terrestrial counterparts, being permanently water saturated, growing in thickness, and creating favorable conditions to accumulate OM, are traits common to most of them. Those characteristic are partially fulfilled as well by subaerial soils from peatlands, tidal or freshwater marshes and mangroves (Rydin and Jeglum 2013; Ellison 2018; French 2018; Tobias and Neubauer 2018).

4. Implications of soil recognition

Despite the effects seagrass have over their substrate are widely acknowledged by marine scientist and that seagrasses are recognized as soil forming (i.e pedogenetical) agents by soil scientists, a consensus has not yet been reached about which should be the specific substrate denomination. An attempt to clarify this issue was made by Kristensen and Rabenhorst (2015), who proposed that <<[…] *the terms "sediment" and "soil" are not necessarily mutually exclusive. Materials that have been transported to and deposited on the floor of an aquatic environment should be denoted sediment. Soil may be an appropriate notation when pedogenically formed "horizons" can be observed.*>>. Their view agrees with the ST-USDA in that the important factor for classifying a substrate as soil or sediment is not the presence of vegetation but the existence of a transformation of the parental material leading to the vertical structuration of the deposit, denoted by the horizons.

The relevance for seagrass substrates to be recognized as soils may go beyond than a mere change in nomenclature. This recognition, by itself, may help to clarify the nature of the deposit more efficiently. As stated by the several studies focused on highlighting the difference between seagrass meadows substrates and the adjacent bare sediments (e.g. Delille et al. 1996; Enríquez et al. 2001; Duarte et al. 2005b; Bernard et al. 2014), seagrass substrate fulfilling soil standards and sediments are radically different. On the other hand, when compared with subaerial soils also formed by accumulation processes (e.g. peatlands or wetland soils), they are quite similar, even though they are formed in entirely different environments (Mateo et al. 2006).

Their recognition as soils would shift several ecosystem services from the seagrass meadow to the substrate beneath them. Although some of the ecosystem services are provided through the presence of the plant, other services like long-term OM stabilization or reef fish sheltering are not provided by the plant itself but by the substrate (Mateo et al. 2006; Serrano et al. 2017). Thus, a young seagrass meadow that has not yet formed a biochemical differentiated substrate – a soil - would not provide these services. The shift of these ecosystem services to the substrate – promoted by soil recognition - would (1) better reflect the processes through which ecosystem services are provided and (2) highlight that even when the plant cover has disappeared (i.e., the meadow has died), ecosystem services will be still provided and the “dead” substrate will still be a functional ecosystem and not a barren bottom (e.g. Borg et al. 2006). As said before, young seagrass meadows had not necessarily developed soil yet and, even though they are already providing valuable ecosystem services, soil-related ecosystem services may take tens to hundreds of years to be provided, making the recognition, protection and restoration of bare seagrass-derived soils more crucial.

GENERAL OBJECTIVES

The overall aim of this thesis is to study the biogeochemistry of marine phanerogams soils and, using the available pedological information, to establish a preliminary soil description. To this end, a generic exploration of geochemical signals is presented in Chapters I and II, and studies focused on OM degradation and its interaction with the microbial communities are presented in Chapters III and IV. Finally, a review of the main characteristics of seagrass soils and a preliminary classification is presented in Chapter V.

The specific objectives of each chapter are:

1. To study the biogeochemical signals in a single core from a well-developed *P. oceanica* meadow, looking for vertical structuration of the soil that could be related to its horizonation and provide a preliminary classification following the ST-USDA and WRB-FAO. To this end, the elemental composition and the carbonate and OM contents were analyzed along a 475 cm-long core encompassing the last 4000 years, using the available information about the Portlligat seagrass mat to contextualize the processes found (**Chapter I**).
2. To explore the main biogeochemical processes determining soil composition in the two main seagrass Mediterranean species (*P. oceanica* and *Cymodocea nodosa*). For this purpose, fifteen stations were sampled along the Andalusian eastern coast and analyzed for elemental geochemical composition, magnetic susceptibility, organic carbon (C_{org}) density, particle size distribution and sediment accretion rate. A Principal Component Analysis was used to summarize the main processes leading to soil formation (**Chapter II**).

3. To assess the potential microbial communities' activity with depth in a *P. oceanica* soil and their potential carbon source consumption. Soil samples along a 130 cm-long core were incubated in 31 different carbon sources (Biolog EcoPlates^{TM}) under aerobic and anaerobic conditions (**Chapter III**).

4. To determine the soil OM degradation pattern and microbial community structuration with depth and its changes after seagrass cover loss. Three cores from the same meadow were sampled under different ecological conditions: (1) one area where the seagrass has died-off showing only dead mat, (2) another one adjacent to the previous but presenting an intermediate plant density as compared to the meadow average density, and (3) a third area presenting the full canopy density characteristic of the high health status of the bay. The three cores were analyzed for total, inorganic and organic carbon and nitrogen, as well as for molecular OM composition by analytical pyrolysis. Bacteria and Archaea communities were assessed by 16S rRNA gene metabarcoding (**Chapter IV**).

5. To preliminary classify seagrass soils using the available pedological information (**Chapter V**).

GENERAL METHODS

In this thesis *P. oceanica* soils were used to explore soil formation processes in seagrass substrates. This species constitutes an ideal model due to the high impact this seagrass has over the substrate, i.e. soil development (Boudouresque and Meinesz 1983), and to the large quantity of information already available about biogeochemistry of its substrate. The soils studied were sampled in two areas: The Portlligat Bay and the Andalusian coast, in the north and south of the Spanish Mediterranean peninsular shores, respectively.

Portlligat Bay (NW Mediterranean) is a shallow bay (<10 m) that connects to the sea by a 213 m wide opening to the North East. It hosts a well-developed *P. oceanica* meadow that was established since at least 6000 yr ago (Mateo et al. 2002), forming a highly organic soil that reaches at least 4.75 m depth (Serrano et al. 2011). The present ecological status of the meadow was described by Hereu et al. (2016), and its past history has been addressed using paleo-ecological reconstructions of human impacts (Serrano et al. 2011; López-Merino et al. 2017) and of ecosystem productivity (Mateo et al. 2010; Leiva-Dueñas et al. 2018). The large quantity of information published about the bay and its meadow and the and the coexistence of dead and healthy, well developed meadow areas, makes Portlligat bay an ideal location to study the soil biogeochemistry and its response to plant cover loss. The studies from Chapters I, III and IV are focused on cores sampled in the Portlligat Bay meadow.

The Andalusian coast (S Iberian Peninsula, SW Mediterranean Sea) presents a large environmental heterogeneity with three main areas, the Atlantic coast (with no *P. oceanica* meadows), and two areas inside the Mediterranean Sea. One with the characteristics of the Mediterranean Sea and the other, the Alboran Sea, with intermediate characteristics between the Atlantic Ocean and the Mediterranean Sea (Arroyo et al. 2015; Leiva-Dueñas et al. 2021). Furthermore, the geological features along the Andalusian coast, such as its lithology, are highly heterogeneous (Red de Información Ambiental de Andalucia 2020). This large environmental variability together with the large area occupied by seagrass meadows (>10,000 ha; Mateo et al. 2018), makes a wide range of soil types available allowing to look for common biogeochemical processes and for the main factors controlling seagrass soils formation and composition. The cores sampled along the Andalusia coast are studied in Chapter II.

Each chapter presented in this thesis has its own approach an objectives and any reader interested in the methods used for any of those approaches is directed to the specific methods section of that chapter. Below, the main field, laboratory and numerical methods are summarized.

1. Sampling techniques:

Three different sampling techniques were used. The core studied in Chapter I was collected from a floating drilling platform. A PVC tube was pushed into the soil with a self-powered pneumatic hammer (Cobra, Atlas-Copco) that combined pneumatic percussion and rotation (see Serrano et al., 2012). Most of the cores studied in chapter II and all the cores used in chapters III and IV were sampled by slowly hammering and rotating a PVC tube (150-200 cm long, internal diameter 7.5 cm) into the soil by SCUBA divers. The tube had a core catcher fitted at its bottom end to avoid loss of material during retrieval. One of the cores used in the second chapter was taken using a vibrocore (Geo-Corer 3000, Igeotest) fitted with a polycarbonate core pipe (600 cm long, internal diameter 10 cm). The first two methods resulted in core compression, which was mathematically corrected afterwards (Morton and White 1997). The vibrocore technique does not result in core compression but may disturb the layered structure of the top section of the core, hindering its use as an environmental archive.

2. Laboratory methods:

The soil cores were cut transversally at 1-2 cm slices and dried in the oven (60°C) until constant weight. Except for the microbiological analyses, XRF-core scanner, magnetic susceptibility and the grain size distribution, all the other analyses were conducted over homogenized sample.

Grain size was determined by digesting the samples with hydrogen peroxide at 30% to remove the OM, sieved at <1 mm and measured using laser diffraction (Mastersizer2000, Malvern Instruments, Centre d'Estudis Avançats de Blanes). OM values were obtained by the mass-loss-on-ignition technique (450 °C for 5 h). Samples for C_{org} were digested by adding HCl 1M to eliminate carbonates and measured in an elemental analyzer using standard procedures.

Two different techniques were used to determine the elemental composition: XRF over homogenized bulk sample (Chapter I) and XRF-core scanner (Chapter II). While the later can be applied to undisturbed cores to obtain semi quantitative measures, the former provides quantitative measures using processed soil samples.

The composition of the OM was analyses by analytical pyrolysis. This technique is based in the fragmentation of the organic chemical compounds of a homogenized sample through a thermal impact. The resulting fragments are sorted by gas chromatography and measured by gas spectroscopy (Moldoveanu 2010). The identification of the fragments and original compounds is possible thanks to the available extensive databases and literature.

The study of the microbial community was approached using two techniques: Biolog Ecoplates ^{TM} and metabarcoding. The Ecoplates^{TM}

are a semi-quantitative method developed to characterize microbial functional activity by measuring the respiration activity of the microbial community on different carbon sources. The respiration of is revealed by the reduction of a tetrazolium dye that is included with the carbon source. Metabarcoding is a species identification technique that uses high-throughput DNA sequencing to identify multiples species from a mixed sample (see van der Reis and Lavery 2020).

3. Soil sample dating

Age-depth models of the cores studied in chapter II were built to estimate their average accretion rate using ^{210}Pb profiles (on bulk soil sample) and Acceleration Mass Spectrometry ^{14}C dating (on seagrass macro-debris). The concentration profile of ^{210}Pb was determined at every centimeter for the uppermost 30 cm of the cores. Age-depth models were obtained using the *rbacon* package for R software (Blaauw and Christeny 2011; R Core Team 2019).

4. Statistical methods:

All the cores used in this thesis were compressed during retrieval except for the core sampled by vibrocoring. The core length measured at the laboratory was corrected to the approximate field length using an exponential function, under the assumption that compaction increases from the bottom to the top of the core (Morton and White 1997).

The main statistical method used in this thesis was principal component analysis, aiming at summarizing the correlation between our proxies and to reduce the dimension of the variables involved. The resulting principal components were then interpreted as reflecting biogeochemical processes/signals. When correlation between two variables was tested, the Spearman method was utilized as neither a normal distribution nor a linear relationship was expected in the soil core data sets. Furthermore, change-point modelling (CPQtR1.0.3;

Gallagher et al. 2011), Chaos 1 and Shannon index, permanova, non-parametric manova, FAPROTAX, and non-metric multidimensional scaling were occasionally used (see methods section of each chapter).

Statistical analysis were run in Excel and R software (Microsoft 2016a; R Core Team 2019), packages *phyloseq* and *psych* (McMurdie and Holmes 2013; Revelle 2017).

5. Literature review:

A literature review was conducted to gather the information published about some of the main parameters used in pedological studies in seagrass soils (Chapter V). Data has been gathered through a literature review using the *Web of Knowledge* (https://www.webofknowledge.com/, accessed from 6th to 22th of July 2020). The variables collected were clay and silt content (mud <0.063 mm), redox potential, pH, carbonates content, organic carbon or organic matter content, dry bulk density, porosity and color. Search terms used were as follows: TS= (seagrass AND (sediment* OR soil) AND *Variable*); where *Variable* was replaced with "bulk density", "grain size", "redox", "pH", "carbonate*", "organic matter OR organic carbon" or "porosity". The period comprised by the search was since 1980 to June 2020.

6. Graphical representation:

Graphical representation of data was conducted by Excel (Microsoft 2016a) and package *ggplot2* for R software (Wickham, 2009; R Core Team, 2019). Diagrams were built using PowerPoint (Microsoft 2016b) and symbols from the Integration and Application Network (University of Maryland Center for Environmental Science). Graphical representation of geographic data was built with QGIS software (QGIS Development Team 2020). GIMP 2 software was used to improve representation quality and merge plots (The GIMP Development Team 2019).

GENERAL DISCUSION

Despite their recognition as soils by the ST-USDA, pedological studies on seagrass substrates are anecdotic. To our knowledge, only four attempts have been made to classify them (Bradley and Stolt 2003; Balduff 2007; Serrano et al. 2012; Nóbrega et al. 2018). However, there is an extensive literature about the rhizosphere biogeochemistry, specially from *Zostera* or *Posidonia* meadows (Chapter V). In this thesis, I have explored the biogeochemistry of these soils, above and below the rhizosphere, aiming to identify long-term pedogenic processes. Furthermore, a preliminary description and classification is attempted.

The *Posidonia oceanica* soils were used as a model for seagrass soil biogeochemistry, due to the high impact of this seagrass over their substrate and the large amount of available information about the biogeochemistry of its rhizosphere. I have explored the changes with depth, as a proxy for time, of a number of biogeochemical proxies (i.e. soil properties) and found several common processes and a large compositional heterogeneity between and within meadows. The differences in composition seem to be highly controlled by terrestrial sedimentary inputs. Two main compartments stand out, that under the influence of the seagrass roots and rhizomes (rhizosphere) and the substrate below (subsoil). The differences observed between these compartments were mainly related to the dominant processes: within the rhizosphere these processes are led both by the plant and the associated microbiota, while in the subsoil the processes are dominated by the mineralization of OM by the microbial community. The main processes found were somehow related to the accumulation and remineralization OM. This may be due to the used of *P. oceanica* as a model, as those meadows accumulate high concentrations of OM in its soils compared to other seagrasses (Chapter V). Therefore, processes involving the inorganic phases may have not been properly addressed in this thesis.

The techniques used include basic geochemical characterization, XRF, microbial functional activity (Biolog Ecoplates^{TM}), metabarcoding and analytical pyrolysis. The XRF allowed to compare the composition of the different meadows studied and to link that composition to soil formation processes (Chapter I and II). Microbial functional activity was used to explore the potential stratification of carbon sources consumption in the soil (Chapter III). Metabarcoding and analytical pyrolysis were used in tandem to look into the degradation of OM compounds and the microbial communities involved, considering the presence of the seagrass and within specific soil compartments - rhizosphere or subsoil (Chapter IV). Furthermore, a review of the main pedological features has been made (Chapter V). However, this information was far from being enough to allow for a proper soil classification, making evident the need of a more adhoc methodology to address this challenge.

1. The stratification of seagrass soils

The presence of two biogeochemically different compartments turned to be particularly evident when studying the stratification of the microbial communities and the OM composition and mineralization processes (Chapter III and IV). On the other hand, differences in the bulk composition between these compartments were smaller and mainly related to the proportion between organic/inorganic materials (Chapter I). When several meadows were compared, differences between meadows were higher than the differences within the meadow soil (between rhizosphere and subsoil; Chapter II).

Since the transformations produced/induced by the seagrass over the substrate always operate in the rhizosphere, sediment accumulation rate is a key factor controlling the degree of substrate transformation.

The time spam that a given substrate layer would be under the influence of the rhizosphere would be necessarily linked to the sediment accretion rate, as this would determine the time it would take to bury this layer below the lower limit of the active living roots (Fig. 4). Therefore, meadows with lower accretion rates would likely present more pedogenetically developed soils.

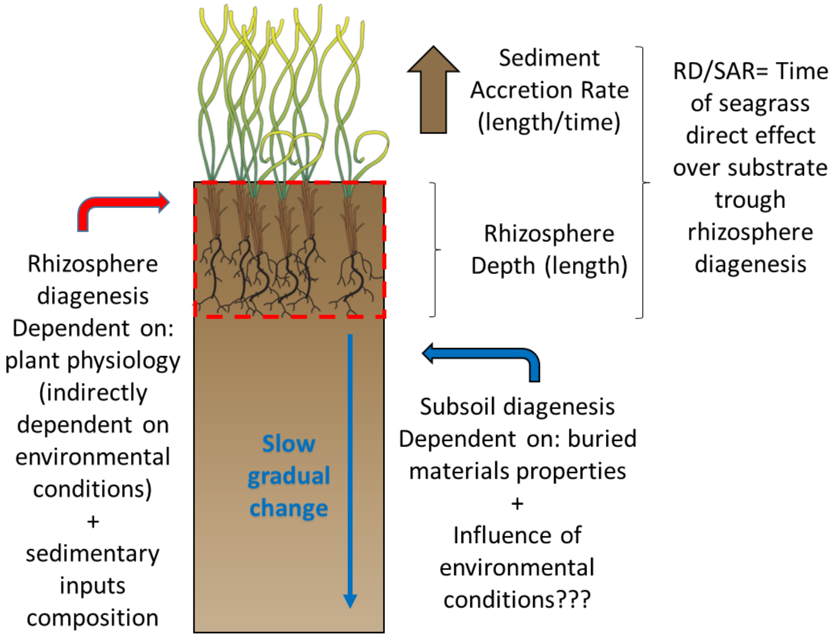

Figure 4: summary of seagrass soil diagenesis (RD: Rhizosphere Depth; SAR: Sediment Accretion Rate)

1.1. The rhizosphere

The highest potential microbial activity corresponded to aerobic communities, although anaerobic metabolic activity was also detected in the rhizosphere (Chapter III). This contrasts with the reducing conditions that are expected to prevail in marine sediments and can be linked to the formation of aerobic micro-niches sustained by the O_2

pumped by the seagrass (Jensen et al. 2007; Marbà et al. 2010). The predominance of the potential aerobic activity over bulk microbial activity, even being those micro environments restricted to a few millimeters from the rhizomes and root tips, may be explained by the high metabolic efficiency of the aerobic microorganisms compared to anaerobic ones. Aerobic microorganisms are able to fully decompose organic molecules while anaerobic microorganisms usually need to form a consortium where several microbial species collaborate in the degradation (Kirchman 2012). Furthermore, the microbial communities within the micro-niches would be the first to access the easy degradable OM leached by the seagrass. The formation of micro-niches with high OM mineralization activity may be related to the pH heterogeneity found in the seagrass rhizosphere, as it has been associated with OM degradation (Brodersen et al. 2016, 2017).

In terms of overall composition, the rhizosphere shows a higher OM content compared with the subsoil (Chapter I), being also enriched in easily degradable organic compounds (Chapter IV; Kaal et al. 2016). However, not all of these compounds are accessible to microbial degradation (Chapter III), as part of this OM corresponds with the living plant or is deposited as macro-debris (Serrano et al. 2012). The source of OM in seagrass soils can be the seagrass itself, in the form of organic exudates released through the roots or as belowground organs that remain in the soil after plant death (Moriarty et al. 1986; Blaabjergl et al. 1998; Nielsen et al. 2001). This OM can also be sourced by other meadow primary producers or by the deposition of allochthonous OM particles (Marbà et al. 2006). The proportion between seagrass derived OM and other sources varies among meadows, but seagrass derived OM is usually the main source (Kennedy et al. 2010). Therefore, it would be expected that seagrass productivity would partially control de accumulation of OM in the soil. Unexpectedly, in this thesis, the minimum C_{org} content did not occurred at the deepest bathymetric range of the meadow (e.g., cores sampled at Aguamarga and Terreros, Fig. 3, Chapter II), where seagrass biomass is at its lowest (Mateo et al. 2018). These discrepancies may be partially explained by differences in inorganic inputs. OM density would be a result of the accumulation of inorganic matter as well. Therefore, at the same rate of OM accumulation a meadow with a lower accretion rate (i.e. lower inorganic sediment inputs) would have a higher OM density than a meadow with a higher accretion rate, owing to a lower OM dilution by the inorganic inputs.

1.2. The subsoil

As expected, the predominant potential microbial activity found in the subsoil was anaerobic (Chapter III). The OM mineralization was slower than in the rhizosphere and it seemed to reach equilibrium after ≈1000 yr. (Chapter I). Although at a slower rate, the anaerobic communities seem to have the capacity to degrade a wider range of organic compounds (Chapter III). This would agree with a lower availability of OM in the environment (Chapter IV).

Losses of OM in the subsoil can change the proportion of other components. The PCA analysis in Chapter I, showed that the concentrations of the lithogenic elements and carbonates increase below the rhizosphere at the same pace as OM content decreases. The enrichment in inorganic fraction with time in the subsoil due to OM mineralization is an expected phenomenon, as part of that OM is released as CO_2 and new OM inputs are quite limited (or negligible) below the rhizosphere. The intensity of the enrichment would depend on the rate of OM mineralization. OM degradation also results in the enrichment of recalcitrant organic compounds with time (see section below). However, this process may have a much lower overall effect in soils below other seagrasses compared to *Posidonia* mats, as they hold far lower concentrations of OM (Chapter V).

Although few published studies report redox measurements for the subsoil, they suggest that the values would resemble those of bare marine sediments, as the positive anomaly caused by the rhizosphere seems to fade with depth (Chapter V). Bulk density increased naturally in the subsoil by autocompaction. Autocompaction refers to the increased density of substrate layers due to the accumulation of new substrate layers above them (Allen 2000). This affects the concentration of the different fractions or compounds but does not affect their relative abundance.

Differences in OM composition and microbial communities structure between cores from the same meadow, sampled in areas showing a different health status (Core L, Cores I and D; Chapter IV), involved the whole length of the cores, not only the rhizosphere that was affected by the change in meadow health status. Furthermore, samples from the same core showed similar composition and grouped together in the PCA biplots (Fig. 5, Chapter II). These differences among cores are likely to derive from the different composition and texture of the sedimentary inputs to each area (Chapter II), but also to the spatial variability in the productivity of the meadow that promotes the accumulation of carbonates and OM at a different rate. This suggests that some of the subsoil properties still reflect the influence of the seagrass. For example, paleoreconstruction studies using *Posidonia oceanica* mats have found signals of past plant productivity in soil layers up to 4.75 m depth (≈4,000 years old) (Leiva-Dueñas et al. 2018, 2020).

2. Organic matter accumulation and mineralization

Most of the seagrass meadows studied in this thesis do not seem to follow a decreasing OM trend with depth (Chapter II), as the balance between inorganic and OM inputs to the meadow and the stability of environmental factors influencing OM accumulation may have varied through time. However, the core sampled at Portlligat bay (Gulf of Roses, Northwest Mediterranean, Chapter I) did show a clear OM decay trend with depth. This can be explained by the high stability of the meadow area where the core was sampled. The chronological model obtained in a previous study (Serrano et al. 2012) suggests none or negligible changes in sediment accretion rates with time, and a recent study suggested that the productivity of the meadow was fairly stable along the time span encompassed by the core – with the only exception of a decreasing trend for the last 800 yr (Leiva-Dueñas et al. 2018). As indicated before, long-term stability seems to be uncommon in seagrass meadows, as it was found in other areas of the same meadow (Chapter IV) and reflected by the study of several meadows from the SE of Andalusia (Chapter II). The results obtained for the Portlligat core may be due to its geophysical setting: a sheltered area on a semi-enclosed bay, and in the inner part of a well-developed, healthy meadow (Figure 5). Furthermore, the large distance to the discharging point of the only creek in the bay and the small size of the catchment may also account for a lower impact that changes in pluviometry may have had over the continental sediment fluxes. These characteristics provide a unique chance to study the degradation of soil OM with time.

This core showed two main OM decay trends, a fast decay above 35 cm and a slower decay below 35 cm; very likely reflecting changes within (<35 cm) and below (>35 cm) the rhizosphere (Chapters I, III and IV). The slow decay trend can be further subdivided, as OM degradation seems to stabilize below 150 cm (Fig 6). Trevathan-Tackett et al. (2020) suggested that root and rhizomes of *Zostera muelleri* incubated in the field may follow a three phases decomposition pattern with a first leaching phase, a microbial degradation phase and a stabilization phase. However, the three phases found in our core do not seem to be directly comparable to those.

The first degradation phase seems to take place in the rhizosphere (Chapters I, III and IV). Here there are two OM sources. The OM buried due to sedimentation, which starts its degradation at the surface and gets older with depth, and the OM leached by the belowground organs. Thus, the leaching and microbial degradation phases may occur at once. Moreover, incubations in the laboratory are held either under aerobic or anaerobic conditions, while in the seagrass rhizosphere both conditions can be found due to the formation of oxic micro-niches around rhizomes and root tips (Jensen et al. 2007; Holmer 2018). The higher mineralization rates found in this phase can be attributed to the presence of aerobic metabolisms, more efficient than the anaerobic ones (Kirchman 2012). Furthermore, the <2mm OM fraction of the

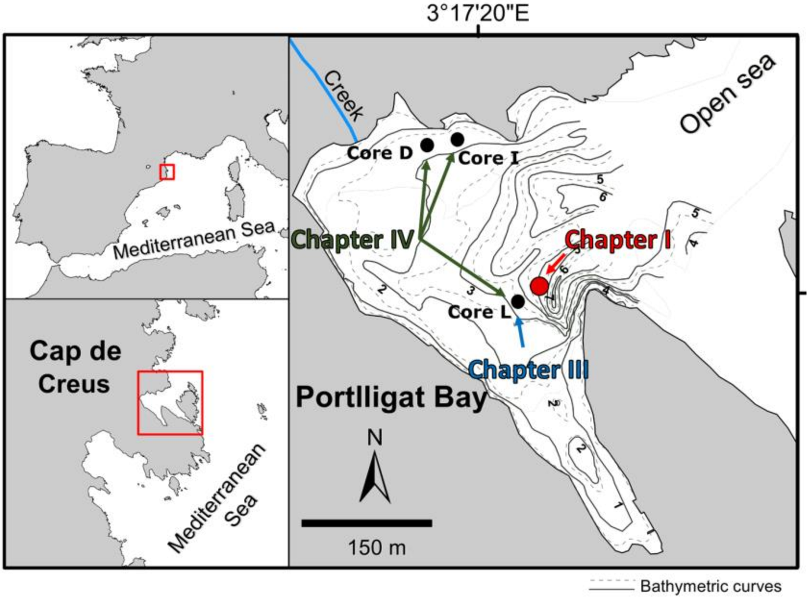

Figure 5; sampling summary of Portlligat bay (modified from Chapter IV). Red dot indicates the location of the Core2000 studied in Chapter I and an ecosystem productivity reconstruction published elsewhere (Leiva-Dueñas et al., 2018). Core L, core studied in Chapters III and IV; Cores I and D studied in Chapter IV.

rhizosphere, the one more accessible to microbial breakdown, is enriched in labile components compared to the subsoil <2mm OM fraction, either for burial or leaching, which are decomposed faster (Chapter IV).

It is interesting to note that, although OM in the rhizosphere decreases with depth (COM and SOM, Chapter I; indirectly measured as C_{org} in Chapter IV), the ratio between labile and recalcitrant compounds remains constant (rhizosphere PC1 and PC2 of core L, Chapter IV). This may be explained by the fact that, while detrital tissues (from seagrass or other sources) are degraded with depth leaving the more recalcitrant compounds, the roots constantly provide easy degradable compounds maintaining the labile OM/recalcitrant OM ratio through the rhizosphere depth.

The second phase would occur almost all, if not entirely, below the rhizosphere (Chapters I, III and IV). This phase seems to affect predominantly to the <2mm OM fraction (Chapter I). At that depth, there are no more oxic microenvironments promoting aerobic degradation, nor leaching of OM from the roots. The anaerobic conditions would slow the decay rate. Moreover, most of the OM arriving to the subsoil has already undergone degradation in the rhizosphere and contains a low proportion of labile compounds, which would become increasingly scarcer with depth (Chapter IV). The microbial communities of the subsoil seem to have adapted to this more exhausted OM, as they are able to degrade a wider range of carbon sources (Chapter III). At this phase, *p*-hydroxybenzoic acid moieties and methylene chain compounds are selectively preserved while polysaccharides and guaiacyl and syringyl lignin moieties are depleted from the <2mm OM fraction (Chapter IV).

Below 150 cm the OM content remains almost stable. Two factors may explain this cessation in OM mineralization. First, the OM

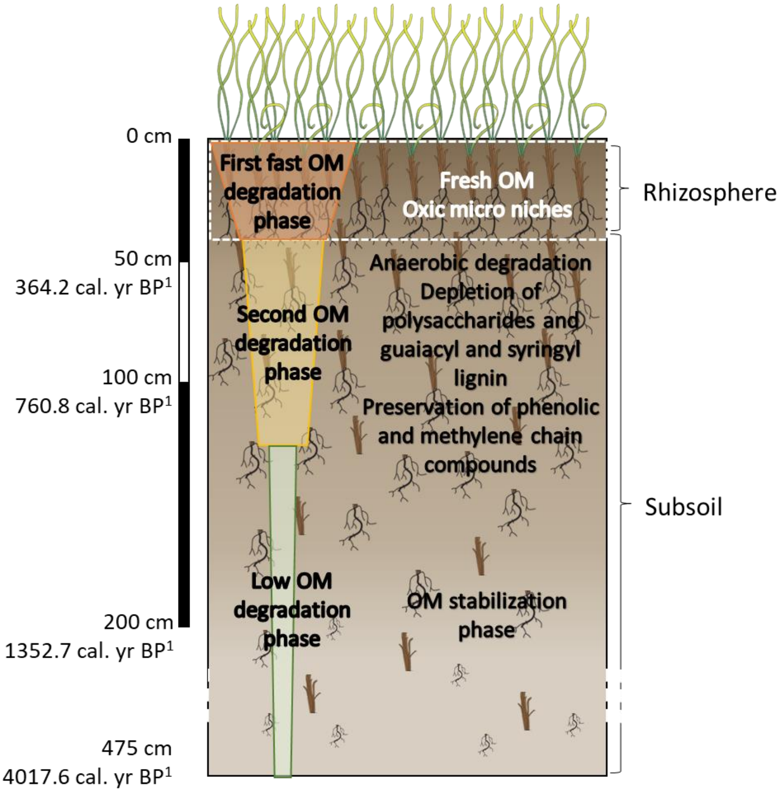

Figure 6; summary of OM degradation in the stable area of Portlligat meadow from Chapters I, III and IV. Chronology from Leiva-Dueñas et al. (2018). Modified from Piñeiro-Juncal et al. (2020) graphical abstract.

accumulated may be highly recalcitrant or even unavailable to microbial degradation. An example of this is the 4-hydroxybenzoic acid which, although found in relative abundance in *P. oceanica* tissues (Kaal et al. 2016), does not seem to be consumed by the soil microbial communities (Chapter III) and is selectively preserved with depth (Chapter IV). Second, electron acceptors available to the microbial community may be far less energetic than those present in upper layers of the soil (Kirchman 2012). In this thesis there is no data about the OM composition of this phase, as the cores analyze by analytical pyrolysis did not reach this depth.

3. Effects of meadow cover loss on soil organic matter mineralization

After cover loss, the death areas of the *P. oceanica* meadow of Portlligat underwent a quick mineralization of the <2mm OM fraction in the rhizosphere - the effect of cover loss over the >2mm OM fraction was not assessed (Chapter IV). The <2mm OM fraction is considered to be the most biogeochemically reactive while the >2mm OM fraction will usually undergo a previous fragmentation and a concomitant increase in specific surface area, enhancing its accessibility to microorganisms. As OM macro debris could still be observed in the Portlligat death meadow (Core D Fig. 2, Chapter IV), this process does not seem to have been accelerated by cover loss. The >2mm OM fraction is the most abundant in the rhizosphere (Serrano et al. 2012), thus *P. oceanica* soils may still show limited CO_2 emissions even after cover loss. The <2mm OM fraction increases with depth, but those layers in which this fraction is the largest part of the OM would belong to the subsoil and are not affected by cover loss.

The high content of macro debris (>2mm OM) may be a particularity of the *Posidonia* genus (Mateo et al. 2006), and particularly of *P. oceanica*, due to the high recalcitrance of their tissues (Trevathan-Tackett et al. 2017; Kaal et al. 2018; Rencoret et al. 2020), which promotes the accumulation of macro debris and the development of organic soils. Therefore, other seagrasses may undergo a more throughout mineralization of their rhizosphere OM. However, further research would be needed to test that: (1) >2mm OM is not affected by the priming effect promoted by cover loss (Chapter IV), and (2) that other seagrasses accumulate OM in their soils predominantly in the <2mm fraction.

If the effect found in the Portlligat meadow is universal, recurrent transitory meadows would accumulate far less OM in their substrates, even when they have not been impacted by erosive phases between colonization events, as cover loss would promote the mineralization of part of the OM accumulated when the meadow was present.

4. *Posidonia oceanica* vs other seagrasses substrate transformation

As any soil, seagrass soils are as heterogeneous as their environmental setting (Demas and Rabenhorst 2001). *Posidonia oceanica* is a temperate Mediterranean seagrass that forms meadows up to 45 m depth (Telesca et al. 2015), but is not found anywhere else. In this thesis *P. oceanica* was used as a model for seagrass soil formation, due to the high impact it has over the substrate, i.e. soil development (Boudouresque and Meinesz 1983), and to the large quantity of information available on its substrate geochemistry. The same paths through which *P. oceanica* alters the substrate have been found in other seagrasses and are recognized as common traits, e.g. O_2 pumping (Borum et al. 2006), OM leaching (Mateo et al. 2006) or texture modification (Bos et al. 2007). However, there are important differences in the intensity of substrate modification that would clearly differentiate *P. oceanica* soils from other seagrass soils.

Posidonia oceanica is a large, slow growing persistent species that forms enduring meadows with small seasonal variations in abundance, assuring a steady transformation of the substrate. However, seagrass meadows may be persistent or transitory. The impact over the substrate and the potential for soil formation of transitory meadows is far lower and would depend on the fluctuation time between meadows stages. Those transitory meadows would be usually formed by colonizing or opportunistic species, like *Halophila* or *Zoostera*, and be located in areas with wide environmental fluctuation or near the species tolerance limit. After the disappearance of the seagrass in transitory meadows, erosive events may happen, removing the incipient soil. More information about seagrass life cycle and colonization patterns can be found at Kilminster et al. (2015).

Many processes that may alter the substrate would be specific-dependent, as they are linked to physiological or morphological traits that vary among species. Plant productivity and total biomass are highly variable among species and environmental conditions, exhibiting *P. oceanica* one of the highest belowground organs biomass (Duarte and Chiscano 1999, Chapter V). Furthermore, the *Posidoniaceae* family has more OM content and more refractory OM in non-photosynthetic above ground tissues than other seagrasses (Trevathan-Tackett et al. 2017) and, among them, *P. oceanica* shows high contents of lignin (Kaal et al. 2018), what could partially explain the high amount of C_{org} found in their soils (Chapter V).

The range of substrates colonized by *P. oceanica* is a fraction of the substrates that can be colonized by seagrasses, not growing in muddy sediments as other species do (e.g., *Zostera* or *Ruppia;* Chapter V). On the other hand, the enrichment in fine fractions of the sediment due to the enhanced precipitation and avoided resuspension shown by *P. oceanica* (Terrados and Duarte 2000; Gacia and Duarte 2001) may not be found, or be fairly lower, in meadows of small seagrass species (Mellors et al. 2002), as the small size of their canopy may not be enough to effectively promote sediment precipitation (Gacia et al. 1999; Bos et al. 2007).

5. Seagrass substrates as soils

The presence of the seagrass causes physico-chemical changes in the substrate matching soil formation processes, i.e. additions, removals, transfers and transformations. The time involved in the formation of the soil would depend on the species and on environmental factors such as temperature or the photosynthetic active radiation available. Whether the influence of the plant would last enough to form a soil or not, and how developed would it be, would be constricted by the sediment accretion rate and the persistence of the meadow. Meadows formed by small species are likely to form less developed soil as these species tend to form transitory meadows (Kilminster et al. 2015) and to develop a smaller belowground compartment (Duarte and Chiscano 1999).

The available pedological information about seagrass soils belongs largely to the epipedon. The most studied genera are *Zostera* and *Posidonia* and the most studied region is Europe and the least South America. There are very few publications that report the color of the soil (Chapter V), a physical property extensively used in soil description and classification.

The inorganic composition of seagrass soils seems to be highly influenced by the terrestrial basin (Chapter II) and, even though their organic fraction can have seagrass or non-seagrass sources (Kennedy et al. 2010), the predominant seagrass species seems to play a role in the total OM accumulated (Chapter V). The more common texture in seagrass soils is sandy, being some seagrasses able to grow over substrates of finer textures and finer texture soils may be developed (Chapter V).

The most likely classification of seagrass-derived soils is as *Entisols*, ST-USDA, or as *Fluvisols* or *Gleysols*, WRB-FAO. The formation of organic soils (e.g., Histosols) seems to be a rare event associated with the *Posidonia* genus (Chapter V).

GENERAL CONCLUSIONS

There are two distinct biogeochemical compartments in seagrass soils, the rhizosphere and the subsoil. The biogeochemistry of seagrass rhizosphere substrates has been profusely studied by marine scientist. This thesis contributes to expand the biochemical research interest to deeper parts of the substrate, that continue to change through paths influenced by their previous interaction with the seagrasses, even if at a much slower rate. Functional aerobic activity was potentially predominant in the rhizosphere, while potential functional anaerobic activity was predominant in the subsoil. Furthermore, the anaerobic communities of the subsoil seemed to be able to degrade a wider range of carbon sources.

The main processes found were somewhat related to OM accumulation and mineralization. This may be due to the soil model chosen, *P. oceanica* mats, as their exceptional content in OM may hinder other biogeochemical processes. The OM content of seagrass soil do not follow any general trend with depth, very likely due to changes in organic and inorganic matter inputs with time. In the Portlligat bay area where a decay trend with depth can be observed, the mineralization seems to follow three phases: a quick mineralization phase in the rhizosphere, and a slow mineralization phase and a stabilization phase in the subsoil.

Cover loss seems to have affected the rhizosphere chemistry, whereas processes occurring in deepest parts of the soil may remain unaltered. Therefore, the subsoil may reflect the ecological status of the meadow in the past, as shown in paleoecological studies.

Not all substrates below seagrass meadows meet the characteristics of a soil, but the physiological characteristics of the seagrasses promote their development and, given the time, all substrates below seagrass meadows are likely to be transformed into soils. As seagrasses colonize a wide range of substrates and climatic settings, their soils can be highly heterogeneous, but they tend to be weakly developed sandy soils.

RECOMMENDATION FOR FUTURE RESEARCH

The use of *P. oceanica* soils as a model may have over-represented the importance of OM linked processes. Similar studies comparing different seagrass with contrasting live strategies, e.g. fast growing vs slow growing or persistent vs transitory meadows forming, would help to further understand the biogeochemistry of these soils.

As is the case for the Portlligat meadow, it is likely that many seagrass meadows would be highly heterogeneous and an examination of the spatial distribution, not only in terms of bathymetry but also in terms of sediment discharge points and hydrodynamics, is recommended to select the area more suitable for an experiment or for samples retrieval.

The analysis of OM-free soil samples may help understand inorganic processes in the meadows, as the influence of the OM in the statistical analysis is suppressed. It would be particularly interesting to compare the inorganic chemistry of meadows with contrasting land basin composition, e.g. carbonate vs siliciclastic basins.

Metal behavior in the soil and its partitioning between plant tissues and the mineral fraction is unclear. This was not specifically addressed in this thesis, as the goal was to determine which were the main soil processes without selecting them beforehand. However, further research on the biogeochemistry of metallic elements in the soil would contribute to the efforts devoted to fully explore the potential of these soils as environmental archives of past human activities, as metal content is a key proxy for mining, metallurgy and industrial development.

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CHAPTER I

Pedogenic processes in a *Posidonia oceanica* mat.

Soil Systems, 2020, 4, 18, 1-15

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Corrigendum to

“Pedogenic processes in a *Posidonia oceanica* mat”

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In the paper “Pedogenic processes in a *Posidonia oceanica* mat” (Soil Systems, 4, 18, 1-5, 2020) there is an error in the soil classification described in the last section of the discussion. The upper 34-44 cm of the soil studied were classified as “organic soil material”, following the Soil Taxonomy (ST), but this is actually incorrect as all of the soil profile is dominated by mineral material. This mistake was due to the incorrect use of total organic matter content instead of organic carbon content as proxy for the soil material classification. Therefore, the epipedon cannot be regarded as a histic epipedon and the soil should be classified as Fluvaquent Entisol and not as Haplofibrist or Humaquept.

CHAPTER II

Processes driving seagrass soils composition along the western Mediterranean: the case of the southeast Iberian Peninsula

Submitted for publication.

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Abstract

Seagrasses are distributed all along the coast of the Mediterranean Sea being *Posidonia oceanica* and *Cymodocea nodosa* the most common species. They promote sedimentation, leading to the formation of well-structured soils. Over the last decade, a growing attention has been paid to their role as chemical sink, especially for CO_2 in the form of organic carbon (C_{org}) and to their use as environmental archives. However, knowledge about the pedogenetic processes occurring in these soils is still in its early stages. This study represents a step forward in identifying and understanding the processes that, in the long-term, determine the composition of seagrass meadows substrates, which in turn can help to understand their role as blue carbon sinks and environmental archives. Fifteen cores were strategically sampled along a 350 km stretch of the Southeast Iberian coast, and analyzed for elemental composition (XRF core-scanning), magnetic susceptibility, C_{org} content and gran size distribution. The cores were dated by ^{210}Pb and AMS ^{14}C techniques to estimate soil accretion. Principal component analysis was used to explore the main geochemical processes linked to soil formation. The results showed that terrestrial runoff plays a key role in meadow soil composition. Furthermore, C_{org} accumulation did not follow any general depth trend in our soil records, suggesting that temporal variation in C_{org} inputs is an important factor in determining carbon depth distribution within the soil. We obtained evidence that the establishment of well-developed, stable *C. nodosa* meadows in the Mediterranean Sea may be promoted by adverse environmental conditions to *P. oceanica* settlement. Metal's behavior within the meadow deposit and their interaction with OM and carbonates is unclear. The results presented in this paper highlight the importance of the influence of land-based inputs in the characteristics of seagrass meadow deposits, highly determining their C_{org} content, as well as the need for further studies on metal behavior, to understand their full potential as environmental records.

Key words: seagrass sediments, subaquatic soils, blue carbon, pedogenetical processes, coastal zone

1. Introduction

Seagrasses are a polyphyletic group of aquatic angiosperms that colonize coastal areas of all continents except Antarctica (Hartog and Kuo 2006). They can settle from intertidal areas to several meters deep in the subtidal, depending on local factors such as light availability and coastal hydrodynamics (Duarte 1991; Koch 2001). They are known to promote sedimentation by reducing the hydrodynamic forces, directly trapping suspended particles (Agawin and Duarte, 2002; Hendriks et al., 2008; Gruber and Kemp, 2010; Hansen and Reidenbach, 2012) and by avoiding particle-resuspension (Terrados and Duarte, 2000; Gacia and Duarte, 2001; Hendriks et al., 2010), forming well-ordered deposits than can be used as environmental archives (Mateo et al., 2002, 2010; Serrano et al., 2016a; López-Merino et al., 2017). Nevertheless, seagrass substrates are continuously modified by the overlaying living plants, which can change soil characteristics such as texture (Rueda et al. 2008; van Katwijk et al. 2010), composition (Kennedy et al., 2004; Smit et al., 2005; Fourqurean et al., 2012a; Mazarrasa et al., 2015) or redox conditions (Duarte et al., 2005). Plant derived changes in the substrate are held in the rhizosphere and can vary with meadow maturity (Holmer 2018). Rhizosphere depth differs largely between species but is usually restricted to the uppermost 40 cm of the marine sedimentary floor. It has been reported that it occupies from 3 to 80% of the substrate volume and has a total absorptive area often exceeding 1 m^2 m^{-2} (Duarte et al. 2005a). The rhizomes and roots of seagrass release O_2 generating oxic microenvironments and preventing the formation of phytotoxins (Borum et al. 2006; Jensen et al. 2007) and OM which promotes microbial activity (Mateo et al. 2006).

Over the last decade, great attention has been paid to the role of these meadows as chemical filters, especially as CO_2 sinks (Romero et al., 1994; Duarte et al., 2005b; Fernandes et al., 2009; Serrano et al., 2011; Fourqurean et al., 2012a). Organic matter (OM) accumulates in seagrass soils because of (1) particles-trapping and deposition favored by the seagrass canopy, (2) limited mineralization due to the anoxic conditions in the soil and (3) the refractory nature of the seagrass tissues, which can be preserved over millennia (Mateo et al., 1997; Lavery et al., 2013; Serrano et al., 2016b). The carbon sequestered in these ecosystems, together with mangroves and salt marshes, is known as blue carbon (Nellemann et al. 2009) and represents close to half of the carbon buried in the ocean floor, despite covering less than 2% of the ocean extension (Duarte et al., 2005b).

The particular physicochemical characteristics of the soil would vary according to environmental factors operating in the course of its development (e.g. Cebrian et al., 2000; Mazarrasa et al., 2015). Demas and Rabenhorst (2001) propose a combination of factors affecting subaqueous soils formation: climatic temperature regime, organisms, bathymetry, flow regime, parent material, time, water column attributes and catastrophic events. Several of these factors have been found to have an impact on seagrass soils (e.g. Thomson et al., 2019; Alcoverro et al., 1997). Their biogeochemistry has been largely studied by marine scientist (e.g., Holmer, 2018; Marbà et al., 2006). However, the available information focuses mainly in the uppermost part of the soils, where the rhizosphere is found. In the present work, we apply principal component analysis to summarize the information about soil composition and to explore the main geochemical signals in seagrass soils from the two most abundant seagrass species in the Mediterranean Sea, encompassing both rhizosphere and subsoil. To this end, we analyzed 15 soil cores from meadows along ca. 350 km of the Southern coast of the Iberian Peninsula, allowing us to characterize the common processes driving their geochemical composition. Understanding these common geochemical processes can shed some light into the role of marine meadows soils as blue carbon sinks as well as environmental archives.

2. Site description and methods

2.1. Study area

We sampled 15 stations in seagrass meadows along a ca. 350 km stretch of the eastern Andalusian coast, southeast of the Iberian Peninsula, where outcrops of volcanic, metamorphic, and sedimentary rocks can be found (Red de Información Ambiental de Andalucia 2020) (Fig. 1). The most abundant seagrass species in these coasts are *Posidonia oceanica* and *Cymodocea nodosa* (Luque and González 2004). *Posidonia oceanica* is a slow-growing species with high biomass and productivity, that can colonize both sandy and rocky bottoms, often forming thick lignin-rich biogenic reefs, called “mats” (Boudouresque and Meinesz 1982; Kaal et al. 2016), and whose meadows are considered a climax community. *Cymodocea nodosa* is a pioneer species that usually grows over sandy and muddy bottoms and can be found growing over degraded or dead *P. oceanica* meadows (Luque and González, 2004).

Fifteen stations distributed in 9 locations were sampled: Melicena (ME.S), Almerimar (AL.S), Roquetas (RO.S, RO.S-C and RO.S-CN), El Alquián (BA.S), Aguamarga (AG.S, AG.I and AG.D), Palomares (PA.I), Villaricos (DE.I), Terreros (TE.S and TE.D), and Calaburras (CA.S-C and CA.S-CN) (Table 1). These stations were selected to maximize bathymetry range, species and conservation status variability. At least three cores were retrieved per station, among which the longest was selected for this study (Table 1, Fig. 2). The stations were located in monospecific meadows of *P. oceanica* or *C. nodosa*, at water column depths ranging from 0.5 to 18.5 m (Table 1). The cores collected in El Alquián, Palomares and one from Roquetas (ROS.CN) belong to *C. nodosa* meadows. Both El Alquián and Palomares cores were retrieved in extensive well-formed meadows while ROS.CN core was sampled from a small lagoon formed between a *P. oceanica* reef and the shore (Moreno and Guirado 2003). The remaining cores were

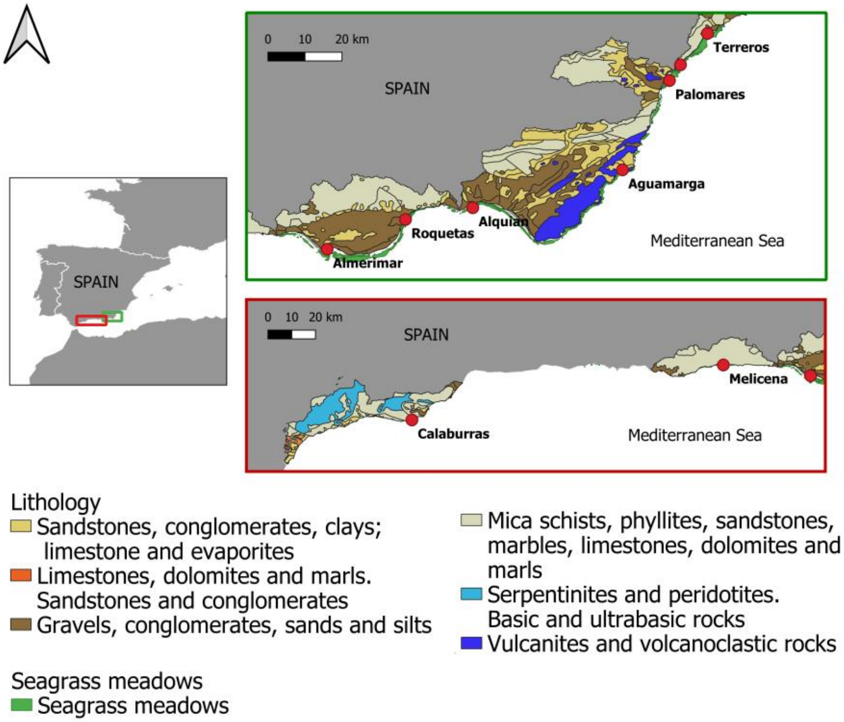


Figure 1: Localities sampled and the lithology of their catchments obtained from the Geological Map of the Iberian Peninsula, Baleares and Canarias, 1:1.000.000 (Instituto Geológico y Minero de España 1995).

sampled in *P. oceanica* meadows. Aguamarga and Terreros meadows were sampled at more than one water depth. In Aguamarga, stations were located at shallow (AG.S, 4.8 m), intermediate (AG.I, 10.8 m) and deep (AG.D, 18 m) waters, while in Terreros cores were only obtained at shallow (TE.S, 5.5 m) and deep (TE.D, 18.5 m) ones. Two cores were sampled in degraded meadows: Villaricos (DE.I) and Melicena (ME.S). The meadow at Villaricos is in an advanced state of degradation, with a very low shoot density, high shoot mortality rate and extensive areas of dead mats (areas where plant cover has been lost). The Villaricos meadow is highly degraded mainly due to the influence of wastewater

Table 1: Summary of the stations studied.

Region /Province	Location	Coordinates		Depth (m)	Species	Observations	Code
Mediterranean, Almería	Terreros	1°40´36.37´´W	37º21´0.12´´N	5.5	*Posidonia oceanica*		TE.S
Mediterranean, Almería	Terreros	1°39´10.60´´W	37º20´37.00´´N	18.5	*P. oceanica*		TE.D
Mediterranean, Almería	Villaricos	1°45´29.53´´W	37º15´18.93´´N	15.9	*P. oceanica*	Chemically degraded	DE.I
Mediterranean, Almería	Palomares	1°47´30.20´´W	37º12´27.13´´N	10.2	*Cymodocea nodosa*		PA.I
Mediterranean, Almería	Aguamarga	1°56´0.42´´W	36º56´15.66´´N	4.8	*P. oceanica*		AG.S
Mediterranean, Almería	Aguamarga	1°55´55.32´´W	36º56´10.20´´N	10.8	*P. oceanica*		AG.I
Mediterranean, Almería	Aguamarga	1°55´55.32´´W	36º55´59.40´´N	18	*P. oceanica*		AG.D
Mediterranean, Almería	El Alquián	2°23´8.04´´W	36º49´23.5´´N	6.8	*C. nodosa*		BA.S
Alborán, Almería	Roquetas	2°35´20.10´´W	36º47´15.50´´N	1.5	*P. oceanica*		RO.S
Alborán, Almería	Roquetas	2°35´24.10´´W	36º47´11.35´´N	0.7	*P. oceanica*	Dead mat	RO.S-C
Alborán, Almería	Roquetas	2°35´24.20´´W	36º47´12.2´´N	1	*C. nodosa*		RO.S-CN
Alborán, Almería	Almerimar	2°49´32.46´´W	36º41´51.72´´N	4.5	*P. oceanica*		AL.S
Alborán, Granada	Melicena	3°14´3.78´´W	36º44´53.99´´N	4.2	*P. oceanica*	In decline	ME.S
Alborán, Málaga	Calaburras	4°41´36.40´´W	36º29´26.60´´N	0.5	*P. oceanica*	Dead mat	CA.S-CN
Alborán, Málaga	Calaburras	4°41´36.40´´W	36º29´26.60´´N	0.5	*P. oceanica*	Dead mat	CA.S-C

from a chemical plant that manufactures ethyl derivatives, among others, since the late 1960s (Moreno et al., 2001; Marbà et al., 2015; Consejería de Agricultura Ganadería Pesca y Desarrollo Sostenible, 2017). Although a waste water treatment plant was installed in 1999, the meadow is still declining, because either the water treatment is not efficient enough, and/or the pollutants trapped in the soil are still being processed by the plants (Agustín Barrajón and Diego Moreno, personal communication, technicians of the Andalusian Government Environment and Water Agency, AMAyA). The Melicena station is located in a degraded meadow, adjacent to an area where dead meadow has been observed, very likely related to an uncontrolled release of agriculture waste waters and sediments (Consejería de Agricultura Ganadería Pesca y Desarrollo Sostenible 2017). We also sampled two dead *P. oceanica* meadows in Roquetas (RO.S-C) and in Calaburras (CA.S). In Calaburras two stations were recovered, one over a dead mat area covered with algae, and another over dead mat overgrown by *C. nodosa* (CA.S-C and CA.S-CN, respectively). Two different climatic areas can be found in the sampled coast. The Terreros, Villaricos, Palomares, Aguamarga, Alquian, Roquetas and Almerimar locations belong to a subdesertic Mediteranean climate, while the Calaburras and Melicena locations belong to a subtropical climate with more abundant annual precipitations (CAGPDS, 2014; Leiva-Dueñas et al., 2021).

2.2. Sampling and laboratory methods

Cores were retrieved over the course of two sampling campaigns in October 2016 and 2017. All cores, except the core from station TE.D (Table 1, Fig. 2) were sampled by gently hammering and slowly rotating a PVC tube (150-200 cm long, internal diameter 7.5 cm) into the soil in SCUBA diving. The tube had a core catcher fitted at its bottom end to avoid loss of material during its retrieval. Core compaction was observed and core-length corrections were done as described below. The core at station TE.D was taken using a vibrocore

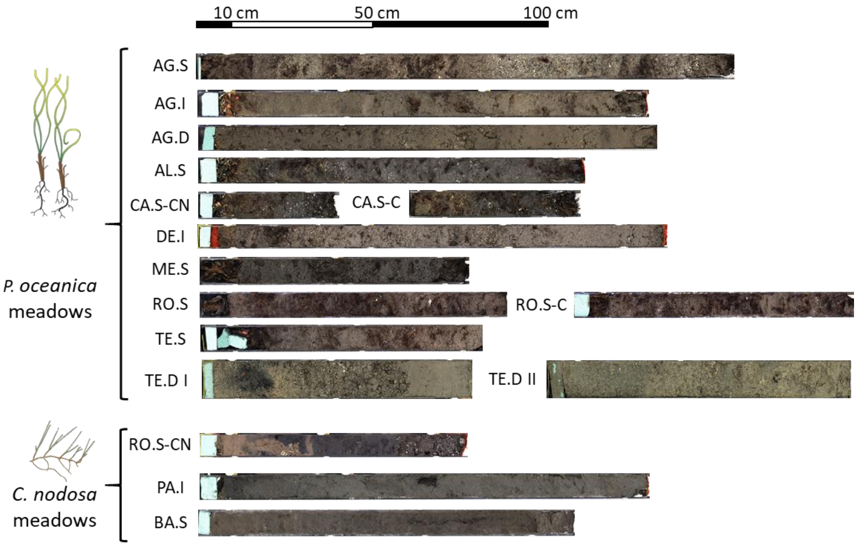


Figure 2: Images of the cores studied. Seagrass symbols from the Integration and Application Network (University of Maryland Center for Environmental Science; UMCES)

(Geo-Corer 3000, Igeotest) into a plastic core pipe (600 cm long, internal diameter 10 cm).

Cores were halved longitudinally in the laboratory. One of the halves was imaged and analyzed using non-destructive techniques at 1 cm steps at the CORELAB laboratory of the University of Barcelona. The elemental geochemical composition of the soil - aluminum (Al), silicon (Si), sulfur (S), chlorine (Cl), potassium (K), calcium (Ca), titanium (Ti), manganese (Mn), iron (Fe), nickel (Ni), zinc (Zn), bromine (Br), rubidium (Rb), strontium (Sr), zirconium (Zr) and lead (Pb) - was obtained by means of an Avaatech XRF-core scanner. Magnetic susceptibility (MS) was obtained with a Bartington Instruments MS2E point sensor mounted on a Geotek Multi-Sensor Core Logger. Some sections along the core, especially at the top, were impossible to measure by XRF or MS owing to their intrinsic nature (presence of plant macro-debris, shells or stones): AG.I 0-16 cm; AG.D 0-10 cm; DE.I 14-18 cm; TE.S 0-20 cm; AL.S 0-8 cm; ME.S 0-8 cm; RO.S 0-18 cm; RO.S-C 0-13 cm; CA.S 0-15 cm; CA.S-CN 0-30 cm; RO.S-CN 0-22 cm; PA.I 1-14, 44-50, 62-65, 77-89, 96-101 and 105-109 cm; and BA.S 0-7 and 57-96 cm. Afterwards, this half core was stored in a dark cold room at 4 °C as a backup, while the other half was used for further analyses. The analyzed half was subsampled every other 2 cm and the samples dried at 60 °C for four days. The vibrocore, TE.D, was subsampled every 10 cm, by recovering 20 ml with 3 cm wide un-capped plastic syringes. Even samples were measured for grain size distribution and total organic carbon (C_{org}). Grain size was determined by digesting the samples with hydrogen peroxide at 30% to remove the OM, sieved at <1 mm and measured using laser diffraction (Mastersizer2000, Malvern Instruments, Centre d'Estudis Avançats de Blanes). The grain size fractions obtained were clay (<0.002 mm), silt (0.002-0.050 mm) and fine (0.05-0.50 mm, FSand), medium (0.5-1.0 mm, MSand) and coarse (>1 mm, CSand) sand. Samples for C_{org} were ground using an agate mortar (Mortar Grinder RM-200 RETSCH) and measured by mass-loss-on-ignition technique (450 °C for 5 h) to obtain the OM%. In 10 to 12 subsamples per core, around 1 g of ground sample was digested by adding HCl 1M to eliminate carbonates, centrifuged and rinsed with distilled water until pH ≈7 before drying at 60°C. The digested sample aliquot was used to measure C_{org} at the IACT-CSIC center in Granada using an elemental analyzer NA 1500 2 (Carlo Erba).

2.3. Dating and age-depth models

Although temporal variations in soil formation are out of the scope of this study, ^{210}Pb profiles and AMS ^{14}C dates were used to build age-depth models. From this models the average accretion rates of the soils were inferred. The concentration profile of ^{210}Pb was determined at every centimeter for the uppermost 30 cm of all cores except for TE.D, CA.S and RO.S-C (see supplementary material), through quantification of ^{210}Po using alpha spectrometry on a PIPS detector (CANBERRA, Mod. PD-450.18 AM) following Sanchez-Cabeza et al. (1998), at the Universitat Autònoma de Barcelona. Furthermore, seagrass macro debris were selected for radiocarbon dating (S1 supplementary material). The materials selected were previously treated to remove soil particles as detailed in Belshe et al., (2019). Radiocarbon analysis was performed by accelerator mass spectrometry using an NEC Pelletron 500 kV AMS (DirectAMS - Accium BioSciences). Radiocarbon ages were corrected for the reservoir effect (Reimer et al. 2013) and the local anomaly ($\Delta R=2 \pm 26$ years, Siani et al., 2000). Radiocarbon dates are expressed as calibrated years before present at 2-sigma confidence interval. Age-depth models were elaborated using the available ages, either ^{210}Pb derived, radiocarbon derived or both, and the *rbacon* package for R software (Blaauw and Christeny 2011; R Core Team 2019). The age at the surface of the core (the sampling year) was included in the models.

2.4. Statistical analysis

Cores collected manually were compressed as a result of percussion during sampling (0.8-59.9%; Table 2) (Glew et al. 2001). Core length measured at the laboratory was corrected to approximate field length using an exponential function, under the assumption that compaction increases from the bottom to the top of the core (Morton and White 1997). From now on, all depths are expressed as decompressed ones. OM data were transformed to C_{org} using a calibration curve (Fourqurean et al. 2012a) for each core calculated as a linear relation between OM and C_{org} with the 10 to 12 samples that were analyzed for C_{org} (r^2= 0.96-0.63). To compare cores with different lengths and time spans, accretion rates (mm yr^{-1}) were calculated as the average of the top meter, by dividing 1000 mm by the age at that depth according to the age-depth model. The data matrix was resampled to select samples with data for all the variables. A principal component analysis (PCA) on the correlation matrix was performed in R version 3.4.3 (R Core Team 2019), package *psych* (Revelle 2017), using varimax rotation to maximize the variance of the variables in each component. C_{org} data was previously transformed by a logarithmic transformation while grain size distribution data were transformed by center log ratio to avoid spurious correlation typical of compositional data (Aitchison 1982). The whole data matrix was scaled to mean 0 and 1 standard deviation. All components with eigenvalues > 1 were considered. Given that the clay content was very low in all samples (Table 2), changes of less than 0.5% would have a high loading in the PCA after scaling the data matrix, although its geochemical significance would be negligible. For this reason, clay was not included in the analysis. The samples from the two cores from Calaburras (CA.S-C and CA.S-CN) were pooled in the same category (CA.S), as they can be considered replicate cores. Correlations between variables and depth used in the discussion have been calculated using the Spearman method ($P<0.005$) as our variables did not follow a normal distribution and a linear relationship is not always expected in soil data.

3. Results

Plant macro-debris were identified during sieving along all cores, except for core PA.I, where macro-debris could not be found between 60 and 120 cm. No general downcore trend was found for the debris not for C_{org}, but for AG.I (rho: 0.59, $P<0.001$), DE.I (rho: 0.42, $P<0.001$), ME.S (rho: 0.6, $P<0.001$) and CA.S, (rho: 0.58, $P<0.001$). However, C_{org} values were always below 10 % of the total weight of the bulk sample (Fig. 3). The predominant inorganic fraction in the cores was FSands and the less abundant fraction was clay, below 1% in all the cores (Table 2). The uppermost layers of BA.S, RO.S-CN and AL.S

Table 2: Main characteristics of the cores studied. FSands, MSands, and CSands stand for Fine, Medium and Coarse sands, respectively.

Code	Samp. date	Comp. %	Core length (cm)	Accretion rate top meter (mm y^{-1})	Dating method	C_{org} (gcm^{-3})	Clay (%)	Silts (%)	FSands (%)	MSands (%)	CSands (%)
TE.S	oct-16	20.4	88.7	1.09 ± 0.14	^{210}Pb, ^{14}C	0.0218	0.04	13.41	72.43	8.87	5.26
TE.D	oct-17	-	200	0.99 ± 0.18	^{14}C	0.083	0.31	15.69	33.58	31.07	19.3
DE.I	oct-16	15.9	157.2	0.71 ± 0.15	^{210}Pb, ^{14}C	0.0096	0.27	23.18	30.7	19.98	25.86
PA.I	oct-17	14.3	147.9	7.57 ± 3.82	^{210}Pb	0.0025	0	4.94	94.93	0.01	0.13
AG.S	oct-17	13.1	172.9	1.88 ± 0.44	^{210}Pb, ^{14}C	0.0268	0.04	6.24	57.5	30.16	6.05
AG.I	oct-17	31.4	166.4	3.56 ± 0.92	^{210}Pb, ^{14}C	0.0138	0.18	16.15	78.01	2.61	3.03
AG.D	oct-17	11.3	136.8	0.42 ± 0.05	^{210}Pb, ^{14}C	0.0191	0.3	20.64	41.58	14.51	22.93
BA.S	oct-16	9.9	117.3	4.41 ± 1.07	^{14}C	0.0025	0.03	13.95	85.81	0	0.2
RO.S	oct-16	41.5	137.7	1.36 ± 0.19	^{210}Pb, ^{14}C	0.0226	0.01	8.45	81.28	6.47	3.78
RO.S-C	oct-16	40.3	141.7	-	-	0.0279	0.01	7.61	87.7	3.1	1.57
RO.S-CN	oct-16	59.9	173.5	-	-	0.0015	0	0.68	78.3	1.62	16.84
AL.S	oct-17	0.8	106.9	0.88 ± 0.12	^{14}C	0.0195	0.1	16.71	72.94	6.77	3.49
ME.S	oct-17	10.9	77.8	1.98 ± 0.85	^{210}Pb, ^{14}C	0.0133	0.02	8.58	45.12	26.68	19.59
CA.S	oct-17	21.2	78.5-102.9	-	-	0.0173	0	4.48	57.89	12	25.63

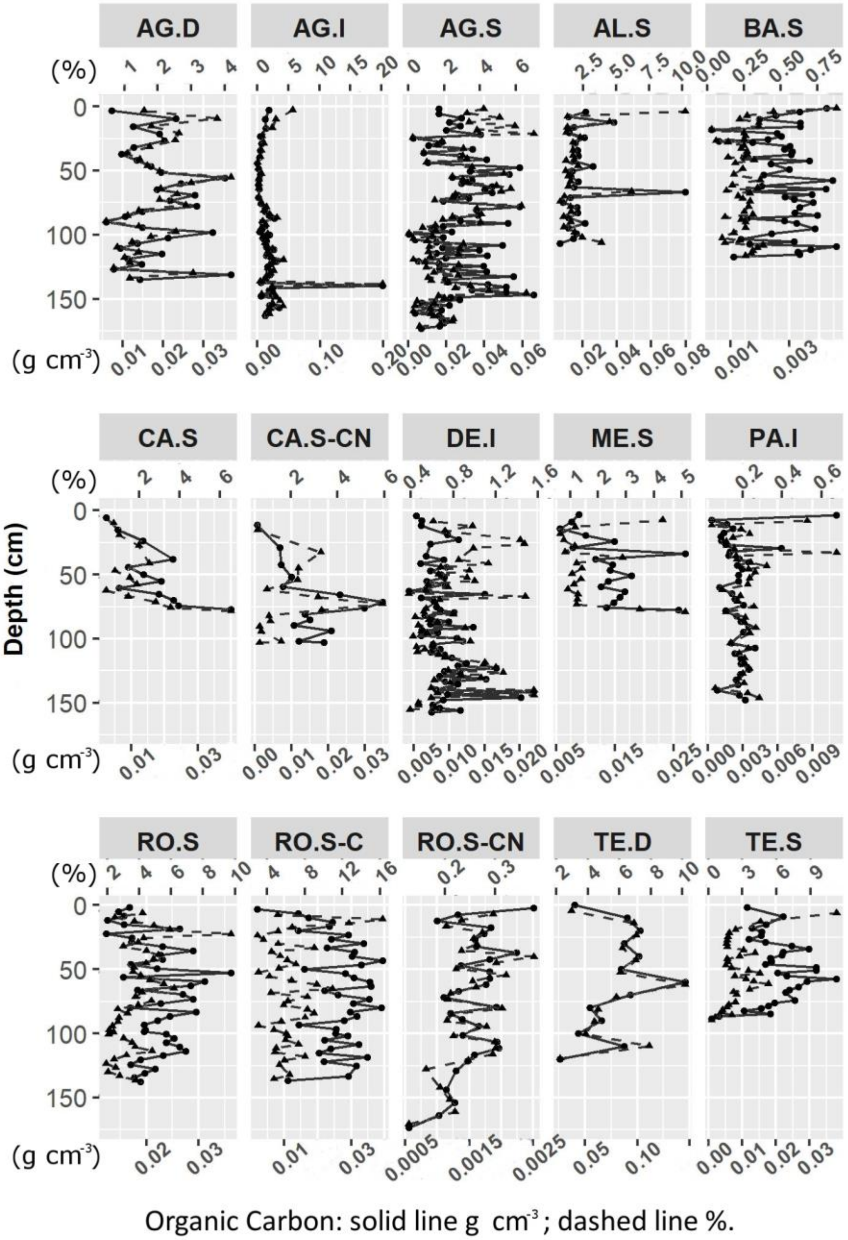


Figure 3: Distribution of C_{org} in each core expressed as carbon density (solid line, g cm^{-3}) and carbon percentage (dashed line).

cores could not be dated by ^{210}Pb because the profile was altered or mixed. Cores PA.I and RO.S-CN were not ^{14}C-dated due to the lack of enough C_{org} rich suitable material. Thus, age-depth models were not obtained for RO.S-CN station and in the dead meadow stations (RO.S-C and CA.S), the estimation of sediment accretion rates was not attempted as erosion was likely to have occurred (Table 2).

According to the age-depth models the lowest accretion rate was recorded in AG.D, 0.42±0.05 mm yr^{-1} (Table 2, Fig. 4), while the core with the highest accretion rate was PA.I, 7.6±3.8 mm yr^{-1} (Table 2, Fig. 4). The most abundant element was Ca with 45% of the total counts, followed by Fe and Cl (20-10%); Si and Sr (10-5%); Zr, K and Ti (5-1%); Br, Rb, Al, Mn, Pb and Zn (1-0.1%), and Ni (<0.1%), although these figures changed importantly according to the location of the studied core, as well as their nature and mineralogical composition. As expected, owing to the main sedimentological features of the cores, MS was highly variable (94 ± 455 SD; S3, supplementary material).

The PCA yielded five components accounting for 70.1 % of the total variance (27.5%, 18.3%, 9.3%, 8%, and 7%, respectively; Table 3). Most cores were well clustered in the PCA scores projections (Fig. 5), indicating that they differed in the weights of the geochemical gradients represented by the components. All variables but MS showed high communalities (> 0.5, Table 3). PC1 clustered Rb, Fe, Zn, K, Ti, Al, Zr, Si, Mn, Silts, and Pb with positive loadings, against C_{org}, Br and MSand with negative loadings (Table 3, Fig. 5). Overall, samples from cores BA.S, DE.I, PA.I, AL.S, ME.S, RO.S-CN and TE.S showed positive PC1 scores (Fig. 6), while cores AG.S, AG.I, AG.D, RO.S, RO.S-C, CA.S and TE.D presented negative scores (Fig. 6). PC2 clustered Sr, Cl, Ca, CSand and MSand with positive loadings against FSand, Si and Zr with negative loadings (Table 3, Fig. 5). Samples from AG.D, DE.I, TE.S and TE.D showed positive scores (Fig. 6) and samples from AG.S, AG.I, BA.S, PA.I, RO.S, RO.S-C, AL.S, CA.S, ME.S, and RO.S-CN had negative scores (Fig. 6). PC3 clustered silts, FSands and Si against MSand, CSand and MS (Table 3, Fig. 5), and essentially separated core ME.S, and to a lesser extent CA.S and AG.S, from the other cores (Fig. 6). PC4 clustered Ni and Pb against Mn and Ca (Table 3, Fig. 5) and distinguished CA.S and RO.S-CN from the rest of the cores (Fig. 6). PC5 clustered S, Br and C_{org} (Table 3, Fig. 5). Cores DE.I, RO.S, RO.S-C, AL.S, ME.S and TE.S showed positive PC5 scores (Fig. 6), while cores AG.S, AG.I, AG.D, BA.S, PA.I, CA.S, RO.S-CN and TE.D had negative scores (Fig. 6).

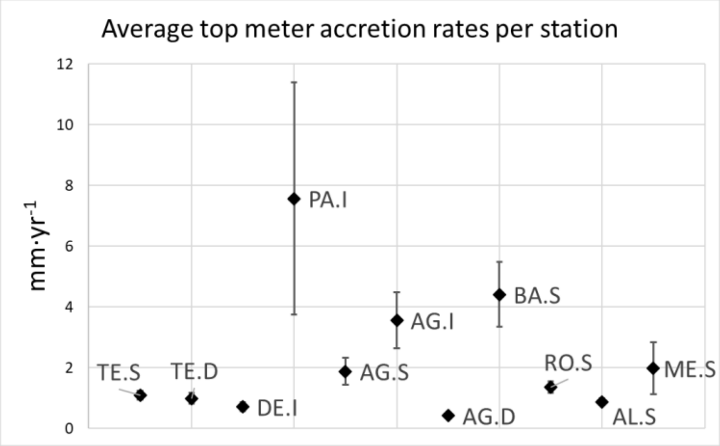


Figure 4: Average of the uppermost meter accretion rate per station (mm yr^{-1}) and its standard error (hanging bars, propagated from the age-depth model).

Table 3: Loadings of chemical elements, magnetic susceptibility (MS), grain sizes (silts, FSand, MSand and CSand) and organic carbon density (C_{org}) for each component as yielded by the principal components analysis (PCA). Com: communality (total variance of each variable explained by the extracted components), Var. %: percentage of variance accounted for by each component; Ac. Var. %: cumulative variance. Loadings > 0.35 in bold.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**Com**
Rb	**0.92**	-0.04	-0.10	-0.02	0.04	0.85
Fe	**0.90**	-0.18	-0.07	0.10	-0.15	0.87
Zn	**0.79**	0.02	0.11	-0.08	0.19	0.69
K	**0.78**	0.25	0.00	-0.10	-0.02	0.68
Ti	**0.77**	-0.29	0.27	-0.05	-0.27	0.83
Al	**0.76**	-0.34	0.31	-0.11	-0.29	0.89
Zr	**0.73**	**-0.37**	0.07	0.12	0.13	0.71
Si	**0.58**	**-0.50**	**0.35**	-0.28	-0.27	0.86
C_{org}	**-0.48**	0.32	0.08	0.20	**0.35**	0.50
Mn	**0.47**	-0.28	-0.10	**-0.42**	-0.17	0.51
Sr	-0.07	**0.88**	0.21	-0.01	-0.06	0.83
FSand	0.06	**-0.78**	**0.37**	-0.26	0.01	0.82
Cl	-0.06	**0.75**	-0.07	0.04	0.29	0.66
Ca	-0.24	**0.72**	0.24	**-0.40**	-0.07	0.79
CSand	-0.07	**0.61**	**-0.50**	0.18	-0.27	0.74
MSand	**-0.37**	**0.47**	**-0.60**	0.09	0.16	0.75
Silt	**0.39**	-0.07	**0.67**	0.19	0.20	0.68
MS	0.23	-0.16	**-0.62**	0.06	0.07	0.47
Ni	-0.14	-0.10	-0.13	**0.69**	-0.16	0.55
Pb	**0.38**	0.22	0.10	**0.57**	0.06	0.52
Br	-0.32	0.06	0.05	**0.55**	**0.48**	0.64
S	0.02	-0.02	0.00	-0.06	**0.76**	0.58
Var %	27.51	18.28	9.30	7.99	6.97	
Ac. Var %	27.51	45.79	55.08	63.08	70.05	

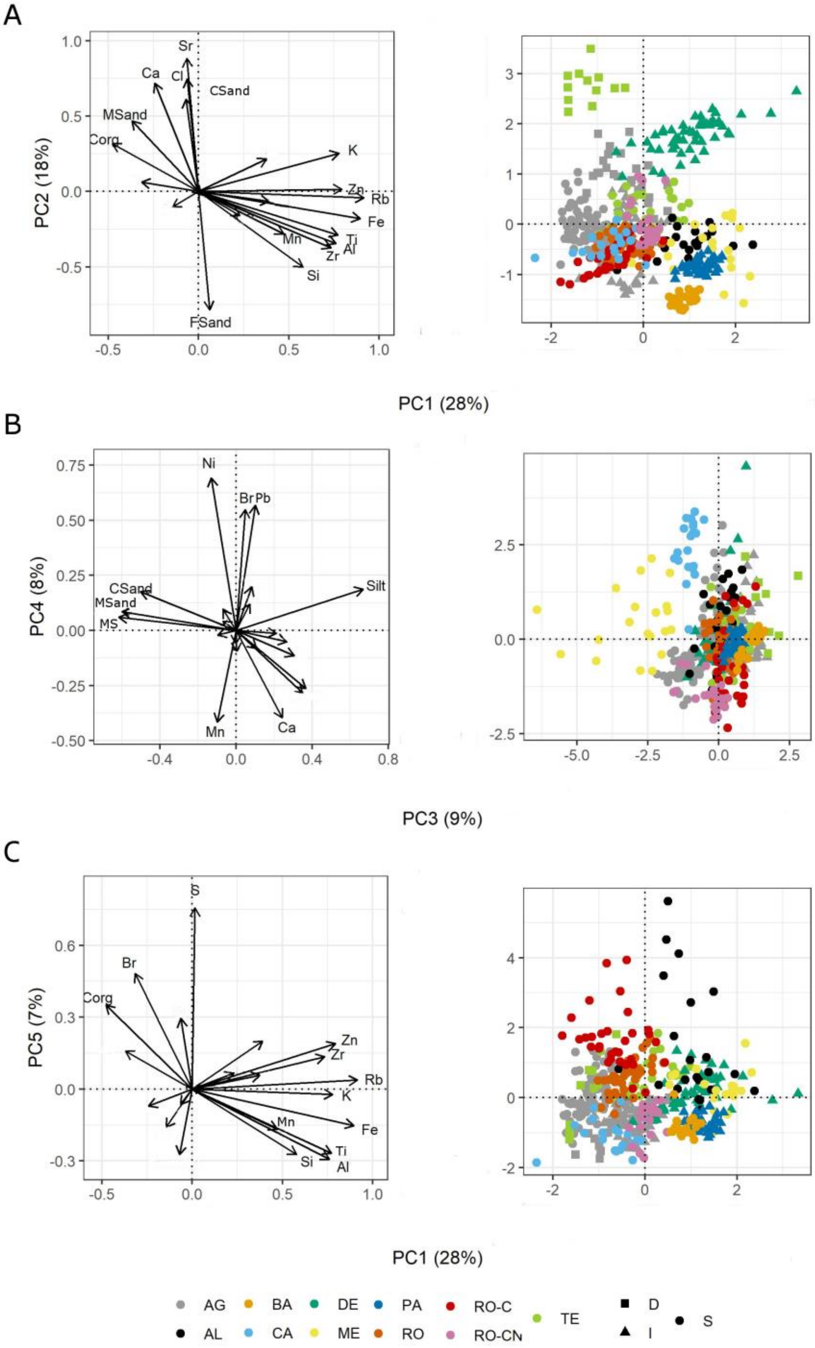
4. **Discussion**

4.1 Inputs of silty terrestrial material vs organic matter accumulation

High positive loadings in PC1 include elements generally related with silty lithogenic materials (Rb, Fe, Zn, K, Ti, Al, Zr, Si, Mn and Pb) (Rothwell and Croudace 2015) against C_{org}, Br and MSands, with moderate negative loadings (Table 3). This component is likely indicating inputs of terrestrial silty sediments either from river discharge or runoff of ephemeral streams. Cores with positive scores may thus reflect a higher influence of terrestrial silty material in meadow composition, as it happens in BA.S, DE.I, PA.I, AL.S and ME.S meadows (Fig. 6). Positive PC1 scores can be explained by the interaction of several local factors like the catchment area, the slope and the runoff. BA.S and PA.I are the station with the higher sediment accretion rate, however, DE.I, AL.S and ME.S do not show particularly high accretion values (Table 2, Fig. 4). Therefore, specific geological features of the catchment, such as its lithological composition and its degree of fracturation due to tectonic processes, and coastal dynamics (i.e. sediment redistribution) would influence PC1 scores as well as total mineral fluxes from the continental catchments.

On the other hand, the covariation between C_{org} and Br was already expected, as Br tends to bind to OM during humification (Leri et al. 2014; Martínez-Cortizas et al. 2016) and it can be used as a proxy for marine OM (e.g. Gribble, 2000; Dembitsky, 2002; Ziegler et al., 2008).

Figure 5: Biplots of the variables studied in the PCA. A, PC1 vs PC2; B, PC3 vs PC4; C, PC1 vs PC5. The arrows in the left panels indicate the loading of each of the variables for each component. Dots in the right panel indicate the score of each sample grouped by station (colors). The shape of the dots indicates at which water depth the meadow was sampled, D: Deep (18-19 m), I: intermediate (10-16 m), S: Shallow (0.5-7m).


A
Sr
Ca
Cl
CSand
MSand
Corg
K
Zn
Rb
Fe
Ti
Mn
Al
Zr
Si
FSand
PC2 (18%)
PC1 (28%)
B
Ni
Br
Pb
CSand
MSand
MS
Silt
Mn
Ca
PC4 (8%)
PC3 (9%)
C
S
Br
Corg
Zn
Zr
Rb
K
Mn
Fe
Ti
Si
Al
PC5 (7%)
PC1 (28%)
AG
AL
BA
CA
DE
ME
PA
RO
RO-C
RO-CN
TE
D
I
S

This component seems to be reflecting a balance between meadow OM production and silty lithogenic inputs. A similar balance was also found in the elemental composition analysis of a *P. oceanica* meadow soil from the northeast of the Iberian Peninsula (Piñeiro-Juncal et al., 2020). In that soil, OM%, and consequently C_{org}%, was highest at the top and declined downcore in the first 100 cm, following an exponential curve linked to OM decay (Serrano et al. 2012). However, the C_{org} distribution with soil depth in our data (Fig. 3) does not seem to show this exponential decay curve, like cores from Florida Bay (USA), Shark Bay (Australia), Mallorca Islands (Spain) or in a collection of *Zostera marina* cores from the Northern hemisphere (Fourqurean et al., 2012b; Mazarrasa et al., 2017; Kindeberg et al., 2019). The C_{org} content is not only the result of how much of the buried C_{org} has been mineralized but also of how much C_{org} was buried in the first place. In stable environments, were C_{org} inputs to the meadow do not change noticeably over time, decay may be expected to be the leading process controlling C_{org} content with soil depth. Moreover, in our analysis the C_{org} content was expressed as C_{org} density (g cm^{-3}), instead of as percentage (%), to allow the comparison of carbon accumulation among cores with different densities. The vertical distribution between the C_{org} expressed in percentage or in density is quite different (Fig. 3), but still, neither distribution fits a decay curve.

On the contrary, C_{org} density increased significantly with depth in four of our stations, as found in *Posidonia spp.* cores from Cockburn Sound (Australia) and Cabrera Island (Spain) (Serrano et al., 2016c; Belshe et al., 2019). The increase of C_{org} density with depth in our deposits may be related to the progressive soil compaction of older soil due to accretion. Even when OM mineralization is lowering the OM content in the sample, compaction results in an increase in soil density and a concomitant increase in the amount of carbon per volume unit. If OM degradation and soil compaction were the only processes taking

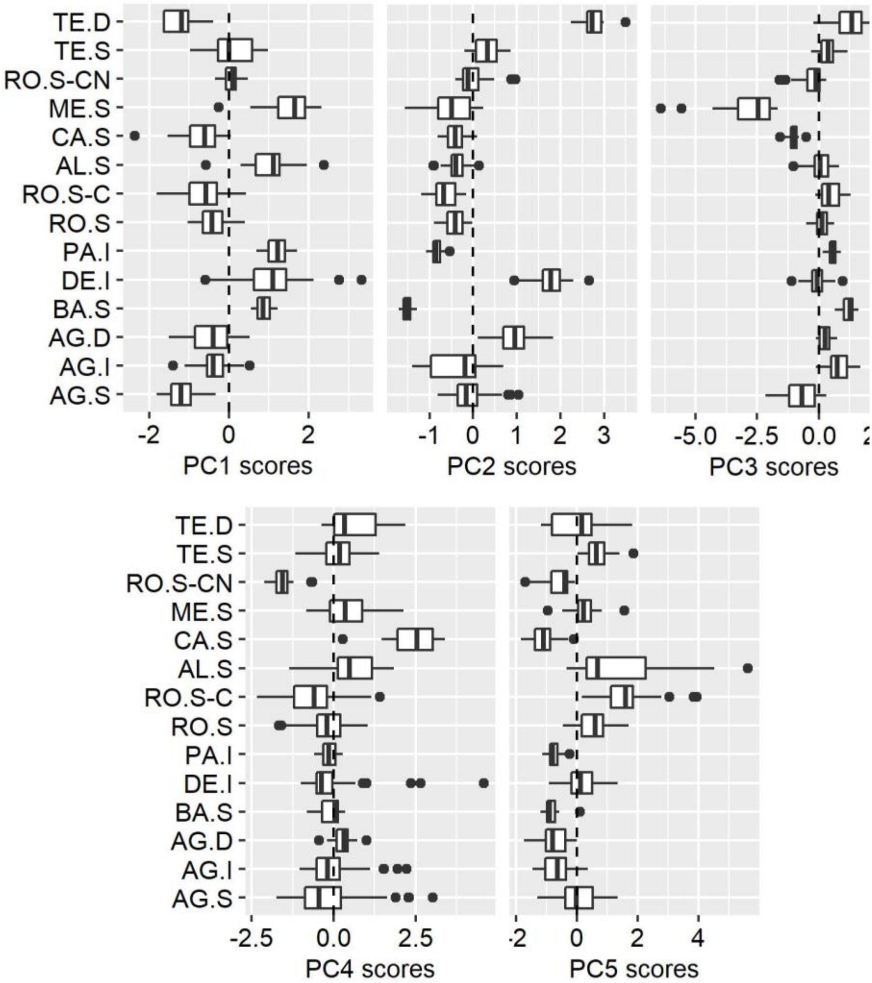


Figure 6: Tukey boxplot of PCA scores per station. For each station the solid line indicates the median of the scores; the box indicates the interquartile range; the hanging bars indicate the range excluding "outliers"; and the dots indicate outliers.

place, C_{org} content would follow a trend with depth, either increasing or decreasing depending on which one predominates. However, this is hardly the case in our data (Fig. 3). Hence, to our best understanding, the vertical fluctuations in soil C_{org} content is probably reflecting temporal variability in OM inputs, which would thus play an important role in C_{org} accumulation in the studied seagrass deposits.

4.2 Grain-size distribution in the soil cores

The second component of the PCA seems to reflect differences in soil texture (Table 3, Fig. 5). Higher Sr and Ca concentrations occur in coarser substrata (positive PC2 loadings) and are probably linked to biogenic carbonates and bioclasts (Croudace and Rothwell 2015), as seagrasses facilitate bio-precipitation of carbonates (Hendriks et al. 2014). However, along the Andalusian coast there are several outcrops of carbonate rocks (Fig. 1) and the contribution of this continental terrigenous fraction to Ca content cannot be completely discarded. Chlorine has been found to be a water saturation indicator in marine sediments (Hennekam and De Lange 2012). Soils made up with coarse particles present large porosity and would have a lower water residence time and a higher content of marine water indicators, such as Cl, compared to soils composed by finer particles with higher water resident times, in which the interstitial water would be enriched in compounds derived from chemical reactions in the soil; e.g. OM mineralization, carbonate dissolution (Marbà et al. 2006). On the other hand, Si and Zr showed negative loadings in PC2, indicative of the siliciclastic nature of the fine sandy sediments (see 4.1).

The cores with coarser textures, and thus higher porosity, are TE.D, AG.D and DE.I (Table 2). The three cores have been collected below 15 m of water column, farther from the coast than in shallow stations, in relatively open waters. The coarser substrates in these stations could be the result of higher resuspension and export of fine particles (van Katwijk et al. 2010) but the ^{210}Pb profile of AG.D and DE.I did not show any signal of post-depositional disturbances (S2, supplementary material), being resuspension unlikely. Therefore, it is plausible that the bulk of the sediment discharged from inland areas may have been trapped in the shallower meadow areas closest to the shore, those further offshore receiving a much smaller input as *Posidonia oceanica* canopy is known to increase sedimentation, promoting fine fraction deposition (Terrados and Duarte, 2000; Hendriks et al., 2008). When the hydrodynamic force or the sediment load is high enough to bring sediments to more distal parts of the meadow, the deposit may become enriched in coarser material, as those high energy environments usually transported coarser materials (van Rijn 1993).

As said before, DE.I core was sampled in a polluted area in which the meadow was in an advanced state of degradation (Marbà et al., 2015; Consejería de Agricultura Ganadería Pesca y Desarrollo Sostenible, 2017). Field observations during sampling also indicated that there was a very soft substrate, confirmed by an anomalously low density in the upper parts of the core. This has been interpreted as the effect of the chemical degradation of the OM deposited that implied an increased porosity and, consequently a decreased density. However, increasing shoot mortality is likely to have an impact over the rhizosphere, but not over deeper sections of the soil (Piñeiro-Juncal et al. 2020a). DE.I showed high PC2 scores along the core and not only in the upper part (S5, supplementary material), but OM degradation, promoted by the demise in plant cover, is not likely to be the sole explanation. As no other core was sampled in this location we cannot ascertain if there is a change in texture between the shallower and the deeper part of the meadow as found for TE.D and AG.D. The shallower meadow in front of Deretil has completely disappeared in a coastal extension of more than 2 km (Moreno et al. 1999). Nevertheless, this loss is relatively recent (in the last 5 decades), and thus would not have affected the processes that formed the soil in the last 3620 cal. yr BP (Table 2), the time encompassed by the DE.I core.

Two of the *C. nodosa* cores, BA.S and PA.I, are the ones presenting the lowest PC2 scores, the largest content of FSands (Fig. 5 and 6), the lowest content of MSand (0 for both cores) and CSand (<1% for both cores) and the highest accretion rates (BA.S 4.4±1.1 mm yr^{-1}, PA.I 7.6±3.8 mm yr^{-1}; Fig. 4; Table 2). *Cymodocea nodosa* is known to be a pioneer species, earlier colonizer of areas that could be later colonized by larger species, as *P. oceanica* (Molinier and Picard 1952). However, the *C. nodosa* meadow at BA.S has existed for at least some hundreds of years (BAS 355 cal. yr BP at the bottom of the core; Table 2), as *C. nodosa* macro debris could be found along the whole core, with no remains of *P. oceanica*. Although no assurance can be provided that the PA.I meadow was stable over the time covered by this soil record, as there were no traces of *C. nodosa* macro debris between 60 and 120 cm deep, *P. oceanica* debris were also absent along the whole core as well. This may be due to the unsuitability of the environment for the colonization of larger seagrass species. *Posidonia oceanica* has been found to grow from fine sandy to rocky bottoms, but not on muddy ones (i.e. silt+clay, Mazzella et al., 1993, Bellan-Santini et al., 1994; De Falco et al., 2006; Gobert et al., 2006). Although silt have a low loading in this component, it is possible that a high content in FSand with almost no MSand or CSand content would negatively affect *P. oceanica* performance. Furthermore, punctual sediment burial of the leaves beyond 5 cm triggers a decline in the shoot population of well-developed *P. oceanica* meadows (Manzanera et al., 2011; Gera et al., 2014), while *C. nodosa* seedlings have been found to tolerate up to 7 cm of punctual burial and its vertical growth is promoted by < 4 cm of punctual burial (Marbà and Duarte 1994). Therefore, *C. nodosa* would be more suited for high accretion environments than *P. oceanica*. Although our accretion rates are lower, two conditions need to be considered. First, the accretion rates are averages of the top meter, where soil compaction is very likely to have already occurred, and may be underestimating punctual sedimentation rates. Second, the studies cited are experiments of punctual burial while our accretion rates integrate long term burial. It is possible that the maintained burial stress of stations PA.I and BA.S (the highest of our stations) may have further diminished *P. oceanica* performance, preventing the establishment of a meadow. The AG.I station showed similar accretion rates to BA.S, but a much coarser sediment and ME.S showed a high content of fine sediments but a much lower accretion rate and both areas host a *P. oceanica* meadow. This suggests that both factors, grain size and high accretion rates, are playing a synergic role in the exclusion of *P. oceanica* from the area.

4.3 High energy transport of coarse material

The third component clustered CSand and MSand with MS, with negative loadings, against silt, with positive loading (Table 3, Fig. 5). The high anti-covariation between silts and MS (0.67 and -0.62 loadings respectively, Table 2) indicates that minerals with higher MS were probably linked to medium and coarse materials. MS in seagrass deposits has been related to influxes of magnetic particles eroded from catchment topsoils and incorporated into marine sediments and seagrasses soils, due to changes in land use or flooding events (López-Merino et al. 2017). The possibility of PC3 being the signal of flooding episodes seems to be reinforced by the association between the MS and coarse grain-sized particles in our cores, as the arrival of larger particles is related to high energy transport (van Rijn 1993). This component would be interpreted as the signal of coarse material discharges, contrary to PC1 that relates to the continuous silty inputs - transported in low energy environments - and its balance with OM accumulation in the meadows. The most outstanding core in PC3 scores is ME.S (Fig. 6), with the lowest scores. Core ME.S was sampled near a steep slope coastal area (Instituto de Cartografía de Andalucia 2007) that could have promoted high energy runoff. The distribution of PC3 scores in ME.S shows a sharp decrease at 25-30 cm (S6, supplementary material), pointing towards a punctual event of coarse material discharge as the main source of its low PC3 values. Other two cores show low PC3 scores, CA.S and the upper part of AG.S core (S6, supplementary material). Scores in CA.S are quite stable along the core (S6, supplementary material), which can be implying that the sedimentary particles arriving to the meadow were always generated in a high-energy environment. On the other hand, scores from AG.S are low between 25 and 50 cm and again between 100 and 140 cm (S6, supplementary material), suggesting the alternation between phases of high and low energy sediment transport.

4.4 Metals bind to organic matter

The fourth component of the PCA clusters Ni, Pb and Br against Ca and Mn (Table 3). The association of Ni and Pb with Br could be indicating the bonding of metals and halogens to humified OM (Leri et al. 2014; Martínez-Cortizas et al. 2016). Furthermore, Pb has been found to be selectively preserved during the degradation of seagrass tissues (Lyngby and Brix 1989). The low loading of C_{org} in this component could be indicating that not all OM but only humified OM is active in metal binding. However, in a *P. oceanica* meadow from the northeast of the Iberian peninsula (Portlligat, Spain) a positive covariation with the fine OM fraction (<2 mm) was found, but not with the humified OM (inferred by the covariance of S, P, Br and Cl; Piñeiro-Juncal et al., 2020). A specific study would be needed to clarify the behavior of metals in seagrass deposits. As found in our study, the core of the Portlligat meadow also showed a negative relationship between Pb and Ca (also to $CaCO_3$) concentrations. This correlation was interpreted as a negative effect of Pb over bio-calcifying organisms or as relative dilution effect between OM and carbonates, as Pb was associated with OM (Piñeiro-Juncal et al., 2020). However, this correlation can also be an indication of a positive relationship between heavy metals content and fine particles, previously observed in other marine areas (e.g., Dang et al., 2015; Yao et al., 2015; Remeikaitė-Nikienė et al., 2018), as $CaCO_3$ is often found in the form of coarse particles.

4.5. Humified organic matter

The main variables associated with the fifth component of the PCA were S and Br, and a moderate loading of C_{org} (Table 3, Fig. 5). Both Br and S are proxies for OM (Rothwell and Croudace, 2015). As stated before, the first one bonds to OM during humification (Leri et al. 2014; Martínez-Cortizas et al. 2016). This balance has been already detected in an XRF analysis in the core of Portlligat mentioned above (Piñeiro-Juncal et al. 2020b). Cores with higher loadings in PC5 were all the shallow *P. oceanica* cores, except CA.S (Fig. 6). While *C. nodosa* cores showed values similar to those of deeper *P. oceanica* meadows. *Posidonia oceanica* carbon stock has been found to be maximum at shallow waters, linked to higher light penetration and primary production (Serrano et al., 2014). *Cymodocea nodosa* has a lower primary production than *P. oceanica* and accumulates far less carbon in its soils (Luque and González 2004), resulting in much lower C_{org} average content in our cores (0.025±0.010 vs 0.002±0.001 C_{org} g cm^{-3}), that would necessarily derive in less humified OM. The station with the lowest scores in this component was CA.S, despite being a shallow *P. oceanica* meadow. CA.S together with RO.S-C, is one of the two dead *P. oceanica* meadows sampled in this study. Despite of this, RO.S-C showed one of the highest values in PC5. The lack of accumulation or faster degradation and wash of the humified OM in the mat could be related to specific impacts derived from the loss of the canopy in dead meadows, from differences in the time elapsed since the loss, or to intrinsic physico-chemical traits of the soil. A specific study would be necessary to explore these possible factors, which are of great interest to model carbon stocks loss after blue carbon habitat degradation.

5. Conclusions

In this study we found five geochemical signals that could be linked to seagrass soil formation processes: (1) accumulation of terrestrial silty material, balanced with organic matter accumulation; (2) soil grain size changes, which might be affected by the orientation and distance from the discharging point of sediments, and by local hydrodynamism; (3) coarse sediments discharge, that we related to high energy transport; (4) the accumulation of metal-OM compounds (and negative correlation with carbonate), by mechanisms that need further research; and, finally, (5) OM humification, linked to OM degradation within the soil. The first three processes are related to the continental catchment that furnishes the meadows with terrigenous materials. Together, they explain 55% of the total variance of our data, revealing the determinant terrestrial influence over these marine coastal ecosystems, working as a juncture between land and sea. As discussed for PC2, sediment grain size and amount may play a central role in controlling species colonization along the Mediterranean coast. Knowledge about environmental conditions promoting the establishment of a given seagrass species would help to understand the causes for meadow deterioration and to develop more efficient restoration projects. Here we show that the study of current and past conditions of stable monospecific meadows can shed light on this question. In our cores, C_{org} depth distribution did not follow any particular trend, pointing to temporal changes in OM inputs to the meadow as an influential factor in its accumulation. Finally, our results on metal-OM bonding, in line with those found in a previous study, suggest the need of specific research to clarify metal's behavior in seagrass beds and the apparent relation between Pb deposition and carbonates accumulation.

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CHAPTER III

Potential microbial functional activity along a *Posidonia oceanica* soil profile

Aquatic Microbial Ecology, 2018, 81, 189-200

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CHAPTER IV

Cover loss in a seagrass Posidonia oceanica meadow accelerates soil organic matter turnover and alters soil prokaryotic communities.

Organic Geochemistry, 2020

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CHAPTER V

Reviewing soil seagrass data for its preliminary description and classification.

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Abstract

Seagrasses are marine angiosperms that colonize coastal areas of all continents with the exception of Antarctica. Due to their terrestrial evolution, they developed belowground organs that interact with and transform their substrates. The presence of seagrasses in soft marine bottoms leads to chemo-physical changes analogous to those taking place during inland soils formation (i.e. additions, removals, transfers and transformations). Although, the Unite States Department of Agriculture Soil Taxonomy (ST-USDA) recognized the possibility of soil formation under seagrasses and that subaqueous soils are recognized by the World Reference Base for Soil Resources (WRB-FAO), seagrass meadows substrates have been largely regarded as sediments by marine scientist. Therefore, very few studies have utilized standard pedological methods, hindering the utilization of those databases for proper soil description and classification. Here, we aim to review the large effort invested in seagrass substrates research to contribute to the amendment of the lack of pedological studies in subaquatic marine environments, by summarizing the data typically used for soil description and classification. A literature review comprised from 1980 to June 2020 yielded more than 3,800 papers from which the available information about dry bulk density, grain size, redox, pH, carbonate content, organic carbon content and porosity was collected. Large knowledge gaps were found in relation to the geographical area of the studies and the species examined. Temperate meadows and genus *Posidonia* and *Zostera* were the areas and species having received the most attention. Nonetheless, the data reviewes allowed to draw some general conclusions. (1) Most seagrasses grow on sandy substrates, the *Posidonia* genus being excluded from muddy substrates. (2) Although they promoted organic matter accumulation, the seagrasses are unlikely to form organic soils. The formation of Histosol seems to be a rare situation restricted to the *Posidonia* genus.

(3) The most likely classification of seagrass-derived soils is as Entisols according to the ST-USDA, and as Fluvisols or Gleysols under the WRB-FAO standard.

Key words: dry bulk density, porosity, grain size, redox, pH, carbonate content, organic carbon

1. Introduction

Seagrasses are a polyphyletic group of angiosperms that colonized marine environments by, at least, three independent lineages (Les et al. 1997). Due to their evolution in terrestrial environments, they developed belowground organs that interact with and transform their substrate (Kuo and den Hartog 2006; Marbà et al. 2006). Seagrasses are distributed in coastal areas of all continents except for the Antarctica (Hartog and Kuo 2006), from soft to rocky bottoms (Koch 2001). In the upper limit of their depth distribution range, seagrasses are limited by exposure to desiccation, to solar heat and radiation, and to hydrodynamism (Infantes et al., 2009, and references therein). Lower limits are mostly defined by the photosynthetic active radiation arriving to the canopy and have been reported as deep as 90 m (Duarte 1991). Their canopies promote sediment accretion by direct trapping of particles, by lowering the hydrodynamic force (Agawin and Duarte 2002; Hendriks et al. 2008; Gruber and Kemp 2010; Hansen and Reidenbach 2012) and by reducing sediment resuspension (Ward et al. 1984; Terrados and Duarte 2000; Gacia and Duarte 2001; Widdows et al. 2008). This results in increased rates of burial of both organic and inorganic particles. The deposits below seagrass meadows grow in thickness forming, when undisturbed, well-structured soils following a chronological sequence in which deeper equals older (Mateo et al. 2002).

Although the presence of seagrasses in soft marine bottoms leads to chemo-physical changes analogous to inland soil formation (i.e. additions, removals, transfers and transformations) (Simonson 1959), the substrates they root in have been largely regarded as sediments by marine scientist (Kristensen and Rabenhorst 2015). The Unite States Department of Agriculture Soil Taxonomy (ST-USDA) definition of soil recognized the possibility of soil formation under seagrasses since its first edition (Soil Survey Staff 1975). However, subaqueous soils have been largely neglected in soil science research (Demas 1993). Furthermore, subaqueous soils are only recognized by the World Reference Base for Soil Resources (WRB-FAO) up to 2 m water depth at low spring tide (IUSS Working Group 2015). This partial recognition allows substrata from the same seagrass meadow, with the same age and characteristics, to be considered or not a soil on the sole basis of depth, an approach not consistent with the soil-continuum.

Seagrass meadows substrates have been widely studied, especially over the last decade, paralleling the growing interest in its role as carbon sink by the scientific community and institutions (Nellemann et al. 2009). Despite the large quantity of data published, very few studies have utilized standard pedological methods (e.g. Bradley and Stolt, 2003; Nóbrega, 2017), hindering the utilization of those databases for proper soil description and classification. Here, we aim to review the large effort invested in seagrass substrates research to contribute to the amendment of the lack of pedological studies in subaquatic marine environments, by summarizing the data typically used for soil description and classification.

2. Material and methods

Data has been gathered through a literature review using the web of knowledge (https://www.webofknowledge.com/, accessed from 6th to 22th of July 2020). The variables collected were clay and silt content (mud <0.063 mm), redox potential, pH, carbonates content, organic carbon or organic matter (C_{org} or OM) content, dry bulk density (DBD), porosity and color. Search terms used were as follows: TS= (seagrass AND (sediment* OR soil) AND *Variable*); where *Variable* was replaced with "bulk density", "grain size", "redox", "pH", "carbonate*", "organic matter OR organic carbon" or "porosity". The period comprised by the search was 1980-2020.

Data from those works reporting replicate values were pooled into one single average value. Data from multi-specific meadows were assigned to the dominant species. If the most abundant was not reported it was noted as a mixed meadow. For those soil samples where OM content was reported but not C_{org} content, the last was estimated from the former using widely accepted linear functions relating them (Fourqurean et al. 2012a). The data was distributed in self-made geographical regions, having a higher resolution those areas were more data was available (Fig. 1).

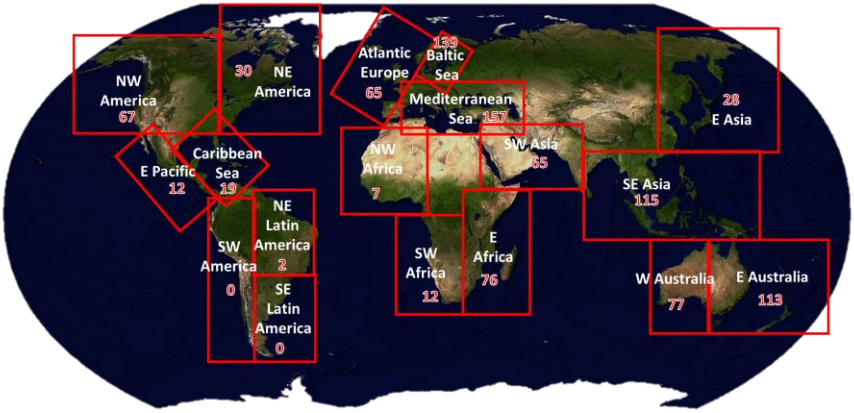

Figure 1: Number of total observations -cores or superficial samples- (red numbers) distributed by selfmade geographic regions. Each of them has at least data for dry bulk density, mud, $CaCO_3$ or C_{org}.

3. Results and discussion

3.1. Literature review

A total of 3,815 papers were obtained from the search of BDB, mud, carbonates and C_{org} content. Among these, 96 reported values of all or some of those variables. These data belong to 10 different genera from all five seagrass families, although only three observations were found for *Rupiaceae*. No data were found for *Syringodium*, *Heterozostera* and *Phyliospadix* genera. Most of the observations (405) correspond to *Zostera spp.*, followed by *Posidonia spp.* (190; Table 1 Sup. material).

The search for “porosity” only yielded 19 publications of which 13 reported values for 186 soil cores, mainly from *Zostera spp.* (Table 2 supplementary material). The term “redox” prompted 57 results from which 15 studies reported data on 67 soil cores (Table 3 Sup. material). Searching for “pH” resulted in 149 papers among which 12 of them reported values for 33 soil cores (Table 4 Sup. material). We only found 4 papers were color descriptions were reported (Table 5 Sup. material).

The main gaps in published data were from seagrass meadows of South America, where only two observations from Brazil were gathered (Fig. 1). By far, the most studied region was Europe (Fig. 1). This contrast with the distribution of seagrass species, with higher diversity is found in tropical areas (Larkum et al. 2006), but agrees with the known knowledge gaps in seagrass distribution (Green and Short 2003). The available pedological information about seagrass soils belongs largely to the epipedon (Supplementary material).

3.1.1. Soil texture, porosity and color

Most of the values reported for mud content fall below 30%, with some families consistently growing in substrates below 20%, like *Thalassia* or *Posidonia* (Fig. 2). In the case of *Posidonia*, for which data of 136 cores were gathered, this review provides support to the general assumption that muddy substrates are not suited for the growth of these species (Mazzella et al. 1993; Bellan-Santini et al. 1994; De Falco et al. 2006; Gobert et al. 2006). The data collected seems to suggests that, although some seagrasses are able to grow in muddy sediments, they are better adapted to sandy substrates (Fig. 2). In seagrass meadows of

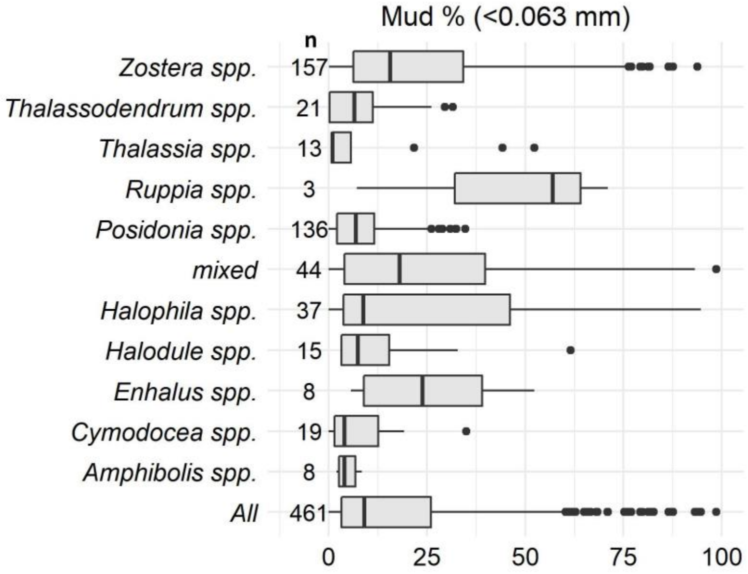

Figure 2: Boxplot of the Mud % distribution per family. Those meadows where a predominant species was not reported are clustered in "mixed". Vertical line, median; black dots, outliers; n, number of observations per genus.

SE Asia, seagrass richness decreases sharply when mud content exceeds 15% (Terrados et al. 1998).

Porosity values ranged from 0.05 to 0.89, average 0.36 and median 0.31 (Table 2 Sup. material). However, we could only gather 186 observations, most of them from *Z. marina* meadows (87%) and the northern hemisphere (96%).

The lack of a pedological approach to seagrasses soils studies explains the virtual lack of works addressing the description of the color of the substrate. The colors reported seem to range from brown to grey (Table 3 Sup. material). However, the soils from *P. oceanica* meadows of Cabrera Island (Balearic Islands, Spain), for instance, showed light

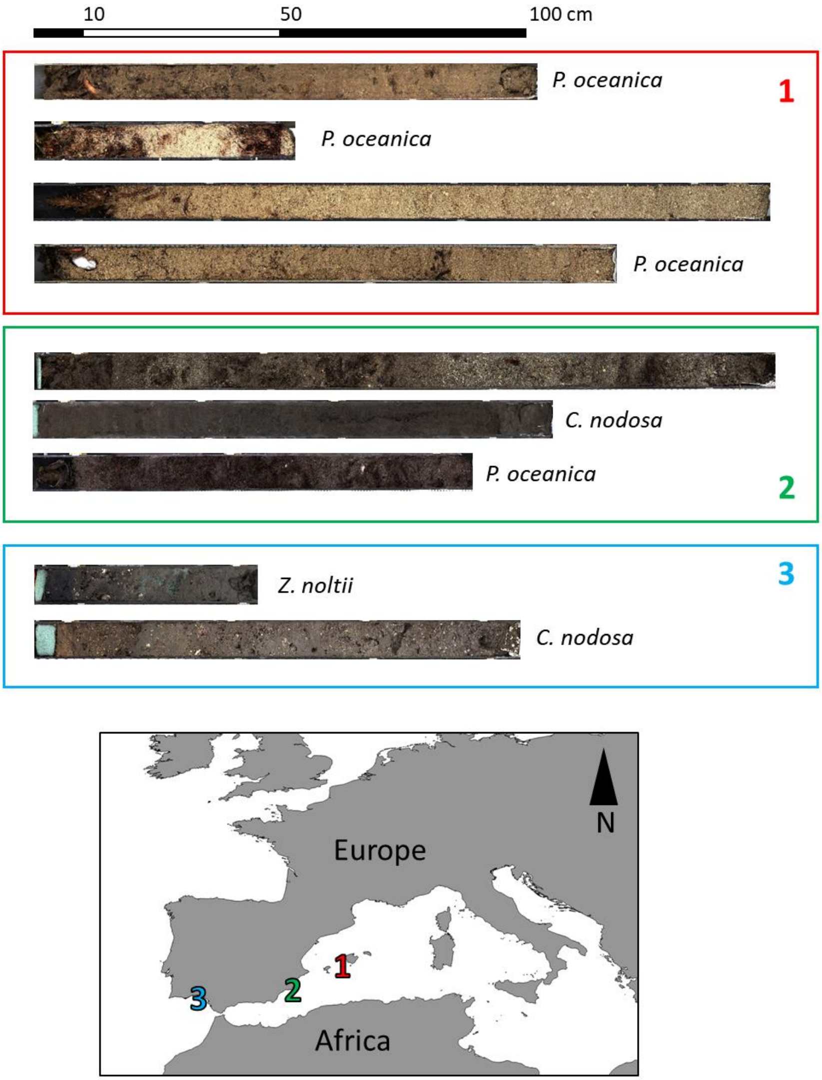

Figure 3: High-resolution images of cores sampled in Posidonia oceanica and Cymodocea nodosa meadows of the Western Mediterranean Sea. Group 1, meadows from Cabrera Island (Belshe et al. 2019); group 2, meadows from east Andalusia (Mateo et al. 2018); group 3, meadows from Bahía de Cádiz (Mateo et al. 2018).

yellow colors (Fig 3, Area 1), probably resulting from a high content of carbonates (>83%). Cabrera Island is mainly composed of limestone, which may influence the carbonate content of the meadows. This suggests that, apart from the redox condition, one of the main factors controlling color may be the composition of the adjacent lithosphere and contributing watershed.

3.1.2. Bulk density

Although data for seagrass soils has increased exponentially in the last decade, due to the quantification of their carbon stocks for which DBD was used as part of the calculations, very few publications provide raw DBD values. We found 643 observations of DBD, most of them from *Zostera spp.* (Fig. 4; Table 1 Sup. material). Among the seagrasses for which data are available, there are not significant differences in DBD (Fig 4). This was expected as DBD would likely depend on other factors, such as texture or parental material.

3.1.3. Redox potential and pH

Most redox data correspond to the upper part of the soil (Table 4 Sup. material). At this depth, the presence of the rhizosphere causes a positive redox anomaly in the soil compared to bare sediments, which is related to the photosynthetic activity of the plant through root O_2 release (Enríquez et al. 2001; Gacia et al. 2005; Marbà et al. 2010). Several studies report a tendency of redox potential to decrease with depth, with very variable values (Table 4 Sup. material). Field experiment with reduced seagrass biomass and light availability found a lowering of the redox potential in the rhizosphere (Gacia et al. 2005; Marbà et al. 2010), suggesting that, in soil layers where the influence of the plant disappears, the soil would exhibit the negative redox values

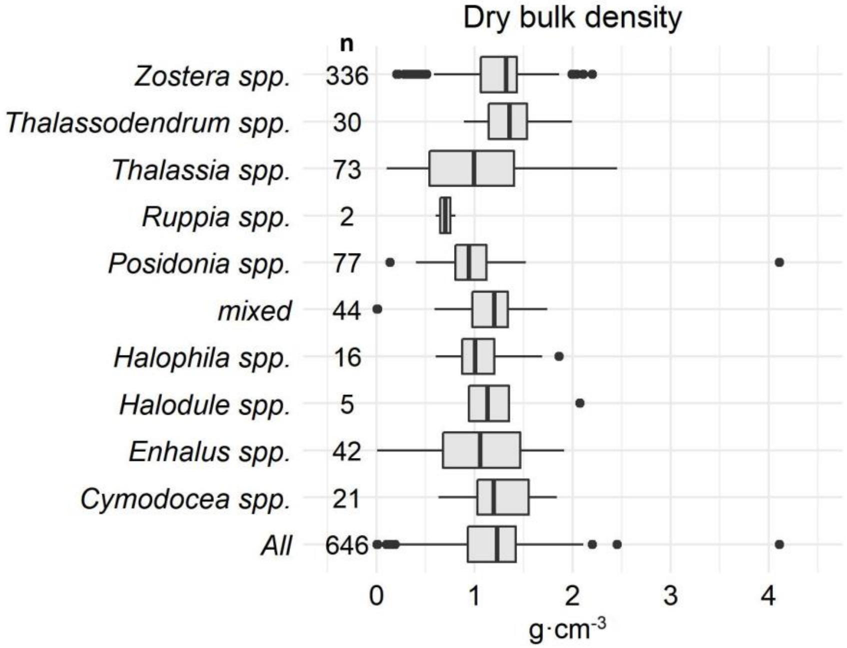

Figure 4: Boxplot of the DBD (g cm-3) distribution per family. Those meadows where a predominant species was not reported are clustered in “mixed”. Vertical line, median; black dots, outliers; n, number of observations per genus.

typical of adjacent unvegetated sediments. Serrano et al. (2020) reported redox values up to 135 cm depth, finding the most negative values below the first half meter of the soil (Table 4 Sup. material).

Average pH values reported in the bibliography were between 6.9 and 8.2 (Table 5 Sup. material). pH in seagrass soils is related to the dissolution of carbonates driven by OM mineralization (Marbà et al. 2006). Burdige and Zimmerman (2002) found that pore water pH reached maximum values at the soil surface (2 cm) of a seagrass meadow. The changes were consistent with changes in carbonate saturation values. The seagrass rhizosphere seems to lower pH, which may result from the humic acids and CO_2 production during OM decomposition (Morse et al. 1987; Burdige and Zimmerman 2002; Nobi and Dinesh Kumar 2014). At a higher resolution, low and high pH micro-niches have been found in *Cymodocea serrulata* and *Z. marina* rhizospheres, pointing to a high pH heterogeneity within the rhizosphere (Brodersen et al. 2016, 2017).

3.1.4. Carbonates and C_{org} content

Carbonate content in seagrass meadows substrates was found to be highly variable, from 0.2 to close to 100 % (Mazarrasa et al., 2015; Table 1 Sup. material). Seagrasses promote the preciptation of carbonates by increasing the pH within their canopies (Hendriks et al. 2014). This effect was expected to be higher in larger seagrass species and tropical areas. Although tropical meadows accumulated more carbonates than temperate ones, the soils of meadows formed by larger species were not found to have a higher carbonate content (Mazarrasa et al. 2015). This may be explained by the predominance of other factors in carbonate accumulation, like the geology of the catchment, the parental material or water depth. Recent studies suggest that most of the carbonates accumulated in seagrass meadows are not produced *in situ* but imported as allochthonous sediment particles (>90% of the carbonates accumulated) (Saderne et al. 2019).

Whether locally formed or imported, the carbonates would be buried and incorporated to the soil as primary carbonates. The formation of secondary carbonates in the soil seems unlikely, as most studies found that the seagrasses lower the pH of the soil. However, coupled dissolution and reprecipitation of carbonates has been found in superficial samples of Bahamas meadows (Burdige et al. 2010).

Organic matter, hence C_{org}, is accumulated in seagrass soils by (1) particles trapping and deposition favored by the seagrass canopy, (2) limited mineralization due to the anoxic conditions in the soil and (3) the refractory nature of the seagrass tissues, which can be preserved

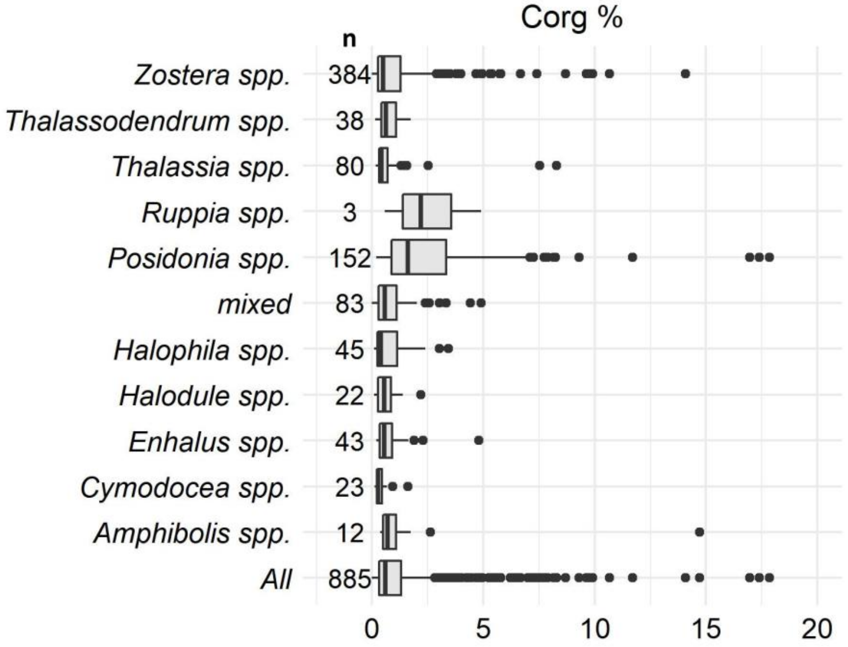

Figure 5: Boxplot of the Corg % distribution per family. Those meadows where a predominant species was not reported are clustered in "mixed". Vertical line, median; black dots, outliers; n, number of observations per genus.

over millennia (Mateo and Romero 1997; Lavery et al. 2013; Serrano et al. 2016e; Kaal et al. 2018). Larger seagrass usually species show larger soil carbon stocks (Lavery et al. 2013). In Australia, despite showing similar sequestration rates, tropical seagrasses showed lower carbon stocks, suggesting higher mineralization rates (Serrano et al. 2019).

Organic carbon values gathered in this review ranged widely, from 0 to 17.85 % of dry weight. The highest values corresponding to *Posidonia spp.* and *Ruppia* meadows. Most meadows show values below 1.5 % (Fig 6). *Ruppia* observations show a surprisingly high concentration of C_{org}, but were based in only three observations.

3.2. Soil classification

The wide range of environmental conditions where seagrass meadows are present would necessarily lead to a wide range of soil types. Some of the properties used in soil classification are not standard measures for seagrass substrate research, like color or cation exchange capacity, hampering the use of published data to this end. Nóbrega (2017) analyzed seagrass substrate using pedological techniques and classified the soils researched as Fluvic Sodic Subaquatic Solonchak (Loamic, Hypersalic, Hypersulfidic), Fluvic Sodic Subaquatic Solonchak (Loamic, Hypersalic, Hyposulfidic) and Eutric Subaquatic Gleysol (Loamic, Sodic, Hypersulfidic), following the WRB-FAO (IUSS Working Group 2015).

Although determining to which soil type would a seagrass soil belong without the proper measurements is not possible, there are some soil types that can be unambiguously discarded and others likely to be a good match. Following the ST-USDA, a seagrass derived soil could not be an Aridisol, where "*[...] water is not available to mesophytic plants for long periods [...]*"; a Gelisol, "*[...] soils with gelic materials underlain by permafrost [...]*"; or a Vertisol, "*[...] clayey soils that have deep, wide cracks for some time during the year [...]*" (Soil Survey Staff 1999). In those cases where a mat is developed and the rhizosphere occupies near 80% of the substrate volume, the soil would correspond to a Histosol, however those cases are likely to be exceptional. The most probable classification for seagrass soils are as Entisols, "*[...] soil material is not in place long enough for pedogenic processes to form distinctive horizons. Some of these soils are on steep, actively eroding slopes, and others are on flood plains or glacial outwash plains that receive new deposits of alluvium at frequent intervals.*" It is very likely that most seagrass meadows would develop an Entisol in the first stages of their development and some of them, due to the small impact of the seagrass species or the high accretion rate, would not develop any other.

The ST-USDA added a suborder within Entisol for substrates permanently saturated with water – Wassents – to improve the classification of subaqueous soils (Soil Survey Staff 2014), although doubts have been raised about its adequacy to describe seagrass soils (Kristensen and Rabenhorst 2015).

Following the WRB-FAO, a seagrass derived soil could not be Cryosols, "*[…] mineral soils formed in a permafrost environment […]*"; Durisols, "*[…] moderately well- to well-drained soils […]*"; Ferralsols, "*[…] have diffuse horizon boundaries, a clay assemblage dominated by low-activity clays (mainly kaolinite) and a high content of sesquioxides.*"; Gypsisols, "*[…] found in the driest parts of the arid climate zone […]*"; Kastanozems, "*[…] dry grassland soils […]*"; Nitisols, "*[…] well-drained, red tropical soils […]*"; Regosols, "*[…] not with fluvic materials […]*"; Retisols, "*[…] characterized by a partial removal of clay and free iron oxides […]*"; Stagnosols, "*[…] soils with perched water […]*"; or Vertisols, "*[…] form deep wide cracks from the surface downward when they dry out, which happens in most years […]*". As in the ST-USDA, in the exceptional case a mat develops a rhizosphere occupying near 80% of the substrate volume, it would very likely be classified as a Histosol. However, the most probable classification for seagrass soils is as Fluvisols "*[…] genetically young soils in fluvial, lacustrine or marine deposits.*" or Gleysols "*[…] soils saturated with groundwater for long enough periods to develop reducing conditions resulting in gleyic properties, including underwater and tidal soils.*" The WRB-FAO added the qualifier Subaquatic (Sb) for those soils permanently underwater (but only until 200 cm depth) (IUSS Working Group 2015).

4. Conclusions

There are large gaps in the information available about seagrass soils. While *Posidonia* and *Zostera* are profusely studied, information from meadows of other genus is scarce. On the other hand, temperate seagrass meadows are far more studied than tropical ones, despite holding the tropical regions a highest seagrass diversity. Nonetheless, some conclusions can be inferred.

Most seagrass substrates have sandy textures, being the *Posidonia* genus not able to grow in muddy substrates. Although they promoted OM accumulation, the seagrasses are unlikely to form organic soils. The formation of Histosol seems to be a rare event linked to the *Posidonia* genus. The most likely classification of seagrass soils is as Entisols, following the ST-USDA, or as Fluvisols or Gleysols following the WRB-FAO.

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APPENDIX. SUPPLEMENTARY MATERIAL

1. Chapter II

Dating and age-depth models

As part of the stimation of the Andalusian blue carbon inventory, the cores used in this study were dated and cronological models were built. Two methods were used: ^{210}Pb and ^{14}C. From the 30 first cm aliquots of 3 g of ground soil were sent to the Unit of Physics of Radiations from the Autonomous University of Barcelona (UAB), to estimate recent sediment accretion rates through ^{210}Pb method. The concentration profile of ^{210}Pb was determined every centimeter for the uppermost 30 cm through quantification of ^{210}Po using alpha spectrometry on a PIPS detector (CANBERRA, Mod. PD-450.18 AM) following Sanchez-Cabeza et al. (1998), at the Universitat Autònoma de Barcelona. The excess of ^{210}Pb (^{210}Pb$_{xs}$) was obtained by subtracting the total ^{210}Pb from the constant value of the ^{210}Pb concentration at the bottom of the soil records, which was taken as representative of the supported ^{210}Pb. ^{210}Pb$_{xs}$-derived sedimentation rates were calculated by applying a CRS model (Appleby and Oldfield 1978). The cores BA.S, RO.S-CN and AL.S could not be dated by ^{210}Pb as reworking of the material did not allow as to find a decay profile. Moreover, the ^{210}Pb dating methods was not attempted in TE.D as the vibrocore sampling may cause disturbance in the upper part of the core. In each core, we selected 2-3 ancient seagrass debris (preferably from leaf tissue) for ^{14}C dating. ^{14}C datings was performed by accelerator mass spectrometry (DirectAMS - Accium BioSciences), using a NEC Pelletron 500 kV AMS. Cores PA.I and RO.S-CN were not dated by ^{14}C, as seagrass debris could not be found and bulk organic matter was very unlikely to have been originated in the year of deposition (Belshe et al. 2017).

If both ^{210}Pb and ^{14}C dates were available, the age-depth model was built by a combination. If not, only the available dates were used. The models were elaborated using the “rbacon” package for R software (Blaauw and Christeny 2011). The year of sampling: 2016 or 2017, was also considered in the model. Radiocarbon dates are expressed as calibrated years before present. Dates were corrected for isotopic fractionation (^{13}C/^{14}C), for the reservoir effect (Reimer et al. 2013) and for the local anomaly ($\Delta R = 2 \pm 26$ years, Siani et al., 2000). In ROS-CN station wasn’t possible to obtain dates and in dead meadow stations (RO.S-C, CA.S and CA.S-C) sediment accretion was not calculated as erosion was likely to have occurred.

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S1: dates used to build the age-depth models per core.

Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
TE.S	^{210}Pb	0	-66	2
	^{210}Pb	1.85	-64	2
	^{210}Pb	3.6	-61	2
	^{210}Pb	5.4	-60	2
	^{210}Pb	7	-53	2
	^{210}Pb	8.75	-42	2
	^{210}Pb	10.4	-34	3
	^{210}Pb	12	-28	3
	^{210}Pb	13.55	-12	4
	^{210}Pb	15	0	5
	^{210}Pb	16.6	34	11
	^{210}Pb	18	60	20
	^{14}C	44.5	414	30
	^{14}C	49.6	597	27
	^{14}C	53.5	562	29
	^{14}C	62.75	821	28
	^{14}C	68.5	1135	32
	^{14}C	76.5	1223	27

Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
TE.D		0	-66	1
	^{14}C	110	1499	28
	^{14}C	190	3042	32
	^{14}C	240	3839	32
DE.I	^{210}Pb	0	-66	3
	^{210}Pb	1.09	-61	3
	^{210}Pb	3.18	-55	3
	^{210}Pb	5.18	-51	3
	^{210}Pb	7.15	-45	4
	^{210}Pb	9.08	-39	4
	^{210}Pb	10.98	-30	5
	^{210}Pb	12.85	-21	5
	^{210}Pb	14.68	-14	6
	^{210}Pb	16.49	-7	7
	^{210}Pb	18.27	3	8
	^{210}Pb	20.02	8	9
	^{210}Pb	21.74	17	9
	^{210}Pb	23.44	40	13
	^{14}C	64	1297	29
	^{14}C	90	1578	27
	^{14}C	101	1273	32
	^{14}C	122	3178	35
	^{14}C	136	3435	36
	^{14}C	153	3614	33
PA.I	^{210}Pb	0	-67	6
	^{210}Pb	3.79	-62	7

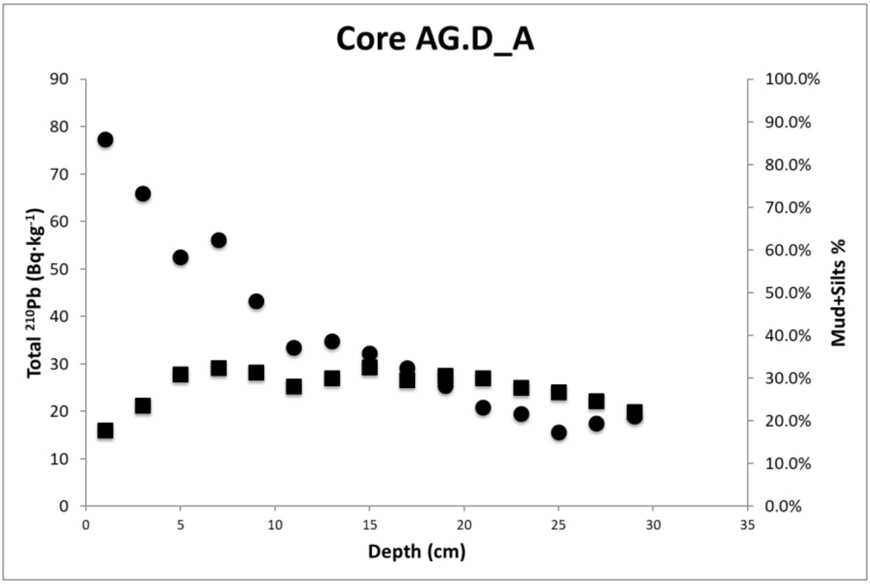
Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
	^{210}Pb	7.38	-54	8
	^{210}Pb	10.85	-47	8
	^{210}Pb	14.2	-38	9
	^{210}Pb	17.44	-29	11
AG.S	^{210}Pb	0	-67	1
	^{210}Pb	0.96	-63	1
	^{210}Pb	2.82	-59	2
	^{210}Pb	4.58	-54	2
	^{210}Pb	6.32	-49	2
	^{210}Pb	8.04	-42	2
	^{210}Pb	9.73	-34	2
	^{210}Pb	11.39	-28	3
	^{210}Pb	13.03	-24	3
	^{210}Pb	14.65	-19	3
	^{210}Pb	16.24	-16	3
	^{210}Pb	17.82	-11	4
	^{210}Pb	19.37	-5	4
	^{210}Pb	20.91	7	6
	^{210}Pb	22.42	17	8
	^{210}Pb	23.92	24	8
	^{210}Pb	25.4	44	13
	^{210}Pb	26.86	65	18
	^{210}Pb	59	471	28
	^{14}C	73	454	30
	^{14}C	88	868	31
	^{14}C	115	1023	28

Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
	$^{14}\mathrm{C}$	127	996	25
	$^{14}\mathrm{C}$	148	2030	31
	$^{14}\mathrm{C}$	162	2315	29
AG.I	$^{210}\mathrm{Pb}$	0	-66	1
	$^{210}\mathrm{Pb}$	3.35	-61	1
	$^{210}\mathrm{Pb}$	6.08	-57	1
	$^{210}\mathrm{Pb}$	8.75	-52	2
	$^{210}\mathrm{Pb}$	11.36	-47	2
	$^{210}\mathrm{Pb}$	13.92	-41	2
	$^{210}\mathrm{Pb}$	16.43	-36	2
	$^{210}\mathrm{Pb}$	18.88	-20	2
	$^{210}\mathrm{Pb}$	21.29	-24	2
	$^{210}\mathrm{Pb}$	23.65	-17	3
	$^{210}\mathrm{Pb}$	25.97	-11	3
	$^{210}\mathrm{Pb}$	28.24	-1	4
	$^{210}\mathrm{Pb}$	30.47	4	4
	$^{14}\mathrm{C}$	88.7	495	26
	$^{14}\mathrm{C}$	119.4	686	28
	$^{14}\mathrm{C}$	157.8	1132	34
AG.D	$^{210}\mathrm{Pb}$	0	-67	2
	$^{210}\mathrm{Pb}$	3.38	-61	2
	$^{210}\mathrm{Pb}$	6.55	-54	2
	$^{210}\mathrm{Pb}$	9.63	-47	2
	$^{210}\mathrm{Pb}$	12.64	-38	3
	$^{210}\mathrm{Pb}$	15.57	-28	3
	$^{210}\mathrm{Pb}$	18.42	-19	4

Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
	^{210}Pb	21.22	-8	5
	^{210}Pb	23.95	7	6
	^{210}Pb	26.63	27	10
	^{210}Pb	29.26	58	21
	^{210}Pb	31.84	88	37
	^{14}C	100	2708	28
	^{14}C	128	3551	31
	^{14}C	136	3884	35
BA.S		0	-66	1
	^{14}C	50	334	23
	^{14}C	86	524	21
	^{14}C	94	567	22
RO.S	^{210}Pb	0	-66	3
	^{210}Pb	0.85	-60	3
	^{210}Pb	2.55	-53	3
	^{210}Pb	4.25	-45	4
	^{210}Pb	5.95	-38	4
	^{210}Pb	7.65	-32	4
	^{210}Pb	9.35	-29	4
	^{210}Pb	11.05	-27	5
	^{210}Pb	12.75	-22	5
	^{210}Pb	14.45	-19	5
	^{210}Pb	16.15	2	7
	^{210}Pb	17.85	6	9
	^{210}Pb	19.55	15	9
	^{210}Pb	21.25	22	11

Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
	^{210}Pb	22.95	42	19
	^{14}C	91.8	1151	28
	^{14}C	136	1501	33
RO.S-C	^{210}Pb	0	-66	3
	^{210}Pb	1.7	-60.8	3
	^{210}Pb	3.4	-51.7	3
	^{210}Pb	5.1	-44.1	4
	^{210}Pb	6.8	-35.1	4
	^{210}Pb	8.5	-29.7	4
	^{210}Pb	10.2	-24.1	4
	^{210}Pb	11.9	-21.2	5
	^{210}Pb	13.6	-14.7	5
	^{210}Pb	15.3	-11.8	5
	^{210}Pb	17	-4.2	7
	^{210}Pb	18.7	-1.5	9
	^{210}Pb	20.4	2.7	9
	^{14}C	116	1036	22
	^{14}C	135	1199	28
RO.S-Cn	-	-	-	-
AL.S		0	-66	1
	^{14}C	104	1601	23
ME.S	^{210}Pb	0	-66	1
	^{210}Pb	3	-59	1
	^{210}Pb	6	-37	4
	^{210}Pb	9	-16	7
	^{210}Pb	12	-6	10

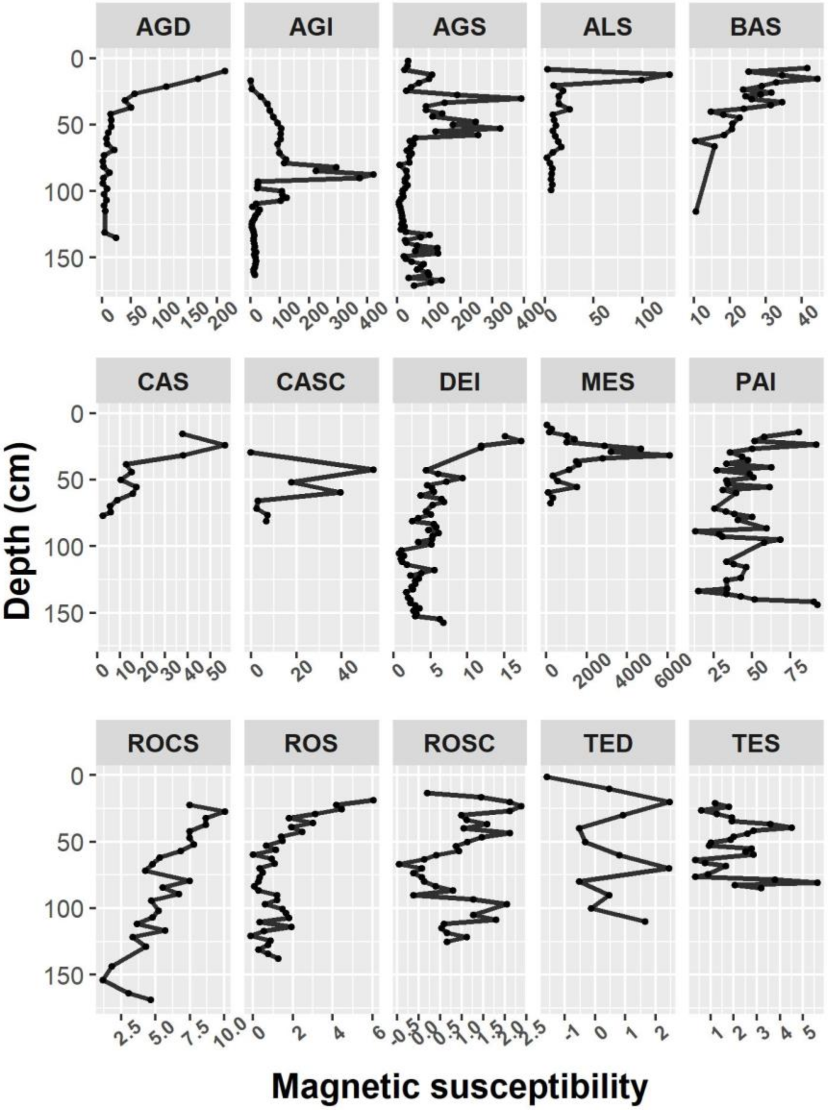
Code	Method	Depth (cm)	Age (cal. yr BP)	Error (yr)
	^{210}Pb	14	32	14
	^{210}Pb	17	63	18
	^{14}C	44.6	339	32
	^{14}C	61.4	515	28



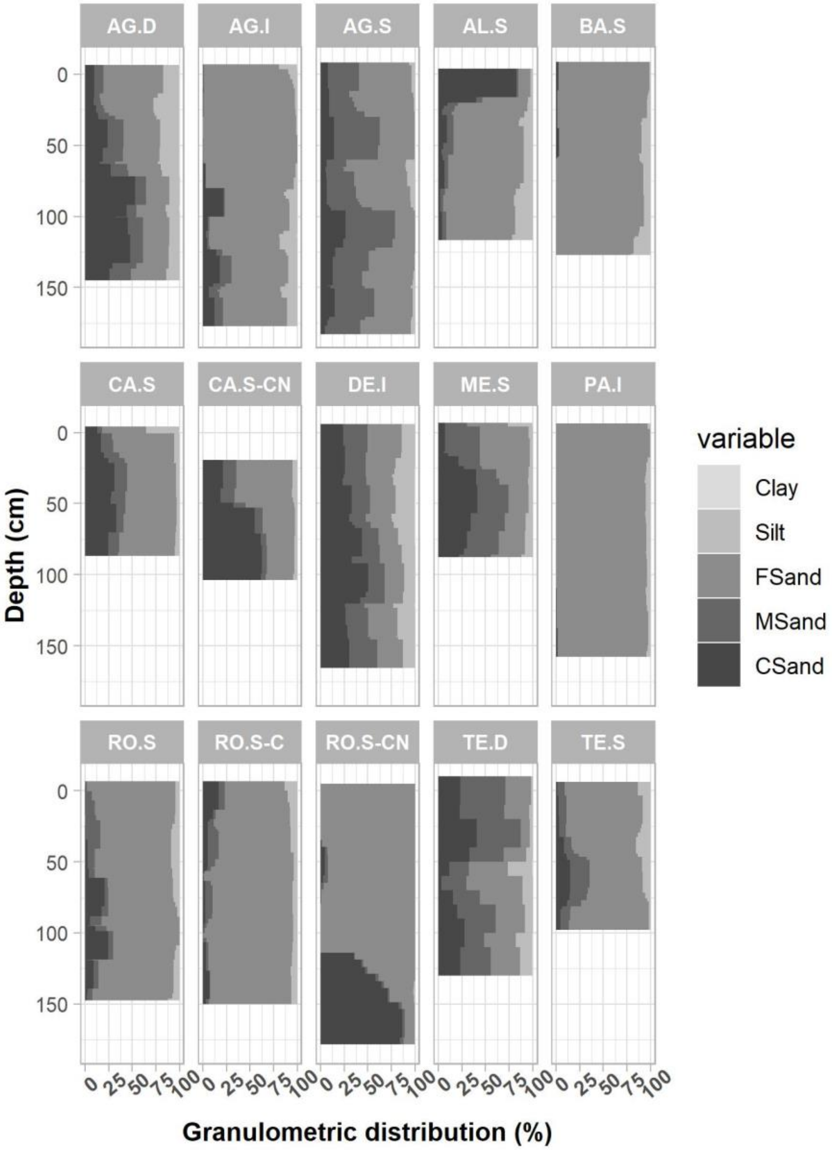
S2: depth profile of ^{210}Pb used to estimate the decaiment curve. Cyrles, total ^{210}Pb (Bq·Kg^{-1}); squares, % of fine materials (clay+silts).

Variables and principal components depth distribution

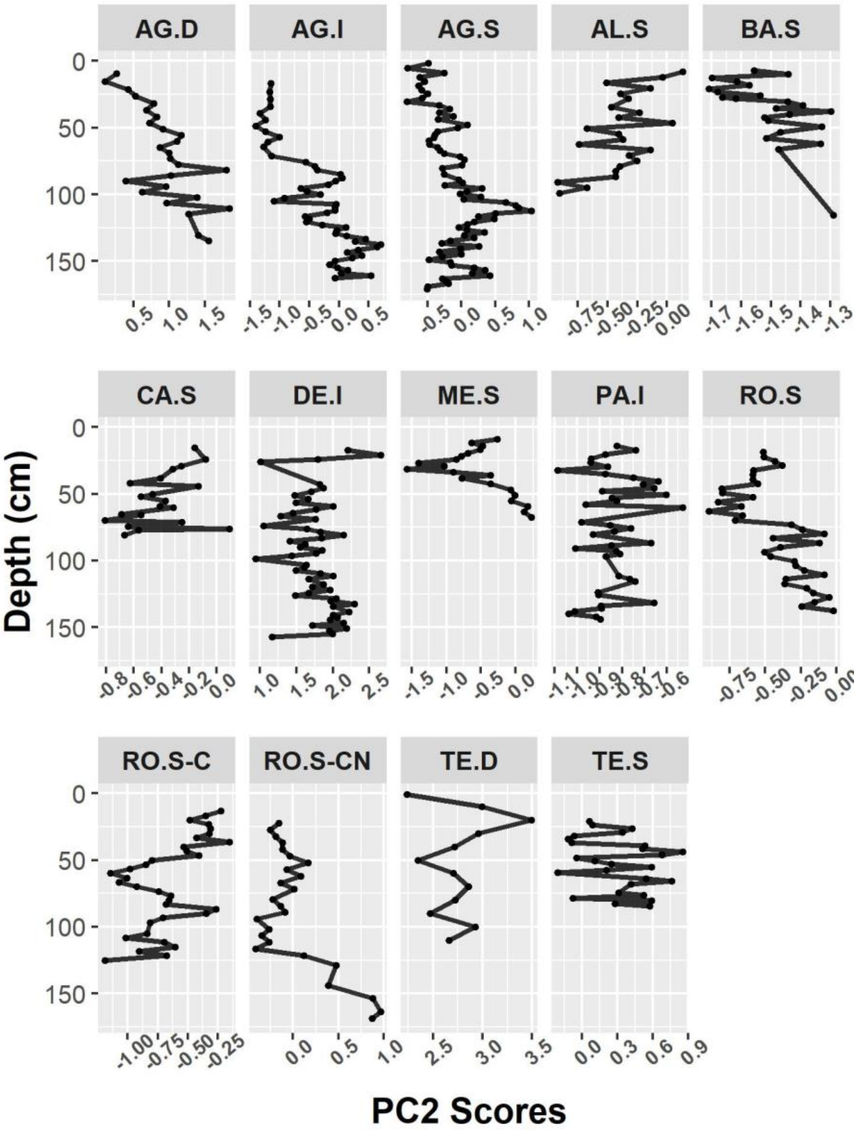
The variables resolution here display is the original resolution. To build the principal component analysis the data matrix was resampled to obtain those samples were all variables where measured.



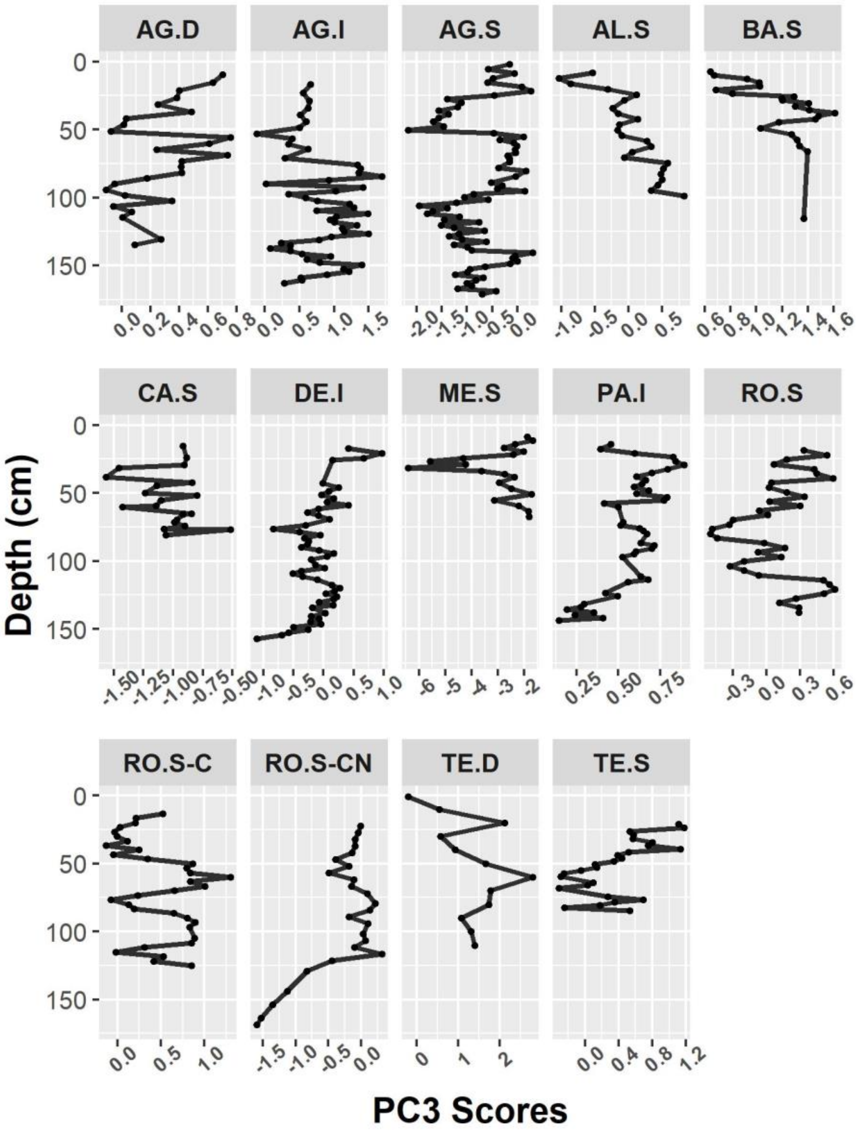
S3: depth distribution of magnetic susceptibility (MS) per core.



S4: grain size distribution per core (%). Clay <0.002 mm, silts 0.002-0.05 mm, fine sands 0.05-0.5 mm (FSand), medium sands 0.5-1 mm (MSand) and coarse sands >1 mm (CSand).



S5: depth distribution of PC2 scores per core.



S6: depth distribution of PC3 scores per core.

2. Chapter IV

S1

Supplementary material 1 from: Cover loss in a seagrass Posidonia oceanica meadow accelerates soil organic matter turnover and alters soil prokaryotic communities.

The S1 supplementary material contains tables of the detected Py-GS-MS compounds, the Py-GS-MS PCA loadings, and the Bacterial and Archaeal ASVs (rarified and non rarified). All of those tables but for the Py-GS-MS PCA loadings table are too large to be reproduced here and any interested reader is directed to its electronic supplementary material of the manuscript.

Table S1.2: Loadings of the Py-GS-MS compounds for each component as yielded by the principal components analysis (PCA). Var. %: percentage of variance accounted for by each component; Ac. Var. %: cumulative variance.

		PC1	**PC2**	**PC3**	**PC4**	**PC5**
CARB	acetic acid	0.759	0.073	-0.222	-0.101	-0.229
OTHER	Me-iodide	0.618	-0.039	-0.376	-0.015	-0.057
OTHER	toluene	0.375	0.754	-0.323	-0.020	0.134
CARB	2-methylfuran	0.649	0.485	-0.278	0.071	0.196
CARB	2-cyclopenten-1-one	0.702	0.075	-0.157	0.283	0.180
CARB	3/2-furaldehyde	0.538	-0.553	-0.061	0.198	0.096
CARB	5-methyl-2-furaldehyde	0.641	-0.183	-0.363	0.062	-0.025
CARB	4-hydroxy-5,6-dihydro-(2*H*)-pyran-2-one	-0.486	-0.394	0.414	-0.319	-0.185
PHENOL	phenol	0.776	0.298	-0.093	-0.023	0.020
CARB	3-methyl-1,2-cyclopentanedione	-0.295	-0.434	0.126	-0.400	-0.154
PHENOL	2-methylphenol	0.263	0.861	-0.230	-0.123	0.029
PHENOL	3/4-methylphenol	0.131	0.906	-0.267	-0.062	0.031
LIG G	guaiacol	-0.505	0.406	0.153	-0.210	-0.102
CARB	levoglucosenone	-0.195	-0.802	0.047	-0.022	-0.131
PHENOL	C2-phenol	0.034	0.849	-0.134	-0.041	-0.148
PHENOL	C2-phenol	-0.077	0.886	-0.186	-0.125	-0.189

		PC1	**PC2**	**PC3**	**PC4**	**PC5**
CARB	3-hydroxy-2-methyl-(2*H*)-pyran-4-one	-0.127	-0.740	-0.297	-0.233	-0.356
OTHER	naphthalene	0.082	-0.478	0.283	-0.288	0.005
OTHER	methoxycatechol	0.849	0.133	0.017	0.182	-0.056
LIG G	4-methylguaiacol	-0.710	0.159	0.257	-0.257	-0.118
CARB	5-hydroxymethyl-2-dihydrofuraldehyde-3-one	-0.289	-0.784	-0.243	-0.226	-0.266
CARB	1,4:3,6-dianhydro-α-D-glucose	-0.262	-0.449	0.110	-0.217	0.059
OTHER	C1-naphthalene	0.788	0.449	-0.015	0.073	0.187
OTHER	C1-naphthalene	0.742	0.379	0.031	0.069	0.335
LIG H	4-vinylphenol	-0.211	0.207	-0.110	-0.169	-0.296
LIG G	4-ethylguaiacol	-0.599	0.284	0.267	-0.146	-0.044
LIG G	4-vinylguaiacol	-0.790	-0.200	0.408	-0.240	-0.085
LIG S	syringol	-0.522	-0.306	0.478	-0.146	-0.079
LIG H	*trans*-4-propenylphenol	-0.129	0.266	0.482	0.038	0.189
LIG G	4-(1-propenyl)guaiacol	-0.497	-0.066	0.618	-0.209	-0.122
LIG G	4-(2-propenyl)guaiacol (*cis*)	-0.487	-0.011	0.667	-0.249	-0.103
LIG G	4-(2-propenyl)guaiacol (*trans*)	-0.720	-0.117	0.565	-0.196	-0.168
	4-methoxybenzoic acid methyl ester	0.856	-0.088	-0.037	0.091	0.037
LIG G	4-formylguaiacol (vanillin)	-0.584	-0.195	0.442	-0.267	-0.272
LIG G	4-acetylguaiacol	-0.544	-0.227	0.288	-0.257	-0.226
LIG G	4-ethylsyringol	-0.230	-0.031	0.800	0.005	-0.082
	p-hydroxybenzoic acid methyl ester	0.012	-0.382	-0.274	-0.068	0.127
LIG G	C3H3-guaiacol	0.238	-0.224	-0.021	0.074	0.190
LIG S	4-vinylsyringol	-0.214	-0.309	0.467	-0.032	-0.050
	4-hydroxybenzoic acid	-0.420	-0.301	-0.014	0.244	-0.163
CARB	levoglucosan	-0.477	-0.106	0.171	0.203	-0.148
LIG GS	4-formylsyringol (syringaldehyde)	0.899	-0.059	0.322	0.143	0.058
LIG GS	4-acetylsyringol	0.365	-0.020	0.741	0.111	-0.077
LIG GS	4-(propan-3-one)syringol	0.374	-0.060	0.767	0.124	-0.041
OTHER	diketodipyrrole	0.231	0.277	0.130	0.234	0.000

		PC1	**PC2**	**PC3**	**PC4**	**PC5**
LIG S	4-(1-propenyl)syringol	0.320	-0.218	0.850	-0.047	-0.125
LIG S	4-(2-propenyl)syringol (*cis*)	0.310	-0.110	0.889	-0.010	-0.066
LIG S	4-(2-propenyl)syringol (*trans*)	-0.425	-0.167	0.800	-0.142	-0.118
LIG S	4-(propan-2-one)syringol	-0.410	-0.189	0.788	0.030	0.002
MCC	phytadiene 2	0.863	0.108	-0.101	0.172	0.178
MCC	C16-fatty acid	-0.457	-0.105	-0.477	0.050	-0.095
MCC	C18-fatty acid	-0.418	-0.040	-0.410	0.116	-0.075
OTHER	alkylcyclohexane (C20H40)	0.814	0.103	0.050	0.331	0.013
OTHER	retene	0.139	0.116	-0.190	-0.013	0.938
OTHER	dehydroabietic acid methyl ester	0.332	0.079	-0.089	0.033	0.908
OTHER	dehydroabietic acid	0.930	0.063	0.030	0.151	0.196
MCC	prist-1-ene	0.660	0.208	-0.053	0.265	0.172
MCC	fatty acid propyl ester?	0.835	0.105	0.277	0.037	0.123
MCC	fatty acid propyl ester?	0.880	0.067	0.229	0.090	0.113
MCC	C16-fatty acid methyl ester	0.310	0.097	-0.362	0.222	0.550
MCC	C18-fatty acid methyl ester	0.256	0.080	-0.356	0.225	0.587
MCC	C24-fatty acid methyl ester	0.559	-0.039	-0.119	0.663	0.137
MCC	C26-fatty acid methyl ester	0.288	-0.125	-0.167	0.806	0.029
MCC	C28-fatty acid methyl ester	0.475	-0.153	-0.107	0.547	0.087
MCC	C23-alkane	0.635	0.492	-0.193	0.145	0.122
MCC	C24-alkane	0.581	0.408	-0.210	0.229	0.281
MCC	C25-alkane	0.634	0.512	-0.198	0.173	0.145
MCC	C26-alkane	0.741	0.314	-0.138	0.220	0.281
MCC	C27-alkane	0.789	0.345	-0.200	0.257	0.082
MCC	C28-alkane	0.705	0.182	-0.036	0.623	0.053
MCC	C29-alkane	0.927	0.124	0.028	0.224	0.048
MCC	C30-alkane	0.749	0.056	0.058	0.620	0.033
MCC	C23-alkene	0.626	0.503	-0.158	0.083	0.109
MCC	C24-alkene	0.548	0.405	-0.256	0.199	0.287
MCC	C25-alkene	0.625	0.531	-0.147	0.109	0.198
MCC	C26-alkene	0.734	0.316	-0.145	0.317	0.190

		PC1	PC2	PC3	PC4	PC5
MCC	C27-alkene	0.877	0.290	-0.087	0.206	0.116
MCC	C28-alkene	0.328	0.140	-0.019	0.870	0.061
MCC	C29-alkene	0.935	0.046	0.082	0.204	0.147
MCC	C30-alkene	0.255	-0.029	0.061	0.904	-0.018
	Var %	25.673	10.513	9.602	6.091	4.074
	Acc var%	25.673	36.186	45.788	51.880	55.954

S2:

Supplementary material 2 from: Cover loss in a seagrass *Posidonia oceanica* meadow accelerates soil organic matter turnover and alters soil prokaryotic communities.

Nerea Piñeiro-Juncal, Joeri Kaal, Julio Cezar Fornazier Moreira, Antonio Martínez Cortizas, Marcio Rodrigues Lambais, Xose Luis Otero and Miguel Ángel Mateo.

This file provides background information on the datasets of Py-GC-MS and 16S rRNA gene metabarcoding. It includes example chromatograms (total ion current) of one sample from the middle-rhizosphere of each of the three cores (Fig. 1), abundance of subgroups of lignin products (Fig. 2), abundances and ratios of (groups of) other products (Fig. 3), PC scores distributions of PC4 (Fig. 4) and PC5 (Fig. 5) from principal components analysis, all from pyrolysis-GC-MS, a description of the microbial taxonomic composition (Fig. 6 and 7) and taxonomic assignment of the microbial ASVs of the annotated FAPROTAX functional groups (Table 1, Table 2).

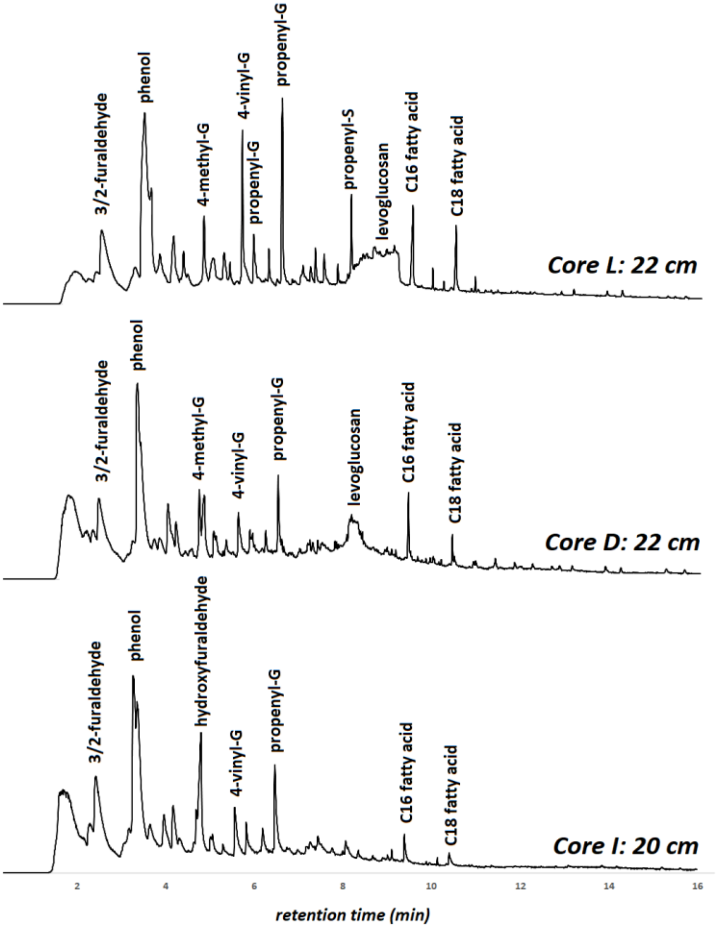


Figure 1: Example of a Py-GC-MS spectra from the rhizosphere of each core. Main peaks are labelled. Guaiacyl lignin compounds are referred to with G, and syringyl products with S. The large and broad peak in the sample from Core L (intact Posidonia canopy) corresponds to levoglucosan, a marker of intact polysaccharides.

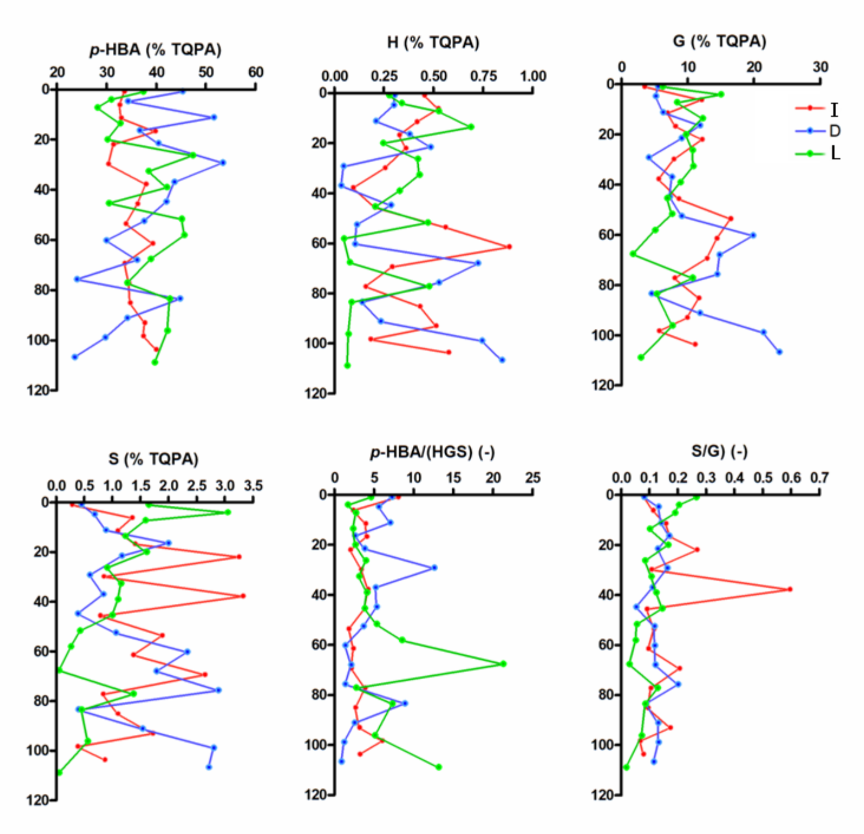


Figure 2: Py-GC-MS. Distributions of subgroups of pyrolysis products of polyphenolic origin along the cores (y-axis represent depth in cm). HBA = hydroxybenzoic acid, H = *p*-hydroxyphenyl products (e.g. 4-vinylphenol), G = guaiacyl, S = syringyl. Ratios of p-HBA to the sum of H-, G- and S-type products, and the S/G ratio, are also provided.

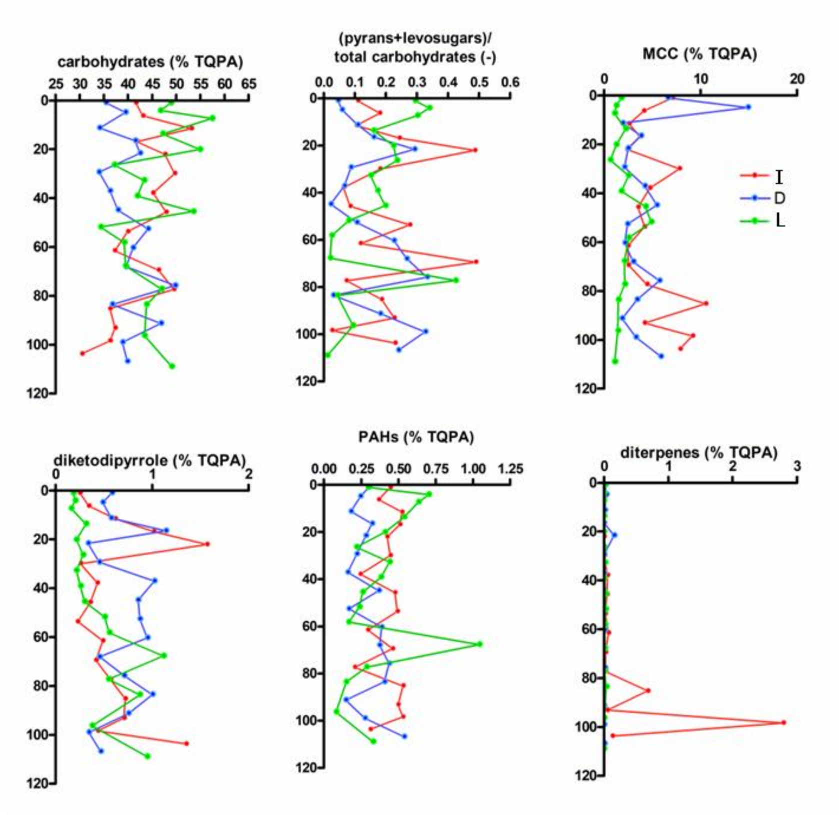


Figure 3: Py-GC-MS. Distributions of (groups of) pyrolysis products, i.e. carbohydrates (furans, furaldehydes, pyrans, anhydrosugars, etc.), methylene chain compounds (MCC, i.e. alkanes, alkenes, fatty acids, etc.), diketodipyrrole, polycyclic aromatic hydrocarbons (PAHs) and diterpene products. The ratio of different carbohydrate products is also given (proxy of carbohydrate preservation).

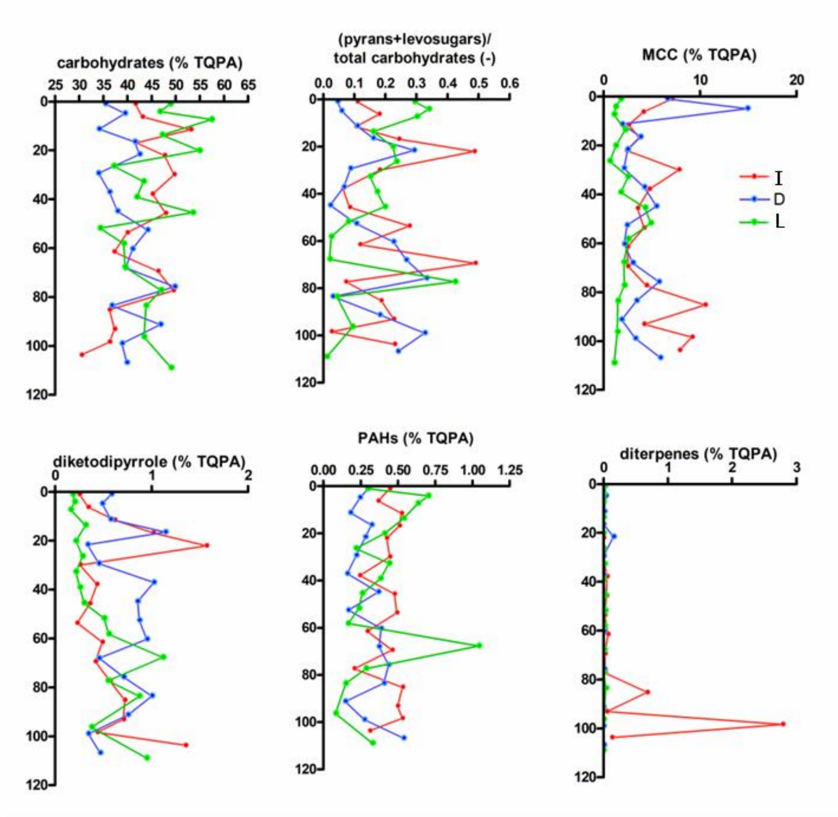


Figure 3: Py-GC-MS. Distributions of (groups of) pyrolysis products, i.e. carbohydrates (furans, furaldehydes, pyrans, anhydrosugars, etc.), methylene chain compounds (MCC, i.e. alkanes, alkenes, fatty acids, etc.), diketodipyrrole, polycyclic aromatic hydrocarbons (PAHs) and diterpene products. The ratio of different carbohydrate products is also given (proxy of carbohydrate preservation).

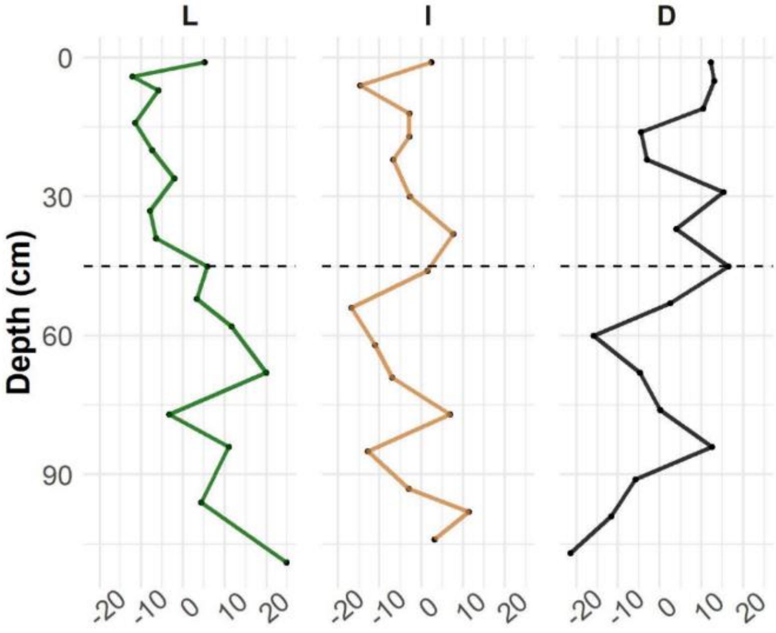


Figure 4: Depth distribution of PC4 scores in Cores L, I and D, obtained by PCA of Py-GC-MS data. The black, dashed, horizontal line indicates the lower limit of the rhizosphere (c. 45 cm).

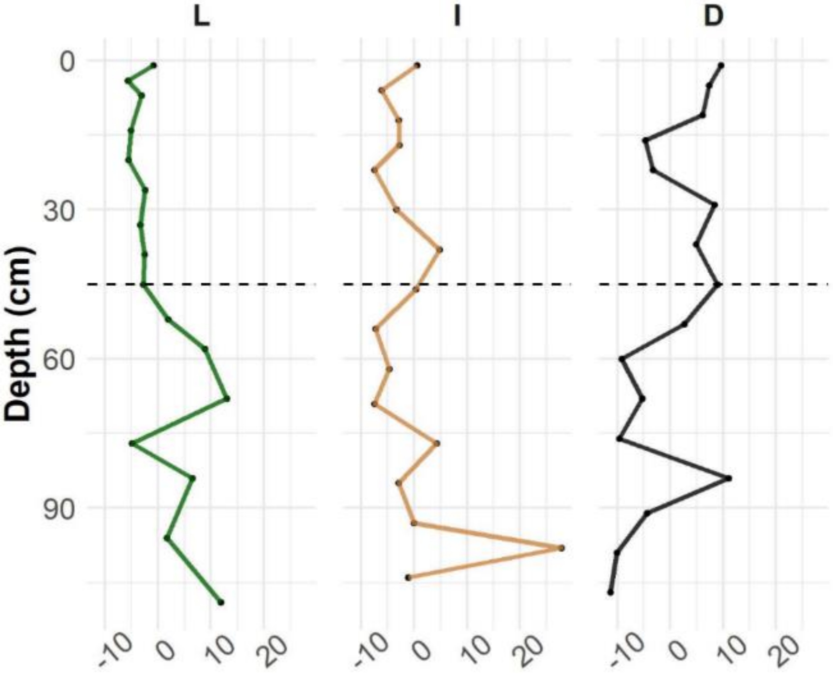


Figure 5: Depth distribution of PC5 scores in Cores L, I and D, obtained by PCA of Py-GC-MS data. The black, dashed, horizontal line indicates the lower limit of the rhizosphere (c. 45 cm).

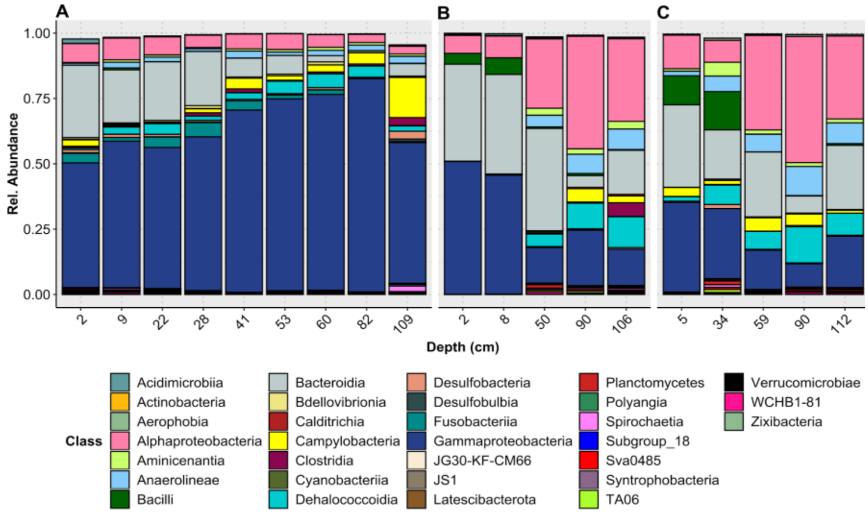


Figure 6: Relative abundance of top abundance bacteria classes (>1%) along profiles depths in the Core L (A), I (B) and D (C).

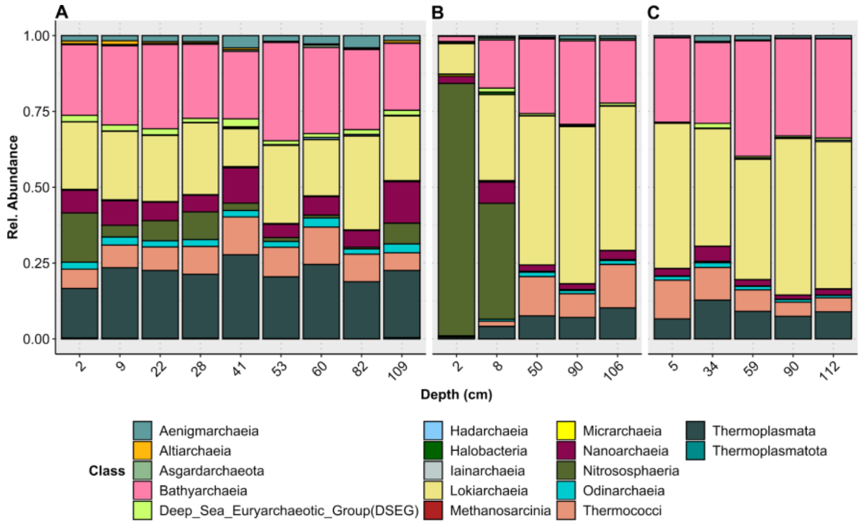


Figure 7: Relative abundance of top abundance archaea classes (>1%) along profiles depths in the Core L (A), I (B) and D (C).

Bacterial and archaeal taxonomic composition

The taxonomic compositions of the bacterial communities, at the class level, along the core profiles are shown in Figure 6. Only classes representing more than 1% abundance in the whole dataset are depicted in the figure.

Overall, our results showed that ASVs assigned to Gammaproteobacteria, Bacteroidia and Alphaproteobacteria were the most abundant in the communities (Figure 6A, B, C). Gammaproteobacteria represented approximately 48-81% in core L, 13-50% in core I and 9-34% in Core D. In Core L, the relative abundance of ASVs assigned to Gammaproteobacteria increased with depth down to 82 cm, whereas in Cores I and D it decreased, specially below 50 cm depth.

ASVs assigned to Bacteroidia represented approximately 2-27% in core L, 4-39% in core I and 6-31% in

Core D. Bacteroidia relative abundance represented approximately 23% in the 2-28 cm depth in core L, and decreased to an average of approximately 4% at the 41-109 cm depth. In Cores I and D, Bacteroidia relative abundance were in average 38% at 2-50 cm depth and decreased at higher depths in Core I. In contrast, in Core D, Bacteroidia showed an average decrease in relative abundance of 3.8-fold at 90 cm depth, as compared to the other depths sampled.

ASVs assigned to Alphaproteobacteria represented approximately 3-8% in core L, 7-43% in Core I and 8-48% in Core D. Significant variations in the relative abundance of Alphaproteobacteria with depths were observed in Cores I and D. In Core I, the relative abundance of Alphaproteobacteria at the top layers (2-8 cm depth) were approximately 4.4-fold lower than at the bottom layers (50-106 cm depth), whereas in Core D, the relative abundance of Alphaproteobacteria at the top layer (5 cm depth) was approximately 3-fold lower than at the bottom layers (59-112 cm depth).

Other less abundant groups of bacteria also contributed to the shifts in community structure observed (Figures 6A, B, C). ASVs assigned to Bacilli was either not-detected or detected at very low relative abundance in Core L

(0-0.7%), while this class of bacteria represented 0.3-6.3% and 0.03-14% of the ASVs in Core I and Core D, respectively. The relative abundance of Bacilli, in general, decreased with depth, especially in Cores I and D. In Core I, Bacilli relative abundance was approximately 5% at 2-8 cm depth and decreased to approximately 0.5% at 50-106 cm depth. In Core D, Bacilli relative abundance was approximately 12% at 5-34 cm depth and decreased to approximately 0.3% at 59-112 cm depth. In contrast, Campylobacteria relative abundance, overall, increased with depth. In Core L, Campylobacteria relative abundance was 2.4% at 2 cm depth and increased to approximately 15% at 109 cm depth. In Core I, Campylobacteria relative abundance increased from 0.05% at 2 cm depth to approximately 5% at 90 cm depth, and from approximately 3% at 5 cm depth to approximately 4% at 90 cm depth of Core D. Similarly, the relative abundance of Clostridia increased from 0.5% at 2 cm depth to 3% at 109 cm depth in core L, <0.01% at 2 cm depth to approximately 5% at 106 cm depth of Core I, and approximately 0.04% at 5 cm depth to 0.4% at 90 cm depth of Core D. Dehalococcoidia relative abundance in the subsoil (53-109 cm) was approximately 1.8-fold higher than in the rhizosphere (2-41 cm) of Core L (2.9 to 4.1%), whereas it was approximately 4,400-fold higher in subsoil (50-106 cm) than in the top layers (2-8 cm) of Core I (0.002 to 8.8%), and approximately 2.1-fold higher in the subsoil (59-112 cm) than in the rhizosphere (5-34 cm) of Core D (4.5 to 9.6%).

The taxonomic compositions of the archaeal communities, at the class level, along the core profiles are shown in Figure 7. Only classes representing more than 1% abundance in the whole dataset are depicted in the figure. The most abundant archaea ASVs in the core profiles examined were assigned to the classes Bathyarchaeia, Lockiarchaeia, Nanoarchaeia, Nitrososphaeria, Thermococci and Thermoplasmata (Figure 7A, B, C).

Overall, the relative abundance of ASVs assigned to Bathyarchaeia did not show significant variations with depth in Cores L and D, ranging from approximately 22 to 32% and 27 to 38% of the archaeal communities, respectively (Figure 7A, C). In Core I, Bathyarchaeia relative abundance increased with depth ranging from approximately 1.7% at 2 cm depth to 27% at 90 depth. At 50-106 cm depth, Batyarchaeia relative abundance was approximately 2.8-fold higher than at 2-8 cm depth.

Similarly, the relative abundance of ASVs assigned to Lockiarchaeia did not show significant variations with depth in Cores L and D, ranging from approximately 12 to 31% and 39 to 51% of the archaeal communities, respectively. In Core I, Lockiarchaeia relative abundance increased with depth, from 10% at 2 cm depth to 28% at 8 cm depth, and reached approximately 52% at 90 cm depth. In the subsoil layers (50-106 cm), Lockiarchaeia relative abundance was 2.6-fold higher than in the top layers (2-8 cm depth).

Nanoarchaeia relative abundance ranged from approximately 4 to 14%, 2 to 6% and 1 to 5% in Cores L, I and D, respectively. Major variations with depth were observed in Cores I and D. In Core I, the relative abundance of Nanoarchaeia at 2 cm depth was approximately 2.4% and increased 2.9-fold at 8 cm depth. At higher depths, Nanoarchaeia relative abundance was approximately 2.3%. In Core D, variations with depth were similar to core I. The relative abundance of Nanoarchaeia at 5 cm depth was approximately 2.4% and increased 2-fold at 34 cm depth. At higher depths, Nanoarchaeia relative abundance was approximately 1.8%. In Core L, the relative abundance of Nanoarchaeia in the rhizosphere (2-41 cm depth) and subsoil (53-109 cm depth) did not show difference, whereas in Core I it was 2-fold higher in the rhizosphere (2-8 cm depth) than in the sub-soil (50-106 cm depth), and in Core D it was 2.2-fold higher in the rhizosphere (5-34 cm depth) than in the sub-soil (59-112 cm depth).

Nitrososphaeria relative abundance showed the highest levels of variation with depth, especially in Cores L (0.05-16%) and I (0.3-83%), as compared to Core D (0.1-0.4%). In Core L, Nitrososphaeria relative abundance decreased from 16% at 2 cm depth to an average of approximately 3.9% at higher depths. In the rhizosphere (2-41 cm depth) of Core L, the Nitrososphaeria relative abundance was approximately 3.2-fold higher than in the sub-soil (53-109 cm depth). In Core I, Nitrososphaeria relative abundance decreased from 83% at 2 cm depth to 38% at 8 cm depth, and an average of 0.3% at higher depths. In the rhizosphere (2-8 cm depth) of Core I, the Nitrososphaeria relative abundance was approximately 203-fold higher than in the sub-soil (50-106 cm depth). In Core D, even though the relative abundance of Nitrososphaeria was lower than in Cores L and I, it increased from 0.14% at 5 cm depth to 0.43%

at 34 cm depth. In the rhizosphere (5-34 cm depth) of Core D, the relative abundance of Nitrososphaeria was approximately 2.2-fold higher than in the sub-soil (59-112 cm depth).

Thermococci relative abundance also showed high levels of variation with depth, especially in core I (0.1-14%), as compared to cores L (6-12%) and D (5-13%). In Core L, Thermococci relative abundance was approximately 8.6% in the rhizosphere (2-41 cm depth) and 9.2% in the subsoil (53-109 cm depth). In core I, Thermococci relative abundance was 0.1% at 2 cm depth and increased increased approximately 17-fold at 8 cm depth and 130-fold at 50 cm depth. In the rhizosphere of Core I (2-8 cm depth), the relative abundance of Thermococci was approximately 13-fold lower than in the sub-soil (50-106 cm depth). In contrast, in Core D, Thermococci relative abundance decreased from approximately 12,8% at 5 cm depth to 4.6% at 112 cm depth. In the rhizosphere of Core D (5-34 cm depth), the relative abundance of Thermococci was approximately 2-fold higher than in the sub-soil (59-112 cm depth).

Thermoplasmata relative abundance ranged from 16 to 27%, 0.5 to 10% and 7 to 13% in Cores L, I and D, respectively. Variations with depth were observed mainly in Cores I and D. In Core I, relative abundance of Thermoplasmata increased from 0.5% at 2 cm depth to 4.1% at 8 cm depth and 10.2% at 106 cm depth. In the subsoil of Core I (50-106 cm depth) the relative abundance of Thermoplasmata was approximately 3.6-fold higher than in the rhizosphere (2-8 cm depth). In contrast, in Core D, the relative abundance of Thermoplasmata increased from 6.6% at 5 cm depth to 12.8% at 34 cm depth, and then decreased to approximately 8.5% in the 59-112 layer.

Table 1. Taxonomic assignment of the bacterial ASVs of the annotated FAPROTAX functional groups.

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
Carbon	Methanol oxidation	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus Proteobacteria; Gammaproteobacteria; Burkholderiales; Methylophilaceae; Methylotenera Proteobacteria; Gammaproteobacteria; Nitrosococcales; Methylophagaceae; Methylophaga

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
Carbon	Aliphatic non methane hydrocarbon degradation	Proteobacteria; Gammaproteobacteria; Oceanospirillales; Alcanivoracaceae1; Alcanivorax
Carbon	Methylotrophy	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus Proteobacteria; Gammaproteobacteria; Burkholderiales; Methylophilaceae; Methylotenera Proteobacteria; Gammaproteobacteria; Methylococcales; Methylomonadaceae; pItb-vmat-59 Proteobacteria; Gammaproteobacteria; Nitrosococcales; Methylophagaceae; Methylophaga
Carbon	Chitinolysis	Proteobacteria; Gammaproteobacteria; Cellvibrionales; Microbulbiferaceae; Microbulbifer
Carbon	Dark hydrogen oxidation	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Carbon	Cellulolysis	Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Lewinella Proteobacteria; Gammaproteobacteria; Cellvibrionales; Microbulbiferaceae; Microbulbifer
Carbon	Xylanolysis	Bacteroidota; Bacteroidia; Bacteroidales; Marinilabiliaceae; [Cytophaga] xylanolytica group Proteobacteria; Gammaproteobacteria; Cellvibrionales; Microbulbiferaceae; Microbulbifer
Carbon	Fermentation	Bacteroidota; Bacteroidia; Bacteroidales; Bacteroidaceae; Bacteroides Bacteroidota; Bacteroidia; Bacteroidales; Barnesiellaceae; Barnesiella Bacteroidota; Bacteroidia; Bacteroidales; Marinilabiliaceae; [Cytophaga] xylanolytica group Bacteroidota; Bacteroidia; Bacteroidales; Rikenellaceae; Alistipes Bacteroidota; Bacteroidia; Flavobacteriales; Crocinitomicaceae; Brumimicrobium Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Algibacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Muricauda Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfobulbaceae; Desulfobulbus Firmicutes; Bacilli; Lactobacillales; Enterococcaceae; Enterococcus Firmicutes; Bacilli; Lactobacillales; Lactobacillaceae; Lactobacillus

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Firmicutes; Bacilli; Lactobacillales; Leuconostocaceae; Weissella Firmicutes; Bacilli; Lactobacillales; Streptococcaceae; Streptococcus Firmicutes; Clostridia; Oscillospirales; [Eubacterium] coprostanoligenes group; [Eubacterium] coprostanoligenes group Firmicutes; Clostridia; Oscillospirales; Ruminococcaceae; Faecalibacterium Firmicutes; Clostridia; Oscillospirales; Ruminococcaceae; Subdoligranulum Firmicutes; Clostridia; Peptostreptococcales-Tissierellales; Peptostreptococcaceae; Paraclostridium Firmicutes; Clostridia; Peptostreptococcales-Tissierellales; Peptostreptococcaceae; Romboutsia Firmicutes; Clostridia; Peptostreptococcales-Tissierellales; Peptostreptococcaceae; Tepidibacter Fusobacteriota; Fusobacteriia; Fusobacteriales; Fusobacteriaceae; Ilyobacter Fusobacteriota; Fusobacteriia; Fusobacteriales; Fusobacteriaceae; Propionigenium Halanaerobiaeota; Halanaerobiia; Halanaerobiales; Halobacteroidaceae; uncultured Proteobacteria; Gammaproteobacteria; Alteromonadales; Colwelliaceae; Colwellia Proteobacteria; Gammaproteobacteria; Enterobacterales; Enterobacteriaceae; Enterobacter Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; Aliivibrio Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; Photobacterium Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; Thaumasiovibrio Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; Vibrio Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; NA Spirochaetota; Spirochaetia; Spirochaetales; Spirochaetaceae; Spirochaeta Spirochaetota; Spirochaetia; Spirochaetales; Spirochaetaceae; Spirochaeta 2
Carbon	Aerobic chemoheterotrophy	Acidobacteriota; Holophagae; Acanthopleuribacterales; Acanthopleuribacteraceae; Acanthopleuribacter

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Actinobacteriota; Actinobacteria; Corynebacteriales; Mycobacteriaceae; Mycobacterium
		Actinobacteriota; Actinobacteria; Frankiales; Geodermatophilaceae; Blastococcus
		Actinobacteriota; Actinobacteria; Micrococcales; Demequinaceae; Demequina
		Actinobacteriota; Actinobacteria; Micrococcales; Microbacteriaceae; Microbacterium
		Actinobacteriota; Actinobacteria; Propionibacteriales; Nocardioidaceae; Nocardioides
		Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Aureispira
		Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Lewinella
		Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Portibacter
		Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Rubidimonas
		Bacteroidota; Bacteroidia; Chitinophagales; Saprospiraceae; Saprospira
		Bacteroidota; Bacteroidia; Cytophagales; Cyclobacteriaceae; Algoriphagus
		Bacteroidota; Bacteroidia; Cytophagales; Cyclobacteriaceae; Fabibacter
		Bacteroidota; Bacteroidia; Cytophagales; Cyclobacteriaceae; Reichenbachiella
		Bacteroidota; Bacteroidia; Cytophagales; Flammeovirgaceae; Flexithrix
		Bacteroidota; Bacteroidia; Cytophagales; Flammeovirgaceae; Luteivirga
		Bacteroidota; Bacteroidia; Flavobacteriales; Crocinitomicaceae; Crocinitomix
		Bacteroidota; Bacteroidia; Flavobacteriales; Cryomorphaceae; Owenweeksia
		Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Actibacter
		Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Aquimarina
		Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Arenibacter
		Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Bizionia
		Bacteroidota; Bacteroidia Flavobacteriales; Flavobacteriaceae; Cellulophaga

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Dokdonia Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Flavobacterium Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Formosa Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Gillisia Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Gramella Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Leeuwenhoekiella Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Lutibacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Maribacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Mesonia Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Nonlabens Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Olleya Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Polaribacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Psychroserpens Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Robiginitalea Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Salegentibacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Sediminicola Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Tenacibaculum Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Ulvibacter Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Winogradskyella Firmicutes; Bacilli; Bacillales; Planococcaceae; Planomicrobium Planctomycetota; Planctomycetes; Pirellulales; Pirellulaceae; Blastopirellula Planctomycetota; Planctomycetes; Pirellulales; Pirellulaceae; Rhodopirellula Proteobacteria; Alphaproteobacteria; Caulobacterales; Hyphomonadaceae; Hyphomonas

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Proteobacteria; Alphaproteobacteria; Rhizobiales; Devosiaceae; Devosia Proteobacteria; Alphaproteobacteria; Rhizobiales; Devosiaceae; Pelagibacterium Proteobacteria; Alphaproteobacteria; Rhizobiales; Hyphomicrobiaceae; Filomicrobium Proteobacteria; Alphaproteobacteria; Rhizobiales; Hyphomicrobiaceae; Hyphomicrobium Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Dinoroseobacter Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Jannaschia Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Litoreibacter Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Roseobacter clade NAC11-7 lineage Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Roseovarius Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Ruegeria Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Shimia Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Sulfitobacter Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Thalassobius Proteobacteria; Alphaproteobacteria; Rhodospirillales; Thalassospiraceae; Thalassospira Proteobacteria; Alphaproteobacteria; Sphingomonadales; Sphingomonadaceae; Altererythrobacter Proteobacteria; Alphaproteobacteria; Sphingomonadales; Sphingomonadaceae; Erythrobacter Proteobacteria; Alphaproteobacteria; Sphingomonadales; Sphingomonadaceae; Sphingorhabdus Proteobacteria; Alphaproteobacteria; Sphingomonadales; Sphingomonadaceae; NA Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Aestuariibacter

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Alteromonadaceae Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Alteromonas Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Catenovulum Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Paraglaciecola Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; Salinimonas Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; uncultured Proteobacteria; Gammaproteobacteria; Alteromonadales; Alteromonadaceae; NA Proteobacteria; Gammaproteobacteria; Alteromonadales; Colwelliaceae; Thalassotalea Proteobacteria; Gammaproteobacteria; Alteromonadales; Colwelliaceae; uncultured Proteobacteria; Gammaproteobacteria; Alteromonadales; Colwelliaceae; NA Proteobacteria; Gammaproteobacteria; Alteromonadales; Marinobacteraceae; Marinobacter Proteobacteria; Gammaproteobacteria; Alteromonadales; Moritellaceae; Moritella Proteobacteria; Gammaproteobacteria; Alteromonadales; Moritellaceae; Paramoritella Proteobacteria; Gammaproteobacteria; Alteromonadales; Moritellaceae; uncultured Proteobacteria; Gammaproteobacteria; Alteromonadales; Pseudoalteromonadaceae; Pseudoalteromonas Proteobacteria; Gammaproteobacteria; Alteromonadales; Pseudoalteromonadaceae; Psychrosphaera Proteobacteria; Gammaproteobacteria; Alteromonadales; Pseudoalteromonadaceae; NA Proteobacteria; Gammaproteobacteria; Alteromonadales; Psychromonadaceae; Agarivorans Proteobacteria; Gammaproteobacteria; Alteromonadales; Psychromonadaceae; Psychromonas Proteobacteria; Gammaproteobacteria; Alteromonadales; Psychromonadaceae; NA

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Proteobacteria; Gammaproteobacteria; Alteromonadales; Shewanellaceae; Ferrimonas Proteobacteria; Gammaproteobacteria; Alteromonadales; Shewanellaceae; Shewanella Proteobacteria; Gammaproteobacteria; Alteromonadales; NA; NA Proteobacteria; Gammaproteobacteria; Legionellales; Legionellaceae; Legionella Proteobacteria; Gammaproteobacteria; Oceanospirillales; Alcanivoracaceae1; Alcanivorax Proteobacteria; Gammaproteobacteria; Oceanospirillales; Endozoicomonadaceae; Endozoicomonas Proteobacteria; Gammaproteobacteria; Oceanospirillales; Halomonadaceae; Cobetia Proteobacteria; Gammaproteobacteria; Oceanospirillales; Halomonadaceae; Halomonas Proteobacteria; Gammaproteobacteria; Oceanospirillales; Kangiellaceae; Aliikangiella Proteobacteria; Gammaproteobacteria; Oceanospirillales; Marinomonadaceae; Marinomonas Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Amphritea Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Marinobacterium Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Motiliproteus Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Neptuniibacter Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Nitrincola Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; Profundimonas Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; uncultured Proteobacteria; Gammaproteobacteria; Oceanospirillales; Nitrincolaceae; NA Proteobacteria; Gammaproteobacteria; Oceanospirillales; Oceanospirillaceae; Oceanospirillum Proteobacteria; Gammaproteobacteria; Oceanospirillales; Oleiphilaceae; Oleiphilus Proteobacteria; Gammaproteobacteria; Oceanospirillales; P13-46; P13-46

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Proteobacteria; Gammaproteobacteria; Oceanospirillales; Pseudohongiellaceae; Pseudohongiella Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Oceaniserpentilla Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Oceanobacter Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Oleibacter Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Oleispira Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Reinekea Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; Saccharospirillum Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; uncultured Proteobacteria; Gammaproteobacteria; Oceanospirillales; Saccharospirillaceae; NA Proteobacteria; Gammaproteobacteria; Oceanospirillales; NA; NA Proteobacteria; Gammaproteobacteria; Pseudomonadales; Moraxellaceae; Acinetobacter Proteobacteria; Gammaproteobacteria; Pseudomonadales; Moraxellaceae; Psychrobacter Proteobacteria; Gammaproteobacteria; Pseudomonadales; Pseudomonadaceae; Pseudomonas Verrucomicrobiota; Verrucomicrobiae; Opitutales; Puniceicoccaceae; Cerasicoccus Verrucomicrobiota; Verrucomicrobiae; Opitutales; Puniceicoccaceae; Pelagicoccus Verrucomicrobiota; Verrucomicrobiae; Verrucomicrobiales; Rubritaleaceae; Rubritalea
Carbon	Aromatic compound degradation	Proteobacteria; Gammaproteobacteria; Cellvibrionales; Microbulbiferaceae; Microbulbifer
Carbon	Hydrocarbon degradation	Proteobacteria; Gammaproteobacteria; Methylococcales; Methylomonadaceae; pItb-vmat-59
Nitrogen	Nitrate respiration	Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfocapsaceae; [Desulfobacterium] catecholicum group

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
Nitrogen	Aerobic nitrite oxidation	Nitrospinota; Nitrospinia; Nitrospinales; Nitrospinaceae; Nitrospina
Nitrogen	Nitrification	Nitrospinota; Nitrospinia; Nitrospinales; Nitrospinaceae; Nitrospina
Nitrogen	Nitrate denitrification	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Nitrogen	Nitrite denitrification	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Nitrogen	Nitrous oxide denitrification	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Nitrogen	Nitrate reduction	Bacteroidota; Bacteroidia; Flavobacteriales; Crocinitomicaceae; Brumimicrobium Bacteroidota; Bacteroidia; Flavobacteriales; Flavobacteriaceae; Sediminicola Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfocapsaceae; [Desulfobacterium]_catecholicum_group Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus Proteobacteria; Gammaproteobacteria; Alteromonadales; Colwelliaceae; Colwellia Proteobacteria; Gammaproteobacteria; Alteromonadales; Shewanellaceae; Shewanella Proteobacteria; Gammaproteobacteria; Enterobacterales; Enterobacteriaceae; Enterobacter Proteobacteria; Gammaproteobacteria; Vibrionales; Vibrionaceae; Vibrio
Nitrogen	Nitrite respiration	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Nitrogen	Denitrification	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Nitrogen	Nitrogen fixation	Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetospira
Nitrogen	Nitrite respiration	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Paracoccus
Phototrophy	Cyanobacteria	Cyanobacteria; Cyanobacteriia; Cyanobacteriales; Xenococcaceae; Xenococcus_PCC-7305 Cyanobacteria; Vampirivibrionia; Gastranaerophilales; Gastranaerophilales; Gastranaerophilales
Phototrophy	Anoxygenic photoautotrophy S oxidizing	Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; Thiogranum

Metabolism	FAPROTAX functional profile	Taxonomy (Phylum; Class; Order; Family; Genus)
		Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; uncultured Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; NA
Phototrophy	Photoheterotrophy	Proteobacteria; Alphaproteobacteria; Rhizobiales; Rhodomicrobiaceae; Rhodomicrobium
Phototrophy	Chemoheterotrophy	Proteobacteria; Gammaproteobacteria; Burkholderiales; Methylophilaceae; Methylotenera Proteobacteria; Gammaproteobacteria; Nitrosococcales; Methylophagaceae; Methylophaga
Phototrophy	Anoxygenic photoautotrophy	Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; Thiogranum Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; uncultured Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; NA
Phototrophy	Oxygenic photoautotrophy	Cyanobacteria; Cyanobacteriia; Cyanobacteriales; Xenococcaceae; Xenococcus_PCC-7305 Cyanobacteria; Vampirivibrionia; Gastranaerophilales; Gastranaerophilales; Gastranaerophilales
Phototrophy	Photoautotrophy	Cyanobacteria; Cyanobacteriia; Cyanobacteriales; Xenococcaceae; Xenococcus_PCC-7305 Cyanobacteria; Vampirivibrionia; Gastranaerophilales; Gastranaerophilales; Gastranaerophilales Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; Thiogranum Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; uncultured Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; NA
Phototrophy	Phototrophy	Cyanobacteria; Cyanobacteriia; Cyanobacteriales; Xenococcaceae; Xenococcus_PCC-7305 Cyanobacteria; Vampirivibrionia; Gastranaerophilales; Gastranaerophilales; Gastranaerophilales Proteobacteria; Alphaproteobacteria; Rhizobiales; Rhodomicrobiaceae; Rhodomicrobium Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; Thiogranum Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; uncultured

Metabolism	**FAPROTAX functional profile**	**Taxonomy (Phylum; Class; Order; Family; Genus)**
		Proteobacteria; Gammaproteobacteria; Ectothiorhodospirales; Ectothiorhodospiraceae; NA
Sulphur	Sulfate respiration	Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacter Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacteraceae Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; uncultured Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; NA Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfobulbaceae; Desulfobulbus Desulfobacterota; Desulfovibrionia; Desulfovibrionales; Desulfovibrionaceae; Desulfovibrio
Sulphur	Dark sulfite oxidation	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Sulfitobacter
Sulphur	Sulfite respiration	Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacter Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfobulbaceae; Desulfobulbus
Sulphur	Thiosulfate respiration	Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacter Firmicutes; Clostridia; Peptostreptococcales-Tissierellales; Fusibacteraceae; Fusibacter
Sulphur	Respiration of sulfur compounds	Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacter Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; Desulfobacteraceae Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; uncultured Desulfobacterota; Desulfobacteria; Desulfobacterales; Desulfobacteraceae; NA Desulfobacterota; Desulfobulbia; Desulfobulbales; Desulfobulbaceae; Desulfobulbus Desulfobacterota; Desulfovibrionia; Desulfovibrionales; Desulfovibrionaceae; Desulfovibrio Firmicutes; Clostridia; Peptostreptococcales-Tissierellales; Fusibacteraceae; Fusibacter

Metabolism	**FAPROTAX functional profile**	**Taxonomy (Phylum; Class; Order; Family; Genus)**
Sulphur	Dark sulfide oxidation	Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetovibrio Proteobacteria; Gammaproteobacteria; Thiomicrospirales; Thiomicrospiraceae; Thiomicrospira
Sulphur	Dark sulfur oxidation	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Sulfitobacter Proteobacteria; Gammaproteobacteria; Thiomicrospirales; Thiomicrospiraceae; Thiomicrospira
Sulphur	Dark thiosulfate oxidation	Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetospira Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetovibrio
Sulphur	Dark oxidation of sulfur compounds	Proteobacteria; Alphaproteobacteria; Rhodobacterales; Rhodobacteraceae; Sulfitobacter Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetospira Proteobacteria; Alphaproteobacteria; Rhodospirillales; Magnetospiraceae; Magnetovibrio Proteobacteria; Gammaproteobacteria; Thiomicrospirales; Thiomicrospiraceae; Thiomicrospira

Table 2. Taxonomic assignment of the archaeal ASVs of the annotated FAPROTAX functional groups.

Metabolism	**FAPROTAX functional profile**	**Taxonomy (Phylum; Class; Order; Family; Genus)**
Carbon	Methanogenesis by CO2 reduction with H2	Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; Methanobrevibacter Halobacterota; Methanomicrobia; Methanomicrobiales; Methanomicrobiaceae; Methanogenium Halobacterota; Methanosarcinia; Methanosarciniales; Methanosarcinaceae; Methanosarcina
Carbon	Methanogenesis by reduction of methyl compounds with H2	Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; Methanosphaera
Carbon	Hydrogenotrophic methanogenesis	Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; NA

Metabolism	**FAPROTAX functional profile**	**Taxonomy (Phylum; Class; Order; Family; Genus)**
Carbon	Methanogenesis	Halobacterota; Methanocellia; Methanocellales; Methanocellaceae; Methanocella Halobacterota; Methanocellia; Methanocellales; Methanocellaceae; Rice_Cluster_I Halobacterota; Methanocellia; Methanocellales; Methanocellales; uncultured
Carbon	Dark hydrogen oxidation	Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; Methanobrevibacter Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; Methanosphaera Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae; NA Halobacterota; Methanosarcinia; Methanosarciniales; Methanosarcinaceae; Methanosarcina
Nitrogen	Aerobic ammonia oxidation	Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; Candidatus_Nitrocosmicus Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; Candidatus_Nitrososphaera Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; NA
Nitrogen	Nitrification	Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; Candidatus_Nitrocosmicus Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; Candidatus_Nitrososphaera Crenarchaeota; Nitrososphaeria; Nitrososphaerales; Nitrososphaeraceae; NA

3. Chapter V

Supplementary material of: Reviewing soil seagrass data for its preliminary description and classification.

Nerea Piñeiro-Juncal, Antonio Martinez-Cortizas and Miguel Ángel Mateo.

Table 1: dry bulk density (DBD), silt+clay % (Mud) and carbonate ($CaCO_3$) and organic carbon content (C_{org}) data gathered in the literature revision. *Mud value <0.074; ** Mud value <0.125; *** organic carbon calculated from organic matter data (see methods section).

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	5	4		41.4		1.8	(Relexans et al. 1992)
Zostera	5	4		52.9		2.62	
mixed	10	12		4.7 *	98.0	0.3	(Erftemeijer and Middelburg 1993)
Enhalus	10	12		48.2 *	10.8	1.89	
mixed		2-10		11.3	98.0	0.29	(Erftemeijer 1994)
mixed		2-10		11.2	99.0	0.36	
mixed		2-10		13.7	99.0	0.34	
mixed		2-10		17.8	97.0	0.29	
mixed		2-10		39.1	10.0	1.89	
mixed		2-10		26	7.5	0.58	
Posidonia	3				26.3	0.69 ***	(Invers et al. 1995)
Posidonia	3				13.1	0.47 ***	
Posidonia	3				83.0	0.20 ***	
Posidonia	3				81.4	0.26 ***	
Posidonia	3				30.7	0.25 ***	
Posidonia	3				38.3	0.22 ***	
Posidonia	3				89.1	0.48 ***	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Posidonia	3				75.7	0.91 ***	
Posidonia	3				40.6	0.49 ***	
Posidonia	3				61.5	0.60 ***	
Posidonia	3				36.7	0.40 ***	
Posidonia	3				17.5	0.69 ***	
Posidonia	3				18.9	1.59 ***	
Posidonia	3				13.0	1.12 ***	
Posidonia	3				28.0	0.90 ***	
Cymodocea	10				31.7		(Pedersen et al. 1997)
Cymodocea	10				27.7		
mixed		19				0.41	(Vinithkumar et al. 1999)
Zostera	10					2.90	(Sfriso and Marcomini 1999)
Zostera						0 ***	(Holmer and Laursen 2002)
Zostera						3.93 ***	
Posidonia	15	3			96.0	1.22	(Holmer et al. 2003a)
Posidonia	15	3			98.0	0.38	
Posidonia	15	3			96.0	0.71	
Posidonia	15	3			93.0	0.55	
Posidonia	15	3			94.0	0.47	
Posidonia	15	3			88.0	2.56	
Posidonia	10	3		0.0		0.53***	(Cancemi et al. 2003)
mixed		1		27.8	0.4	1.26***	(Fisher and Sheaves 2003)
mixed		1		17.8	0.3	0.69***	
mixed		1		26.0	0.3	0.83***	
mixed		1		45.2	0.7	1.16***	
mixed		1		68.3	0.7	3.32***	
mixed		1		39.2	0.4	4.90***	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
mixed		1		38.1	2.6	2.49***	
mixed		1		70.9	2.2	2.00***	
mixed		1		60.4	2.3		
mixed		1		98.6	2.7	1.24***	
mixed		1		43.8	2.8	0.74***	
mixed		1		34.4	2.7	0.75***	
Posidonia	5					9.30	(Holmer et al. 2004)
Posidonia	5					1.00	
Posidonia	5					4.40	
Posidonia	5					3.10	
Cymodocea	5					1.60	
Thalassodendrum	Sup	1		0.0			(Perry and Beavington-Penney 2005)
Thalassodendrum		1		0.1			
Thalassodendrum		1		0.1			
Thalassodendrum		1		0.2			
Thalassodendrum		1		0.1			
Thalassodendrum		1		0.1			
Thalassia		1		1.0	11.8		
Thalassia		1		0.8	13.5		
Thalassia		1		0.6	14.1		
Thalassia		1		0.6	12.0		
Thalassia		1		0.8	10.6		
Thalassia		1		0.9	13.4		
Halophila	5	2		0.2	4.9	0.10	(Al-Rousan et al. 2005)
Halophila	5	2		0.5	8.2	0.17	
Halophila	5	2		0.5	9.8	0.16	
Halophila	5	2		0.7	3.0	0.14	
Halophila	5	2		1.7	8.6	0.17	
Halophila	5	2		1.0	4.9	0.14	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	CaCO$_3$ %	C$_{org}$ %	Reference
Halophila	5	2		1.8	3.8	0.13	
Enhalus	25	1			3.8	0.37	(Holmer et al. 2006)
Thalassia	25	1			1.2	0.16	
Halophila	25	1			0.9	0.15	
Posidonia	2	3		13.1		0.74	(Apostolaki et al. 2007)
Posidonia	2	3		4.8		1.92	
Posidonia	2	3		15.3		2.19	
Posidonia	2	8			42.3	11.70	(Como et al. 2007)
Posidonia	2	8			29.5	6.30	
Posidonia	2	8			26.7	4.30	
Posidonia	2	8			18.2	3.30	
Zostera	10	3		20.1		0***	(Bos et al. 2007)
Zostera	10	4	2.0	12.0		0.53***	(Matheson and Schwarz 2007)
Zostera	10	4	1.5	7.0		0.51***	
Zostera	10	4	2.2	4.0		0.39***	
Zostera	10	4	1.4	39.0		2.12***	
Zostera	10	4	1.4	29.0		1.60***	
Zostera	10	4	1.6			0.43***	
Zostera	10	4	1.5			0.66***	
Zostera	10	4	1.4			0.59***	
Zostera	10	4	1.1			1.99***	
Zostera	10	4	1.3			1.17***	
Zostera	10	4	1.4			0.53***	
Zostera	10	4	1.4			0.57***	
Zostera	10	4	1.5			0.39***	
Zostera	10	4	1.4			0.74***	
Zostera	10	4	1.7			0.31***	
Zostera	5	3		86.5	6.3		(Cabaço et al. 2008)
Zostera	5	3		81.6	8.6		
Zostera	5	3		87.6	8.1		

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	5	3		65.8	5.2		
Zostera	30	3		49.1		0.03***	(Honkoop et al. 2008)
mixed		6		93.1			(Kiswara et al. 2009)
mixed		6		27.2			
mixed		3		2.0			
Zostera	3	74		40.7		2.94***	(Figueiredo da Silva et al. 2009)
Zostera	10	1		1.3		0.54	(Herkül and Kotta 2009)
Zostera	10	1		1.6		0.60	
Zostera	10	1		1.7		0.55	
Zostera	10	1		1.6		0.57	
Posidonia	Sup	1		0.3	60.2		(Frezza et al. 2011)
Posidonia	Sup	1		0.7	58.3		
Posidonia	Sup	1		0.8	41.7		
Posidonia	Sup	1		0.7	52.7		
Posidonia	Sup	1		1.9	45.7		
Posidonia	Sup	1		1.3	64.1		
Posidonia	Sup	1		0.9	44.2		
Posidonia	Sup	1		0.6	67.3		
Posidonia	Sup	1		0.7	59.8		
Posidonia	Sup	1		0.9	56.5		
Posidonia	Sup	1		2.2	60.8		
Posidonia	Sup	1		4.1	43.8		
Posidonia	Sup	1		4.6	36.7		
Posidonia	Sup	1		2.6	19.1		
Posidonia	Sup	1		2.3	15.5		
Posidonia	Sup	1		3.8	13.8		
Posidonia	Sup	1		3.0	12.2		
Posidonia	Sup	1		1.4	12.3		
Posidonia	Sup	1		1.7	9.4		

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Posidonia	Sup	1		1.4	9.6		
Posidonia	Sup	1		1.6	10.6		
Posidonia	Sup	1		2.4	19.5		
Posidonia	Sup	1		1.8	10.5		
Posidonia	Sup	1		3.8	11.9		
Posidonia	Sup	1		10.8	50.0		
Posidonia	Sup	1		7.0	31.7		
Posidonia	Sup	1		7.1	23.3		
Posidonia	Sup	1		6.3	28.4		
Posidonia	Sup	1		5.3	22.6		
Posidonia	Sup	1		12.3	42.3		
Posidonia	Sup	1		5.9	62.4		
Posidonia	Sup	1		6.3	55.2		
Posidonia	Sup	1		6.3	33.5		
mixed		26		2.3		0.22	(Sim Ooi et al. 2011)
mixed	1	695	0.8		82.1	2.39	(Fourqurean et al. 2012b)
mixed		307	0.8		71.4	3.03	
Zostera	10	3		7.0	11.7	14.07***	(Pagès et al. 2012)
Zostera	5	57		47.0			(Dubois et al. 2012)
Amphibolis					10.5		(Holmer and Kendrick 2013)
Amphibolis					96.6	0.39	
Amphibolis					96.6	0.38	
Amphibolis					39.2	1.74	
Halophila					7.7	0.17	
Halophila					96.7	0.37	
Halophila					96.6	0.47	
Posidonia					21.2		
Posidonia					96.2	0.43	
Posidonia					96.6	0.41	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	CaCO$_3$ %	C$_{org}$ %	Reference
Posidonia					73.5	6.99	
Posidonia					24.3		
Posidonia					96.5	0.40	
Posidonia					96.2	0.45	
Posidonia					87.9	5.44	
Zostera					9.3	0.34	
Zostera					96.6	0.36	
Zostera					96.5	0.40	
Posidonia		47				1.31	(Lavery et al. 2013)
Halophila		15				1.18	
Zostera		15				1.33	
Cymodocea		15				0.68	
Halodule		27				0.69	
Amphibolis		59				0.36	
mixed		15				0.32	
Posidonia		43				0.28	
mixed		28				0.28	
mixed		15				0.30	
Posidonia		7				17.85	
Posidonia	1		1.1		89.5	0.91	(Serrano et al. 2014)
Posidonia	1		1.1		92.0	0.88	
Posidonia	1		1.0		92.5	0.29	
Posidonia	1		1.3		89.7	0.23	
Posidonia	2.7		0.8		82.5	7.84	
Posidonia	2.7		0.7		85.4	6.62	
Posidonia	0.4		1.3		86.7	3.21	
mixed	Up to 100	469	1.4		84.6	0.58	(Campbell et al. 2014)
Zostera	200		0.9			0.01	(Miyajima et al. 2015)
Zostera	120		1.0			0.01	
Zostera	200		1.1			0.01	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	120		0.7			0.01	
Zostera	110		0.6			0.01	
Zostera	200		1.2			0.00	
mixed	95		1.3			0.00	
mixed	150		1.3			0.00	
mixed	130		1.3			0.01	
mixed	200		1.3			0.01	
mixed	200		1.5			0.00	
mixed	193		1.4			0.01	
mixed				28		1.10	(Phang et al. 2015)
Halophila	20	3				0.25	(Rattanachot and Prathep 2015)
Thalassia	20	3				0.27	
Cymodocea	20	3				0.34	
mixed	20	3				0.23	
mixed	20	3				0.25	
mixed	20	3				0.26	
mixed	20	3				0.34	
Halophila	20	3				0.37	
Thalassia	20	3				0.24	
Cymodocea	20	3				0.11	
mixed	20	3				0.33	
mixed	20	3				0.26	
mixed	20	3				0.29	
mixed	20	3				0.35	
Thalassodendrum				8.4	32.0	0.53***	(Khalafallah et al. 2016)
Thalassodendrum				9.4	33.8	0.55***	
Thalassodendrum				10.2	31.8	0.43***	
Thalassodendrum				4	32.8	1.73***	
Thalassodendrum				5	30.4	1.13***	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Halophila				5	30.8	1.48***	
Halophila				8	32.5	1.35***	
Halodule				7.4	28.5	1.22***	
Halodule				7.5	31.2	1.39***	
mixed				3.6	39.5	1.30***	
mixed				6	30.2	1.26***	
Halophila				6.7	45.0	1.13***	
Halophila				4.9	42.5	0.92***	
Halophila				8	46.7	1.09***	
Thalassodendrum				8	39.0	0.83***	
Thalassodendrum				6.5	42.2	0.55***	
Thalassodendrum				4	41.5	0.53***	
Posidonia	150	3			26.4	2.24	(Rozaimi et al. 2016)
mixed		7	0.8		82.8	1.76	(Serrano et al. 2016f)
mixed		7	0.9		85.8	1.41	
Thalassia	30	6	0.8			1.38	(Dahl et al. 2016b)
mixed	9	98	1.4	0		0.10	(Samper-Villarreal et al. 2016)
mixed	9	66	1.2	3.3		0.50	
Posidonia	35	1	0.4	31.6 **	40.2	2.10	(Serrano et al. 2016b)
Halophila						0.58	(Serrano et al. 2014)
Amphibolis	85	1		2.0		14.70	(Serrano et al. 2016c)
Amphibolis	213	1		8.4		0.52	
Halodule	209	1		19.9		1.17	
Halodule	10	1		3.5		0.79	
Halodule	10	1		3.2		0.57	
Halodule	10	1		3.2		0.84	
Halodule	10	1		3.5		0.84	
Halodule	10	1		3.2		0.57	
Halodule	10	1		3.2		0.84	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Amphibolis	116	1		2.2		0.84	
Amphibolis	60	1		3.4		0.85	
Amphibolis	106	1		2.8		0.82	
Amphibolis	167	1		8.4		0.53	
Amphibolis	68	1		4.5		2.61	
Amphibolis	74	1		6.3		0.56	
Halophila	10	1		56.4		1.11	
Halophila	10	1		75.6		1.36	
Halophila	33	1		3.3		2.38	
Halophila	70	1		3.7		0.24	
Halophila	120	1		94.7		0.14	
Halophila	20	1		8.9		3.42	
Halophila	10	1		7.5		0.32	
Halophila	10	1		7.5		1.03	
Posidonia	163	1		16.6		1.03	
Posidonia	184	1		11.3		2.03	
Posidonia	178	1		11.6		1.89	
Posidonia	172	1		14.1		2.25	
Posidonia	88	1		14.0		2.48	
Posidonia	136	1		17.2		1.37	
Posidonia	100	1		17.5		1.47	
Posidonia	147	1		4.8		1.62	
Posidonia	87	1		7.5		1.21	
Posidonia	122	1		28.0		2.10	
Posidonia	82	1		5.5		2.53	
Posidonia	475	1		12.0		4.24	
Posidonia	270	1		11.1		3.19	
Posidonia	270	1		10.4		7.10	
Posidonia	270	1		11.8		5.52	
Posidonia	270	1		7.9		5.73	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Posidonia	270	1		7.6		16.97	
Posidonia	270	1		6.3		17.39	
Posidonia	39	1		2.0		8.16	
Posidonia	76	1		2.0		0.78	
Posidonia	76	1		2.5		0.57	
Posidonia	29	1		8.9		0.98	
Posidonia	29	1		8.9		0.81	
Posidonia	30	1		7.1		1.00	
Posidonia	76	1		3.4		1.04	
Posidonia	121	1		0.6		1.26	
Posidonia	69	1		0.8		0.71	
Posidonia	56	1		0.9		1.07	
Posidonia	86	1		0.9		0.43	
Posidonia	82	1		0.3		0.35	
Zostera	10	1		31.4		0.64	
Zostera	10	1		75.9		0.84	
Zostera	10	1		28.9		1.12	
Zostera	10	1		16.6		0.79	
Zostera	10	1		13.7		0.28	
Zostera	10	1		15.3		0.31	
Zostera	10	1		16.5		0.32	
Zostera	10	1		15.0		0.42	
Zostera	10	1		18.4		0.32	
Zostera	10	1		16.1		0.49	
Zostera	10	1		9.9		0.73	
Zostera	10	1		12.3		0.69	
Zostera	10	1		9.5		0.68	
Zostera	10	1		12.3		0.94	
Zostera	10	1		7.7		0.37	
Zostera	10	1		9.7		0.20	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	10	1		8.3		0.24	
Zostera	10	1		18.4		0.37	
Zostera	10	1		35.6		0.45	
Zostera	10	1		12.5		0.58	
Zostera	10	1		14.1		0.32	
Zostera	10	1		56.9		0.48	
Zostera	10	1		11.6		0.74	
Zostera	10	1		18.6		0.44	
Zostera	10	1		16.1		1.78	
Zostera	430	1		41.2		1.97	
Zostera	170	1		37.6		1.08	
Posidonia		1	0.9	11 **		1.28	(Serrano et al. 2016e)
Posidonia		1	1.0	6 **		1.06	
Posidonia		1	0.9	5 **		0.59	
Posidonia		1	1.2	4 **		0.38	
mixed	18	3	0.6			2.57	(Howard et al. 2016)
Zostera	228	1	1.2			2.28	(Brown et al. 2016)
Zostera	228	1	1.3			1.81	
Zostera	210	1	1.6			0.73	
Zostera	300	1	1.9			0.22	
Zostera	25	3	1.3	5		0.13	(Röhr et al. 2016)
Zostera	25	3	1.3	9		0.35	
Zostera	25	3	1.4	7.1		0.33	
Zostera	25	3	1.3	1.9		0.13	
Zostera	25	3	1.3	4.9		0.45	
Zostera	25	3	1.4	4.4		0.19	
Zostera	25	3	1.3	2.7		0.16	
Zostera	25	3	1.4	12.4		0.26	
Zostera	25	3	1.3	9.2		0.20	
Zostera	25	3	1.4	6.3		0.20	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	3	1.2	29.4		2.30	
Zostera	25	3	1.4	27.3		0.29	
Zostera	25	3	1.4	8.1		0.12	
Zostera	25	3	1.2	27.1		3.23	
Zostera	25	3	1.2	17.3		1.53	
Zostera	25	3	1.2	33		1.71	
Zostera	25	3	1.2	4		0.31	
Zostera	25	3	1.2	0.5		0.10	
Zostera	25	3	1.3	34.6		5.78	
Zostera	25	3	1.3	21		2.18	
Zostera	37.5	6	0.7	62.8		2.79	(Dahl et al. 2016a)
Zostera	37.5	6	1.1	17.9		0.61	
Zostera	37.5	6	1.4	3.7		0.18	
Zostera	37.5	6	1.3	2.6		0.17	
mixed	10	1				0.16	(Jankowska et al. 2016)
mixed	10	1				0.04	
mixed	10	1				0.12	
Posidonia	20	5	0.9	3.3			(Ricart et al. 2017)
Posidonia	20	5	1.1	0.6			
Posidonia	20	5	1.2	0.2			
Halodule	12	1				0.09***	(Trevathan-Tackett et al. 2018)
Halodule	12	1				0.22***	
Thalassia	15	1				0.31***	
Thalassia	15	1				0.35***	
Halodule	12	1				0.53***	
Halodule	12	1				0.42***	
Thalassia	15	1				0.26***	
Thalassia	15	1				0.38***	
Halodule	12	1				0.34***	
Halodule	12	1				0.30***	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Thalassia	15	1				0.80***	
Thalassia	15	1				0.65***	
Zostera	40	1	1.7		1.2	0.14	(Marbà et al. 2018)
Zostera	39	1	1.7				
Zostera	34	1	1.6		1.2	0.17	
Zostera	36	1	1.6		1.3	0.19	
Zostera	42	1	1.7		0.8	0.02	
Zostera	42	1	1.6		0.9	0.06	
Zostera	38	1	1.6				
Zostera	38	1	1.6		1.1	0.14	
Zostera	16	1	1.5		3.9	0.43	
Zostera	41.5	3		1.2		0.70	(Barañano et al. 2018)
mixed	12					0.01	(Oreska et al. 2017)
Zostera		9				0.01	(Miyajima et al. 2017)
Thalassia	50	1	1.2			1.50	(Githaiga et al. 2017)
Thalassia	50	1	1.3			1.17	
Thalassia	50	1	1.4			0.87	
Thalassia	50	1	1.3			0.72	
Thalassia	50	1	1.3			0.58	
Thalassia	50	1	1.5			0.66	
Thalassia	50	1	1.5			0.74	
Thalassia	50	1	1.4			0.67	
Thalassia	50	1	1.4			0.53	
Thalassia	50	1	1.5			0.80	
Thalassia	50	1	1.3			1.32	
Thalassia	50	1	1.4			1.56	
Thalassia	50	1	1.4			0.57	
Thalassia	50	1	1.3			0.50	
Thalassia	50	1	1.6			0.71	
Enhalus	50	1	1.4			1.33	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	CaCO$_3$ %	C$_{org}$ %	Reference
Enhalus	50	1	1.3			1.03	
Enhalus	50	1	0.9			1.90	
Enhalus	50	1	1.2			0.78	
Enhalus	50	1	1.0			0.56	
Enhalus	50	1	1.3			0.63	
Enhalus	50	1	1.5			0.79	
Enhalus	50	1	1.6			0.99	
Enhalus	50	1	1.6			0.98	
Enhalus	50	1	1.4			1.22	
Enhalus	50	1	1.3			2.29	
Enhalus	50	1	1.5			1.63	
Enhalus	50	1	1.5			0.61	
Enhalus	50	1	1.5			0.82	
Enhalus	50	1	1.4			0.82	
Thalassodendrum	50	1	1.4			1.19	
Thalassodendrum	50	1	1.6			0.43	
Thalassodendrum	50	1	1.6			1.41	
Thalassodendrum	50	1	1.4			1.29	
Thalassodendrum	50	1	1.4			1.09	
Thalassodendrum	50	1	1.4			0.82	
Thalassodendrum	50	1	1.4			1.08	
Thalassodendrum	50	1	1.3			1.19	
Thalassodendrum	50	1	1.3			1.05	
Thalassodendrum	50	1	1.2			0.73	
Thalassodendrum	50	1	1.1			0.66	
Thalassodendrum	50	1	1.2			0.66	
Thalassodendrum	50	1	1.1			1.09	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Thalassodendrum	50	1	1.4			0.42	(Stankovic et al. 2017)
Thalassodendrum	50	1	1.2			0.65	
Enhalus	100	1				0.72	
Thalassia	100	1				0.70	
Halophila	100	1				0.43	
mixed	30	13	0.0			0.62	(Rozaimi et al. 2017)
mixed	30	6	0.0			0.35	
Enhalus	30	3	0.0			0.31	
Halophila	5	2	1.9	20.4		1.20	(Jiang et al. 2017)
mixed	5	2	1.5	1.8		1.50	
Thalassia	5	2	1.4	0.7		0.33	
Halophila	5	2	1.2	59.9		1.15	
Halophila	5	2	1.7	18.5		0.51	
mixed	5	2	1.3	65.8		0.87	
mixed	5	2	1.4	41.4		1.30	
mixed	5	2	1.5	19.2		0.39	
Cymodocea	54	2		0.0			(Samper-Villarreal et al. 2018)
Halophila	50	3		0			
Zostera	22	5		1.4			
Zostera	93	4		0.6			
Halodule	114	1		9.1		2.18	(Nóbrega et al. 2018)
Ruppia	111	1		7.1		0.57	
Thalassia	30		1.8	5.5			(Jiang et al. 2018)
Thalassia	30		1.8	5.6			
Thalassia	30		1.7	1.5			
Enhalus	30		1.7	9.3			
Enhalus	30		1.7	5.6			
Enhalus	30		1.7	7.8			
mixed	109	1	1.3			0.54	
mixed	90	1	1.3			0.56	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
mixed	110	1	1.1			0.50	(Cusack et al. 2018)
mixed	35	1	1.3			0.76	
mixed	118	1	0.9			0.98	
mixed	116	1	1.2			1.12	
mixed	106	1	1.2			0.74	
mixed	61	1	1.2			0.60	
mixed	104	1	1.1			0.68	
mixed	93	1	1.1			0.49	
mixed	87	1	1.0			0.56	
mixed	76	1	0.9			0.59	
Zostera		3	1.2			0.24	(Postlethwaite et al. 2018)
Zostera		3	1.2			0.21	
Zostera		3	1.1			0.24	
Zostera		3	1.2			0.37	
Zostera		3	1.2			0.46	
Zostera		3	1.4			0.48	
Thalassia	15		0.2			0.46	(Tanaya et al. 2018)
Thalassia	15		0.2			0.23	
Thalassia	15		0.3			0.31	
Thalassia	15		0.4			0.19	
Thalassia	15		0.4			0.25	
Thalassia	15		0.3			0.33	
Thalassia	15		0.4			0.25	
Thalassia	15		0.2			0.27	
Thalassia	15		0.1			0.47	
Thalassia	15		0.2			0.35	
Thalassia	15		0.2			0.24	
Thalassia	15		0.3			0.42	
Thalassia	15		0.1			0.73	
Thalassia	15		0.3			0.32	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Thalassia	15		0.6			0.21	
Thalassia	15		0.3			0.26	
Thalassia	15		0.2			0.32	
Thalassia	15		0.6			0.21	
Thalassia	15		0.1			0.22	
Thalassia	15		0.6			0.24	
Thalassia	15		0.9			0.59	
Thalassia	14		0.9			0.36	
Thalassia	15		0.9			0.31	
Thalassia	16		0.8			0.39	
Thalassia	13		1.1			0.40	
Thalassia	13		1.1			0.41	
Thalassia	15		1.2			0.39	
Thalassia	14		1.2			0.49	
Thalassia	10		0.9			0.42	
Thalassia	13		0.7			0.30	
Thalassia	13		0.7			0.41	
Thalassia	15		1.0			0.64	
Thalassia	14		0.7			0.35	
Thalassia	12		0.9			0.23	
Thalassia	14		1.1			0.42	
Thalassia	14		0.8			0.38	
Enhalus	7.3		0.5			0.29	
Enhalus	4.3		0.7			0.25	
Enhalus	14		0.4			0.30	
Enhalus	16		0.3			0.30	
Enhalus	15		0.5			0.40	
Enhalus	15		0.5			0.18	
Enhalus	15		0.6			0.19	
Enhalus	15		0.3			0.19	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	CaCO$_3$ %	C$_{org}$ %	Reference
Enhalus	13		0.6			0.55	
Enhalus	12		0.7			0.67	
Enhalus	12		0.8			0.39	
Enhalus	13		0.6			0.44	
Enhalus	14		0.7			0.53	
Enhalus	13		0.7			0.35	
Zostera		1		12.4		1.41	(Lundquist et al. 2018)
mixed		7		0.5			(Belshe et al. 2018)
mixed		10		0.8			
mixed		4		1.1			
mixed		8		0.7			
Posidonia	Sup	1		23.0		8.23	(Kletou et al. 2018)
Posidonia	Sup	1		21.2		7.87	
Posidonia	Sup	1		19.4		7.26	
Posidonia	Sup	1		19.7		7.74	
Thalassia	50	1	1.1			7.52***	(Rattanachot et al. 2018)
Enhalus	50	1	0.9			4.79***	
Zostera	35	1	1.0			1.20	(Green et al. 2018)
Zostera	35	1	1.1			1.25	
Zostera	35	1	0.9			1.62	
Zostera	35	1	0.8			4.94	
Zostera	35	1	1.1			1.30	
Zostera	35	1	0.9			1.37	
Zostera	35	1	1.0			1.04	
Zostera	35	1	1.1			1.33	
Zostera	35	1	1.1			1.10	
Zostera	35	1	1.0			1.28	
Zostera	35	1	1.1			0.95	
Zostera	35	1	0.3			3.82	
Zostera	35	1	1.2			0.86	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	CaCO$_3$ %	C$_{org}$ %	Reference
Halophila		3	1.3	44		0.24	(Serrano et al. 2018)
Halophila		3	1.2	44.2		0.24	
Halophila		3	1.1	42.7		0.27	
Thalassia		3	0.7	52.3		0.80	
Thalassia		3	0.6	44.2		0.72	
Thalassia		3	0.9	21.7		0.50	
Enhalus		3	0.7	40.42		0.57	
Enhalus		3	0.9	52.3		0.45	
Enhalus		3	0.9	38.6		0.32	
Enhalus		3	1.1	30.6		0.40	
Thalassodendrum		3	1.0	6.3		0.16	
Thalassodendrum		3	0.9	21.1		0.36	
Thalassodendrum		3	1.1	11.2		0.21	
Thalassodendrum		3	1.1	31.6		0.14	
Thalassodendrum		3	0.9	15.1		0.95	
Thalassodendrum		3	1.0	26.1		0.18	
Thalassodendrum		3	1.0	29.5		0.24	
Halodule		3	1.4	10.8		0.17	
Halodule		3	1.1	26.7		0.22	
Halodule		3	0.9	32.8		0.26	
Halophila		3	0.8	40.6		0.29	
Halophila		3	1.0	44.8		0.38	
Halophila		3	0.9	46.1		0.39	
Halophila		3	1.0	43.7		0.37	
Halophila		3	1.0	57		0.42	
Halophila		3	0.9	60.8		0.45	
Halodule		3	0.9	61.5		0.44	
Zostera	25	3	1.4	14		0.28	(Röhr et al. 2018)
Zostera	25	3	1.4	11.5		0.41	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	3	1.4	26.6		0.45	
Zostera	25	3	1.6	30.3		0.08	
Zostera	25	3	1.3	15.5		0.27	
Zostera	25	3	1.5	34.2		0.29	
Zostera	25	3	2.0	15.6		0.62	
Zostera	25	3	1.3	7.6		0.22	
Zostera	25	3	1.1	19.9		0.31	
Zostera	25	3	1.4	9		0.17	
Zostera	25	3	0.9	36.9		0.77	
Zostera	25	3	1.7	21.5		0.36	
Zostera	25	3	1.5	24.3		0.55	
Zostera	25	3	1.0	60.3		0.89	
Zostera	25	3	1.0	75.9		1.22	
Zostera	25	3	1.0	81.3		1.28	
Zostera	25	3	1.3	76.3		2.34	
Zostera	25	3	1.3	43.6		0.44	
Zostera	25	3	1.2	25		1.65	
Zostera	25	3	1.3	2.3		2.35	
Zostera	25	3	1.3	7.5		4.68	
Zostera	25	3	1.5	3.1		0.12	
Zostera	25	3	0.5	40.4		5.37	
Zostera	25	3	1.5	32.2		0.41	
Zostera	25	3	0.2	55.6		10.65	
Zostera	25	3	0.9	61.1		0.66	
Zostera	25	3	1.4	61		0.86	
Zostera	25	3	0.6	29.7		3.96	
Zostera	25	3	0.5	27.6		2.44	
Zostera	25	3	0.4	68.1		3.78	
Zostera	25	3	1.0	52		2.61	
Zostera	25	3	1.2	2.6		0.26	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	3	1.5	4.3		0.45	
Zostera	25	3	1.4	5.4		0.42	
Zostera	25	3	1.2	0.5		0.10	
Zostera	25	3	1.2	27.1		3.23	
Zostera	25	3	1.2	4		0.31	
Zostera	25	3	1.2	17.8		1.53	
Zostera	25	3	1.2	30.4		2.30	
Zostera	25	3	1.3	23		2.18	
Zostera	25	3	1.2	33.2		1.71	
Zostera	25	3	1.3	34.7		5.78	
Zostera	25	3	1.4	27.9		0.29	
Zostera	25	3	1.4	8.1		0.12	
Zostera	25	3	1.4	12.5		0.26	
Zostera	25	3	1.4	4.2		0.20	
Zostera	25	3	1.3	1.9		0.13	
Zostera	25	3	1.3	2.7		0.16	
Zostera	25	3	1.3	9.2		0.20	
Zostera	25	3	1.3	5.1		0.13	
Zostera	25	3	1.3	3.2		0.45	
Zostera	25	3	1.4	2.9		0.19	
Zostera	25	3	1.3	9		0.35	
Zostera	25	3	1.4	7.2		0.33	
Thalassia	10	3	1.0			0.79	(Barry et al. 2018)
Thalassia	10	3	0.2			8.29	
Thalassia	10	3	0.5			2.52	
Thalassia	50-86	6	1.5			0.70	(Gullström et al. 2018)
Enhalus	50-86	6	1.4			1.02	
Thalassodendrum	50-86	6	1.3			1.44	
Thalassia	50-86	6	1.4			0.76	
Enhalus	50-86	6	1.5			0.81	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Thalassodendrum	50-86	6	1.6			0.59	
Thalassia	50-86	6	1.5			0.46	
Thalassodendrum	50-86	6	1.5			0.47	
Thalassia	50-86	6	1.6			0.47	
Cymodocea	50-86	6	1.8			0.54	
Enhalus	50-86	6	1.9			0.28	
Thalassodendrum	50-86	6	1.7			0.28	
Thalassia	50-86	6	1.9			0.28	
Cymodocea	50-86	6	1.8			0.27	
Thalassodendrum	50-86	6	1.7			0.22	
Thalassia	50-86	6	1.8			0.35	
Cymodocea	50-86	6	1.8			0.40	
Enhalus	50-86	6	1.6			0.51	
Thalassodendrum	50-86	6	1.7			0.81	
Thalassia	50-86	6	1.8			0.20	
Thalassodendrum	50-86	6	1.7			0.20	
Thalassia	50-86	6	2.5			0.32	
Cymodocea	50-86	6	1.7			0.22	
Thalassodendrum	50-86	6	2.0			0.52	
Thalassia	50-86	6	1.7			0.31	
Cymodocea	50-86	6	1.7			0.25	
Zostera	41.3	3		1.2		0.07***	(Barañano et al. 2018)
Zostera	40.6	3		0.8		0***	
Cymodocea			1.2	2.5			(Vizzini et al. 2019)
Cymodocea			1.6	1			
Zostera	25	1	1.3			0.71	(Prentice et al. 2020)
Zostera	25	1	0.8			1.55	
Zostera	25	1	1.6			2.56	
Zostera	25	1	1.7			1.04	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	1	1.6			0.65	
Zostera	25	1	1.6			0.47	
Zostera	25	1	1.0			1.08	
Zostera	25	1	1.3			0.88	
Zostera	25	1	0.9			1.56	
Zostera	25	1	1.3			0.87	
Zostera	25	1	1.0			1.48	
Zostera	25	1	1.3			2.90	
Zostera	25	1	1.5			2.21	
Zostera	25	1	1.4			0.69	
Zostera	25	1	1.0			1.52	
Zostera	25	1	1.8			0.51	
Zostera	25	7	1.5			0.18	
Zostera	25	7	1.3			0.23	
Zostera	25	7	1.7			0.32	
Zostera	25	7	1.6			0.71	
Zostera	25	7	1.5			0.62	
Zostera	25	7	1.2			0.74	
Zostera	25	3	1.4			0.60	
Zostera	25	3	1.3			1.02	
Zostera	25	3	1.0			1.72	
Zostera	25	3	1.4			0.19	
Zostera	25	3	1.4			0.38	
Zostera	25	4	1.7			0.42	
Zostera	25	3	1.7			0.29	
Zostera	25	3	1.5			0.42	
Zostera	25	8	1.4			0.44	
Zostera	25	4	1.4			0.63	
Zostera	25	6	1.3			0.41	
Zostera	25	3	1.1			0.22	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	3	1.1			0.36	
Zostera	30	3		0.4			(Prentice et al. 2019)
Zostera	30	3		1			
Zostera	30	3		6			
Zostera	30	3		0.1			
Zostera	30	3		0.7			
Zostera	30	3		0.2			
Posidonia	25	1	1.2	15	2.7	1.00	(Sanders et al. 2019)
Ruppia	25	1	0.6	71	3.7	4.90	
Halophila	25	1	1.4	7	1.3	0.40	
Zostera	25	1	0.7	77	3.4	3.20	
Ruppia	25	1	0.8	57	1.2	2.20	
Zostera	25	1	0.6	58	1.9	2.20	
Halophila	25	1	0.6	56	18.9	2.30	
Halophila	25	1	1.1	65	0.6	1.90	
mixed	5	2	1.5	2.4		0.33	(Jiang et al. 2019)
mixed	5	2	1.7	7.3		0.31	
Zostera	25	1	1.3			3.23	(Kindeberg et al. 2019a)
Zostera	20	1	0.8			3.00	
Zostera	23	1	1.3			3.86	
Zostera	25	1	1.0			1.09	
Zostera	25	1	1.0			1.12	
Zostera	25	1	1.0			1.13	
Zostera	25	1	1.5			0.52	
Zostera	20	1	1.2			0.37	
Zostera	25	1	1.4			0.36	
Zostera	25	1	1.5			0.63	
Zostera	25	1	1.6			0.21	
Zostera	25	1	1.8			0.44	
Zostera	25	1	1.5			0.44	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	1	1.5			0.38	
Zostera	25	1	1.6			0.32	
Zostera	25	1				0.73	
Zostera	25	1				0.82	
Zostera	25	1				0.75	
Zostera	20	1	1.3			0.32	
Zostera	25	1	1.3			0.22	
Zostera	25	1	1.3			0.38	
Zostera	25	1	1.4			0.15	
Zostera	25	1	1.3			0.23	
Zostera	25	1	1.3			0.29	
Zostera	35	1	0.5			3.91	
Zostera	38	1	0.4			5.74	
Zostera	35	1	0.4			5.29	
Zostera	42	1	1.5			0.67	
Zostera	36	1	1.6			0.27	
Zostera	30	1	1.7			0.21	
Zostera	35	1	0.2			8.70	
Zostera	38	1	0.2			9.63	
Zostera	40	1	0.2			7.40	
Zostera	30	1	0.9			2.68	
Zostera	35	1	0.8			3.01	
Zostera	35	1	0.8			3.03	
Zostera	42	1	1.4			0.74	
Zostera	38	1	1.3			0.96	
Zostera	29	1	1.1			1.39	
Zostera	35	1	0.6			4.00	
Zostera	38	1	0.6			3.40	
Zostera	37	1	0.5			3.78	
Zostera	41	1	0.5			3.15	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	37	1	0.5			3.28	
Zostera	37	1	0.4			3.16	
Zostera	25	1	1.4			0.17	
Zostera	25	1	1.4			0.34	
Zostera	25	1	1.5			0.22	
Zostera	25	1	0.9			1.12	
Zostera	25	1	0.9			1.25	
Zostera	20	1	0.8			1.51	
Zostera	25	1	0.9			1.07	
Zostera	25	1	0.6			1.69	
Zostera	25	1	0.7			1.22	
Zostera	25	1	1.3			0.17	
Zostera	25	1	1.4			0.20	
Zostera	25	1	1.3			0.20	
Zostera	25	1	1.5			0.41	
Zostera	25	1	1.4			0.46	
Zostera	25	1	1.4			0.41	
Zostera	25	1	1.1			0.37	
Zostera	25	1	1.2			0.31	
Zostera	25	1	1.2			0.23	
Zostera	25	1	1.7			0.75	
Zostera	25	1	1.7			0.57	
Zostera	25	1	1.8			0.48	
Zostera	25	1	1.0			0.99	
Zostera	25	1	1.0			0.81	
Zostera	25	1	1.0			0.80	
Zostera	25	1	1.3			0.35	
Zostera	25	1	1.3			0.32	
Zostera	25	1	1.3			0.31	
Zostera	20	1	1.6			0.51	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	1	1.5			0.43	
Zostera	25	1	1.6			0.66	
Zostera	25	1	1.3			0.26	
Zostera	22	1	1.4			0.30	
Zostera	25	1	1.4			0.20	
Zostera	25	1	1.4			0.19	
Zostera	25	1	1.4			0.22	
Zostera	25	1	1.3			0.21	
Zostera	25	1	1.4			0.12	
Zostera	25	1	1.4			0.11	
Zostera	25	1	1.4			0.15	
Zostera	25	1	1.4			0.15	
Zostera	25	1	1.4			0.16	
Zostera	25	1	1.5			0.16	
Zostera	25	1	1.4			0.17	
Zostera	25	1	1.4			0.23	
Zostera	30	1	1.3			0.19	
Zostera	30	1	1.3			0.13	
Zostera	30	1	1.3			0.14	
Zostera	25	1	1.3			0.13	
Zostera	25	1	1.4			0.61	
Zostera	25	1	1.3			0.28	
Zostera	8	1	1.4			0.46	
Zostera	15	1	1.5			0.21	
Zostera	15	1	1.5			0.21	
Zostera	19	1	1.5			0.15	
Zostera	25	1	1.1			0.33	
Zostera	25	1	1.1			0.38	
Zostera	25	1	1.2			0.37	
Zostera	25	1	1.3			0.20	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	1	1.3			0.19	
Zostera	25	1	0.6			0.60	
Zostera	25	1	1.5			0.18	
Zostera	25	1	1.6			0.13	
Zostera	25	1	1.3			0.56	
Zostera	15	1	0.9			2.47	
Zostera	14	1	1.0			2.23	
Zostera	13	1	0.9			2.21	
Zostera	12	1	1.3			1.97	
Zostera	6	1	1.3			1.98	
Zostera	10	1	1.2			2.58	
Zostera	25	1	1.0			1.52	
Zostera	25	1	1.3			1.38	
Zostera	25	1	1.0			1.69	
Zostera	22	1	1.5			0.21	
Zostera	22	1	1.5			0.23	
Zostera	24	1	1.5			0.49	
Zostera	25	1	0.3			4.89	
Zostera	23	1	1.2			6.66	
Zostera	22	1	1.5			5.79	
Zostera	25	1	0.5			1.14	
Zostera	25	1	0.3			0.69	
Zostera	25	1	0.3			3.30	
Zostera	25	1	1.5			0.34	
Zostera	25	1	1.5			0.57	
Zostera	25	1	1.5			0.35	
Zostera	25	1	0.7			2.76	
Zostera	25	1	0.7			3.51	
Zostera	25	1	0.6			3.41	
Zostera	25	1	1.4			0.13	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	25	1	1.4			0.10	
Zostera	25	1	1.4			0.12	
Zostera	25	1	1.6			0.57	
Zostera	25	1	1.6			0.48	
Zostera	22	1	1.4			0.37	
Zostera	25	1	1.4			0.09	
Zostera	25	1	1.3			0.10	
Zostera	25	1	1.4			0.12	
mixed	22-55	2	1.2			0.35	(Rahayu et al. 2019)
mixed	22-55	3	0.8			0.94	
mixed	22-55	3	1.1			0.38	
mixed	22-55	3	1.1			0.78	
mixed		31	1.2			0.59	(Garcias-Bonet et al. 2019)
mixed	1	11		9.0		1.07	(Gallagher et al. 2019)
mixed	1	11		4.1		0.71	
Enhalus	1	11		17.1		0.30	
Zostera	30	1	1.4			0.31	(Poppe and Rybczyk 2018)
Zostera	30	1	1.2			0.60	
Zostera	30	1	1.2			0.59	
Zostera	30	1	1.3			0.38	
Zostera	30	1	1.4			0.30	
Zostera	30	1	1.5			0.30	
Zostera	50	3				9.90	(Dahl et al. 2020)
Zostera	50	3				9.70	
Zostera	50	3				0.30	
Zostera	50	3				2.20	
mixed	10	3	0.63	82.7		4.41	(Ricart et al. 2020)
Zostera	10	3	1.17	51.9		1.90	
mixed	10	3	1.15	66.3		1.48	
Zostera	10	3	2.11	21.9		1.16	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Zostera	10	3	1.18	62.2		0.59	
Halophila	10	3	0.88	75.1		3.03	
Zostera	10	3	1.75	11.0		0.92	
mixed	10	3	1.65	9.6		1.23	
Zostera	10	3	1.48	15.1		0.74	
Zostera	10	3	1.35	16.7		0.78	
mixed	10	3	1.58	18.2		0.83	
Zostera	10	3	1.54	13.0		1.01	
Zostera	10	3	1.54	11.8		0.88	
Halodule	10	3	2.08	3.3		0.17	
Zostera	10	3	2.00	14.9		0.75	
Zostera	30	5	0.72	93.8			(Lima et al. 2020)
Zostera	30	5	0.68	87.5			
Zostera	30	5	0.89	79.3			
Zostera	30	5	0.94	79.7			
Zostera	30	5	1.27	66.6			
Zostera	30	5	1.46	1.1			
Thalassia	100	12	1.24			1.04	(Arney et al. 2020)
Posidonia	135	1		4.5		4.00	(Serrano et al. 2020)
Cymodocea	30	3		1.7			(Bañolas et al. 2020)
Cymodocea	30	3		2.8			
Cymodocea	30	3		0.7			
Cymodocea	30	3		3.9			
Cymodocea	30	3		1.3			
Cymodocea	30	3		2.0			
Posidonia	45	1	1.05	1.6		0.54	(Salinas et al. 2020)
Posidonia	43	1	1.03	1.9		1.05	
Posidonia	50	1	1.15	2.1		0.94	
Posidonia	40	1	0.88	7.1		1.04	
Posidonia	36	1	0.84	8.9		1.00	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Posidonia	41	1	0.80	9.6		0.97	
Posidonia	50	1	1.05	11.0		1.98	
Posidonia	49	1	0.83	1.0		1.63	
Posidonia	49	1	0.88	1.2		1.43	
Posidonia	49	1	0.91	1.1		0.50	
Posidonia	50	1	1.03	0.9		0.40	
mixed	2		1.17	11.0			(Bulmer et al. 2020)
Posidonia	173	1	1.19	5.8	30.0	2.52	Unpublished, Diaz-Almela, Mateo
Posidonia	105	1	0.63	5.6	23.6	3.96	
Posidonia	125	1	0.63	4.9	26.5	3.41	
Posidonia	167	1	0.93	13.5	18.4	1.98	
Posidonia	87	1	0.92	20.9	18.1	1.16	
Posidonia	37	1	0.83	5.3	12.2	0.70	
Posidonia	136	1	1.00	22.5	44.6	1.88	
Posidonia	21	1	0.99	25.3	30.3	1.26	
Posidonia	55.9	1	0.88	28.9	29.0	1.54	
Posidonia	106	1	1.03	15.7	13.5	2.23	
Posidonia	28	1	0.58	6.6	23.8	6.25	
Zostera	66	1	0.91	29.0	7.3	0.27	
Zostera	44	1	1.02		10.4	0.38	
Zostera	65	1	0.98		9.4	0.23	
Zostera	96	1	1.47	30.6	16.4	0.83	
Zostera	101	1	1.20		64.7	0.61	
Zostera	90	1	0.98		13.3	0.31	
Zostera	113	1	1.21	21.8	13.3	0.50	
Zostera	104	1	0.96		17.1	0.31	
Zostera	108	1	0.95		15.5	0.33	
Cymodocea	96	1	1.31	17.6	19.4	0.49	
Cymodocea	96	1	1.06		14.4	0.53	
Cymodocea	56	1	0.71	17.5	6.4	0.93	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Cymodocea	117	1	1.19	16.4	6.5	0.25	
Cymodocea	116	1	0.97		5.6	0.16	
Cymodocea	109	1	0.92		5.6	0.26	
Cymodocea	103	1	1.12	8.8		0.25	
Cymodocea	100	1	1.03	8.8	5.8	0.25	
Cymodocea	111	1	0.99		7.0	0.21	
Posidonia	58	1	0.79	5.4	16.7	2.81	
Posidonia	61	1	0.85	7.2	17.0	1.42	
Posidonia	77	1	0.77	7.3	18.1	2.10	
Posidonia	59	1	0.59	4.4	16.9	1.88	
Posidonia	89	1	0.57	6.1	19.3	1.99	
Posidonia	103	1	1.03	6.8	16.9	1.98	
Posidonia	157	1	1.26	22.8	30.0	0.78	
Posidonia	98	1	1.01	30.9	31.5	1.28	
Posidonia	104	1	1.05	28.1	30.9	1.66	
Posidonia	69	1	1.11	26.1	37.3	1.28	
Posidonia	41	1	0.79	7.5	4.4	1.21	
Posidonia	77	1	0.93	8.5	7.9	1.99	
Posidonia	148	1	1.02	9.5	4.7	1.73	
Cymodocea	102	1	1.24	5.1	11.4	0.21	
Cymodocea	93	1	1.13	7.8	9.3	0.18	
Cymodocea	530	1	1.09	19.2	9.5	0.13	
Cymodocea	138	1	1.47	34.9	13.1	0.27	
Posidonia	108	1	0.66	8.2	20.5	3.79	
Posidonia	93	1	4.11	7.0	24.3	3.97	
Posidonia	94	1	0.94	10.0	23.3	3.75	
Cymodocea	173	1	0.63	0.6	23.9	0.25	
Posidonia	68	1	0.70	7.8	20.0	5.24	
Posidonia	140	1	0.47	8.4	18.6	6.42	
Posidonia	190	1	0.43	10.4	22.0	4.72	

Family	Core length (cm)	n	DBD (g cm^{-3})	Mud % (<0.063 mm)	$CaCO_3$ %	C_{org} %	Reference
Posidonia	200	1	0.40	9.2	22.0	4.43	
Posidonia	134	1	0.85	5.3	22.1	2.74	
Posidonia	48	1	0.13	32.4	48.0	3.38	
Posidonia	260	1	1.26	32.3	46.6	3.40	
Posidonia	544	1	1.52	34.7	52.9	1.39	
Posidonia	395	1	1.42	12.7	33.4	0.84	
Posidonia	89	1	0.82	13.3	20.3	2.69	
Posidonia	89	1	1.14	11.5	19.5	3.07	
Posidonia	65	1	0.71	10.7	19.3	3.55	
Posidonia	528	1	1.41		55.7	2.83	
Posidonia	140	1	0.64	17.4	37.8	2.70	
Posidonia	131	1	0.70	7.2	31.5	0.87	
Posidonia	390	1	1.27	10.3	48.1	3.79	
Posidonia	320	1	1.23	10.8	40.9	6.22	
Posidonia	240	1	1.37	14.9	63.3	5.62	
Posidonia	81	1	1.07	1.6	83.5	2.25	Unpublished, Leiva-Dueñas, Mateo
Posidonia	160	1	1.37	0.6	94.0	1.73***	
Posidonia	138	1	0.99	1.8	89.1	1.12	
Posidonia	89	1	1.51	2.3	87.2	1.03	
Posidonia	98	1	0.81	9.0	83.6	3.05	

Table 2: porosity data gathered in the literature revision.

Specie	Depth (cm)	Av	max	min	References
Zostera marina			0.3	0.25	(Röhr et al. 2016)
Zostera marina			0.4	0.2	
Zostera marina	50	0.67			(Dahl et al. 2016a)
Zostera marina	50	0.43			
Zostera marina	50	0.32			
Zostera marina	50	0.42			

Specie	Depth (cm)	Av	max	min	References
Zostera marina	30	0.36			(Krause-Jensen et al. 2011)
Thalassia testudinum	5	0.77			(Yarbro and Carlson 2008)
Thalassia testudinum	5	0.75			
Thalassia testudinum	5	0.82			
Thalassia testudinum	5	0.88			
Thalassia testudinum	5	0.85			
Thalassia testudinum		0.70			(Jensen et al. 2009)
Thalassia testudinum		0.91			
Thalassia testudinum		0.34			
Thalassia testudinum		0.25			
Thalassia testudinum		0.42			
Zostera japonica	80		0.8	0.77	(Wheatcroft et al. 2013)
Zostera japonica	80		0.63	0.62	
Cymodocea nodosa		0.42			(Vizzini et al. 2019)
Cymodocea nodosa		0.42			
Zostera marina	4-16	0.53			(Dahl et al. 2018)
Zostera marina	4-16	0.36			
Zostera marina	4-16	0.43			
Zostera marina	4-16	0.31			
Zostera marina	4-16	0.42			
Zostera marina	4-16	0.48			
Zostera marina	4-16	0.60			
Zostera marina	4-16	0.76			
Zostera marina	4-16	0.23			
Zostera marina	4-16	0.28			
Zostera marina	4-16	0.47			
Zostera marina	4-16	0.43			
Zostera marina	4-16	0.71			
Zostera marina	4-16	0.66			
Zostera marina	4-16	0.59			
Zostera marina	4-16	0.25			

Specie	Depth (cm)	Av	max	min	References
Zostera marina	4-16	0.29			
Thalassia testudinum	16	0.42	0.56	0.31	(Devereux et al. 2011)
mixed	20	0.45			(Rattanachot and Prathep 2015)
Thalassia hemprichii		0.68			(Dahl et al. 2016b)
Thalassia hemprichii		0.69			
Thalassia hemprichii		0.69			
Thalassia hemprichii		0.67			
Thalassia hemprichii		0.68			
Zostera marina	25	0.32			(Kindeberg et al. 2019a)
Zostera marina	20	0.37			
Zostera marina	23	0.31			
Zostera marina	25	0.38			
Zostera marina	25	0.38			
Zostera marina	25	0.38			
Zostera marina	25	0.32			
Zostera marina	20	0.27			
Zostera marina	25	0.21			
Zostera marina	25	0.42			
Zostera marina	25	0.38			
Zostera marina	25	0.45			
Zostera marina	25	0.32			
Zostera marina	25	0.30			
Zostera marina	25	0.28			
Zostera marina	20	0.28			
Zostera marina	25	0.25			
Zostera marina	25	0.28			
Zostera marina	25	0.33			
Zostera marina	25	0.31			
Zostera marina	25	0.33			
Zostera marina	35	0.31			
Zostera marina	38	0.26			

Specie	Depth (cm)	Av	max	min	References
Zostera marina	35	0.28			
Zostera marina	42	0.37			
Zostera marina	36	0.34			
Zostera marina	30	0.32			
Zostera marina	35	0.18			
Zostera marina	38	0.18			
Zostera marina	40	0.17			
Zostera marina	30	0.37			
Zostera marina	35	0.35			
Zostera marina	35	0.35			
Zostera marina	42	0.40			
Zostera marina	38	0.41			
Zostera marina	29	0.40			
Zostera marina	35	0.32			
Zostera marina	38	0.34			
Zostera marina	37	0.31			
Zostera marina	41	0.30			
Zostera marina	37	0.31			
Zostera marina	37	0.29			
Zostera marina	25	0.29			
Zostera marina	25	0.30			
Zostera marina	25	0.27			
Zostera marina	25	0.37			
Zostera marina	25	0.36			
Zostera marina	20	0.36			
Zostera marina	25	0.38			
Zostera marina	25	0.35			
Zostera marina	25	0.36			
Zostera marina	25	0.27			
Zostera marina	25	0.29			
Zostera marina	25	0.30			

Specie	Depth (cm)	Av	max	min	References
Zostera marina	25	0.38			
Zostera marina	25	0.36			
Zostera marina	25	0.37			
Zostera marina	25	0.33			
Zostera marina	25	0.33			
Zostera marina	25	0.32			
Zostera marina	25	0.30			
Zostera marina	25	0.30			
Zostera marina	25	0.32			
Zostera marina	25	0.35			
Zostera marina	25	0.36			
Zostera marina	25	0.35			
Zostera marina	25	0.31			
Zostera marina	25	0.33			
Zostera marina	25	0.31			
Zostera marina	20	0.08			
Zostera marina	25	0.06			
Zostera marina	25	0.05			
Zostera marina	25	0.22			
Zostera marina	22	0.26			
Zostera marina	25	0.22			
Zostera marina	25	0.21			
Zostera marina	25	0.22			
Zostera marina	25	0.22			
Zostera marina	25	0.20			
Zostera marina	25	0.20			
Zostera marina	25	0.22			
Zostera marina	25	0.23			
Zostera marina	25	0.23			
Zostera marina	25	0.24			
Zostera marina	25	0.26			

Specie	Depth (cm)	Av	max	min	References
Zostera marina	25	0.26			
Zostera marina	30	0.25			
Zostera marina	30	0.25			
Zostera marina	30	0.27			
Zostera marina	25	0.26			
Zostera marina	25	0.27			
Zostera marina	25	0.26			
Zostera marina	8	0.29			
Zostera marina	15	0.23			
Zostera marina	15	0.22			
Zostera marina	19	0.22			
Zostera marina	25	0.27			
Zostera marina	25	0.30			
Zostera marina	25	0.28			
Zostera marina	25	0.22			
Zostera marina	25	0.26			
Zostera marina	25	0.24			
Zostera marina	25	0.28			
Zostera marina	25	0.28			
Zostera marina	25	0.32			
Zostera marina	15	0.36			
Zostera marina	14	0.35			
Zostera marina	13	0.34			
Zostera marina	12	0.31			
Zostera marina	6	0.32			
Zostera marina	10	0.33			
Zostera marina	25	0.36			
Zostera marina	25	0.35			
Zostera marina	25	0.34			
Zostera marina	22	0.26			
Zostera marina	22	0.26			

Specie	**Depth (cm)**	**Av**	**max**	**min**	**References**
Zostera marina	24	0.26			
Zostera marina	25	0.23			
Zostera marina	23	0.31			
Zostera marina	22	0.32			
Zostera marina	25	0.29			
Zostera marina	25	0.21			
Zostera marina	25	0.22			
Zostera marina	25	0.28			
Zostera marina	25	0.27			
Zostera marina	25	0.29			
Zostera marina	25	0.32			
Zostera marina	25	0.31			
Zostera marina	25	0.29			
Zostera marina	25	0.25			
Zostera marina	25	0.24			
Zostera marina	25	0.25			
Zostera marina	25	0.24			
Zostera marina	25	0.23			
Zostera marina	22	0.23			
Zostera marina	25	0.26			
Zostera marina	25	0.25			
Zostera marina	25	0.26			
mixed	10	0.53			(Erftemeijer and Middelburg 1993)
Enhalus acoroides	10	0.72			(Azzoni et al. 2001)
Ruppia cirrhosa	12	0.76			

Table 3: redox potential data gathered in the literature revision.

Specie	Depth (cm)	mV			Commentaries	**References**
		Average	**max**	**min**		
E. acoroides	0-15		400	-120	Decrease with depth	(Holmer et al. 1999)

Specie	Depth (cm)	mV			Commentaries	**References**
		Average	**max**	**min**		
C. serrulata	2-3	40.44				(Alsaffar et al. 2019)
Z. noltii	5	-227				(Cabaço et al. 2008)
Z. noltii	5	-309				
Z. noltii	5	-234				
Z. noltii	5	-192				
R. cirrhosa	0-10		>250	-100	Varies seasonally and decrease with depth	(Azzoni et al. 2001)
mixed	15		400	0	Decrease with depth related to irradiance	(Gacia et al. 2005)
T. testudinum	30		400	<-150	Decrease with depth	(Enríquez et al. 2001)
T. testudinum	40		>300	-100		
T. testudinum	40		>100	-100		
T. testudinum	35		400	<-100		
T. testudinum	25		300	0		
T. testudinum	35		300	-200		
Z. marina	14		300	-100		(Holmer et al. 2006)
C. nodosa	35		400	-100	Decrease with depth	(Marbà and Duarte 2001)
Z. capricorni	10	-18				(Matheson and Schwarz 2007)
Z. capricorni	10	81				
Z. capricorni	10	-19				
Z. capricorni	10	-108				

Specie	Depth (cm)	mV			Commentaries	**References**
		Average	**max**	**min**		
Z. capricorni	10	3				
Z. capricorni	10	42				
Z. capricorni	10	55				
Z. capricorni	10	-5				
Z. capricorni	10	36				
Z. capricorni	10	10				
Z. capricorni	10	-39				
Z. capricorni	10	-3				
Z. capricorni	10	-37				
Z. capricorni	10	23				
Z. capricorni	10	-2				
T. hemprichii	Rhizosphere	-74			Positive anomaly	(Marbà et al. 2010)
C. rotundata	Rhizosphere	-94			Positive anomaly	
S. isoetifolium	Rhizosphere	-26			Positive anomaly	
E. acoroides	Rhizosphere	92			Positive anomaly	
H. uninervis	Rhizosphere	-21			Positive anomaly	

Specie	Depth (cm)	mV			Commentaries	**References**
		Average	**max**	**min**		
E. acoroides	Rhizosphere	-95			Positive anomaly	
T. hemprichii	Rhizosphere	190				
C. serrulata	Rhizosphere	-9.1				
C. serrulata	Rhizosphere	87.9				
E. acoroides	Rhizosphere	172.2			Positive anomaly	
H. ovalis	Rhizosphere	-99			Positive anomaly	
H. ovalis	Rhizosphere	83			Positive anomaly	
Z. japonica	Rhizosphere	41.3				
Z. japonica	Rhizosphere	80.1			Positive anomaly	
H. ovalis	50	-51.44	77.7	-209		(Rattanachot and Prathep 2015)
T. hemprichii	50	-117.4	-18.2	-158		
C. rotundata	50	-146.7	-75	-197.3		
mixed	50	-97.1	44.2	-183.7		
mixed	50	-105.3	-1.3	-187		
mixed	10	-21.6	200	-100		(Terrados et al. 1999)
mixed	20		0	-300	Decrease with depth	(Alongi et al. 2008)
mixed	20		0	-150	Decrease with depth	
mixed	20		0	-250	Decrease with depth	
mixed		-84.1				(Fisher and Sheaves 2003)
mixed		-84.1				
mixed		-64.6				
mixed		-43.5				

Specie	Depth (cm)	mV			Commentaries	**References**
		Average	**max**	**min**		
mixed		-53.3				
mixed		-46.6				
mixed		-137.3				
mixed		-95.5				
mixed		-86.4				
mixed		-149.9				
mixed		134.3				
mixed		-117				
P. australis			-25	-520	Decrease with depth	(Serrano et al. 2020)

Table 4: pH data gathered in the literature revision.

Specie	**Depth (cm)**	**pH**	**Range**		**References**
			max	**min**	
C. serrulata	2		8.2	7.2	(Brodersen et al. 2017)
Zostera spp.	30	7.1			(Lima et al. 2020)
Zostera spp.	30	7.2			
Zostera spp.	30	7.2			
Zostera spp.	30	7.6			
Zostera spp.	30	7.4			
Zostera spp.	30	7.7			
		8.3	8.1	7.9	(Vinithkumar et al. 1999)
Thalassia testudinum	10		8.2	7.5	(Burdige and Zimmerman 2002)
			7.4	7.0	(Nobi and Dinesh Kumar 2014)
Thalassia testudinum	60		8.1	7.2	(Morse et al. 1987)
Thalassia testudinum	20		8.5	7.5	(Burdige et al. 2010)
Halodule spp.	114	6.9	7.1	6.8	(Nóbrega et al. 2018)
Ruppia maritima	111	7.6	7.9	7.0	
	10	8.2			(Hicks 2007)

Specie	Depth (cm)	pH	Range		References
			max	min	
Zostera marina	108	8.0	8.5	7.3	(Bradley and Stolt 2003)
Zostera marina	66	8.2	8.3	7.9	
Zostera marina	60	7.9	8.2	7.8	
Zostera marina	100	7.8	8.1	7.6	
Zostera marina	81	7.9	8.3	7.6	
Zostera marina	107	7.4	8.4	5.1	
Zostera marina	124	7.8	8.1	7.6	
mixed	20		7.2	6.4	(Alongi et al. 2008)
mixed	20		7.1	6.5	
mixed	20		7.2	6.8	
Z. capricorni		8			(Mellors et al. 2002)
Halodule uninervis		8.2			
Halophila minor		7.1			
Z. capricorni		8.1			
Halodule uninervis		8.8			
Halodule uninervis		8.9			
Halodule uninervis		6.8			
Halodule uninervis		8.7			

Table 5: color observations gathered in the literature revision.

Specie	Soil Depth	Color	Munsell code	References
Posidonia oceanica	475	dark brown to grey peaty		(Serrano et al. 2012)
Ruppia maritima	0-10		5GY 3/1, 10YR 3/1	(Nóbrega et al. 2018)
Ruppia maritima	10-26		5G 4/1	
Ruppia maritima	26-37		5GY 4/1	
Ruppia maritima	37-56		10Y 4/1	
Ruppia maritima	56-84		5GY 4/1	
Ruppia maritima	84-114		10B 4/1	

Specie	**Soil Depth**	**Color**	**Munsell code**	**References**
Halodule spp.	0-6		N 2.5, 10Y 3/1	
Halodule spp.	6-13		2.5Y 5/1	
Halodule spp.	13-30		2.5Y 4/1	
Halodule spp.	30-44		N 4	
Halodule spp.	44-70		N 5	
Halodule spp.	70-93		N 3	
Halodule spp.	93-106		5B 3/1, N 3	
Halodule spp.	106-111		5B 3/1	
Posidonia australis	0-5	Greyish-brown	Gley1 4/N	(Serrano et al. 2020)
Posidonia australis	5-10	Greyish-brown	Gley1 4/N	
Posidonia australis	10-15	Greyish-brown	Gley1 4/N	
Posidonia australis	15-20	Greyish-brown	Gley1 4/N	
Posidonia australis	20-25	Greyish-brown	Gley1 4/N	
Posidonia australis	25-30	Lighter brown	10YR 6/3	
Posidonia australis	30-35	Lighter brown	10YR 6/3	
Posidonia australis	50-55	Consistent brown	10 YR 6/ 4	
Posidonia australis	85-90	Consistent brown	10 YR 6/ 4	
Posidonia australis	130-135	Consistent brown	10 YR 6/ 4	
Mixed		dark, brown		(Serrano et al. 2016g)

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Por último, a Carmen. Después de todo lo que hemos tenido que pasar o nos amábamos o nos odiábamos, me alegro de que sea la primera. Porque es la primera, no? Quiero decir… yo creo que es la primera.