Chapter 4
Seagrass Meadows

Seagrass meadows are intertidal and shallow subtidal habitats composed of up to 76 species of marine angiosperms and are important components of global estuarine and coastal ecosystems in boreal, temperate and tropical latitudes. Found on all continents except Antarctica, seagrasses provide habitat, protection and nursery grounds for economically valuable fishery species, act as indicators of and modify local water quality and form close links between benthic and pelagic food chains, and nutrient and carbon cycles (Jackson et al. 2001; Mateo et al. 2006; Unsworth et al. 2014). They have a high level of connectivity with mangroves and coral reefs (Unsworth et al. 2008) and are important habitats for food security and human well-being (Cullen-Unsworth et al. 2014).

Seagrasses are among the most productive primary producers in the sea and, like mangroves and salt marshes, have strong trophic links to the coastal ocean (Holmer 2009). Roughly half of their primary productivity is contributed by the seagrasses themselves with the other half coming from associated epiphytes and macroalgae. In tropical areas where seagrass species diversity (up to 12 species) is greater than in higher latitudes, dugong, sea turtles and parrotfish directly feed on these angiosperms. Many tropical seagrass species are highly productive to the extent that they can provide most of the fixed carbon for some coastal regions.

A large fraction of this fixed carbon is not consumed by herbivores, and seagrass tissue is relatively refractory and decomposes slowly. A significant fraction of seagrass production occurs below-ground as roots and rhizomes where this material can be preserved over long time scales (Duarte et al. 2005). Seagrass meadows are net autotrophic, acting as net CO_2 sinks. Until recently, the role of seagrasses in storing carbon has been ignored.

Like salt marshes and mangroves, seagrass meadows are highly dynamic in time and space with large changes taking place over short intervals. Physical disturbance, herbivory, intraspecific competition, nutrients, pollution and deposition of fine particles all play key roles in influencing seagrass biomass, species composition and area. A number of factors will determine if seagrasses will occur in any given area, including natural biophysical drivers that regulate physiological activity

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and morphology, such as light availability, temperature, water clarity, salinity, wave action, currents, depth, substrate, day length, nutrients, epiphytes and diseases. Also, the availability of seeds and vegetative fragments and anthropogenic inputs, such as sediment loading and excess nutrients may be important determinants in seagrass existence.

Widespread losses of seagrass have occurred globally, and about 24% of all species are at risk of extinction or are now classified as near threatened on the IUCN's Red List (Waycott et al. 2009; Short et al. 2011). The rate of seagrass decline has increased over the past 70 years, from 0.9% per year prior to 1940 to 7% per year since 1980. Direct impacts such as removal of seagrass during dredging cause immediate loss, but a large number of indirect impacts cause much of the permanent and chronic damage to seagrass meadows. These include overfishing, long-term nutrient pollution and climate change.

Few metabolic studies have been conducted in the Southern Hemisphere to investigate whether or not seagrass meadows have potential as carbon sinks (Duarte et al. 2010), but the few studies available indicate that they have large storage capacity (Duarte et al. 2011) and can form the basis for climate change mitigation strategies. Seagrass meadows function to trap and bind sediment by trapping suspended particles from currents and hereby help to clarify the overlying water column. The root and rhizomes stabilise the sediments and help prevent coastal erosion during storms, heavy rains and floods. Seagrass detritus is not only an important trophic link, but accumulates to become an important carbon sink.

4.1 Fluid Dynamics: The Mechanism for Sediment and Carbon Accumulation

Seagrasses, like their salt marsh and mangrove counterparts, are ecosystem engineers capable by their very existence of reducing the velocity of currents and attenuating waves to the extent that sediment particles can deposit on their surfaces and on the seabed. Other factors play important roles in helping to accumulate carbon, such as canopy complexity, turbidity, wave height and water depth (Samper-Villarreal et al. 2016). But the essence of what drives the accumulation of sediment particles and associated carbon is fluid dynamics. The movement of water among, between and around seagrass blades is the key feature of carbon capture (Koch et al. 2006).

The main source of energy required to move water is the sun which causes winds that lead to waves and thermal gradients that lead to expansion, mixing and instabilities in water gradients and thus flow. Seawater, being an incompressible fluid, moves at a flow rate (Q) which is defined by the velocity (u) of the fluid that passes through a cross-sectional area, A. Water flow leads to both hydrostatic and dynamic pressures which are a constant. What this means in practical terms is that the sum of the pressures helps to explain lift that occurs within, around and under seagrass canopies. Drag is another force that operates in the case of water motion and has two components, (1) viscous drag (F_{d}) that exists due to the interaction of the seagrass surface with the water and defined as

$$F_{\mathrm{d}} = 1/2C_{\mathrm{d}}\rho\mathrm{Au}^2 \tag{4.1}$$

where C_{d} is the drag coefficient and ρ is the hydrostatic pressure and (2) the dynamic or pressure drag (F_{p}) that exists under high flows when flows separate from boundaries.

Water flow can be either smooth and regular (laminar flow) or rough and irregular (turbulent flow), depending on the velocity and temporal and spatial scale under investigation as defined by the Reynolds number:

$$R_e = lu/v \tag{4.2}$$

where l is the length scale under observation and v is the kinematic viscosity. R_e defines four flow regimes that may occur: (1) creeping flow where $R_e << 1$ which occurs at very slow flows and spatial scales such as those experienced by microbes, (2) laminar flow ($1 < R_e < 10^3$) which is smooth and regular, (3) transitional flow ($R_e \approx 10^3$) which involves the production of eddies and disturbances in the flow and (4) fully turbulent flow ($R_e >> 3$). These flows are scale-dependent; flow is almost always turbulent across entire seagrass meadows but laminar at the scale of individual seagrass leaves.

Flow conditions become more complex when water approaches a boundary such as the seagrass canopy or seafloor. Water cannot penetrate such boundaries but slips by it, a condition which leads to the development of a velocity gradient perpendicular to the boundary as the velocity at the boundary will be zero relative to the stream velocity (U_0). As water flows downstream, the velocity gradient will get larger and a slower moving layer of water will develop next to the boundary. Vertically, there is a sublayer in which the forces are largely viscous. Consequently, the mass transfer in this layer is slow, dominated by diffusion, which is called a diffusive boundary layer. Such boundary layers can become embedded within one another such that it is possible to define boundary conditions around blade epiphytes, flowers, leaves and the canopy.

At the molecular level, a boundary layer develops on the sediment surface as well as on each leaf, shoot or flower as water flows through a seagrass meadow. The faster the water movement, the thinner the diffusive boundary layer, and thus the transfer of molecules (e.g. CO_2) is faster from the boundary layer to the water column. When currents are weak, the flux of molecules may be diffusion-limited, but after a critical velocity (U_k) is reached, the transfer is no longer limited by diffusion but by the rate of assimilation capacity (i.e. biological or biochemical activity). The mass transfer of molecules also depends on other factors such as the thickness of the periphyton layer on the seagrass leaves, reactions within the periphyton layer and the concentration of molecules in the water adjacent to the leaf-periphyton assemblage.

At the scale of shoots (mm to cm), a feedback mechanism operates as individual shoots are affected by the other shoots and its position within the entire canopy (i.e. edge versus centre of the entire meadow). As water velocity increases, shoots bend which minimises drag, but the forces exerted on individual shoots are more complex when waves are involved as a shoot is exposed to unsteady flows in different directions. This is confirmed by the fact that in wave-swept environments, seagrass leaves become longer as wave exposure increases (de Boer 2007). Flow around shoots results in bending but also pressure gradients on the leeward side of the leaf such that a vertical ascending flow is generated downstream of the shoot. This water then disperses horizontally at the point where the leaves bend over with the flow. Interstitial water is also flushed out at the base of the shoot due to the pressure gradients generated on the sediment surface.

At the whole-canopy level, reduced flows occur within the canopy due to the deflection of the current over the canopy and a loss of momentum within the canopy (van Katwijk et al. 2010). Water speed as a result can be 2 to >10 times slower than outside the meadow. It is this process that allows water and sediment particles to be trapped during low tide; even short seagrass canopies can still reduce water velocity (e.g. *Zostera novazelandica*; Heiss et al. 2000). Vertically, however, water flow intensifies at the height of the sheath or stem as these parts are much less effective at reducing water velocity compared with the leaf component. Canopy flow is nevertheless complex because it is a function of the drag or resistance of the leaves on the water.

Seagrass canopies are overall areas where sediments deposit and carbon accumulates largely due to the reduction in velocity and intensity of turbulence, that is, a reduction in flow strength that leads to a reduction in resuspension within the canopy (de Boer 2007). Although few data (Gacia et al. 2003) exist for empirical measurements of sediment deposition in seagrasses, Duarte et al. (2013a, b) estimate a mean rate of 0.2 ± 0.04 cm year^{-1}. Accumulation may be seasonal, especially during summer when seagrasses are at their maximum density and in winter then resuspension may be greater than accumulation when seagrasses are minimal, although roots and rhizomes may alone be sufficient to stabilise the accumulated deposits (Bos et al. 2007). Epiphytes on seagrass leaves may foster the accumulation of sediment particles by increasing the roughness of the canopy and increasing the thickness of the boundary layer on the leaf surface. However, in highly wave-exposed locations, seagrasses may not accumulate fine sediments due to resuspension. Indeed, in some cases, sediment may be coarser beneath seagrass patches as a result of turbulence generated by the leaves themselves.

4.2 Carbon Sequestration

Rates of carbon sequestration in seagrass meadows ($n = 396$) average 220.7 ± 20.1 g C_{org} m^{-2} year^{-1} (±1 SE) and a median of 167.4 g C_{org} m^{-2} year^{-1} with values ranging from −2094 to 2124 g C_{org} m^{-2} year^{-1} (Table 4.1). As there

Table 4.1 Estimates of annual carbon sequestration rates (g C_{org} m^{-2} $year^{-1}$) in seagrass meadows worldwide. Duarte et al. (2010) were the source for most of these data in addition to those listed below

Location$^{\text{source}}$	Number of observations	Range	Mean
Florida[a]	117	−272 to 1371	71.0
Spain[b]	61	−323 to 620	781.5
Texas[c]	49	−1282 to 1713	−58.4
France[d]	25	−918 to 2335	284.7
Australia[e]	24	−402 to 629	148.8
Denmark[f]	23	−494 to 813	3.0
Mexico[g]	21	−2094 to 1147	233.1
Chesapeake Bay[h]	20	−337 to 1696	377.0
Alabama[i]	14	−475 to 1462	502.3
Indonesia[j]	12	−1434 to 77	−578.5
Greece[k]	6	119–280	172.8
Japan[l]	6	1.8–10.1	5.0
Philippines[m]	4	−34 to 615	213.2
New England[n]	4	−27 to 41	0.7
North Carolina[o]	3	10–66	33.9
The Bahamas[p]	3	731–972	835.9
Norway[q]	2	−0.5 to 44	21.6
Puerto Rico[r]	2	686–2057	1371.0
Portugal[s]	2	276.5–403.2	339.8
Malta[t]	2	133–249	191.0
India[u]	1		2124.2
South Africa[v]	1		365.8
Wadden Sea[w]	1		33.0
The Netherlands[x]	1		51.1
Padilla Bay, Washington[y]	1		−54.9
Corsica[z]	1		41.3
Mauritania[aa]	1		2068.3

(continued)

Table 4.1 (continued)

Location^{source}	Number of observations	Range	Mean
Panama[ab]	1		374.7
Italy[ac]	1		153.3

[a]Sources: Odum (1956), Kenworthy and Thayer (1984), Cebrian (2002), Barrón et al. (2004), Martin et al. (2005), Calleja et al. (2006), Stutes et al. (2007), Herbert and Fourqurean (2008), Yarbro and Carlson (2008), and Long et al. (2015)
[b]Sources: Romero et al. (1994), Mateo et al. (1997), Cebrian et al. (2000), Cebrian (2002), Barrón et al. (2004), Holmer et al. (2004), Gazeau et al. (2005), Vaquer-Sunyer et al. (2012), and Hendriks et al. (2014)
[c]Sources: Odum (1962, 1963) and Ziegler and Benner (1999)
[d]Sources: Frankingnoulle and Bouqueneau (1987), Viaroli et al. (1996), Mateo et al. (1997), Welsh et al. (2000); Desious-Paoli et al. (2001), Ouisse et al. (2014), Cox et al. (2016), Delgard et al. (2016), and Olive et al. (2016)
[e]Sources: Moriarty et al. (1990), Eyre and Ferguson (2002), Adams et al. (2016), Rozaimi et al. (2016), and Serrano et al. (2016)
[f]Source: Risgaard-Petersen and Ottosen (2000)
[g]Source: Reyes and Merino (1991)
[h]Sources: Murray and Wetzel (1987), Caffrey (2004), Lee-Nagel (2007), and Rheuban et al. (2014)
[i]Source: Anton et al. (2009)
[j]Source: Erftemeijer et al. (1993)
[k]Source: Apostolaki et al. (2010)
[l]Source: Apostolaki et al. (2014)
[m]Source: Miyajima et al. (2015)
[n]Source: Gacia et al. (2005)
[o]Sources: Caffrey (2004) and Howarth et al. (2014)
[p]Source: Kenworthy and Thayer (1984) and Cebrian (2002)
[q]Source: Koch and Madden (2001)
[r]Source: Duarte et al. (2002)
[s]Source: Odum (1959)
[t]Sources: Alexandre et al. (2012) and Bahlmann et al. (2015)
[u]Source: Serrano et al. (2016)
[v]Source: Qasim and Bhattathiri (1971)
[w]Source: Baird and Ulanowicz (1993)
[x]Source: Asmus et al. (2000)
[y]Source: Pellikaan and Nieuhuis (1988)
[z]Source: Caffrey 2004 and Caffrey et al. (2014)
[aa]Source: Champenois and Borges (2012)
[ab]Source: Clavier et al. (2014)
[ac]Source: López-Caldeŕon et al. (2013)

are comparatively few sequestration rates derived from dating using radionuclides (Romero et al. 1994; Mateo et al. 1997; Miyajima et al. 2015; Rozaimi et al. 2016), most of these numbers were derived from metabolic measurements of annual primary production and community respiration to determine the amount of carbon available for storage (Cebrian 2002, Duarte et al. 2010, 2013a, b). Like salt marshes and mangroves, there is no clear relationship with latitude as many of the most luxuriant seagrass meadows are composed of *Posidonia oceanica* in the Mediterranean. The data are skewed towards seagrasses of Florida, Spain and Texas, but there are seagrass beds at nearly all locations that show net heterotrophy (those with negative values in Table 4.1), that is, more loss of carbon via respiration than fixed by the plants. Unlike the data for salt marshes and mangroves, nearly all of the seagrass data were derived from metabolic studies rather than from empirical measurements of actual carbon storage; thus these data do not necessarily account for possible export of 'excess' carbon fixed by the plants nor possible import of carbon from adjacent ecosystems, such as mangroves, salt marshes, coral reefs, rivers or oceanic inputs. Nevertheless, on average, seagrass meadows store carbon although apparently less than salt marshes and mangroves. This conclusion was also reached for tropical Indo-Pacific seagrasses, with an estimated average net sink of 155 g C_{org} m^{-2} $year^{-1}$ (Unsworth et al. 2012).

The sequestration of seagrass carbon is likely to be underestimated as seagrasses export a substantial portion of their primary production, both in particulate and dissolved form. Available evidence indicates that the export of seagrass carbon represents a significant contribution for carbon sequestration in sediments outside seagrass meadows and in the deep sea (Duarte and Krause-Jensen 2017).

The effects of physical disturbance on carbon sequestration capacity of seagrasses has recently been experimentally determined by Dahl et al. (2016). In a series of field experiments testing the impact of shading and simulated grazing, they found that treatments of high-intensity shading and high-intensity clipping to simulate grazing show significantly lower net community production and carbon content in belowground biomass than in control plots. This latter effect was caused by erosion of the surface sediment due to the removal of above-ground biomass. Their findings indicate that high-intensity disturbances reduce the ability of seagrass meadows to sequester carbon.

Seagrasses, unlike their marsh and mangrove counterparts, can clearly modify seawater pH to the extent that this phenomenon may have some bearing on their ability to withstand ocean acidification. Near a natural volcanic vent off the Italian coast, Apostolaki et al. (2014) found that at high CO_2 levels in close proximity to the vent, seagrasses have high rates of primary productivity but less biomass possibly due to greater grazing, nutrient limitation or poor environmental conditions. A similar result was found in relation to a CO_2 vent in Papua New Guinea (Russell et al. 2013). Thus, seagrass responses to ocean acidification may be complex rather than a simple overall positive or negative reaction. The capacity of seagrasses to modify their ambient pH may have implications for nearby coral reefs as the presence of seagrasses results in a net increase in pH possibly ameliorating the impacts of acidification (Unsworth et al. 2012).

The net increase in pH suggests a positive trend between seagrass productivity and carbonate deposition. Indeed, a study of particulate inorganic carbon (PIC, mostly $CaCO_3$) in seagrasses has shown that PIC stocks in the top 1 m of sediment average 654 Mg PIC ha^{-1} exceeding POC (particulate organic carbon) stocks by a factor of 5 (Mazarrasa et al. 2015). Meadows dominated by *Halodule*, *Thalassia* or *Cymodocea* support the highest PIC stocks which decrease polewards by 8 Mg PIC ha^{-1} per degree of latitude. Using PIC sediment stocks and estimates of sediment accretion, Mazarrasa et al. (2015) estimated a mean PIC accumulation rate of 126.3 g PIC m^{-2} $year^{-1}$ or roughly one-half of the estimated rate of organic carbon sequestration (Table 4.1). Further, based on the global extent of seagrasses (177,000 to 600,000 km^2), seagrasses globally store between 11 and 39 Pg PIC in the top metre of sediment and accumulate between 22 and 75 Tg PIC $year^{-1}$. This range of values suggests a significant contribution to coastal carbonate carbon sequestration by seagrasses (Gullström et al. 2018; Howard et al. 2018). High rates of carbonate accumulation imply CO_2 emissions from precipitation, but the POC and PIC stocks between vegetated and un-vegetated sediments demonstrate that seagrass meadows are strong overall CO_2 sinks.

4.3 Carbon Stocks

Published and unpublished measurements of the organic carbon content of living seagrass biomass and underlying soils were compiled recently by Fourqurean et al. (2012a, b) based on data from seagrass meadows across the globe. The results show a wide spread of data of soil organic carbon storage (Fig. 4.1) with most observations being <100 Mg C_{org} ha^{-1} from short (<1 m) cores, but much higher carbon inventories from cores taken to at least 1 m depth. Overall, a median value of 69.3 Mg C_{org} ha^{-1} was derived. Median above- and below-ground biomass were 0.264 and 0.540 Mg C_{org} ha^{-1}, respectively, underscoring that nearly all seagrass organic carbon is stored in soil.

Geographically, it is difficult to discern true trends or patterns in the data owing to the scarcity of data from many parts of the globe. Nevertheless, it is clear that meadows of the Mediterranean seagrass *Posidonia oceanica* have the highest average soil storage (372.4 Mg C_{org} ha^{-1}). The median soil C_{org} stock value is about equal to the average for terrestrial soils, but about one-fourth of the median for salt marsh soils and one-tenth that of the median for mangrove soils.

Using estimates of global seagrass area of between 300,000 and 600,000 km^2 and multiplying by the median soil C_{org} value, we derive a range of global C_{org} values of between 2.1 and 4.2 Pg C_{org} for soils and between 75.5 and 151 Tg C_{org} for biomass. If we assume that the 1 m soil data is the most complete inventory, the soil C_{org} stock rises to between 5.8 and 9.8 Pg C_{org}. As with salt marshes and mangroves, soil C_{org} stocks can be much greater in systems where unconsolidated soils accumulate to depths greater than 1 m, such as in *Posidonia oceanica* meadows where 11 m thick deposits have been found. Of course, meadows growing on coarse carbonates may

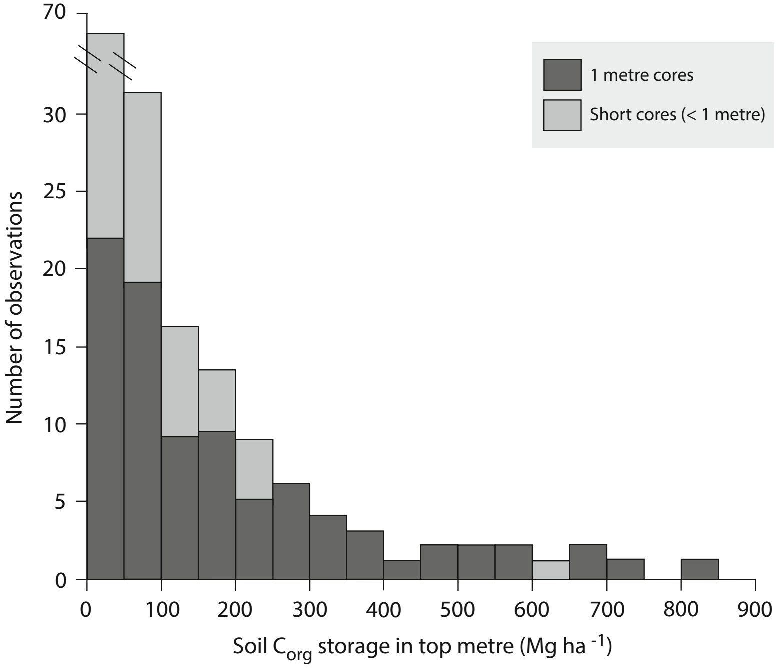

Fig. 4.1 Estimates of soil C_{org} stored in the world's seagrass meadows. Updated from Fourqurean et al. (2012a) using data from Lavery et al. (2013), Campbell et al. (2015), Miyajima et al. (2015), Phang et al. (2015), Alongi et al. (2016), Rozaimi et al. (2016) and Serrano et al. (2016). Bars without shading indicate estimates made based on shallow (<1 m) sediment cores, and black shading indicates estimates based on 1 m length cores

have fairly shallow deposits of less than a metre with correspondingly small C_{org} but large carbonate carbon inventories (Campbell et al. 2015).

Carbon storage in seagrass soils is a reflection of long-term nutrient history. In a comparison of long-term nutrient history versus short-term nutrient enrichment, Armitage and Fourqurean (2016) found that in sites undergoing 17 months of nutrient additions, biomass carbon both above- and below-ground increase but soil carbon content decrease by about 10% in response to phosphorous addition. There is also less than 3% organic carbon in soil when seagrass leaf N:P exceeds a threshold of 75:1 or when below-ground seagrass carbon stock is less than 100 g m^{-2} in the experimental plots and within a naturally occurring long-term gradient of phosphorus availability. Their results show that even under nutrient-limited conditions, seagrass beds have very high potential for carbon storage.

Black carbon may, in some instances, lead to an overestimation of carbon stocks. Chew and Gallagher (2018) found that failure to subtract allochthonous recalcitrant carbon (black carbon) formed outside the ecosystem overvalues the storage of organic carbon. They estimate that current carbon stock estimates are positively biased, particularly for low organic seagrass environments, by 18% for temperate regions and 43% for tropical regions. Obviously, more estimates of black carbon need to be made in order to more accurately assess seagrass blue carbon stocks.

4.4 Potential Losses

Assuming an annual rate of loss of 7% (Waycott et al. 2009) and global area estimates of 300,000 to 600,000 km^2 (Fourqurean et al. 2012), seagrass decline returns to either the atmosphere or to the adjacent coastal ocean (or both) from 0.54 to 1.08 Pg CO_2 equivalents annually. This range is greater than that for salt marshes (0.02–0.24 Pg CO_2 equivalents) and mangroves (0.27–0.59 Pg CO_2 equivalents) and equal to about one-quarter of the average annual deforestation rate of 4.61 Pg CO_2 equivalents.

If all seagrass was destroyed, 7.7 to 15.4 Pg CO_2 equivalents would be lost which is nearly twice to more than three times greater than the annual average rate of deforestation across the globe. Obviously, the loss of seagrass is an ecological catastrophe in terms of species and ecosystem services being lost and carbon that is being either returned to the atmosphere or coastal ocean. Management emphasis is urgently needed to stem the high rates of seagrass lost annually and to conserve and restore presently declining meadows.

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