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REVIEW PAPER

Carbon and nutrient exchange of mangrove forests with the coastal ocean

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Abstract Mangrove forests exchange materials with the coastal ocean through tidal inundation. In this study, we aim to provide an overview of the published data of carbon (C) and nutrient exchange of mangrove forests with the coastal ocean at different spatial scales to assess whether the exchange is correlated with environmental parameters. We collected data on C (dissolved and particulate organic C; DOC and POC) and nutrient exchange (dissolved and particulate nitrogen, N and phosphorus, P) and examined the role of latitude, temperature, precipitation, geomorphological setting, hydrology, dominant mangrove species and forest area in explaining the variability of the exchange. We identified that there are a range of methodologies used to determine material exchange of mangroves with the coastal zone, each methodology providing data on the exchange at different spatial scales. This variability of approaches has limited our understanding of the role of mangroves in the coastal zone. Regardless, we found that mangrove forests export C and nutrients to the coastal zone in the form of litter and POC. We found that precipitation is a major factor influencing the export of C in the form of litter; sites with low annual precipitation and high mean annual temperatures export more C as litter than sites with high precipitation and low temperature. Furthermore, export of POC is higher in zones with low mean annual minimum temperature. Identification of broad-scale trends in DOC and dissolved nutrients was more difficult, as the analysis was limited by scarcity of suitable studies and high variability in experimental approaches. However, tidal amplitude and the concentration of nutrients in the floodwater appears to be important in determining nutrient exchange. The strongest conclusion from our analysis is that mangrove forests are in general sources of C and nutrients in the form of litter and POC and that they are most likely to be exporting C subsidies in dry regions.

Keywords Coastal wetlands · Nitrogen · Phosphorus · Litter · Tidal exchange · Precipitation

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Mangroves, importers or exporters of materials to the coastal ocean?

Mangrove forests are the dominant ecosystems of coastal areas between 30° north and south of the equator (Kangas & Lugo, 1990), covering almost 16 million ha of tropical and subtropical coastal regions (FAO, 2004). Mangrove forests are biogeochemically active and complex. They link terrestrial and marine environments, moderating the water flow and transport of material carried in the floodwater during tidal inundation. The intensity and direction of the exchange of materials has been the subject of recent debate. Mangrove forests can import terrestrially derived dissolved nutrients and carbon (C) by directly absorbing them from the floodwater (e.g. Boto & Wellington, 1988) and indirectly by absorbing them from the deposited sediment (e.g. Robertson & Alongi, 1992). Mangrove forests can also import particulate nutrients and C associated with suspended sediment and organic debris (Adame et al., 2009). The capacity of mangroves to import nutrients and C has been proposed to be important in maintaining the health of adjacent seagrass communities (Wolanksi et al., 1997; Valiela & Cole, 2002).

In addition to the studies showing mangrove forests importing nutrients and C during tidal inundation, there have been an increasing number of publications suggesting that mangrove forests can simultaneously export nutrients and C to the adjacent coastal environment (Dittmar & Lara, 2001; Dittmar et al., 2006). This idea comes from the "Outwelling Theory" by Odum (1968) and has been supported by recent studies that suggest that export of materials is a common feature of mangrove forests (Lee, 1995). For example, exports of dissolved ammonium, silicate and phosphorus (P) have been reported from mangrove forests near the Amazon River (Dittmar & Lara, 2001; Dittmar et al., 2006). Large amounts of nutrients and C associated with litter and detritus can also be exported by tidal flushing (Woodroffe, 1992; Ong, 1993). The export of C and nutrients from mangrove forests to the ocean has been proposed to be important in sustaining coastal productivity (Newell et al., 2004).

The understanding of mangrove forests as importers or exporters of material has direct implications in the perception of the ecosystem services that mangrove forests provide. For example, if nutrient export dominates, then mangrove forests are important in subsidising coastal production. In contrast, if nutrient import is dominant throughout the year, then mangrove forests are important for improving water quality. The variability in nutrient and C exchange supports the idea that different mangrove forests provide different ecological services (Ewel et al., 1998) and that mangrove function is variable across temporal and spatial scales (Farnsworth, 1998). Although, there is a high degree of certainty that mangrove forests have an important role in sustaining coastal health, there is less certainty about the processes that underlie this role and the environmental factors that control these processes.

There are a number of characteristics of mangrove forests that are important in determining the magnitude and direction of material exchange such as latitude, climate, geomorphological setting, hydrology, forest area and species composition. Most studies that have investigated C and nutrient exchange have, often for logistical reasons, only tested one or two variables at a time. In this study, we analyse a range of studies that have investigated C, N and P exchange of mangrove forests within the coastal zone at different spatial scales to assess whether material exchange is correlated with environmental parameters. The aim of this review is to provide an overview of the reported nutrient and C exchange of the mangrove forest with the coastal ocean, and to determine factors that affect the role of mangroves as importers or exporters of materials.

Material exchange at different spatial scales

The exchange of material between the mangrove forest and the coastal ocean has been investigated using a wide range of experimental techniques. Each technique has provided data on mangrove exchange at different spatial scales: exchange between estuarine systems and the ocean, between an estuary basin and the coastal ocean and between a mangrove forest and the adjacent creek. Studies of material exchange have included a wide range of indicators of C and nutrient transport. For example, at least three different types of samples are commonly used as indicators of C and nutrient exchange: (1) C, nitrogen (N) and P associated with leaf litter, (2) C, N and P associated with particulate matter and (3) dissolved C, N and P. Methodologies commonly used to measure C and nutrient exchange in the form of litter and particulate organic carbon (POC) include the following:

Indirect calculations based on litter traps

The difference between litter production and standing litter is used to measure the export of litter and nutrients and C associated with it (e.g. Wafar et al., 1997). The calculated rate represents the integrated export of litter over time. In many studies, it is assumed that most of the export is a result of tidal flushing. Thus, in sites where microbial decomposition and detritivory are high, the rates of litter export calculated using this methodology could be overestimated (Robertson & Daniel, 1989; Holguin et al., 2001). This methodology can be used to estimate the export of the C and nutrients as particulate material and litter from a mangrove forest to the adjacent water body.

Litter and detritus sampled in the mouth of creeks

Litter export has been directly measured by collecting litter during a tidal cycle in the mouth of a tidal creek (Golley et al. 1962; Wattayakorn et al., 1990). To obtain a representative value of litter export using this methodology, sampling should be conducted in various tidal cycles and under different weather conditions (Odum, 2000). This methodology can be used to measure the amount of litter and particulate material (and the C and nutrients associated with it) exported during a tidal cycle from a creek that floods a mangrove forests to the adjacent coastal zone.

Methodologies for sampling dissolved material exchange in mangroves are more variable and include.

Flumes

A physical boundary is constructed inside the mangrove forest and water is sampled throughout tidal cycles as the water enters and leaves the artificial channel (e.g. Childers & Day, 1988, Davis et al., 2001a). Walls of 0.5–1 m tall, separated 1.5–3 m apart are used to prevent lateral water movement without altering water flow as the tide inundates the mangroves (Childers & Day, 1988). This methodology allows detailed study of material exchange of the mangrove forest with the adjacent creek. The limitation of this technique is that the construction of flumes in dense forest or in forests with high prop roots can be difficult. However, the flume technique allows for accurate flux calculations (material exchange per time, per area flooded) of materials exchange from mangroves with the floodwater and provides comparable data of nutrient exchange with other sites. This technique minimises confounding effects of material exchange such as tidal elevation and duration of the flooding.

Island enclosures

This methodology has been applied by artificially enclosing small islands (2.5-4 m diameter) of scrub mangroves. The water is sampled around the enclosures and a flux is calculated from changes in nutrient concentration and a calculation of water inside the enclosure (e.g. Davis et al., 2001b). Similar to the flume technique, this methodology allows comparison of the exchange of material between the mangrove forest and the adjacent estuary. Its use is limited to small islands of mangroves, but it can be useful as a base for comparison of exchange rates in larger mangrove areas.

Sampling in creeks

Water is sampled in the mouth of a creek that floods a known area of mangrove forest (e.g. Dittmar & Lara, 2001; Sánchez-Carrillo et al., 2009). This methodology is appropriate to measure nutrient exchange between the estuarine basin and the coastal ocean. This methodology is one of the most widely used and thus, results are comparable among sites. The exchange rate obtained with this methodology may not accurately reflect exchange between the mangrove forest and the ocean, as it includes processes associated with the tidal creek bed and the water column (Twilley, 1985). This methodology might be impractical for studying exchange of material in mangrove forests in open bays or outside of tidal creeks.

Transects

Water is sampled along transects from the mangrove forest to the adjacent ocean. The aim of using this methodology is to measure the material exchange from a mangrove system to the ocean. This methodology has been used to measure the influence of a lagoon surrounded by mangrove forests in the adjacent coastal zone ($\sim$1 km, Young et al., 2005) and the influence of a large mangrove system in the ocean shelf edge, 100 km from the coast (e.g. Dittmar et al., 2006). This methodology is appropriate for studying material exchange at large spatial scales.

Environmental factors affecting material exchange

There is a wide range of processes involved in determining material exchange in mangrove forests. These processes are influenced by a number of factors ranging from global scales, such as climate and latitude, to local characteristics of the forest, such as species composition.

Global scale: climate and latitude

Mangrove forests are distributed in tropical and subtropical coasts. Their distribution is limited by the occurrence of frost at high latitudes (Kangas & Lugo, 1990; Duke et al., 1998). Mangrove productivity is the highest at low latitudes, in areas of high annual precipitation and temperature (Saenger & Snedaker, 1993). Thus, high productivity might result in high quantities of material available for export (Odum, 2000). However, high productivity might also reflect high metabolic demand, which may result in high rates of nutrient import.

Regional scale: geomorphological setting and hydrology

The physical forces that form a shoreline will continuously influence the ecological processes occurring within it. According to the geomorphological classification, a mangrove forest can be river-dominated, tide-dominated, wave-dominated barrier lagoon, composite-river and drowned bedrock valley (Thom, 1982). Riverine mangroves are proposed to export material to the coastal zone, while tidal mangroves are more likely to import materials (Wolanski et al., 1992, Woodroffe, 1992). This argument is based on the principle that tidal mangroves are dominated by bidirectional flows, while riverine mangroves are dominated by unidirectional flows that favour outwelling. In addition, export of material is also influenced by the "openness" of a mangrove forest to the ocean, with open bays being more likely to have high exports compared to semi-enclosed ones (Odum, 2000). Hydrology has also an important role on material exchange. Frequent flooding and long tidal inundation times can enhance sediment and C retention (Wolanski et al., 1992, Adame et al., 2009), but it can also enhance litter and nutrient export (Twilley, 1985; Childers et al., 2000; Odum, 2000). The effect of the principal physical force acting on a shoreline (e.g. river, tide, wave), its hydrology (e.g. inundation time) and position within the estuary (e.g. low or high intertidal) have been represented as the functional type of mangrove forests, such that mangroves can be classified as riverine, fringe, scrub, overwash, basin and hammock forests (Lugo & Snedaker, 1974).

Local scale: dominant tree species, litter fall, forest area and nutrient concentration of the floodwater

There are numerous local factors that can affect material exchange of mangrove forests with the coastal zone. Litter production in a forest can depend on the species of tree that the forest is composed. For example, in the Mandovi-Zuari estuary, litterfall was higher in stands of *Avicennia officinalis* than in stands of *Sonneratia alba* (Wafar et al., 1997). Different species also have differing decomposition rates. For example, *Rhizophora mangle* leaves decompose more slowly than those of *Avicennia germinans*, which could favour export of leaves of *Rhizophora mangle* over *A. germinans* (Twilley et al., 1986; Wafar et al. 1997). In addition, the soils of mangrove forests dominated by different tree species have particular characteristics that could affect material exchange. For example, in south Brazil, soils of forests dominated by *Avicennia* had higher rates of decomposition compared to soils of a *Rhizophora* dominated forest, which could result in higher nutrient exports from *Avicennia* forests compared to forests dominated by *Rhizophora* (Lacerda et al., 1995).

The area of a mangrove forest can affect material exchange. The export of organic C has been observed to be greater in larger systems compared to smaller ones (Childers et al., 2000). Finally, concentration of nutrients in the floodwater can affect nutrient exchange, with larger import rates in sites where nutrients concentrations are high compared to sites with low nutrient concentrations, where import has been observed to be comparatively lower (Childers et al., 2000; Adame et al., 2010).

Analysis of environmental parameters and material exchange

To analyse the effect of environmental parameters and the spatial scale in the function of mangroves in C, N and P exchange during tidal inundation, we conducted an extensive review of studies published from 1960 to 2010 (Tables 1, 2, 3). We used the following criteria to select the studies for our analysis: (1) studies incorporated fluxes in and out of mangrove forest during tidal inundation; (2) results were presented as a net exchange rate, or alternatively, we were able to extract the net exchange value (inwellings–outwellings) when this was not explicitly provided, (3) data were provided in units consistent with g m^{-2} $year^{-1}$, (4) data were given as an annual flux. If the number of samples in the study were too few to calculate an annual rate, the data were still used but were considered an approximation. Approximate values are highlighted in the tables and figures. The area of the forest was the area used at each study for each spatial scale. The export of litter during tidal inundation was transformed to grams of C using a 50% conversion factor when this was not explicitly stated (Rajkaran & Adams, 2007). Throughout, we refer to exports as negative values and imports as positive values (e.g. Rivera-Monroy et al., 1995).

We separated the analysis in two sections: C exchange and nutrient exchange. The C section was divided in three subsections: C exchange associated with litter (20 studies), C exchange associated with POC (12 studies) and C exchange as DOC (15 studies). The nutrient section focuses on P and N exchange because these elements have a particularly strong impact on ecosystem processes and are regularly reported in the literature. The nutrient exchange section was divided in three subsections: nutrient exchange associated with particulate matter in the form of litter (nine studies), nutrient exchange as dissolved N (inorganic forms of N: NO_x and NH_4) and dissolved P (inorganic forms of P: SRP or PO_4) (15 studies), and nutrient exchange calculated using indirect exchange estimates (10 studies). This final section incorporates all the studies that performed calculations of nutrient budgets based on models of nutrient absorption, growth and export from mangrove forests. In each section the data was analysed to assess the effect of the methodology used and the spatial scale considered (Tables 4, 5).

We assessed the relationships among the exchange of C and nutrients that were directly measured in the field (i.e. not indirect measurements) and quantitative environmental parameters when there was enough data to provide statistically meaningful tests ($n \geq 8$). For each variable, we analysed the data grouped by similar methodologies and spatial scales. The environmental parameters were transformed in order to facilitate the visualisation of the data and to conform to the requirement for normality and homogenous variances when using linear models. Precipitation, mangrove forest area, temperature and nutrient concentration were transformed using the Box-Cox or log transformation. Normality was assessed using Shapiro–Wilk tests. A multiple regression analysis test was conducted in order to assess the relationship of C and nutrient exchange and non-categorical variables (Statistica 7.0. StatSoft In., Tulsa, USA). Using a variance inflation factor (VIF) for each environmental parameter, we selected the parameters for the model that produced the least co-linearity (VIF < 3) and that best explained the variation in the exchange (high R^2 and low P values). When enough data was available ($n \geq 5$), the difference in exchange due to sampling technique was assessed with a t test or with an analysis of variance (ANOVA), where sampling technique was the fixed effect in the model.

Spatial applicability of methodologies used to measure material exchange

The first result of our analysis is the identification of a variety of methodologies that has been used to address the same question: What is the material exchange of mangroves with the coastal ocean? While the main objective and aim of many of studies is similar, the approach to the question has been very variable and so have been the results. For example, all the studies found in this review reported an export of litter to the coastal ocean (Tables 2, 4) and most studies reported export of POC. As a result, the studies that investigated the export of nutrients in the

Table 1 Environmental characteristics of mangrove forests where material exchange with the coastal zone has been investigated

	Location	Latitude	Mean annual T (°C)	Mean min T (°C)	Mean max T (°C)	Annual precipitation (m)	Dominant sp.	Area (km^2)	Litterfall (g m^{-2} $year^{-1}$)	Reference
Caete Coast	Brazil	1	27	22	31	2.5	Mx	10000		Dittmar et al. (2006)
Furo do Meio	Brazil	1	26	22	31	2.6	Mx	2		Dittmar & Lara (2001)
Guayas River	Ecuador	2	26	24	27	0.9	Rh	120	833	Twilley et al. (1997)
Kuala Selangor	Malaysia	3	28	24	33	1.8	Mx	1	706	Mahmood et al. (2005)
Mattang	Malaysia	5	28	25	33	2.5	Rh	408	763[a]	Gong et al. (1984), Gong & Ong (1990)
Sungai Merbok	Malaysia	6	27	25	33	2.1	Rh	50	763[a]	Gong et al. (1984), Simpson et al. (1997)
Klong Ngao	Thailand	9	28	21	35	4.0	Mx	12	670	Christensen (1978), Wattayakorn et al. (1990)
Rio Coco Solos	Panama	9	29	26	27	3.0	Rh			Lin & Dushoff (2004)
Fly Delta	PNG	9	27	25	29	1.1	Rh	874	1430[b]	Robertson et al. (1999), Robertson & Alongi (1995)
Tapi estuary	Thailand	9	27	27	28	1.7		20		Wattayakorn et al. (2001)
Klong Ngao	Thailand	10	28	21	35	4	Mx	12	670	Christensen (1978), Wattayakorn et al. (1990)
Darwin	Australia	13	28	20	32	1.6	Bru	1	686	Woodroffe et al. (1988)
Mandovi-Zuari	India	15	27	26	30	2.9	Mx	16	1268	Wafar et al. (1997)
Magueyes Island	Puerto Rico	18	27	21	32	0.7	Rh	0.01	724[a]	Golley et al. (1962), Pool & Snedaker (1975)
Coral Creek	Australia	18	24	14	32	1.1	Rh	5	891	Boto & Bunt (1981), Duke et al. (1981), Ayukai et al. (1998)
Conn Creek	Australia	18	24	14	32	1.1	Rh	6	960	Duke et al. (1981), Ayukai et al. (1998)
Hinchbrook Island	Australia	18	24	14	32	1.1	Rh	164	1268	Robertson & Alongi (1992)
Terminos Lagoon	Mexico	19	27	18	36	1.7	Rh	835	1043	Day et al. (1987), Rivera-Monroy et al. (1995)
Townsville	Australia	19	25	14	31	1.2	Cr	81	960	Duke et al. (1981), Robertson & Daniel (1989)
Ingham	Australia	19	25	15	31	2.1	Av	64	960	Duke et al. (1981), Robertson & Daniel (1989)
Celestun	Mexico	21	26	20	35	0.8	Rh.	22	1197	Young et al. (2005), Zaldivar et al. (2004)
Red River	Vietnam	20	23	16	28	1.7	Mx	84	1190	Hong & Hoan (1993), Wösten et al. (2003)
Mai Po	Hong Kong	22	23	14	31	2.2	Ka	10	1107	Lee (1989)
Itacuruca	S Brazil	23	23	18	23	2.3	Rh	38	674[a]	Adaime (1985), Silva et al. (1998)
El Verde Lagoon	Mexico	24	25	18	30	0.6	Lg	0.5	1100	Day et al. (1987), Flores-Verdugo et al. (1987)
Sepetiba Bay	Brazil	24	2	18	23	2.3	Rh	38	674[a]	Adaime (1985), Silva et al. (1998)
North River	USA	25	24	19	28	1.4	Rh	14	880[b]	Odum & Heald (1972, 1974[a])
Taylor River	USA	25	24	19	28	1.4	Rh		485	Lugo & Snedaker (1974), Davis et al. (2001a, b)
Shark River	USA	25	24	19	28	1.4	Mx		880[b]	Romigh et al. (2006)

Table 1 continued

	Location	Latitude	Mean annual T (°C)	Mean min T (°C)	Mean max T (°C)	Annual precipitation (m)	Dominant sp.	Area (km^2)	Litterfall (g m^{-2} $year^{-1}$)	Reference
Southern everglades	USA	25	24	19	28	1.3	Rh	460	880[b]	Odum & Heald, (1974), Sutula et al. (2003)
Florida Bay	USA	25	24	19	28	1.3	Rh	865	880[b]	Lugo & Snedaker (1974)
Ten Thousand Is.	USA	26	25	19	28	1.4	Rh	721	880[b]	Lugo & Snedaker (1974)
Rookery forest	USA	26	24	19	28	1.4	Av	16	485	Lugo & Snedaker (1974), Twilley (1985)
Rookery Bay	USA	26	24	19	28	1.3	Av	180	485	Lugo & Snedaker (1974), Twilley et al. (1986)
Moreton Bay	Australia	27	21	16	25	1.6	Av	80	393	Davie (1984)
Bahia de Lobos	Mexico	27	24	18	22	0.2	Av	5	712	Sánchez-Carrillo et al. (2009)
Charlotte Harbour	USA	27	23	19	28	1.4	Rh	262	880[b]	Lugo & Snedaker (1974)
Sarasota Bay	USA	27	23	19	28	1.4	Rh	16	880[b]	Lugo & Snedaker (1974)
Tampa Bay	USA	28	23	19	28	1.4	Rh	85	880[b]	Lugo & Snedaker (1974)
Mngazana estuary	South Africa	32	15	18	25	1	Mx	1	560	Rajkaran & Adams (2007)
Tuff Crater	New Zealand	37	15	11	19	1.3	Av.	0.2	588	Woodroffe (1982), Woodroffe (1985a)

Environmental characteristics include: mean annual, mean minimum and mean maximum annual temperature (°C), annual precipitation (m), dominant mangrove species, mangrove area (km^2) and annual litterfall (g m^{-2} $year^{-1}$). Litter fall (g m^{-2} $year^{-1}$) was obtained from original sources, [a] Saenger & Snedaker review paper (1993) and from [b] Leach & Burgin (1985)

Mix mixed forest, *Rh* Rhizophora, *Av* Avicennia, *Ce* Ceriops, *Br* Brugueira, *Ka* Kandelia, *Lag* Laguncunaria

Table 2 Carbon exchange (g C m^{-2} $year^{-1}$) during tidal inundation in the form of litter, particulate organic carbon (POC) and dissolved organic carbon DOC) and environmental characteristics of a range of mangrove forests

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics	C flux as litter (g C m^2 $year^{-1}$)	POC flux (g C m^2 $year^{-1}$)	DOC flux (g C m^2 $year^{-1}$)	Reference
Guayas River, Ecuador	River dominated	Riverine	Upper regions of the Churute River	sd	4.0		−340.1			Twilley et al. (1997)
Kuala Selangor, Malaysia	River dominated	Fringing Riverine	Mouth of Selangor River	sd	2.8	Tidal inundation class 4 (Watson 1928). Maximum tidal amplitude of 4 m	−122.6			Mahmood et al. (2005)
Mattang, Malaysia	River dominated	Riverine		sd	2.7		−176.0			Gong et al. (1984), Gong & Ong (1990)
Klon Ngao, Thailand	River dominated		Deltaic plain of the Kra River	sd	2.4	1 m at neap; 3 m spring tide. Strongly influenced by tides	∼−1.0			Wattayakorn et al. (1990)
Mngazana, South Africa	River dominated	Fringe	Tidal creeks at mouth of Mngazana River in an open estuary	sd	0.48		−131.6	−0.003	0	Rajkaran & Adams (2007)
Fly Delta, PNG	River dominated	Riverine	Deltaic islands at mouth of river	m	2			−285.0		Roberston et al. (1991), Robertson & Alongi (1995)
Darwin, Australia	Drowned river valley		East arm of Darwin Harbour. Tidal creek and tidal flats within the embayment	sd	3.7	Dominated by tides of up to 7 m. Mean spring range 5.5 m and mean neap range is 1.9 m	−332.0			Woodroffe et al. (1988)
Mandovi-Zuari India	Drowned river valley		Coastal tidal plain estuary at mouth of Mandovi and Zuari Rivers	m	1.3	Important wave and river influence, specially in the monsoon season	−0.1		−0.1	Quasim & Sen Gupta (1981), Wafar et al. (1997)
North River, USA	Carbonate setting River dominated			sd	0.8		−292.0[a]			Odum & Heald (1972, 1974)
Taylor River, USA	Carbonate setting River dominated	Scrub Fringe	Small channel (∼10 m wide) that links shallow ponds to the southern Everglades	sd	0.05	Not significantly affected by tides		0	∼0.46 67.3	Lugo & Snedaker (1974), Davis et al. (2001a, b, 2003)

Table 2 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics	C flux as litter (g C m^2 year^{-1})	POC flux (g C m^2 year^{-1})	DOC flux (g C m^2 year^{-1})	Reference
Rookery forest, USA	Carbonate setting River dominated	Basin	Forest along Hiden River, which drains to Rookery Bay	sd	0.55	152 Tides inundate per year. Standing water for 241 days, cumulative depth of 12 m		−13.4	−36.7	Lugo & Snedaker (1974), Twilley (1985)
Florida, USA	Carbonate setting			sd	0.8		−186.0[a]			Heald (1969), Odum & Heald (1974)[a]
South Florida, USA	Carbonate setting			sd	0.8		−438.0			Heald, (1971), Odum & Heald (1974) in Miller (1979)
Shark River, USA	Carbonate setting	Riverine	Tidal river	sd	0.75	Water level 15–120 cm at creek. Mean tide amplitude of 0.5–1 m. Inundated twice a day			−56.0	Romigh et al. (2006)
Rookery Bay, USA	Carbonate setting Tidal dominated	Basin	Forest adjacent to the bay	sd	0.1	152 tides inundate per year. Standing water for 241 days, cumulative depth of 12 m	−198.0	−15.1	−44.3	Lugo & Snedaker (1974), Twilley et al. (1986)
Celestun, Mexico	Carbonate setting Tidal dominated	Fringe Scrub Basin	Coastal lagoon	sd	0.3			−9.1	−108.1	Young et al. (2005)
Caete Coast, Brazil	Tidal dominated	Riverine Fringe	Coast with large riverine inputs from the Amazon River	d	4	Strong macrotidal influence			∼−138.1	Dittmar et al. (2006)
Furo de Meio, Brazil	Tidal dominated	Riverine Fringe	Tidal creek	sd	4	Forest inundated every fortnight. Creek depth 1 (low tide) to 5 m (high tide) Spring tides 4–5 m			−48.0	Dittmar & Lara (2001)
Magueyes Is, Puerto Rico	Tidal dominated			d	0.3	One tide a day floods forest for approximately 5–17 cm	∼−401.5			Golley et al. (1962)

Table 2 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics	C flux as litter (g C m^2 $year^{-1}$)	POC flux (g C m^2 $year^{-1}$)	DOC flux (g C m^2 $year^{-1}$)	Reference
Itacuruca, S. Brazil	Tidal dominated	Fringe	Tidal creeks within the coastal embayment of Sepetiba Bay	sd	0.8	Underground water inputs	~ −3.9	−165.0	~ −13.1	Adaime (1985), Rezende (1988), Lacerda et al. (1995), Silva et al. (1998), Rezende et al. (2007)
El verde lagoon, Mexico	Tidal dominated		Ephemeral connection to the sea. Seasonal riverine inputs	sd	1.5		−492.8			Flores-Verdugoet al. (1987)
Mai Po, Hong Kong	Tidal dominated		Tidal shrimp pond in Deep Bay at the mouth of river	m	1.4	Modified hydrology by constructed tidal pond	−3.7			Lee (1989)
Tuff Crater, New Zealand	Tidal dominated	Fringe Scrub	Crater with little connection to ocean	sd	1.3	1.80–2.49 m of tidal amplitude	~ −2.2	−109.5		Woodroffe (1982), Woodroffe (1985a)
Townsville, Australia	Tidal dominated		Tidal creek	sd	2.2	Inundated once a day 82 days a year, once every 16.2 days	−194.0			Robertson & Daniel (1989)
Townsville, Australia	Tidal dominated		Tidal creek	sd	2.2	Inundated once a day, 82 days a year, once every 16.2 days	−252.0			Robertson & Daniel (1989)
Ingham, Australia	Tidal dominated		Tidal creek	sd	2.2	Inundated once a day, 66 days a year, once every 18 days	−107.0			Robertson & Daniel (1989)
Coral Creek, Australia	Tidal dominated		Tidal creek in Hinchbrook Island with low freshwater inputs	d	1.8	Elevation 0.25–1.25 cm	−365.0	−0.6/−54.8	7.3/~ 18.7	Boto & Bunt (1981), Ayukai et al. (1998), Boto & Wellington (1988)
						0–1.4 m above MSL				
Conn Creek, Australia	Tidal dominated		Freshwater inputs from runoff and underground. Tidal creek close to Hinchbrook channel	d	1.8			−56.9	~ −20.9	Ayukai et al. (1998)

Table 2 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics	C flux as litter (g C m^2 $year^{-1}$)	POC flux (g C m^2 $year^{-1}$)	DOC flux (g C m^2 $year^{-1}$)	Reference
Lobos Bay, Mexico	Tidal dominated	Fringe Scrub	Semi enclosed coastal lagoon	m	1.2	Inverse estuary. Max spring tides of 1.04–1.25 m. Flood time is 11 h and ebb tide 12.3–13.1 h		0.1	0.4	Sánchez-Carrillo et al. (2009)

Environmental characteristics include: geomorphological setting (according to Woodroffe (1992); Thom (1982)), mangrove functional type (Lugo & Snedaker 1974), tidal regime (*sd* semidiurnal, *d* diurnal, *m* mixed), average tidal amplitude (m) and hydrological characteristics. Positive exchange indicates C import and negative exchange indicates export. Data was obtained from the published literature, from our calculations based on published data, and from [a] Twilley et al. (1992). C exchange values marked with "~" are annual approximations because these values are based on low sample numbers or sampling that was not performed during a whole year

form of litter, and POC concluded that mangroves export nutrients to the coastal zone. On the other hand, investigations of the exchange of dissolved nutrients in mangroves report contrasting results, with some studies showing imports of nutrients and some of exports (Tables 3, 5). Finally, all the studies that estimated material exchange by using the nutrient metabolic demand of the forest showed that mangroves import nutrients (Tables 3, 5).

There are a variety of factors that interact in determining the role of mangroves as importers or exporters of materials (some of them revealed and discussed in the following sections). However, it is evident from our collection of published literature that one of the main limitations to understand the role of mangroves in the coastal zone is the variety of methodological approaches addressing this problem. While each of the approaches is valuable in their own context, not all contribute equally to answering the question of whether mangroves import or export material to the coastal zone. Transects from a mangrove system to the coastal ocean address the influence of large mangrove systems on the ocean (scale of ~10–100 km); samples taken on mouths of creeks deal with the exchange of materials of a creek that floods a mangrove forest with the coastal ocean (~1–10 km), and samples taken at the forest-creek interface with the aid of enclosures or flumes measure the exchange of material of the mangrove forest with the adjacent creek (~1 m–1 km). Additionally, studies that calculate nutrient export based on litter export or nutrient consumption by the forest, address these specific questions, not the role of the mangroves as importers or exporters of materials to the coastal zone.

The variety in approaches limits the comparison among different sites and environmental characteristics. Thus, we recommend that future studies in material exchange address the problem at specific spatial scale (the exchange of a mangrove forest with the floodwater, with the adjacent creek, with the adjacent water body and with the coastal ocean) and provide discussion and conclusion accordingly. Furthermore, future comparisons between different settings at similar spatial scales and with the use of comparable methodologies would help understand the effect of environmental variables in the extent and direction of the exchange. For example, a comparison of studies conducted with the use of flumes in mangroves and saltmarsh showed that carbonate

Table 3 Phosphorus and nitrogen net exchange (g m^{-2} year^{-1}) during tidal inundation and the environmental characteristics of a range of mangrove forests

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics and nutrient concentrations	Particulated N flux (g m^{-2} year^{-1})	Dissolved N flux (g m^{-2} year^{-1})	Particulated P flux (g m^{-2} year^{-1})	Dissolved P flux (g m^{-2} year^{-1})	Reference
Mattang, Malaysia	River dominated	Riverine		sd	2.7		−2.66		−0.28		Gong et al. (1984), Gong & Ong (1990)
Klong Ngao, Thailand	River dominated		Deltaic plain of the Kra River	sd	2.4	1 m at neap; 3 m spring tide. Strongly influenced by tides N = 0.006 mg l^{-1} P = 0.004 mg l^{-1}		∼ −0.49		∼ −0.006	Wattayakorn et al. (1990)
Rio Cocos Solos, Panama	River dominated	Riverine Fringe		m	0.3	N = 0.11 mg l^{-1} P = 0.035 mg l^{-1}		+		+	Lin & Dushoff (2004)
SE Queensland, Australia	River dominated	Fringe Scrub	Sites at the upper limits of mangroves from 3–5 km of mouth of river	sd	1	Depth of and inundation 0.6–0.8 m. Time of inundation 3–6 h in spring tides N = 0.08 mg l^{-1} P = 0.016 mg l^{-1}		+		+	Adame et al. (2010)
Mandovi-Zuari, India	Drowned river valley		Coastal tidal plain estuary at mouth of Rivers Mandovi and Zuari	m	1.3	Wave and river influence in monsoon season	−0.002	−0.002	−0.0003	−0.0002	Wafar et al. (1997), Quasim & Sen Gupta (1981)
Taylor River, USA	Carbonate setting River dominated	Scrub Fringe	Small channel (∼10 m wide) that links shallow ponds to southern Everglades	sd	0.05	Not significantly affected by tides N = 0.084 mg l^{-1} P = 0.003 mg l^{-1}	∼0.02	∼36.76 0.02[b]	∼ −0.12	∼1.41 −0.12[b]	Davis et al. (2001a, b, 2003)
Southern Everglades, USA	Carbonate setting		Drained by two sloughs; Shark and Taylor slough, where five creeks were sampled	sd	0.8	Little tidal influence and freshwater inputs. Tide from 5 cm to 1 m N = 0.084 mg l^{-1} P = 0.003 mg l^{-1}	−0.46	−0.03	−0.007	−0.0008	Odum & Heald (1974), Sutula et al. (2003)

Table 3 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics and nutrient concentrations	Particulated N flux (g m^{-2} $year^{-1}$)	Dissolved N flux (g m^{-2} $year^{-1}$)	Particulated P flux (g m^{-2} $year^{-1}$)	Dissolved P flux (g m^{-2} $year^{-1}$)	Reference
Celestun, Mexico	Carbonate setting	Fringe Basin Scrub	Coastal lagoon	m	0.3	Underground water influence	−4.21	−1.57			Young et al. (2005)
Lobos Bay, Mexico	Tidal dominated		Tide dominated, semi enclosed coastal lagoon. Inverse estuary	m	1.2	Max spring tides of 1.04–1.25 m. Flood time is 11 h and ebb tide is 12.3−13.1 h N = 0.338 mg l^{-1} P = 0.048 mg l^{-1}	−1.46	−1.79	19.71	0.18	Sánchez-Carrillo et al. (2009)
Coral Creek, Australia	Tidal dominated	Fringe Basin	Tidal creek in Hinchbrook Is. Low freshwater inputs	d	1.8	Elevation 0.25–1.25 cm 0–1.4 m above MSL N = 0.001 mg l^{-1} P = 0.003 mg l^{-1}	~1.60	~1.60/ 1.45		~0.34/ 0.50	Boto & Bunt (1981), Boto & Wellington (1988), Ayukai et al. (1998)
Sepetiba, Brazil	Tidal dominated	Fringe	Tidal creek that drains to coastal lagoon	sd	1	Tidal level at creek 0.6–2.6 m	−0.02				Adaime (1985), Silva et al. (1998)
Terminos Lagoon, Mexico	Tidal dominated	Fringe Basin		m	0.3		−0.52	0.61			Day et al. (1987), Rivera-Monroy et al. (1995)
Caete River, Brazil	Tidal dominated	Riverine Fringe	Tidal creek in shallow estuary. Results extrapolated regionally	sd	4	Forest inundated every fortnight. Creek depth 1 (low tide)–5 m (high tide) Spring tides 4–5 m N = 0.21 mg l^{-1} P = 0.016 mg l^{-1}		−5.0		−0.19	Dittmar & Lara (2001)

Table 3 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics and nutrient concentrations	Particulated N flux (g m^{-2} $year^{-1}$)	Dissolved N flux (g m^{-2} $year^{-1}$)	Particulated P flux (g m^{-2} $year^{-1}$)	Dissolved P flux (g m^{-2} $year^{-1}$)	Reference
SE Queensland, Australia	Tidal dominated	Fringe Scrub	Sites from 0.4–2 km from sea	sd	1	Depth of and inundation 0.4–1.3 m. Time of inundation 3–7 h in spring tides $N = 0.055$ mg l^{-1} $P = 0.024$ mg l^{-1}		+		+	Adame et al. (2010)
Conn Creek, Australia	Tidal dominated		Freshwater inputs from runoff and ground. Tidal creek at mouth of Hinchbrook channel	sd	1.8	$N = 0.003$ mg l^{-1} $P = 0.0001$ mg l^{-1}		~ -1.20		~ -0.61	Boto & Bunt (1981), Ayukai et al. (1998)
Indirect estimates											
Nutrients as total N and P											
Sungai, Malaysia	River dominated		Tidal creek that receives numerous riverine inputs. Estuary depth from 3–15 m	m	2.7	Maximum spring tidal range is 2.5 and minimum neap range is 0.4	~ 0				Gong et al. (1984), Simpson et al. (1997)
Tapi River, Thailand	River dominated		Estuary at the mouth of Tapi River	sd	1	Tidal ranges from 0.7–1.9 m	50.3		1.86		Wattayakorn et al. (2001)
Red River, Vietnam	River dominated	Riverine Fringe	Lower estuary of the Red River	d	3.3	No underground water. Important river discharge	112.98		13.47		Hong & Hoan (1993), Wösten et al. (2003)
Hinchbrook Is. Australia	Tidal dominated		Island separated from mainland by Hinchbrook channel	sd	1		+				Robertson & Alongi (1992)
Florida Bay, USA	Carbonate setting			sd	0.8		5.04[a]				Davie (1984), Hyland et al. (1989), Odum & Heald (1974), Deegan et al. (1986), Bianchi et al. (1999)

Table 3 continued

Location	Geomorphological setting	Mangrove functional type	Description of geomorphology	Tidal regime	Average tidal amplitude (m)	Hydrological characteristics and nutrient concentrations	Particulated N flux (g m^{-2} $year^{-1}$)	Dissolved N flux (g m^{-2} $year^{-1}$)	Particulated P flux (g m^{-2} $year^{-1}$)	Dissolved P flux (g m^{-2} $year^{-1}$)	Reference
Ten Thousand Is, USA	Carbonate setting			sd	0.8		0.20[a]				
Charlotte Harbour, USA	Carbonate setting			sd	0.8		5.04[a]				
Tampa Bay, USA	Carbonate setting			sd	0.8		1.41[a]				
Sarasota, USA	Carbonate setting			sd	0.8		2.82[a]				
Moreton Bay, Australia	Wave dominated	Fringe Scrub	Semi enclosed bay	sd	1	Mesotidal with oceanic influence in the east side and riverine influence on the west side	0.66[a]				

Environmental characteristics include: geomorphological setting (Woodroffe, 1992; Thom, 1982), mangrove functional type (Lugo & Snedaker 1974), tidal regime (*sd* semidiurnal, *d* diurnal, *m* mixed), average tidal amplitude (m), hydrological characteristics and nutrient concentration in the floodwater. Positive exchange indicates nutrient imports and negative exchange indicates export. Data was obtained from the published literature, from our calculations based on published data, and from calculations by [a] Valiela & Cole (2002). Nutrient exchange values marked with "∼" are annual approximations

[b] Nutrients were measured as the sum of particulate and dissolved forms, although most of the N was composed of dissolved forms

Table 4 Carbon exchange (g C m^{-2} $year^{-1}$) during tidal inundation in the form of litter, particulate organic carbon (POC) and dissolved organic carbon DOC), the spatial scale considered in the study and methodology used in the field

Spatial scale	Methodology	Net C flux (g m^{-2} $year^{-1}$)	Reference
Litter			
Estuarine basin and coastal ocean	Litter sampled with net at creek	−198.0	Lugo & Snedeaker (1974)
		−131.6	Rajkaran & Adams (2007)
		~−2.2	Woodroffe (1985)
		−1.0	Wattayarkon et al. (1990)
		−401.5	Golley et al. (1962)
Mangrove forest and adjacent creek	Litter production vs standing litter	−340.1	Twilley et al. (1997)
		−122.6	Mahmood et al. (2005)
		−176.0	Gong & Ong (1990)
		−332.0	Woodroffe et al. (1988)
		−0.1	Wafar et al. (1997)
		−194.0	Robertson & Daniel (1989)
		−252.0	Robertson & Daniel (1989)
		−107.0	Robertson & Daniel (1989)
		−3.7	Lee (1989)
		~−3.9	Silva et al. (1998)
		−492.8	Flores-Verdugo (1987)
		−365.0	Boto & Bunt (1981)
		−492.8	Flores-Verdugo (1987)
POC			
Estuarine system and coastal ocean	Transects	−9.1	Young et al. (2005)
Estuarine basin and coastal ocean	Detritus sampled with net at creek	−0.6	Ayukai et al. (1998)
		−56.9	Ayukai et al. (1998)
		−54.8	Boto & Bunt (1981)
		0.1	Sánchez-Carrillo et al. (2009)
		−0.003	Rajkaran & Adams (2007)
		−109.5	Woodroffe (1985)
	Mass balance	−285	Robertson et al. (1999)
Mangrove forest and adjacent creek	Flumes	0	Davis et al. (2001)
		−15.1	Twilley (1985)
		−13.4	Twilley (1985)
DOC			
Estuarine system and coastal ocean	Water sampled in transects from mangrove to ocean	~−138.1	Dittmar et al. (2006)
		−108.1	Young et al. (2005)
Estuarine basin and coastal ocean	Water sampled in creeks	−48.0	Dittmar et al. (2001)
		7.3	Boto & Wellington (1988)
		~18.7	Ayukai et al. (1998)
		~20.9	Ayukai et al. 1998
		0.4	Sánchez-Carrillo et al. (2007)
		0	Rajkaran & Adams (2007)
		~13.1	Rezende et al. (2007)

Table 4 continued

Spatial scale	Methodology	Net C flux (g m^{-2} $year^{-1}$)	Reference
Mangrove forest and adjacent creek	Flumes and island enclosures	67.3	Davis et al. (2001a, b)
		−44.3	Twilley (1985)
		−36.7	Twilley (1985)
		−56.0	Romigh et al. (2006)
Mangrove forest and floodwater	Based on litter decomposition	−0.1	Wafar et al. (1997)

settings release ammonium, while terrigenous settings take up ammonium (Childers et al., 1999). Another comparison using similar spatial scales and methodologies with riverine versus tidal-dominated mangroves revealed that riverine sites were more likely to receive higher nutrient inputs and were most likely to import nutrients than tidal dominate sites (Adame et al., 2010). At this moment, the scarcity of comparable data due to the variability in approaches in the published literature leaves many questions unanswered: Are carbonate settings more likely to import P than terrigenous settings? Do sites with high terrigenous influence export more carbon/nutrients than carbonate settings? Do "open" (e.g. coastal embayment, fringe mangroves) systems of mangroves export more material than closed systems (e.g. basin mangroves)? Does eutrophization of the floodwater increases nutrient import in all kinds of mangroves? Does hydrology (tidal amplitude, velocity of inundation and flooding frequency) affect export of particulate and dissolved material in all mangrove forests? How is export affected by extreme weather conditions (storms, cyclones, droughts)? These and many other questions will help us to understand the role of mangrove forest over the spatial and temporal variability of ecosystem function in the coastal zone. Despite the limitations and the variability of the data, in this review we were able to identify variables that appear to be especially important in determining C and nutrient exchange.

Carbon exchange

Mangroves export litter and POC to the coastal ocean

The studies found in the literature reported an export of C in the form of litter during tidal inundation that ranged from −0.1 g C m^{-2} $year^{-1}$ in mangroves in Hong Kong (Lee, 1989) to −498.8 g C m^{-2} $year^{-1}$ for El Verde Lagoon, Mexico (Flores-Verdugo et al., 1987; Tables 2, 4). The mean litter export was −202.0 ± 158.0 g C m^{-2} $year^{-1}$ (mean ± standard deviation). All the studies of C exchange as litter and most studies for POC (10 out of 12) reported exports, so we can conclude that mangrove forests tend to export litter and POC during tidal inundation. Mean litter export during tidal inundation is approximately 50% of the mean C litterfall observed in mangroves (Saenger & Snedaker 1993) (in the data set from this study, mean export of 51% with a wide range, from 0 to 99% export) and suggests that a large proportion of canopy production is exported.

The multiple regression analysis revealed that precipitation and mean annual temperature were the parameters that best explained the variation in C exchange as litter (Table 6). Precipitation and mean annual temperature explained 77% of the variation in the data across the broad range of environmental factors tested in this study. Sites with low precipitation (≥200 mm in our dataset) and high mean annual temperatures (≤29°C in our dataset) exported more C as litter compared to sites with high precipitation (≤4000 mm) and low mean temperature (≥15°C). C exchange as litter and precipitation (log + 3) were significantly correlated ($F_{1,19} = 22.1$; $P = 0.002$; $R^2 = 0.52$) (Fig. 1). These results suggest that in dry regions (e.g. Magueyes Island, Puerto Rico, Mngazana estuary, South Africa, Laguna Verde, Mexico) export of C in the form of litter could be particularly important in subsiding near-shore food webs. The processes underlying high levels of export in low precipitation/high temperature sites are likely to be complex, involving factors such as physiological characteristics of the forest, biogeochemical characteristics of the soil and microbial decomposition rates. For example, in dry regions, precipitation

Table 5 Phosphorus and nitrogen exchange (g m^{-2} $year^{-1}$) during tidal inundation for a range of mangrove forests

Spatial scale	Methodology	Net N flux (g m^{-2} $year^{-1}$)	Net P flux (g m^{-2} $year^{-1}$)	Nutrient form	Reference
Estuarine system and coastal ocean	Transects	+	+	D	Lin & Dushoff (2004)
		−1.57		D	Young et al. (2005)
		−4.21		P	
Estuarine basin and coastal ocean	Water sampled in creeks	−5.0	−0.19	D	Dittmar & Lara (2001)
		~1.60	~0.34	D	Ayukai et al. (1998)
		~−1.20	~−0.61	D	Ayukai et al. (1998)
		~ −0.49	~−0.006	D	Wattayakorn et al. (1990)
		−1.79	0.18	D	Sánchez-Carrillo et al. (2009)
		1.45	0.50	D	Boto & Wellington (1988)
		−0.53	−0.007	P	Sutula et al. (2003)
		−1.46	19.71	P	Sánchez-Carrillo et al. (2009)
	Nutrients exported as litter based on export estimations	−0.002	−0.0002	D	Wafar et al. (1997)
		−1.60		P	Boto & Bunt (1981)
		−0.02		P	Silva et al. (1998)
		−0.002	−0.0003	P	Wafar et al. (1997)
		−2.66	−0.28	P	Gong & Ong (1990)
Mangrove forest and adjacent creek	Water sampled from island enclosures, flumes and in the forest–creek interface	–	–	D	Wösten et al. (2003)
		0.61		D	Rivera-Monroy et al. (1995)
		−0.52		P	Rivera-Monroy et al. (1995)
		+	+	D	Adame et al. (2010)
		+	+	D	Adame et al. (2010)
Mangrove forest	Indirect estimate of exchange based on primary production and consumption.	0.02	~−0.12	P + D	Davis et al. ((2001a, b)
		~ 0			Gong et al. (1984)
		50.3	1.86		Simpson et al. (1997)
		+			Robertson & Alongi (1992)
		112.98[a]	13.47[a]		Hong & Hoan (1993), Wösten et al. (2003), Bianchi et al. (1999), Deegan et al. (1986), Odum & Heald (1974)
		5.04[a]			
		0.20[a]			
		2.82[a]			
		1.41[a]			
		0.66[a]			Davie (1984), Hyland et al. (1989)

The scale considered in the study and methodology used in the field is included

D dissolved, *P* particulate

[a] Data obtained from Valiela & Cole (2002)

rates are higher than evapotranspiration rates, resulting in high levels of porewater salinity (>32 PSU). Salinity determines many biogeochemical pathways in mangrove forests and is highly variable among sites, values can range from around 10 PSU in tropical sites with riverine inputs (e.g. Davis et al., 2003) to up to more than 70 PSU in subtropical arid zones, such as in Western Australia (M. F. Adame, personal observation). High salinity alters faunal composition, decreases bacterial abundance (Ólafsson et al., 2004; Twilley et al., 1997) and reduces primary productivity (Cintrón et al., 1978; Saenger & Snedaker, 1993). The lower productivity and the slower rates of decomposition in regions with high salinities (>32 PSU) could decrease C recycling within the forest and increase litter exports in

Table 6 Results for a multiple regression for carbon exchange as litter during tidal inundation for a range of mangrove forests

Source	df	Sums of squares	Mean square	*F* ratio	*P*
Regression	5	362774.6	72554.91	9.12	0.0004
Residual	14	111324.8	7951.77		
Variables	VIF	Standardised β	SE of β	*t* Ratio	*P*
Precipitation	1.47	1.018	0.162	6.269	<0.0001
Mean *T*	1.77	−0.540	0.172	−3.133	0.007
Area	1.54	−0.225	0.161	−1.399	0.183
Mean tidal amplitude	1.47	0.102	0.157	0.652	0.525
Litterfall	1.12	−0.031	0.137	−0.233	0.819

Explanatory environmental variables included in the model are annual precipitation, mean annual temperature (*T*), mean tidal amplitude, litterfall and mangrove area

$R^2 = 0.77$, $n = 20$

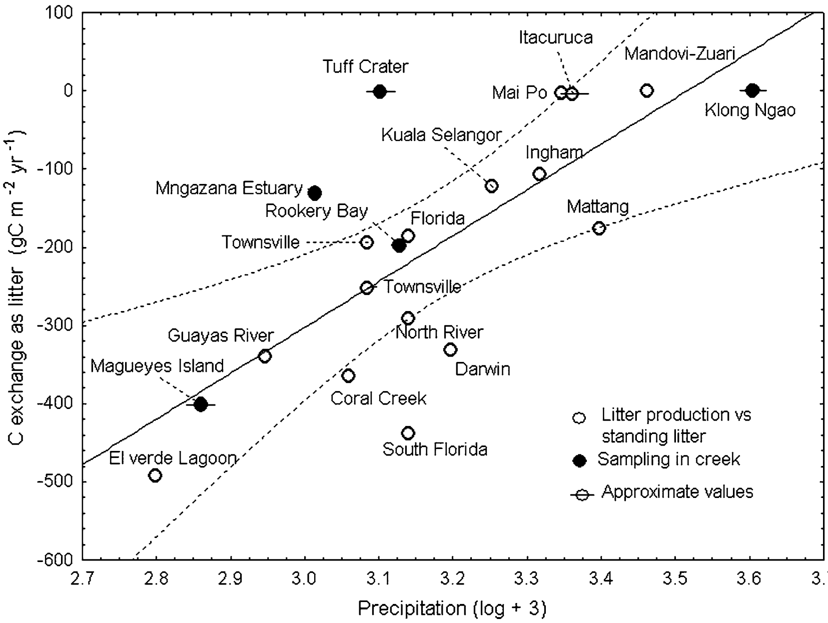

Fig. 1 The relationship between carbon exchange as litter (g C m^{-2} year^{-1}) and precipitation (log transformed + 3). Positive carbon exchange represents import and negative exchange represents export from the mangrove forest. The regression is statistically significant ($F_{1,18} = 22.1$; $P = 0.002$; $R^2 = 0.55$) and is represented by the curve $y = -2061.19 + 586.15x$. The *lines* parallel to the regression line represent the 99% confidence interval. *Open symbols* are samples obtained by the calculation of litter export based on standing litter and litter production; *closed symbols* were data obtained by measurements in tidal creeks. *Symbols with horizontal line* are approximate values

comparison to regions with lower salinities. Furthermore, it is likely that not only mean annual precipitation, but also the seasonality of precipitation, could influence patterns of C export, with higher C exports in the form of litter during the dry season compared to the wet season (e.g. Mahmood et al., 2005).

The variance inflation factor of the parameters used in our model was low (<2) suggesting low multi co-linearity, however, tidal amplitude and mean annual temperature were significantly correlated in the model ($F_{1,18} = 6.86$; $P = 0.02$; $R^2 = 0.27$), suggesting a possible effect of tidal amplitude on litter export. High tides are associated with higher velocity of the ebb compared to flood tides (Wolanski et al., 1992), which may favour export. The comparison of the slope of the two models obtained when assessing sampling method (calculation from standing litter and litter sampled at creek) showed no significant difference of C exchange between these two sampling techniques ($F_{1,16} = 1.23$; $P = 0.47$) (Fig. 1).

Site-specific characteristics also account for some variation observed in the data. Litter accumulation in mangroves has been related to forest type, which in turn is related to tidal inundation frequency (higher inundation frequency in riverine forests > fringe > basin > scrub) (Twilley, 1985; Twilley et al., 1986, Wafar et al. 1997). Within any given site, the effects of forest type, tidal inundation and tree species could be very important in determining C export in the form of litter. However, in our global data set these parameters did not appear to strongly influence C exchange, suggesting that at large spatial scales, their effects are secondary to the influence of precipitation.

A potentially important factor influencing C exchange in the form of litter that was not considered in this study is the activity of benthic fauna. Crabs inhabiting mangrove forests are responsible for burial and retention of litter (Robertson, 1986). They can result in the retention of as much as 79% of the litter fall in Northern Australia (Robertson & Daniel, 1989) and up to 81% in tropical Brazil (Nordhaus et al., 2006), far exceeding rates of microbial decomposition, and therefore having considerable impact on the amount of litter available for export. Crabs can also alter the hydrology of mangrove ecosystems, influencing water flow rates, soil permeability (Stieglitz et al., 2000) and the redox potential of soils, which influences a range of biological and chemical processes (e.g. Alongi, 1988; Clark et al., 1998). The abundance and diversity of crabs in mangrove forest could be affected by latitude, tidal inundation frequency, availability of organic matter and sediment characteristics (Hartnoll et al., 2002; Lee, 2008). Crab abundance was recorded to be similar across a latitudinal gradient in eastern Africa, but biomass increases at higher latitudes (Hartnoll et al., 2002). Crab diversity is also highly variable and it is thought to be linked to mangrove composition, with higher species diversity found in Southeast Asia (Lee, 2008). While it is very likely that crab abundance and composition have an important role in C exchange, there is insufficient data to assess this over a range of sites.

Low mean annual temperatures could favour POC export

The calculated mean exchange of C as POC was -59.1 ± 88.0 g C m^{-2} year^{-1}. Values ranged from a small import to a mangrove basin of 0.1 g C m^{-2} year^{-1} in Baja California Mexico (Sánchez-Carrillo et al., 2009) to an indirect estimated export of -285 g C m^{-2} year^{-1} in the Fly Delta in Papua New Guinea (Robertson & Alongi 1995) (Tables 2, 4).

In the linear model we included data obtained from similar spatial scales and sampling techniques of POC, i.e. sampling in creeks and sampling in flumes or enclosures. These sampling techniques did not show any obvious effects on the rates of exchange reported (Fig. 2). The data set represents the exchange of the mangrove forest with the adjacent creek/coastal zone. POC exchange was significantly correlated with mean minimum temperature; sites with lower minimum temperatures (≥11°C in our dataset) had higher exports than sites with higher temperatures (≤27°C in our dataset) ($R^2 = 61$; $F_{1,7} = 11.102$; $P = 0.013$) (Fig. 2). But, the linear model did not reveal that a combination of parameters could significantly explain the variation in POC exchange (Table 7). The factors most likely to be important in explaining POC exchange besides minimum annual temperature (model with less co-linearity and higher significance) were annual precipitation and the area of the forest, however none of the parameters were significant (Table 7). The effect of minimum annual temperature in POC export can be explained by the physiological requirements of mangrove trees, which limits their productivity and distribution. The geographical location of mangrove forest is mainly determined by minimum temperature, low temperature decreases productivity and diversity of mangrove forests (Lugo & Snedaker, 1974, Morrisey et al., 2010) as well as reducing rates of microbial degradation (Lovelock, 2008) and the activity of benthic fauna (Jimenez & Bennett, 2007). Thus, reduced soil microbial activity and crab activity at sites with low temperatures may increase the availability of POC for export.

Mangrove exchange of DOC with the coastal ocean

The exchange of DOC in mangroves during tidal inundation had a mean of -26.6 ± 88.0 g C m^{-2}

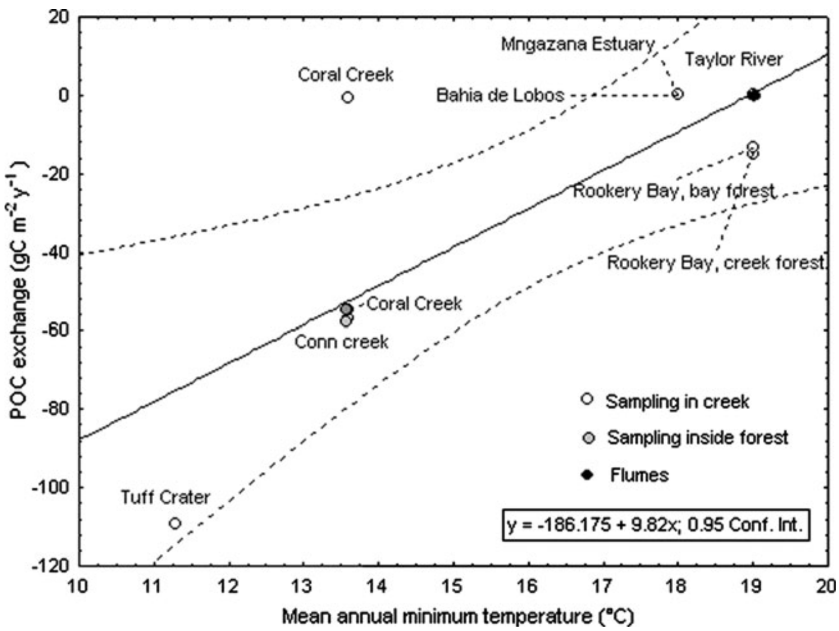

Fig. 2 The relationship among POC exchange (g C m^{-2} $year^{-1}$) and mean annual minimum temperature over a range of mangrove forests. Positive carbon exchange represents import and negative exchange represents export from the mangrove forest. The regression is statistically significant ($F_{1,7} = 11.102$; $P = 0.013$; $R^2 = 0.61$) and is represented by the curve $y = -186.18 + 9.82x$. The *lines* parallel to the regression line are the 95% confidence interval

Table 7 Results for a multiple regression for exchange of particulate organic carbon (POC) during tidal inundation for a range of mangrove forests

Source	df	Sums of squares	Mean square	*F* ratio	*P*
Regression	3	8006.57	2668.86	3.80	0.115
Residual	4	2807.33	701.83		

Variables	VIF	Standardised β	SE of coefficient	*t* Ratio	*P*
Mean min *T*	1.74	0.619	0.336	1.844	0.139
Precipitation (Box–Cox)	1.25	−0.441	0.285	−1.548	0.200
Area (log + 1)	2.06	0.312	0.365	0.854	0.441

Explanatory environmental variables included in the model are annual precipitation, mean annual minimum temperature (min *T*) and mangrove forest area

$R^2 = 0.74$, $n = 8$

$year^{-1}$ which is approximately 13% of the mean C export as litter (-202 ± 240.8 g C m^{-2} $year^{-1}$) and 45% of C export as POC (-59.1 ± 88.04 g C m^{-2} y^{-1}). Exchange rates of DOC ranged from an import to the forest of 67.3 g C m^{-2} $year^{-1}$ in Florida (Davis et al., 2003) to an export of the estuarine basin of -138.0 g C m^{-2} $year^{-1}$ in Brazil (Dittmar et al., 2006) (Tables 2, 4). Nine studies reported exports of DOC and five reported imports. None of the explanatory parameters considered in this study were significantly correlated with DOC exchange. The linear model that explained the most variation in DOC exchange included mean tidal amplitude, precipitation, mean minimum annual temperature and litterfall, but none of the variables were significant (Table 8).

Minimum annual temperature could have an important influence on DOC export, as it was the variable with the highest prediction potential in our multivariate model. Furthermore, it has been proposed that DOC export from mangrove forests could be strongly affected by the activity of sediment bacteria, which are highly efficient in consuming DOC (Alongi et al., 1989; Alongi, 2005). Although DOC is in lower concentration than C as POC or as litter, DOC is highly labile and therefore may be an ecologically important contribution to coastal waters, entering food webs through the microbial loop

Table 8 Results for a multiple regression for dissolved organic carbon exchange during tidal inundation for a range of mangrove forests

Source	df	Sums of squares	Mean square	*F* ratio	*P*
Regression	4	3201.46	800.36	0.50	0.740
Residual	6	9663.36	1610.56		

Variables	VIF	Standardised β	SE of coefficient	*t* Ratio	*P*
Mean min *T*	1.85	−0.529	0.481	−1.099	0.314
Litterfall	2.53	−0.435	0.562	−0.773	0.468
Mean tidal amplitude	2.25	0.072	0.531	0.136	0.896
Mean tidal amplitude	2.25	0.072	0.531	0.136	0.896

Explanatory environmental variables included in the model are mean tidal amplitude, mean annual minimum temperature (min *T*), precipitation and litterfall

$R^2 = 0.25$, $n = 11$

(Alongi, 2009). The dynamics of DOC in mangrove forests is an area that requires further investigation to determine both the factors influencing the magnitude of the DOC fraction of exported C and also its role in supporting the productivity of coastal waters.

We have only considered in this study fluxes of organic C, however, mangrove waters have been observed to be significant sources of CO_2 (Borges et al., 2003). It has been suggested that the export of inorganic C during tidal inundation could exceed the organic fraction (Alongi et al., 2008; Bouillon et al., 2008). The exchange of inorganic C during tidal inundation also requires attention in order to obtain an accurate net C exchange of the mangrove forest with the coastal zone (Bouillon et al., 2008; Alongi, 2009).

Nutrient exchange

Dissolved nitrogen export could be favoured in sites with large tidal amplitudes and low N concentrations

Dissolved N exchange was highly variable and ranged from an export of the estuarine basin to the coastal zone of −5.0 gN m^{-2} year^{-1} (Caete River, Brazil; Dittmar & Lara, 2001) to an import of 1.6 gN m^{-2} year^{-1} to the mangrove basin (Coral Creek, Australia; Ayukai et al., 1998) (Tables 3, 5). The mean N exchange was −0.58 ± 1.64 gN m^{-2} year^{-1}. Dissolved P exchange ranged from an export of −0.61 gP m^{-2} year^{-1} in Conn Creek, Australia (Boto & Bunt, 1981; Ayukai et al., 1998) to an import of 1.4 gP m^{-2} year^{-1} in Taylor River, US (Davis et al., 2001a, b). Mean dissolved P exchange was 0.03 ± 0.34 gP m^{-2} year^{-1}.

We found fewer studies for nutrient exchange that contained quantitative data than for C exchange. The small number studies for particulate nutrient exchange ($n < 8$) constrained our analyses. However, dissolved nitrogen exchange was significantly correlated with tidal amplitude and with N concentration in the floodwater ($F_{1,7} = 5.71$, $R^2 = 0.45$, $P = 0.048$) (Table 9). Sites with higher tidal amplitude (≤2.4 m) and lower N concentrations had higher N exports than those with low tidal amplitude (≥0.05 m) and high N concentrations in the floodwater. The correlation of N export and tidal amplitude has previously been shown in saltmarsh (Childers et al., 2000) and could reflect a range of processes associated with tidal inundation. For example, long inundation times could enhance the time for diffusion of N from sediments, or result in differences in redox of soils and associated biogeochemistry with extended inundation (e.g. rates of denitrification, nitrification, ammonification), or some other suite of processes associated with higher sediment deposition or productivity of trees with extended duration of inundation. Nutrient pollution also appears to be very important in determining N exchange of many coastal wetlands, as has been shown in experimental studies in mangroves around the world (Davis et al., 2003; Taylor et al., 1992; Adame et al., 2010). It is likely that enrichment with N by pollution alters the biogeochemical role of mangroves by altering benthic processes such as enhancing denitrification (Rivera-Monroy et al., 1995), by altering the benthic communities (Schaffelke et al., 2005) as well

Table 9 Results for a multiple regression for dissolved nitrogen (N) exchange for a range of mangrove forests

Source	df	Sums of squares	Mean square	F ratio	P
Regression	3	353103	70620.6	11.6	0.0004
Residual	5	79141.5	6087.8		

Variables	VIF	Standardised β	SE of β	t Ratio	P
Mean tidal amplitude	1.66	−0.903	0.189	−4.775	0.005
N concentration (log + 4)	2.78	−0.834	0.245	−3.410	0.019
Mean min T	2.95	0.218	0.251	0.941	0.426

Explanatory environmental variables included in the model are mean tidal amplitude, N concentration in floodwater and mean annual minimum temperature (min T)

$R^2 = 0.89$, $n = 9$

as increasing forest productivity (Feller et al., 2003) and the growth and abundance of pneumatophore algae (Melville & Pulkownik, 2006).

P exchange was correlated with P concentration in the floodwater. However, contrary to N, there tended to be high exports in sites with low concentrations. This result is difficult to interpret, but could reflect low nutrient uptake in forests that may be limited by other elements e.g. N or iron, (Feller et al., 2002; Alongi, 2010). Although P concentration in the floodwater was significant in the statistical model, the model itself was not significant (Table 10), thereby reducing confidence in a mechanistic link.

Studies of nutrient exchange were in general scarce, and thus the results shown here are supported only by a small number of data points ($n = 9$ for N, 8 for P). For example, the correlation of tidal amplitude with N export was mainly driven by large exports in the macrotidal site of Caete, Brazil. If this point is eliminated, the correlation is not significant. Thus, the conclusions made here can be considered as hypotheses that require testing in future field experiments. Another limitation to studies of nutrient exchange is that many studies are short term, while it is known that comprehensive studies over long periods indicate that nutrient fluxes are highly variable throughout the year, therefore giving rise to uncertainty in annual budgets (Ayukai & Wolanski, 1997; Simpson et al., 1997).

Mangrove exchange of nutrients as particulate matter

Studies of nutrient exchange as particulate matter were variable, although most of them reported export of nutrients (9 studies out of 10 of N; 3 out of 5 of P) (Tables 3, 5). The mean N exchange as particulate matter was -1.32 ± 1.39 gN m^{-2} year^{-1}. The exchange of N in particulate matter ranged from an export of to the coastal zone of -4.21 gN m^{-2} year^{-1} from Celestun Lagoon, Mexico (Young et al., 2005) to

Table 10 Results for a multiple regression for dissolved phosphorus (P) exchange for a range of mangrove forests

Source	df	Sums of squares	Mean square	F ratio	P
Regression	3	0.469	0.156	7.37	0.068
Residual	3	0.064	0.021		

Variables	VIF	Standardised β	SE of β	t Ratio	P
P concentration (log + 4)	1.66	1.331	0.295	4.515	0.020
Litter fall	2.78	0.710	0.306	2.321	0.102
Tidal amplitude	2.95	0.547	0.262	2.089	0.123

Explanatory environmental variables included in the model are P concentration in floodwater (log + 4), litter fall and mean tidal amplitude

$R^2 = 0.88$, $n = 8$

an import to the mangrove forest of 0.02 gN m^{-2} $year^{-1}$ in Taylor Slough, USA (Davis et al., 2001a, b). The mean P exchange as particulate matter was 3.86 ± 8.86 gP m^{-2} $year^{-1}$. Exchange of P in particulate matter ranged from an estimated export of -0.28 gP m^{-2} $year^{-1}$ in Matang, Malaysia (Gong & Ong, 1990) to an import to the mangrove basin of 19.7 gP m^{-2} $year^{-1}$ in Bahia de Lobos, Mexico (Sánchez-Carrillo et al., 2009). There are few data that assess nutrient exchange as particulate matter and sampling methodology is too variable to provide any meaningful statistical analysis (Table 3).

Nutrient exchange measured through indirect estimates

Finally, N exchange calculated from indirect estimates ranged from zero exchange in Sungai Merbrok, Malaysia (Gong & Ong, 1990) to export of -112.98 gN m^{-2} $year^{-1}$ in the Red River, Vietnam (Wösten et al., 2003) (Tables 3, 5). The rest of the estimates were between the range of 1 and 5 gN m^{-2} $year^{-1}$. The mean N exchange estimated was 19.83 ± 38.43 gN m^{-2} $year^{-1}$, which is in the opposite direction (import rather than export) and an order of magnitude different to the exchange of N in particulate and dissolved forms measured in the field during tidal inundation. We compared the nutrient exchange indirect estimates with the nutrient exchange of N obtained from the mouth of creeks and found that, even without the highest and lowest values of -54 and -112.98 gN m^{-2} $year^{-1}$, the results for both techniques were significantly different (Mean of sampling in creeks = -0.928 versus mean of estimates of 1.69; t value = -2.402; df = 12; $P = 0.033$). While mangrove forests use nutrients to sustain their metabolic demands, other studies show that mangrove forests, in fact, tend to export nutrients in the form of litter and detritus, and in many cases, as dissolved material (discussed above). Thus, there is still much to resolve to fully understand the biogeochemical complexity of mangrove forests. Factors that might also help explain variability in nutrient exchange of coastal wetlands and that should be incorporated in future studies are the ecological development of the forest, subsurface flow and temporal variability due to exogenous force such as storms and hurricanes (Childers et al., 2000).

Conclusion

The study of material exchange of mangrove forest to the coastal zone has advanced in the last 50 years. However, there are still many key questions that remain unanswered mainly because the studies have been done at a variety of spatial scales with a range of methodologies, which limits comparison between studies and sites. However, despite these limitations, based on the data set analysed here, we found that mangrove forests tend to export C to the coast ocean in the form of litter and POC. Moreover, precipitation appears to be important in determining the amount of C exported in the form of litter. Sites with lower annual precipitation will make a greater contribution to the coastal environment via C export as litter than sites with higher precipitation. Furthermore, low minimum annual temperatures are likely to be important in increasing POC export to the coastal zone.

Mangrove forests usually export C and nutrients in the form of detritus to the coastal zone, just as Odum (1978) suggested for saltmarsh ecosystems. However, dissolved carbon and nutrients are some times exported and some times imported. There was a tendency for N import to occur with high tidal amplitudes and with high N concentrations in the floodwater, but more studies are needed to improve confidence in the trends observed. The compilation of data in this study highlights the need to investigate mangrove exchange at different spatial scales using appropriate methodological approaches. The results of this study also highlight variables that are important in determining C and nutrient exchange. An enhanced understanding of material exchange in mangroves will aid in understanding the ecological services that different mangrove forests provide, thereby facilitating modelling and prioritisation of mangrove areas for conservation and restoration.

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María Fernanda Adame completed her undergraduate and postgraduate studies (BSc. Biology, MSc. Limnology and Oceanography) at the National University of Mexico (UNAM), where she studied the aquatic ecology of saline lagoons and lakes. She completed her PhD in Marine Sciences at The University of Queensland, Australia. As part of her project, she investigated the exchange of material between mangroves and the coastal ocean in Southeast Queensland and in the arid Exmouth Gulf in Western Australia. She is now working as a Postdoctoral fellow in collaboration with Dr. Lovelock at the University of Queensland and Dr. Herrera-Silveira at the CINVESTAV (IPN), Mexico. Her research focuses on the biogeochemistry, ecology, restoration and environmental valuation of mangroves and adjacent plant communities, such as saltmarsh and cyanobacteria mats. She is currently measuring and evaluating ecosystem services provided by mangroves in the Mexican Caribbean.

Catherine E. Lovelock graduated as a PhD from James Cook University, and is now Professor at the University of Queensland. She is the head of the Coastal Plant Laboratory at the School of Biological Sciences. Her research is focused on the ecology and ecophysiology of coastal plant communities. She is particularly interested in the influence of environment, including global climate change, on plant community productivity and diversity. Her group conducts experimental work over a wide range of coastal plant communities that includes macroalgae, mangroves and cyanobacterial mat communities. Some of her current research projects include assessment of how sea level and nutrient enrichment influences mangrove and salt marsh ecosystems, how metabolism of coral reefs varies over latitude and how mangroves mediate exchanges between the land and sea.