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Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies

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ABSTRACT

Seagrass meadows support high primary production rates and their canopies are efficient at filtering particles out of their water column as well as in preventing resuspension of the sediments. In addition, decomposition rates in seagrass sediments are slow, because of low nutrient concentration in seagrass detritus and low oxygen concentration in seagrass sediments. These characteristics result in high carbon burial rates in seagrass meadows, which have the capacity to accumulate large stores of carbon in their sediments, raising the seafloor. Carbon fingerprinting techniques allow to calculate both the age of these deposits and, therefore, the rate of carbon burial and identify the contribution of carbon produced by the seagrass. Yet, data on the regional cover and carbon stocks in seagrass meadows is sparse for some regions, particularly the Indo-Pacific, Africa and South America. In addition, our understanding of the factors regulating the variability in carbon sink capacity among seagrass meadows is limited. These gaps limit the capacity to formulate strategies to mitigate climate change based on the carbon sink capacity of seagrass meadows. A research strategy needs be formulated to address these gaps and provide the necessary protocols to ensure the accountability of mitigation actions involving the conservation and restoration of seagrass meadows.

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1. Introduction

Seagrass are a group of about 60 angiosperm species adapted to life in the sea, whether permanently or temporarily submerged (Hemminga and Duarte, 2000). Seagrass are clonal, rhizomatous plants that develop, largely through clonal growth, large ecosystems termed seagrass meadows, often monospecific but that can include up to 12 species in the tropics (Hemminga and Duarte, 2000). Seagrass meadows occur along the shores of all continents, to maximum depths of up to 50 m, depending on water transparency, except Antarctica (Hemminga and Duarte, 2000). Whereas there is no comprehensive inventory of the area covered by seagrasses globally, different estimates are available. The documented seagrass area is 177,000 km² (Green and Short, 2003), but this is an acknowledged underestimate of the total area covered by seagrass meadows, since many regions with large

seagrass meadows (e.g. Indonesia and Bahamas) have not been fully charted. Hence, the estimates most commonly used in the literature use a low estimate of 300,000 km² and a high estimate of 600,000 km² (Duarte et al., 2005a; Nellemann et al., 2009; Mcleod et al., 2011), with the global area potentially suitable to support seagrass growth estimated at 4,320,000 km² (Gattuso et al., 2006).

Seagrass meadows are highly productive ecosystems (Duarte and Chiscano, 1999) and play a key role as habitats supporting high biodiversity (Hemminga and Duarte, 2000). In addition, they are characterised by their capacity to sequester and store considerable amount of carbon in their carbon-rich sediments (Duarte et al., 2005b), being responsible for 20% of the global carbon sequestration in marine sediments despite occupying 0.1% of the ocean surface (Duarte et al., 2005b; Kennedy et al., 2010). Regrettably, seagrass meadows are being lost globally at fast rates, of about 5% year⁻¹, and at least 1/3 of the area present has been lost since World-War II (Orth et al., 2006; Waycott et al., 2009), which represents the loss of an important carbon sink (Mcleod et al., 2011).

Realisation of the important carbon sink capacity of seagrass meadows has recently led to the proposal that seagrass

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meadows, along with salt-marshes and mangrove forests, could be used to support strategies to mitigate climate change (Nellemann et al., 2009; Laffoley and Grimsditch, 2009; Mcleod et al., 2011). These strategies would be based on both the conservation and reforestation of seagrass meadows. However, the development of management schemes based on the role of seagrass meadows as intense carbon sinks has been precluded to-date by limitations in current knowledge on the mechanisms conducive to their high carbon sink capacity and the rates of carbon burial they do support. Here we provide a synthesis of recent research addressing both these gaps and identify additional elements required to formulate a robust strategy for climate change mitigation based on the role of seagrass meadows as intense carbon sinks. We believe that the knowledge presented here, largely based on papers published within the past 5 years, provides a solid underpinning to launch carbon mitigation strategies based on the conservation and restoration seagrass meadows.

2. Mechanisms of carbon burial in seagrass communities

2.1. Metabolic C capture

Seagrasses rank amongst the most productive populations on the biosphere (Duarte and Chiscano, 1999). On average, net primary production per unit of area of seagrass populations, when considering that of leaves, rhizomes and roots, is about $1012 \text{ g DW m}^{-2} \text{ yr}^{-1}$ (Duarte and Chiscano, 1999), equivalent to $404 \text{ g C m}^{-2} \text{ yr}^{-1}$ or $14.8 \text{ ton CO}_2 \text{ ha yr}^{-1}$, with a ratio aboveground: belowground production of 16.4 ± 8.5 (Duarte and Chiscano, 1999). The most productive seagrass meadows are multispecies meadows in the Indo-Pacific region, those of *Phyllospadix* spp. in the North American Pacific coast and those of *Posidonia oceanica* in the Mediterranean Sea (Duarte and Chiscano, 1999). Despite the small global extension of seagrass populations, their net primary production accounts for about 1% of the global net marine primary production (Duarte and Cebrián, 1996). The production of seagrass species accounts for most of the primary production of seagrass communities, which includes contributions by epiphytic communities. The leaves and rhizomes of seagrasses are colonised by epiphytic autotrophic and heterotrophic organisms. Net primary production of seagrass autotrophic epiphytes, comprising microscopic and macroscopic algae, has been quantified for a few seagrass communities (Hemminga and Duarte, 2000). Net primary production of seagrass autotrophic epiphytes ranges from $13.8 \text{ g DW m}^{-2} \text{ yr}^{-1}$ – $755 \text{ g DW m}^{-2} \text{ yr}^{-1}$, and it typically accounts for 20–60% of total seagrass aboveground productivity (Hemminga and Duarte, 2000). Therefore, the photosynthetic activity of seagrass meadows contributes a significant amount of marine organic carbon.

2.2. Carbon accumulation in seagrass meadows

Whereas seagrass meadows support an important biomass, they represent a minor component of the carbon stocks in seagrass meadows, which are – by far – dominated by the sedimentary pool. Seagrass sediments are organic-rich, with an average organic concentration of 4.1% (Kennedy et al., 2010). Seagrass meadows occupy coastal environments over millenary time scales and are able to form thick carbon deposits, raising the seafloor by about 1 mm per year (Kennedy et al., 2010). The thickest documented sedimentary deposit has been reported at 11 m thick for the *P. oceanica* meadow at Port Lligat, Spain, corresponding to an accumulation of about $0.18 \text{ tons C m}^{-2}$ over 6000 years of seagrass growth at that site (Lo Iacono et al., 2008). Thick seagrass deposits,

several meters in thickness, have been reported for other sites, including other sites in the Spanish Mediterranean, Shark Bay (W. Australia) and Florida Bay (cf. Kennedy et al., 2010).

Hence, seagrass meadows combine a high metabolic capacity to act as carbon sinks with the capacity to accumulate large carbon pools in the sediments over millenary time scales. The long retention times of carbon in sedimentary deposits in seagrass meadows is quite unique and renders seagrass meadows some of the most carbon-rich ecosystems in the Biosphere. Understanding the reasons for the high capacity of seagrass to capture and store carbon is fundamental to manage these ecosystems in support of strategies to mitigate climate change.

3. Understanding the high capacity for carbon burial in seagrass meadows

The high primary production of seagrass communities is matched by high rates of organic matter consumption through respiration (Duarte et al., 2010), largely derived by the contribution of heterotrophic organisms, such as benthic animals and sediment bacteria, present with high biomass in these ecosystems. Yet, more than 80% of seagrass production is not consumed by herbivores (Duarte and Cebrián, 1996), and decomposition rates of seagrass detritus are slow when compared with those of other organisms, because of the low nutrient (nitrogen and phosphorous) concentration in their tissues (Enríquez et al., 1993). Hence, a fraction of the organic carbon produced by seagrass communities is not consumed by heterotrophs, resulting in a tendency for seagrass ecosystems to be generally autotrophic communities acting as carbon sinks (Duarte and Cebrián, 1996; Duarte et al., 2010). Whereas organic matter consumption (respiration) may exceed production (gross primary production) during some periods of the year (Hemminga and Duarte, 2000), the vast majority of metabolic estimates of seagrass communities available at annual time scales reveal that they are autotrophic, and hence act as CO_2 sinks (Duarte et al., 2010). The excess organic carbon produced by seagrass ecosystems is exported or buried (Duarte and Cebrián, 1996).

3.1. Particle trapping: the role of seagrass meadows as filters

Seagrass meadows develop lush canopies that affect the water flow above them, thereby acting as ecosystem engineers modifying their abiotic environment (Jones et al., 1997). The presence of seagrass canopies at the benthic boundary layer alters the roughness of the bottom (Granata et al., 2001; Nepf and Vivoni, 2000) and thereby the vertical flow profile over the sediments and the associated turbulence structure (Ackerman and Okubom, 1993; Fonseca et al., 1982; Gambi et al., 1990; Koch et al., 2006; Koch and Gust, 1999), especially when canopy height represents more than 10% of the height of the water column (Nepf and Vivoni, 2000). Depending on shoot density and seagrass species, flow reduction resulting from current deflection by the canopy ranges from 2- to more than 10-fold compared to water flow outside the seagrass bed (Ackerman, 1986; Gambi et al., 1990; Hendriks et al., 2008). Seagrass canopies also have a dampening effect on waves (Bouma et al., 2005; Fonseca and Cahalan, 1992). When waves enter the near shore region, they encounter the friction (shear stress) of the seagrass canopy and become shallow water waves. This leads to wave-induced transport in a process referred to as Stokes drift, which may be of considerable impact in many coastal environments. Although wave attenuation is maximal when the meadow occupies a large portion of the water column (Fonseca and Cahalan, 1992), reduction in wave energy and orbital velocity occurs even when beds are located at 5–15 m

depth and the plants occupy a small portion of the water column (Granata et al., 2001). However, the capacity of seagrasses to trap sediment might be lost under extreme flow conditions in wave-exposed environments (Fonseca and Bell, 1998; Koch and Gust, 1999).

Apart from the direct effect of dampening of waves and currents by seagrass canopies leading to increased sediment deposition (Gacia and Duarte, 2001; Gacia et al., 1999; Hendriks et al., 2008) and decreased resuspension (Lopez and Garcia, 1998; Terrados and Duarte, 2000), seagrass can also directly intercept suspended sediment particles with their canopies. Seagrass canopies increase the effective benthic surface by as much as twenty times thereby providing a large surface for sediment deposition and the probability of contact. The collision of suspended particles with seagrass leaves increases particle path length and causes momentum loss (Hendriks et al., 2008), which results in increased deposition. Field estimates indicate that the potential for particle contact with leaf surfaces sometimes approaches 100% in *Zostera marina* canopies (Ackerman, 2002). In addition, exopolymeric substances secreted by epiphytes can bind sediment particles to seagrass leaves (Duarte 2002). Epiphytic layers on seagrass leaves may also contribute to the trapping of particles in seagrass beds by increasing the roughness of the canopy and increasing the velocity gradient layer on the leaf surface (Koch et al., 2006). The capacity of seagrass meadows to trap particles can be quite high, and, for instance, Barron et al. (2004) calculated, using carbon budgets across seagrass patches of different age, that the input of carbon originating elsewhere, trapped into sediments of *Cymodocea nodosa* patches in a Mediterranean lagoon, must be about $157 \text{ mmol C m}^{-2} \text{ day}^{-1}$.

Hence, seagrass meadows act as filters trapping and retaining particles suspended in the water column, which drives an additional carbon flow contributing to carbon sequestration in seagrass sediments (Kennedy et al., 2010).

3.2. High carbon preservation in seagrass sediments

High metabolic carbon sink capacity and high carbon trapping capacity supports a large flow of carbon to seagrass sediments. However, in order for seagrass meadows to be effective as carbon sinks this carbon must be effectively preserved in the sediments for centuries to millennia, as can be the case. The mechanisms conducive to high carbon preservation rates in seagrass sediments include (1) low nitrogen and phosphorus content in seagrass tissues (Duarte, 1990), which renders seagrass detritus a poor substrate to support microbial growth and results in low decomposition rates (Enríquez et al., 1993); (2) low oxygen concentration in seagrass sediments. Seagrass sediments are often anaerobic, which leads to inefficient microbial metabolism and enhances seagrass preservation; (3) the fact that a fraction of seagrass production (up to 50%), that of roots and rhizomes, is placed directly into the sediments, often at depths of tens of centimetres (Duarte et al., 1998), contributing to the high preservation efficiency for these tissues; (4) the fact that being underwater, seagrass sediments are free of fires, which are responsible for the emission as CO₂ of much of the organic carbon accumulated in forest soils on land, and (5) the dissipation of waves and turbulence by seagrass canopies prevents sediment resuspension and increases the retention of sediments and the associated carbon. The combination of all these factors leads to high carbon preservation in seagrass sediments, which together with high metabolic inputs and particle trapping rates explain the role of seagrass meadows as intense carbon sinks in the biosphere.

4. Assessing seagrass carbon burial

4.1. Assessment of the net community metabolism of seagrass meadows

Available estimates of seagrass community metabolism, described by gross primary production, respiration and net community production, have been recently reviewed and synthesised to quantify the role of seagrass meadows as carbon sinks (Duarte et al., 2010). Most seagrass metabolic estimates have been derived from changes in oxygen concentration in incubation chambers deployed in situ and from diel oxygen concentration curves measured in the field (Duarte et al., 2010). However, metabolic rates of seagrass communities have been also calculated from changes in CO₂, ¹⁴C uptake and incubations of sediment cores, containing seagrass communities, in the laboratory. Since year 1956, seagrass community metabolism has been quantified for 155 sites. These estimates are unevenly distributed, with most of them (67%) assessing the metabolism of tropical and subtropical seagrass meadows and more than one forth that of Mediterranean ones (Duarte et al., 2010). There is a substantial gap of information on community metabolic rates for seagrass meadows along the coasts of the Southern Hemisphere and North and West Pacific regions (Duarte et al., 2010).

The synthesis of available estimated revealed that gross primary production (GPP) of seagrass communities averages $224.9 \pm 11.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and tends to exceed respiration (R, average \pm standard error = $187.6 \pm 10.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$) for most meadows (Duarte et al., 2010). This indicates that seagrass meadows tend to be autotrophic ecosystems, with an average net community production (NCP) of $27.2 \pm 5.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Duarte et al., 2010). Two-thirds (63%) of the seagrass meadows examined acted as CO₂ sinks. Seagrass community metabolic rates vary across geographical regions and species, with tropical seagrass meadows tending to have lower (although not significantly) NCP than temperate ones (Duarte et al., 2010). Meadows of fast-growing seagrass species have the highest GPP, and together with those of *Thalassia testudinum*, the highest R (Duarte et al., 2010). GPP and R are positively related, but seagrass meadows tend to be net autotrophic ecosystems (i.e. $\text{GPP}/\text{R} > 1$) when GPP exceeds $186 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Duarte et al., 2010), and seagrass meadows tend to act as CO₂ sinks when average aboveground biomass exceeds 41 g DW m^{-2} (Duarte et al., 2010).

The average net metabolic capture of carbon by seagrass communities ($9.9 \pm 2.22 \text{ mol C m}^{-2} \text{ yr}^{-1}$, Duarte et al., 2010) is more than five times the C sink capacity of that of North American wetlands and the net carbon captured by the 10% seagrass meadows with the largest carbon sink capacity is well above the rates of carbon sink in undisturbed Amazonian forests, assumed to be the largest terrestrial carbon sinks (Duarte et al., 2010). Considering a global area of seagrass meadows ranging from $300,000 \text{ km}^2$ to $600,000 \text{ km}^2$ and the average (\pm SE) NCP per unit of area, seagrass meadows would bury, only through their metabolic activity, between 20 and $50 \text{ Tg C year}^{-1}$ using the low estimate of global seagrass extension and between 41 and $101 \text{ Tg C year}^{-1}$ using the high estimate of seagrass cover. These estimates confirm that seagrass meadows rank amongst the strongest CO₂ sinks in the biosphere, and that despite their small global extension (less than 0.1% of ocean surface) they bury about 20% of the total carbon buried in the global ocean.

4.2. Assessment of carbon storage

The extent to which seagrass organic matter accumulates in the sediment can be determined in a number of ways (Table 1). In

Table 1
Summary of estimates of sediment accumulation and carbon burial rate in seagrass meadows.

Location	Dating technique	Sediment accumulation rate (mm m ⁻² y ⁻¹)	Carbon burial (g C m ⁻² y ⁻¹)	Seagrass	Reference
Fanals point, NW Mediterranean	Direct measure of sedimentation rate		198	<i>P. oceanica</i>	Gacia et al., 2002
Ischia, NW Mediterranean	Radiocarbon, ¹⁴ C, Annual carbon budget	1.65	30, 19.5	<i>P. oceanica</i>	Mateo et al., 1997, 2006
Culip, NW Mediterranean	Radiocarbon, ¹⁴ C	0.61	9	<i>P. oceanica</i>	Mateo et al., 1997
Port Lligat, NW Mediterranean	Radiocarbon, ¹⁴ C	4.14	75	<i>P. oceanica</i>	Mateo et al., 1997
Campello, NW Mediterranean	Radiocarbon, ¹⁴ C	2.03	112	<i>P. oceanica</i>	Mateo et al., 1997
Tabarca 1, NW Mediterranean	Radiocarbon, ¹⁴ C	1.14	62	<i>P. oceanica</i>	Mateo et al., 1997
Tabarca 2, NW Mediterranean	Radiocarbon, ¹⁴ C	1.88	104	<i>P. oceanica</i>	Mateo et al., 1997
Medas, NW Mediterranean	Radiocarbon, ¹⁴ C, Annual carbon budget	0.79	12.6, 72.5	<i>P. oceanica</i>	Mateo et al., 1997, 2006
Bay of Calvi, Corsica	Annual carbon budget		16.6	<i>P. oceanica</i>	Mateo et al., 2006
Spencer Gulf, S. Australia	²¹⁰ Pb	2–2.7		<i>P. australis</i>	Belperio et al., 1984
Spencer Gulf, S. Australia	¹⁴ C	0.2–1.4		<i>P. australis</i>	Belperio et al., 1984
Port Lligat, NW Mediterranean	¹⁴ C	1.1		<i>P. oceanica</i>	Lo Iacono et al., 2008
Ebro delta, NW Mediterranean	Carbon content of different aged sand waves		43.8	<i>C. nodosa</i>	Barron et al. 2004
Cala Jonquet, NW Mediterranean	Annual carbon budget		52.4	<i>Zostera marina</i>	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		4.4	<i>Cymodocea nodosa</i>	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		2.9	<i>Zostera noltii</i>	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		66.4	<i>Posidonia oceanica</i>	Cebrian et al., 1997

studies examining the fate of organic carbon, estimates of losses due to herbivory, decomposition and export can be compared with seagrass primary production to determine how much carbon is unaccounted for and hence is assumed to accumulate in the sediment. Duarte and Cebrián (1996) compiled the available data and estimated that, on average, 16% of seagrass primary production accumulates in the sediment. There are limitations to this technique as it generally provides only an indirect estimate of carbon accumulation. In addition, data compilations may have a mismatch between the amount of data available for primary production relative to that available for herbivory, decomposition and export. The data provided are also average values and do not therefore identify the relative importance of different seagrass species, which may be substantial. For example, Cebrian et al. (1997) followed the fate of carbon in four Mediterranean seagrass species and found that *P. oceanica* had about 23 times higher capacity to accumulate organic carbon stocks than *Zostera noltii*. This kind of carbon budgeting provides short-term (annual) estimates of carbon accumulation in seagrass meadows. A more direct approach to studying short-term carbon accumulation is provided by sediment traps. Sediment traps are instruments that can be deployed in seagrass meadows to measure the quantity of sinking particles (Gacia et al., 1999). The traps can be deployed on a weekly or monthly basis and the organic (and inorganic) content of collected particles determined. As yet, there is little data available that uses this technique (Table 1).

Analyses of radioactive components of sediments coupled with estimates of carbon concentration can provide longer term estimates of carbon accumulation. The two most common techniques use the naturally occurring radioactive isotopes of lead (²¹⁰Pb) and carbon (¹⁴C). Both techniques rely on the radioactive decay of these isotopes, the rate of which is well known. The ²¹⁰Pb has a half-life of 22.3 years, which means that after 22.3 years, only half of the original amount is undecayed. If the sediment layers are undisturbed, then as the sediment ages it slowly loses its radioactivity. The age of a sediment layer can therefore be determined by how much ²¹⁰Pb it contains. For ¹⁴C, its half-life of 5730 years and so the age of much older sediments can be dated. This radiocarbon dating can be used to estimate the age of carbon containing materials up to

about 58,000–62,000 years. In sediments the ¹⁴C of refractory seagrass organic matter such as roots and rhizomes is commonly measured (Table 1).

Estimates of the short-term carbon storage in sediments (years) averages about 53 g C m⁻² yr⁻¹ and compares well with direct estimates of longer term carbon burial, averaging 58 g C m⁻² a⁻¹ (Table 1). The data sets used in these calculations are, however, from a restricted geographical area and represent meadows of only a few of all seagrass species.

4.3. Isotopic fingerprinting and accountability of seagrass carbon burial

Organic matter sources that contribute and accumulate in the sediments of seagrass meadows have different, and identifiable, organic carbon stable isotope signatures that can be tracked and quantified. Besides the seagrass tissues themselves, other potential sources of organic carbon are plankton, (usually collected as suspended particulate organic matter), seagrass epiphytes, micro-phytobenthos, macroalgae and terrestrial organic matter, including that of mangroves. All these organic matter sources have isotopic signatures that are generally different from those of seagrass tissues (Moncreiff and Sullivan, 2001). So by measuring the stable isotopic signature of organic carbon ($\delta^{13}\text{C}$) in seagrass sediments the proportions of seagrass and other organic matter sources that have accumulated can be estimated. Kennedy et al. (2010) compiled a data set containing 219 analyses of the organic carbon stable isotopic signature of seagrass sediments which have been collected at 88 locations around the world and showed that 50% of the organic matter that accumulates is derived from the seagrass tissues, with the other 50% of the organic matter that accumulates was derived from the trapping of phytoplankton and terrestrially derived particles by the seagrass canopy.

Using the range of organic carbon accumulation rates reported for seagrass meadows as between 83 and 133 g C m⁻² y⁻¹ (Duarte et al., 2005b), and combining this with the estimate that 50% of this organic matter is derived from seagrass tissues, it can be calculated that between 41 and 66 g C m⁻² y⁻¹ of the organic matter produced by seagrasses become buried in the sediment (Kennedy et al., 2010). The burial rate of seagrass-derived organic matter can be now

compared with the net amount of organic matter produced in seagrass meadows (net community production) of around $120 \text{ g C m}^{-2} \text{ y}^{-1}$ (Duarte et al., 2010) to conclude that the amount buried represents 30–50% of the net community production. The organic matter not retained in seagrass sediments could have been exported away from the seagrass meadows to be decomposed or stored elsewhere. Overall, the total organic carbon sink sustained by seagrass meadows is the sum of their net community production and the non seagrass-derived carbon that has been trapped and accumulates in their sediments. The sum of these two terms gives a range of between 160 and $186 \text{ g C m}^{-2} \text{ y}^{-1}$, comparable to other recent estimates (e.g. $138 \pm 38 \text{ g C m}^{-2} \text{ y}^{-1}$ in Mcleod et al., 2011), and further demonstrates the importance of seagrass meadows for carbon sequestration.

5. Limitations in the assessment of seagrass carbon sink capacity

The initial calculations by Duarte et al. (2005a) that seagrass meadows act as intense carbon sinks and contribute a significant fraction of all carbon sequestered in marine sediments allowed the formulation of climate change mitigation strategies based on the conservation and recovery of seagrass meadows (Nellemann et al., 2009; Laffoley and Grimsditch, 2009). Parallel research, improved our understanding of the processes conducive to the role of seagrass meadows as carbon sinks (e.g. Hendriks et al., 2008) and delivered improved estimates of the carbon pools stored in seagrass sediments (Lo lacono et al., 2008). The adoption of climate change mitigation strategies based on the conservation and recovery of seagrass meadows requires that current uncertainties be resolved. This need prompted recent synthesis assessing the metabolic capacity of seagrass meadows to act as carbon sinks (Duarte et al., 2010) and the identification of sources of carbon to seagrass sediments (Kennedy et al., 2010).

Our knowledge on the role of seagrass meadows as carbon sinks has improved rapidly in the past years. However, substantial uncertainties and gaps remain. These uncertainties need to be addressed to provide the robust underpinnings required to implement climate change mitigation strategies based on the conservation and recovery of seagrass meadows. The actions require to address current uncertainties include:

1. Improved estimates of global seagrass cover. Present estimates of global seagrass are based on extrapolations and a canonical estimate of seagrass cover is lacking, largely due to difficulties in resolving seagrass cover using remote sensing tools. As a result, current estimates of global seagrass cover range two fold (see above). This uncertainty results from insufficient mapping of seagrass meadows in some regions, including Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank, Africa and South America. Some of these regions (Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank) have extensive carbonate platforms, suitable to support seagrass meadows, but have not been mapped. Research effort, including mapping, on seagrass ecosystems in the coast of Africa and South America has been rather limited, and present estimates of the area covered by seagrass meadows in these regions are likely to be severely underestimated. Robust estimates of global and regional estimates of CO_2 sequestration by seagrass meadows require reliable estimates of the area they cover. Moreover, seagrass cover is a dynamic property, as meadows are declining worldwide (Orth et al., 2006; Waycott et al., 2009). Hence, global estimates need also be revised regularly to account for losses and, where present, gains.
2. A more comprehensive investigation of carbon stocks and burial rates over different time scales, including estimates of the thickness of sediments deposits under extant seagrass meadows. Current estimates of carbon stocks and burial rates in seagrass sediments are remarkably few, representing an insufficient basis to estimate carbon stocks accumulated in seagrass sediments.
3. Elucidation of the fate of the carbon exported from seagrass meadows. About 50%–70% of the net community production of seagrass meadows is exported and could be buried elsewhere, as suggested recently (Kennedy et al., 2010). Assessing burial rates of seagrass-derived carbon in sediments with distance from seagrass beds will help resolve the size of the footprint of seagrass burial, since existing evidence indicates that seagrass carbon can be found buried in sediments at least tens of meters away from seagrass meadows (Kennedy et al., 2010). Hence, assessing carbon pools in seagrass sediments alone underestimates the carbon sink capacity of seagrass meadows. Resolving the footprint of seagrass meadows for carbon sequestration is essential to ensure the accountability of carbon removal by seagrass meadows in mitigation strategies based on conservation and restoration of seagrass meadows.
4. Identification of the factors responsible for variability in seagrass carbon sink capacity. Seagrass meadows range greatly, over an order of magnitude in their capacity to act as carbon sinks (e.g. Duarte et al., 2010). Whereas this variability is partially associated with changes in the biomass and species composition of the meadows (Duarte et al., 2010), models to predict the carbon sink capacity of seagrass meadows are still lacking. Yet, understanding of the factors controlling the carbon sink capacity of seagrass meadows will be fundamental to underpin the development of sound management strategies to maximise carbon sink capacity by, for instance, giving priority to the conservation of meadows with high carbon sink potential or managing the environment to maximise carbon removal by seagrass meadows.
5. Improved models to identify suitable areas for seagrass growth. Mitigation strategies based on seagrass carbon sinks include efforts to conserve seagrass meadows and efforts to restore seagrass meadows. The success of seagrass restoration projects depends critically on the choice of adequate sites to support seagrass growth. However, guidelines on the environmental requirements conducive to successful restoration efforts are still lacking. The light requirements to support seagrass growth have been sufficiently documented as to allow delineation of areas receiving adequate light to support seagrass growth (e.g. Gattuso et al., 2006). However, more comprehensive guidelines are needed, including consideration of adequate sediment characteristics and dynamics (e.g. Cabaço et al., 2008), wave and energy environment and even biotic requirements to support adequate seagrass growth.
6. Assessments of the impacts of seagrass loss on the fate of the carbon deposits stored by the seagrass meadow. The accelerated decline of seagrass meadows represents a loss of carbon sink capacity and is, therefore, an issue of concern. However, seagrass meadows also protect, by dissipating wave energy and reducing resuspension the massive sedimentary stocks of organic carbon accumulated over time. Current understanding of the functioning of seagrass meadows suggest that the loss of seagrass cover may, therefore, render the associated sedimentary carbon deposits vulnerable to be lost through erosive and resuspension processes. If seagrass decline rendered sedimentary carbon stocks vulnerable conservation strategies

would be even more needed, since the consequences for carbon cycling will not be limited to the loss of carbon sink capacity but may include the remobilisation and eventual emission as CO₂ of carbon stocks accumulated over millennia. However, the fate of sedimentary carbon stocks following seagrass loss is as yet unknown, and resolving this unknown is, therefore, a matter of urgency.

6. Future strategies

The uncertainties listed above need be articulated into a research agenda conducive to a robust understanding of seagrass carbon burial to underpin climate change mitigation programs based on the conservation and restoration of seagrass meadows. These programs also require the development of reliable protocols for the cost-effective measurement of carbon sequestration ensuring the accountability of the carbon sequestered by seagrass meadows.

Whereas the benefits of conservation programs to preserve the carbon sink capacity of seagrass meadows can be readily evaluated, those of seagrass restoration programs involve greater uncertainties. Seagrass restoration programs are costly and have typically shown limited success at the time scales at which they have tested, typically two to four years. However, models show that the clonal nature of seagrasses leads to an exponential growth (Sintes et al., 2005, 2006), where seedlings or patches containing a few shoots may grow after a few decades to millions of shoots extending over significant areas, as documented in some field studies (e.g. Duarte and Sand-Jensen 1990). The explosive clonal growth of seagrasses offers a distinct advantage relative to reforestation projects on land, as the larger initial planting costs may be offset by the explosive clonal growth coupled with the distinct carbon sink intensity of seagrass meadows. There is, therefore, a need to develop and validate models to predict the cumulative carbon sink associated with seagrass restoration projects and to evaluate their cost efficiency.

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