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A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂

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Recent research has highlighted the valuable role that coastal and marine ecosystems play in sequestering carbon dioxide (CO_2) . The carbon (C) sequestered in vegetated coastal ecosystems, specifically mangrove forests, seagrass beds, and salt marshes, has been termed "blue carbon". Although their global area is one to two orders of magnitude smaller than that of terrestrial forests, the contribution of vegetated coastal habitats per unit area to long-term C sequestration is much greater, in part because of their efficiency in trapping suspended matter and associated organic C during tidal inundation. Despite the value of mangrove forests, seagrass beds, and salt marshes in sequestering C, and the other goods and services they provide, these systems are being lost at critical rates and action is urgently needed to prevent further degradation and loss. Recognition of the C sequestration value of vegetated coastal ecosystems provides a strong argument for their protection and restoration; however, it is necessary to improve scientific understanding of the underlying mechanisms that control C sequestration in these ecosystems. Here, we identify key areas of uncertainty and specific actions needed to address them.

Front Ecol Environ 2011; 9(10): 552–560, doi:10.1890/110004 (published online 20 Jun 2011)

The global average atmospheric carbon dioxide (CO_2) concentration rose to 387 parts per million (ppm) in December 2009 (ESRL/NOAA 2009), the highest level it has reached over the past 800 000 years (Lüthi *et al.* 2008)

In a nutshell:

- Despite their relatively small global extent, vegetated coastal ecosystems (mangrove forests, seagrass beds, salt marshes) are disproportionately important in sequestering carbon dioxide when compared with terrestrial ecosystems
- Although the importance of vegetated coastal ecosystems as natural sinks is partly due to their high primary productivity, a key mechanism is their efficiency in trapping sediments and associated carbon from outside their ecosystem boundaries
- These "blue carbon" sinks are being lost at critical rates and action is urgently required to prevent further degradation and loss
- Improved scientific understanding of the factors that influence carbon sequestration in these ecosystems is needed to identify sites that are high priorities for restoration and/or conservation management

¹The Nature Conservancy, Honolulu, HI ^{*}(emcleod@tnc.org); ²Department of Geography and Centre for Climate and Global Change Research, McGill University, Montreal, Canada; ³Department of Earth and Environmental Sciences, Katholieke Universiteit Leuwen, Leuven, Belgium; ⁴Botany Department, Stockholm University, Stockholm, Sweden; ⁵Global Change Research Department, IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, Esporles, Spain; ⁶The UWA Oceans Institute, University of Western Australia, Perth, Australia; ⁷School of Biological Sciences, The University of Queensland, St Lucia, Australia; ⁸Cary Institute of Ecosystem Studies, Millbrook, NY; ⁹Department of Biology, University of Florida, Gainesville, FL and more than 38% above the pre-industrial value of roughly 280 ppm (Raupach and Canadell 2008). There is a broad consensus among the scientific community that this increase in CO_2 is driven primarily by the burning of fossil fuels and changes in land use (Solomon et al. 2007). Landuse change results in CO₂ emissions through clearance of natural vegetation, forest fires, and agricultural activities, as well as through the deterioration of ecosystems that serve as natural carbon (C) sinks (Solomon et al. 2007). The Intergovernmental Panel on Climate Change estimates that, by the year 2050, global CO₂ emissions must be reduced by 85% from levels seen in 2000 to prevent a global mean temperature increase of 2°C (IPCC 2007). This calculation assumes that the reduction in emissions is the only mechanism by which we can reduce CO_2 concentrations. A more recent approach suggests refocusing efforts from a single emissions reduction strategy to a plan that combines reducing anthropogenic sources of CO_2 (mitigation) with supporting CO₂ uptake and storage through the conservation of natural ecosystems with high C sequestration rates and capacity (Canadell and Raupach 2008). However, the net C sink provided by an ecosystem will not mitigate anthropogenic emissions of CO_2 unless its C sequestration rate increases over time (eg through an increase in areal extent or increased primary productivity). Ecosystems can shift from being a net sink of C to a source of C as a result of changes in climate (eg changes in precipitation and temperature), atmospheric composition effects (eg CO₂ fertilization, nutrient deposition, damage by pollution), and land-use-change effects (eg deforestation, afforestation, agricultural practices; IPCC 2007). Therefore, while efforts to conserve and restore natural sinks will help to

reduce the impacts of increases in anthropogenic CO_2 emissions, they should not be viewed as a replacement for emissions reduction strategies.

Human activities and interactions among the major C pools will determine the rate of future increases in atmospheric CO_2 concentration. The major global C pools include the atmosphere, oceans, fossil fuels, and - collectively - vegetation, soils, and detritus (Figure 1: Sarmiento and Gruber 2002; IPCC 2007). The oceans are the largest C pool, encompassing an estimated 38 000 gigatons of C (Gt C). The geological C pool, composed primarily of fossil fuels, is the next largest pool, estimated at nearly 4000 Gt C. Vegetation, soils, and detritus hold around 2000 Gt C. followed by the atmosphere, which holds about 760 Gt C (IPCC 2007). It is not clear whether the C sequestered by vegetated coastal ecosystems (eg mangroves, salt marshes, seagrasses) is included in these estimates.

Research on natural C sinks has focused predominantly on either ocean ecosystems (Sabine et al. 2004) or terrestrial forest ecosystems (IPCC 1999). The oceans have absorbed about one-third of anthropogenic CO₂ emissions through physical, chemical, and biological processes. The oceans' role as a sink for CO_2 is driven by two processes: the solubility pump and the biological pump. The solubility pump is a function of differential CO₂ solubility in seawater and the thermal stratification of the ocean. Cold, deep waters are generally rich in dissolved inorganic C because the solubility of CO_2 increases in cold water. When deep water upwells into warmer equatorial regions, there is extensive outgassing of CO_2 to the atmosphere resulting from the reduced solubility of the gas. The biological C pump refers to the uptake of CO_2 by marine plankton from the surface waters through photosynthesis; as a result of this process, a small fraction of the biomass produced is transferred to the deep ocean and buried in sediments. In terrestrial ecosystems, C is sequestered in vegetation and soils (Houghton et al. 1999). Terrestrial plants capture CO_2 from the atmosphere, and C is converted through photosynthesis and stored in plant biomass and in soils. Carbon is returned to the atmosphere as CO_2 or methane under anaerobic conditions through respiration (including decomposition of dead biomass; IPCC 2007). Terrestrial ecosystems are subject to saturation of soil C storage, and the longevity of the above- and belowground C sink is uncertain (Schlesinger and Lichter 2001).

The terrestrial C sink often is quantified as the difference between fossil-fuel and land-use emissions and the sum of the uptake by the oceans and accumulation in the atmosphere. However, major uncertainties exist in estimates of average net C uptake for terrestrial ecosystems (Sarmiento and Gruber 2002). Given the methodological



Figure 1. A simplified diagram of the global C cycle, showing major C pools (gigatons [Gt] C) and fluxes (data from IPCC 2007).

approaches used to quantify terrestrial and oceanic C sinks, vegetated coastal ecosystems are not explicitly included in estimates of either of these C sinks, creating a gap in global extrapolations. Such a gap has also been proposed for the possible role of freshwater ecosystems in the global C budget (Aufdenkampe *et al.* 2011). The losses of vegetated coastal ecosystems (eg as a result of land-use change) need to be taken into account when estimating C sources and sinks in these ecosystems.

Although the critical role that vegetated coastal ecosystems play in C sequestration has been largely overlooked, recent reports have highlighted the natural capacity of these ecosystems in sequestering C, and this has catalyzed research among academic institutions and conservation organizations (Laffoley and Grimsditch 2009; Nellemann et al. 2009). This new recognition of "blue carbon" (Nellemann et al. 2009) is based primarily on research demonstrating that seagrass meadows, mangrove forests, and tidal salt marshes are highly efficient C sinks (Chmura et al. 2003; Duarte et al. 2005a; Bouillon et al. 2008; Lo Iacono et al. 2008; Duarte et al. 2010; Kennedy et al. 2010). Building on these recent ecosystem-specific reviews, we synthesize current evidence regarding the C sequestration potential of these ecosystems and re-evaluate their potential role in comparison to terrestrial forest types. We also identify the main uncertainties that must be addressed to strengthen the science underpinning this important area of research.

Blue carbon sinks

Coastal ecosystems dominated by plants – such as mangroves, salt marshes, and seagrasses – play a critical role in the global sequestration of C that would otherwise



Figure 2. Mangrove forest (Rhizophora mucronata in the background; pneumatophores of Avicennia marina in the foreground) in Gazi, Kenya. Complex root systems slow down tidal waters and trap carbon-rich particles from the water column and store them in sediment.

remain as atmospheric CO_2 and exacerbate climate change (Chmura *et al.* 2003; Duarte *et al.* 2005a; Bouillon *et al.* 2008; Laffoley and Grimsditch 2009; Nellemann *et al.* 2009; Duarte *et al.* 2010; Kennedy *et al.* 2010). These ecosystems sequester C within their underlying sediments, within living biomass aboveground (leaves, stems, branches) and belowground (roots), and within non-living biomass (eg litter and dead wood). Blue carbon is sequestered over the short term (decennial) in biomass and over longer (millennial) time scales in sediments (Duarte *et al.* 2005a; Lo Iacono *et al.* 2008).

Unlike terrestrial soils, the sediments in which healthy



Figure 3. Shallow seagrass meadow (Cymodocea serrulata) in Zanzibar, Tanzania. Roots and rhizomes trap and store sediments and associated organic carbon.

mangroves, salt marshes, and seagrass meadows grow do not become saturated with C because sediments accrete vertically in response to rising sea level, assuming ecosystem health is maintained (eg McKee et al. 2007). The rate of sediment C sequestration and the size of the sediment C sink may therefore continue to increase over time (Chmura et al. 2003). For example, at the extreme end, the seagrass (Posidonia oceanica) meadows in Portlligat Bay, Spain, and mangrove (Rhizophora mangle) systems in Belize have accreted C-rich deposits >10 m thick and are over 6000 years old (McKee et al. 2007; Lo Iacono et al. 2008). The longevity of blue carbon sinks is impressive when compared with rainforests, which are reported to sequester C for decades or centuries at most (Chambers et al. 2001).

The structural complexity of vegetated coastal ecosystems (root systems, dense vegetation, leafy canopy in seagrass systems; Figures 2–4) predisposes salt marshes, man-

grove forests, and seagrass beds to be highly efficient in trapping sediment and associated organic C originating from internal and external riverine and oceanic sources ("laterally imported C"). Because vegetated coastal ecosystems can sequester C from both internal and external sources, they represent a C sink for a larger area. Several studies based on stable C-isotope signatures in sediments have demonstrated the importance of the importation and burial of organic C from outside the ecosystem boundaries. An estimated 50% of C sequestered in seagrass meadow sediments is thought to be of external origin (Kennedy *et al.* 2010), and for man-

groves and salt marshes, cross-system data compilations indicate a full spectrum of situations, from dominance of locally produced C burial to dominance of laterally imported C sources, depending on, for example, tidal range (Middelburg *et al.* 1997; Bouillon *et al.* 2003). Furthermore, given that part of the C fixed by the dominant vegetation in these ecosystems may also be exported, the C sequestration rates of vegetated coastal systems may actually be higher than those reported here, if a substantial fraction of that exported C is buried outside the ecosystems' boundaries (see Kennedy *et al.* 2010).

Estimates of long-term C burial in sediments

Estimates of the long-term C burial capacity in blue carbon sinks are highly variable. There are no definitive studies of spatial variability within mangrove forests, salt marshes, or seagrass meadows other than studies addressing C burial differences among different marsh (Craft 2007) and mangrove (Sanders et al. 2010) habitats. Carbon burial rates within a salt marsh or mangrove forest may be affected by variability in hydroperiod, salinity, nutrient status (eg nutrient input from pollution), and suspended sediment supply. Variations in C burial capacity are linked to changes in allocation among plant parts (eg roots versus leaves), decomposition, and primary productivity, which are in turn driven by both physical (eg temperature, precipitation, sea level, nutrients, sediment type) and biological (eg species composition, plant competition, herbivory, bioturbation, trophic cascades) variables.

Salt marsh, mangrove, and seagrass ecosystems all have relatively high rates

of sediment C burial (Table 1). Recent syntheses of C burial by seagrass ecosystems have revised earlier estimates upward by almost 70% (Duarte *et al.* 2010; Kennedy *et al.* 2010). Long-term rates of C accumulation in sediments of all three ecosystems ranged between 18 and 1713 g C m⁻² yr⁻¹ (Table 1). By contrast, long-term rates of C accumulation in soils of temperate, tropical, and boreal forests from chronosequences of 8000–10000 years ranged between 0.7 and 13.1 g C m⁻² yr⁻¹ (Table 2). However, higher rates of C accumulation have been documented after disturbances in terrestrial forests (eg accumulation rates ranged between 21 and 55 g C m⁻² yr⁻¹ in abandoned agricultural soils in temperate forest areas that were allowed to return to native vegetation; Schlesinger 1997).

Although mangroves, seagrass meadows, and salt marshes represent a much smaller area than terrestrial



Figure 4. Salt marsh (Dipper Harbour Marsh) in the Bay of Fundy, New Brunswick, Canada. At low tide, greater than 2 m of marsh peat is clearly visible.

forests (Tables 1 and 2), their total contribution to longterm C sequestration is comparable to C sinks in terrestrial ecosystem types. The total global C burial is estimated at 31–34 teragrams (Tg) C yr⁻¹, 5–87 Tg C yr⁻¹, and 48–112 Tg C yr⁻¹ for mangroves, salt marshes, and seagrass beds, respectively (Table 1). These global C burial rates are comparable to those of terrestrial forest types $(53.0 \text{ Tg C yr}^{-1} \text{ for temperate}, 78.5 \text{ Tg C yr}^{-1} \text{ for tropical},$ and 49.3 Tg C yr^{-1} for boreal forests; Table 2). Despite the smaller aboveground biomass and areal coverage of vegetated coastal ecosystems, they have the potential to contribute substantially to long-term C sequestration resulting from the higher rate of organic C sequestration in sediments (Figure 5). However, global losses of vegetated coastal ecosystems threaten their ability to function as long-term C sinks.

Carbon burial and global area of vegetated coastal ecosystems Carbon burial rate						
Ecosystem	$(g C m^{-2} yr^{-1})$ mean ± SE	Global area (km²)	$(Tg C yr^{-1})$ mean ± SE	Sources		
				Global area	Carbon burial	
Salt marshes	218 ± 24	22 000**-	4.8 ± 0.5	Chmura et al. (2003);	Chmura et al. (2003);	
	(range = 18–1713) n = 96 sites	400 000	87.2 ± 9.6	Duarte et al. (2005a)	Duarte et al. (2005a)	
Mangroves	226 ± 39 (range = 20–949) n = 34 sites	37 760 – 52 36	31.1 ± 5.4 34.4 ± 5.9	Giri et <i>al.</i> (2010); Spalding et <i>al.</i> (2010)	Chmura et <i>al.</i> (2003); Bird et <i>al.</i> (2004); Lovelock et <i>al.</i> (2010); Sanders et <i>al.</i> (2010)	
Seagrasses	38 ± 38 (range = 45–190) n = 123 sites	177 000 – 600 000	48–112	Charpy-Roubaud and Sournia (1990); Green and Short (2003); Duarte et <i>al</i> . (2005b)	Duarte et <i>al.</i> (2005a); Duarte et <i>al.</i> (2010); Kennedy et <i>al.</i> (2010); Duarte (unpublished data)	

Notes: ^{*}We calculated global carbon burial values using the mean carbon burial rate and the minimum and maximum global area values for salt marshes and mangroves. Global carbon burial values for seagrasses are from Kennedy et al. (2010). ^{**}No global inventory of salt marshes has been published, so Chmura et al. (2003) estimated 22 000 km² of salt marshes based on inventories for Canada, Europe, the US, and South Africa. SE = standard error.



Figure 5. Mean long-term rates of C sequestration (g C $m^{-2} yr^{-1}$) in soils in terrestrial forests and sediments in vegetated coastal ecosystems. Error bars indicate maximum rates of accumulation. Note the logarithmic scale of the y axis. Data sources are included in Tables 1 and 2.

Current threats to blue carbon sinks

Recent assessments suggest that about one-third of mangrove, seagrass, and salt marsh areas have already been lost over the past several decades (Table 3) as a result of reclamation, deforestation, engineering and urbanization, transformation to aquaculture ponds (Green and Short 2003; Duarte et al. 2005b; Silliman et al. 2009), and climate change (Woodroffe 1995; Björk et al. 2008). Coastal eutrophication, siltation, and development have led to seagrass decline (Duarte 2002; Green and Short 2003; Duarte et al. 2005b; Waycott et al. 2009), and mangroves and salt marshes have been damaged by dredging, filling, dyking, drainage, trophic cascades, and invasive species (Valiela et al. 2001; Alongi 2002; Silliman et al. 2005; Silliman et al. 2009). Sea-level rise can erode and flood mangroves and salt marshes (Woodroffe 1995; Silliman et al. 2009), and increase water depths above existing seagrass meadows, thereby reducing available light to support photosynthesis (Björk *et al.* 2008). Increased seawater temperatures may also lead to direct losses of seagrass meadows (Marbà and Duarte 2010).

Currently, blue carbon sinks lose between $\sim 0.7-7\%$ of their area annually (Costanza et al. 1997; Valiela et al. 2001; Alongi 2002; Duarte et al. 2005a; Bridgham et al. 2006; FAO 2007; Duarte et al. 2008; Waycott et al. 2009; Spalding et al. 2010). While the global average annual loss of mangroves has slowed from 1.04% in the 1980s to 0.66% in the 5 years before 2005 (Spalding et al. 2010), seagrass loss rates have accelerated over the past several decades, from 0.9% per year before 1940 to 7% per year since 1990 (Waycott et al. 2009). Such losses reduce their capacity for C storage and have serious implications for human populations that depend on these ecosystems for food, livelihoods, and coastal protection.

Because of the valuable C sequestration capacity of vegetated coastal ecosystems (in addition to the other critical goods and services they provide), and the vast human- and climate-driven threats to these systems, it is imperative that we improve our understanding of how these systems currently function as C sinks, and how they are likely to be affected by future changes.

Considerable research has addressed the driving processes and controls of C dynamics in vegetated coastal systems (Middleton and McKee 2001; Kristensen *et al.* 2008). However, much less emphasis has been placed on how anthropogenic impacts and climate change (specifically sea-level rise and temperature increases) may affect C storage in vegetated coastal systems. Climate change is likely to affect blue carbon sinks and their sequestration potential through alterations in their total area, composition, growth and productivity, and allocation of above-and belowground biomass.

Table 2. Carbon burial and global area of terrestrial forest ecosystems							
	Carbon burial (g $C m^{-2} vr^{-1}$)	Global area	Global carbon burial	Sourc	es		
Forest type	mean ± SE	(km ²)	$(Tg C yr^{-1})$	Global area	Carbon burial		
Temperate	5.1 ± 1.0 (range = 0.7–13.1) n = 18	10 400 000	53.0	Schlesinger (1997)	Schlesinger (1997); Zehetner (2010)		
Tropical	4.0 ± 0.5 (range = 1.4–7.6) n = 15	19622846	78.5	Schlesinger (1997); Asner et al. (2009)	Schlesinger (1997); Zehetner (2010)		
Boreal	4.6 ± 2.1 (range = 0.8–11.7) n = 5	13 700 000	49.3	Schlesinger (1997)	Schlesinger (1997); Zehetner (2010)		

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Key questions

Several critical questions must be addressed to improve our understanding of the fate of C sequestered in vegetated coastal ecosystems, including: (1) how are sequestration rates affected by ecosystem loss, and what is the fate of existing sediment C stocks? (2) How may sequestration rates and C stocks in sediments be affected by climate change? (3) What recommendations can be made to inform future C sequestration research?

How are sequestration rates and existing sediment C stocks affected by ecosystem loss and/or modification?

Human disturbances (eg timber harvesting, clearing, dredging and filling, as well as eutrophication) have caused extensive losses of vegetated coastal ecosystems (Table 3). Thus, analogous to the major impact of land-use changes in the C sink of terrestrial ecosystems (Achard et al. 2004), land-use change and anthropogenic disturbance of coastal ecosystems can have substantial impacts on C sequestration and existing C stocks in these systems. The disruption of C sequestration by coastal ecosystems through human activities may result in a switch from being a net sink to a net source of C. For example, when wetlands are drained, the water level lowers and sediments are exposed to oxygen. This exposure increases the rates of nutrient cycling and microbial activity; in this way, C stocks that were once resistant to decay (under anaerobic conditions) can be lost through aerobic respiration (Couwenberg et al. 2010). In Florida, conversion of freshwater wetlands to grazed pastures caused a 96% decrease in total organic C (Sigua et al. 2009).

Human activities that result in disturbance and exposure of sediments accelerate erosion, enhance leaching of dissolved organic C, and contribute to succession to plant species with lower C-sequestration capacities, thus reducing C stocks accumulated in soils over long periods of time. Clearing of mangrove forests resulted in statistically significant reductions of C stocks in sediments (eg up to ~50% over an 8-year period; Granek and Ruttenberg 2008; Sweetman *et al.* 2010). These results suggest that the total C lost through mangrove deforestation substantially exceeds that due to removal of standing biomass alone.

The impact of large-scale deforestation of mangroves for aquaculture has been well documented (Alongi 2002).

standing biomass and 750 t C ha⁻¹ from oxidation of mangrove sediments that have been accumulating for millennia. If the process occurs over 10 years, the loss of C from sediments (75 t C ha⁻¹ yr⁻¹) is 50 times the C sequestration rate in this forest (Eong 1993). A recent study (Donato *et al.* 2011) explored C emissions resulting from mangrove deforestation and land-use change, and estimated that global emissions would be in the range of 0.01–0.12 petagrams C yr⁻¹. Although these numbers may be preliminary, they confirm that the effects of land-use change in blue carbon sinks are potentially of global importance and need to be better constrained. Such estimates provide a powerful argument for the conservation of mangrove forests, particularly when atmospheric concentrations of CO₂ are considered.

A blueprint for blue carbon

Prolonged eutrophication has led to major seagrass dieoffs. Seagrass roots and rhizomes stabilize sediments, so that such die-offs can result in erosion and release of buried C. Increases in nutrients may reduce the plants' need for extensive roots, and so decrease belowground C allocation. For example, nutrient enrichment in coastal salt marshes in Massachusetts resulted in reductions in root and rhizome biomass and C accumulation (Turner et al. 2009). Similarly, nutrient enrichment of a coastal marsh in South Carolina resulted in a loss of 40 g C m^{-2} yr⁻¹ of soil C (Morris and Bradley 1999). Furthermore, nitrogen fertilization may also stimulate microbial breakdown of recalcitrant organic matter (eg organic matter such as humus or lignin-containing material that few soil organisms can decompose), thus releasing C. By contrast, in some cases eutrophication may actually increase C sequestration. Salt marshes and mangroves are generally nitrogen limited, so increases in nitrogen can increase C fixation. Morris et al. (2002) demonstrated that nutrient enrichment in a South Carolina salt marsh resulted in increased primary productivity and biomass density and the rate of sediment accretion. McKee et al. (2007) found that the addition of nitrogen and phosphorus in mangroves in Belize resulted in both increases and decreases in accretion. Assessing the impacts of eutrophication on vegetated coastal ecosystems is clearly complex.

How may C sequestration rates and storage be affected by climate change?

The impacts of global climate change (eg changes in sea level and temperature) are likely to affect C sequestration

When mangroves are converted to aquaculture ponds, C is released back to the atmosphere as a result of both the removal of the forest and, more importantly, the perturbation (and oxidation) of mangrove sediments during pond construction. For example, in mangrove forests in Malaysia, conversion to aquaculture ponds could result in the release of 150 tons (t) C ha⁻¹ from removal of

Ecosystem	Percent of global loss	Annual rate of global loss	References			
Mangroves	20% (since 1980s) 30–50% (since 1940s)	~0.7–3%	Valiela et <i>al.</i> (2001); Alongi (2002); FAO (2007); Spalding et <i>al.</i> (2010)			
Seagrasses	50% (since 1990s)	~7%	Costanza et al. (1997); Duarte et al. (2005a); Waycott et al. (2009)			
Salt marshes	25% (since 1800s)	I–2%	Bridgham et al. (2006); Duarte et al. (2008			

Table 3, Global loss of blue carbon sinks (total percent loss and annual rate of loss)

rates in vegetated coastal ecosystems, but precisely how is difficult to predict. If mangroves and salt marshes are able to maintain elevation above the sea surface despite accelerated sea-level rise, then their ability to sequester C may be maintained or increased (Langley *et al.* 2009). However, if insufficient sediment or root growth is available to maintain elevation, then they may be eroded or flooded. Studies of C accumulation in salt marshes in South Carolina (Mudd *et al.* 2009) suggest that rates of C accumulation increase with sea-level rise until this reaches a critical rate that drowns the marsh vegetation and stops C accumulation. The critical rate varies, depending on inorganic sediment supply and hydrological conditions.

Erosion of C-rich deposits under mangroves after the loss of tree cover has been documented (Cahoon *et al.* 2003). Once the protective cover that vegetation provides is lost (eg from rapid sea-level rise), the stored C deposits may be eroded by wave action and oxidized back to CO_2 , resulting in a loss of C sink capacity and of past storage. In contrast, flooding of a marsh or mangrove may also permanently bury the accumulated peat layer and prevent its decay, thus maintaining the long-term storage of C. Additionally, increases in sea level may cause organic decay rates to slow, thus increasing the C storage capacity of intertidal sediments. Sea-level rise therefore has the potential to increase, maintain, or reduce C storage in coastal habitats; a better understanding of the fate of buried C when wetlands become submerged or eroded is needed.

Temperature is also an important driver affecting C storage in mangroves, seagrass meadows, and salt marshes, because temperature affects the underlying metabolic processes of C gain through photosynthesis and C loss through plant and microbial respiration. In vegetated coastal systems, slight increases in temperature can increase productivity, but large increases can cause temperature stress, resulting in metabolic changes, altered growth rates, distribution shifts, and changes in C balance and mortality (Ellison 2000). Increasing average annual temperatures correspond to a decline in sediment C density in mangrove swamps and Spartina patens marshes, probably due to increased decay rates at higher temperatures (Chmura et al. 2003). A key question therefore is whether the impacts of warming and increased productivity can compensate for increases in sediment respiration; this issue has not been addressed adequately for coastal wetlands. One recent study (Kirwan and Blum 2011) suggested that increased remineralization of organic matter offsets the gain in plant productivity that may result from higher temperatures.

What recommendations can be made to inform future C sequestration research?

Research on C sequestration in vegetated coastal ecosystems is essential to help address the knowledge gaps identified above. Selection of research sites must be informed by an improved understanding of the driving forces affecting C sequestration rates. Although global C sequestration rates are high for vegetated coastal ecosystems, these rates vary among locations, reflecting the wide array of factors that influence the magnitude of any given C sink. Such factors include primary productivity, respiration, exchange of C with adjacent systems, hydrology, sedimentation rate, changes in nutrient cycles, changes in temperature, changes in sea level, location along tidal gradients, and species composition (Middleton and McKee 2001; Kristensen *et al.* 2008). Research that improves our understanding of the relative roles and importance of such factors in C dynamics is needed to guide restoration of coastal ecosystems and their C sink potential.

To quantify the C sequestration potential of vegetated coastal systems, we need to measure and map the spatial and regional variability of C sequestration rates in and among blue carbon sinks, relating these differences to ecological and environmental characteristics. Such maps may be used to guide conservation planning and restoration efforts. It is also important to determine indicators that can be used to estimate and scale up C cycling data (eg primary productivity for mangroves and seagrasses shows clear latitudinal gradients, whether linked to temperature, irradiance, precipitation, nutrient availability, or combinations thereof). In addition, it would be valuable to assess and quantify the combined C sequestration, as well as the human and ecological benefits (eg fisheries production), associated with preservation and restoration of vegetated coastal ecosystems.

Remote sensing and aerial photography may be useful in identifying land-use changes and blue carbon sinks that are priority areas for protection, based on such combined conservation and social benefits, C sequestration potential, and prospects for surviving the impacts of climate change (particularly sea-level rise). However, additional research on vegetated coastal ecosystems with high C sequestration potential is needed to determine the combined effects of climate change, land-use practices (eg deforestation, coastal development that forms a barrier to mangrove landward migration), and other human impacts (eg pollution, eutrophication) on C sequestration. For example, studies should address the conditions that determine whether sea-level rise increases, maintains, or reduces C storage.

The standardization of methods for measuring sediment C stocks and sediment C accumulation rates – including field-based and remote sensing methods – is essential for improving estimates of C sequestration. Furthermore, accurate quantification and verification of sediment C burial is necessary for C sequestration incentive programs and trade in C credits. In addition, multi-year measurements are needed to assess the amount of C entering long-term storage and to provide the baselines needed to determine the impact of changes in climate and/or human disturbance on C storage.

Future studies should focus on quantifying the export of

C to adjacent systems. Several previous studies (Lee 1995; Dittmar *et al.* 2006) have looked at the export of particulate and dissolved organic C, while more recent research has indicated that export of dissolved inorganic C may be quantitatively greater and could limit our ability to constrain C budgets in mangrove ecosystems (Bouillon *et al.* 2008).

Conclusion

Interest in the role of vegetated coastal ecosystems in C sequestration has increased dramatically over the past several years. This has led to a corresponding increase in case studies that improve our knowledge of C dynamics and the associated biogeochemical processes in mangroves, seagrasses, and salt marshes. Such efforts are important in arguing for the protection and restoration of these ecosystems, based on the valuable goods and services they provide, including their C sequestration capacity. However, we still lack sufficient understanding of the underlying factors that control the variability of C storage in vegetated coastal ecosystems. Specific studies are needed to improve this understanding and strengthen the case for the value of blue carbon sinks.

Improved methods for measuring C storage and the quantification of C storage rates in vegetated coastal ecosystems will help to inform regional and global C management and potential C offset schemes. By strengthening the science supporting the sequestration potential of blue carbon sinks and our understanding of associated biogeochemical processes – specifically our ability to determine the drivers of variability in C sequestration rates and how long-term C storage may be affected by climate change and other anthropogenic impacts – we will improve our ability to identify and manage priority areas for conservation and restoration. In doing so, we will continue to build the case for the protection of these valuable ecosystems that are being lost at such rapid rates.

Acknowledgements

GLC was supported by funding from a Natural Sciences and Engineering Research Council of Canada (NSERC) grant. CMD's participation was supported by project MEDEICG, funded by the Spanish Ministry of Science and Innovation (number CTM2009-07013). MB thanks COST Action ES0906: Seagrass productivity: from genes to ecosystem management.

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