

Mangrove production and carbon sinks: A revision of global budget estimates

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[1] Mangrove forests are highly productive but globally threatened coastal ecosystems, whose role in the carbon budget of the coastal zone has long been debated. Here we provide a comprehensive synthesis of the available data on carbon fluxes in mangrove ecosystems. A reassessment of global mangrove primary production from the literature results in a conservative estimate of $\sim 218 \pm 72 \text{ Tg C a}^{-1}$. When using the best available estimates of various carbon sinks (organic carbon export, sediment burial, and mineralization), it appears that $>50\%$ of the carbon fixed by mangrove vegetation is unaccounted for. This unaccounted carbon sink is conservatively estimated at $\sim 112 \pm 85 \text{ Tg C a}^{-1}$, equivalent in magnitude to $\sim 30\text{--}40\%$ of the global riverine organic carbon input to the coastal zone. Our analysis suggests that mineralization is severely underestimated, and that the majority of carbon export from mangroves to adjacent waters occurs as dissolved inorganic carbon (DIC). CO_2 efflux from sediments and creek waters and tidal export of DIC appear to be the major sinks. These processes are quantitatively comparable in magnitude to the unaccounted carbon sink in current budgets, but are not yet adequately constrained with the limited published data available so far.

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1. Introduction

[2] Mangrove ecosystems thrive along coastlines throughout most of the tropics and subtropics. These intertidal forests play important ecological and socioeconomical roles, e.g., by acting as a nutrient filter between land and sea [e.g., Robertson and Phillips, 1995; Rivera-Monroy et al., 1999], contributing to coastline protection [e.g., Field,

1995; Vermaat and Thampanya, 2006], providing commercial fisheries resources [e.g., Constanza et al., 1997; Barbier, 2000; Diele et al., 2005], and as nursery grounds for coastal fish and crustaceans [Baran and Hambrey, 1998; Rönnbäck, 1999; Mumby et al., 2004]. Tropical forests in general are a disproportionately important component in the global carbon cycle, and are thought to represent $\sim 30\text{--}40\%$ of the terrestrial net primary production [see Malhi and Grace, 2000; Clark et al., 2001a]. Although the area covered by mangrove forests represents only a small fraction of tropical forests, their position at the terrestrial-ocean interface and potential exchange with coastal waters suggests these forests make a unique contribution to carbon biogeochemistry in coastal ocean [Twilley et al., 1992]. The coastal zone ($<200 \text{ m}$ depth, covering $\sim 7\%$ of the ocean surface, Gattuso et al. [1998]) has an important role in the oceanic carbon cycle, and various estimates indicate that the majority of mineralization and burial of organic carbon, as well as carbonate production and accumulation takes place in the coastal ocean [e.g., Gattuso et al., 1998; Mackenzie et al., 2004; Duarte et al., 2005]. The potential impact of mangroves on coastal zone carbon dynamics has been a topic of intense debate during the past decades. In particular, the “outwelling” hypothesis, first proposed for mangroves by Odum [1968] and Odum and Heald [1972] suggested that a large fraction of the organic matter produced by mangrove trees is exported to the coastal ocean, where it should form

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Table 1. Summary of Literature Estimates of Various Components in the Global Mangrove C Budget^a

	Data Sources				
	<i>Twilley et al.</i> [1992]	<i>Jennerjahn and Ittekkot</i> [2002]	<i>Duarte et al.</i> [2005]	<i>Dittmar et al.</i> [2006]	<i>Duarte and Cebrián</i> [1996]
Area, km ²	240,000	200,000	200,000	180,000	110,000
Net Primary Production	280 (litter + wood)	92 (litter)			
Herbivory					9.1 ± 2.4%
Mineralization					40.1 ± 6.5%
Burial	20	23	23.6		10.4 ± 3.6%
Organic carbon export	30–50 (POC + DOC)	46 (POC + DOC)		26.4 (as DOC)	29.5 ± 9.4%

^aFluxes are expressed in Tg C a⁻¹, except for the estimates by *Duarte and Cebrián* [1996] which are in percent of the overall net primary production. Note that the areal extent of mangroves (in km²) differs between some of the data sources.

the basis of a detritus food chain and thereby support coastal fisheries. A number of recent studies have indicated that a direct trophic link between mangrove forest production and offshore secondary production is unlikely for many mangrove systems [e.g., *Lee, 1995*].

[3] Despite the large number of case studies dealing with various aspects of organic matter cycling in mangrove systems [*Kristensen et al., 2008*], there is still no consensus on the magnitude and partitioning of mangrove primary production and the fate of the organic matter produced. Several authors have suggested that mangrove-derived organic matter is of global significance in the coastal zone: estimates indicate that mangrove forests could be responsible for ~10% of the global export of terrestrial particulate and dissolved organic carbon (POC and DOC) to the coastal ocean (*Jennerjahn and Ittekkot [2002]* and *Dittmar et al. [2006]*, respectively), and for ~10% of the global organic carbon burial in the coastal ocean [*Duarte et al., 2005*]. The exchange of carbon between tidal wetlands such as mangrove forests or salt marshes and the coastal ocean, and its ultimate fate in the ocean is therefore increasingly recognized as a potentially important component in the ocean carbon budget [*Twilley et al., 1992*].

[4] Published global estimates on central components of the mangrove carbon budget (summarized in Table 1) have two main shortcomings: (1) information on mangroves is very limited and carbon budgets are therefore based on relatively small data sets; and (2) while there is a wealth of data on litter fall, estimates on belowground allocation and wood production are still scarce because of methodological difficulties and some published budgets are consequently biased because they ignore wood and belowground produc-

tion. Moreover, mangrove systems occur in a wide range of environmental settings, and the degree of organic matter retention and export can therefore be expected to vary considerably according to factors such as geomorphology, tidal amplitude, local climate, vegetation type, and biotic influences, e.g., the activity of litter-retaining crabs [e.g., *Twilley et al., 1986; Smith et al., 1991; McIvor and Smith, 1995; Twilley et al., 1997; Nordhaus et al., 2006*]. This inherent variability among and within mangrove systems evidently complicates global extrapolations.

[5] Nevertheless, when comparing some of the budget estimates (Table 1) with the global riverine organic carbon export (~300–400 Tg C a⁻¹ [see *Schlünz and Schneider, 2000*, and references therein]), it is clear that the potential role of mangrove forests in global coastal zone carbon budgets is significant, and that a more refined assessment of global mangrove carbon budgets is due. Moreover, mangrove forests are being cleared and converted worldwide at alarming rates (~1% of the area a⁻¹ [*FAO, 2003*]) and the past few decades have witnessed a significant decrease in the global mangrove forest cover (with estimates as high as ~35% during the past 20 years according to *Valiela et al. [2001]*).

[6] The purpose of this study is to provide an overview of the current knowledge on quantitative aspects of mangrove carbon dynamics. We performed an intensive literature search for data related to mangrove primary production and the various sinks of organic carbon (Figure 1). The results of our analysis stress the need to include belowground and wood production in primary production estimates. Furthermore, the currently available estimates on organic carbon export, burial and mineralization (see Table 1)

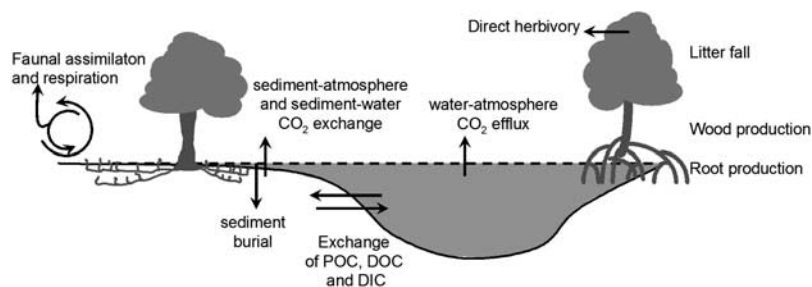


Figure 1. Summary of the major components in mangrove carbon budgets considered: primary production (litter fall, wood, and root production) and various sink terms.

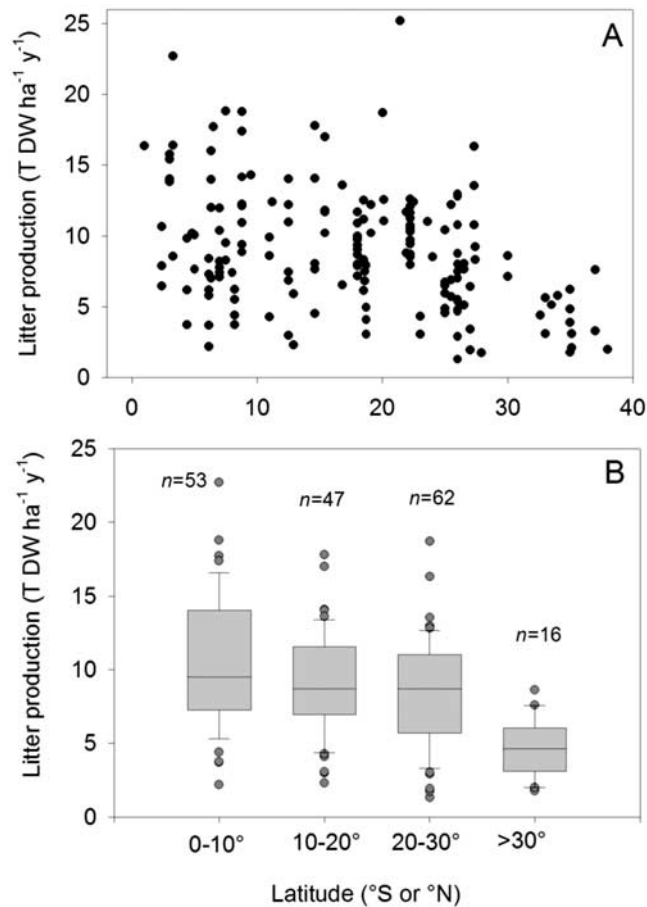


Figure 2. (a) Scatterplot of litter fall data as a function of latitude and (b) boxplot representation of these data, grouped for different latitudinal zones. Boxplot lines represent median, 50, and 75 percentiles, and data outside the 75 percentiles are presented as black circles.

account for <50% of mangrove net primary production (NPP), indicating that major unaccounted loss pathways exist and/or that some of the currently available budget components are severely biased. We propose a number of processes and pathways that might have been overlooked or underestimated in current budgets, and discuss how these important gaps in the global carbon budget for these systems may be resolved.

2. Data Sources

[7] The literature was screened for data relevant to mangrove primary production, assimilation/respiration by fauna, and organic carbon export, burial, and mineralization. A number of earlier reviews [Twilley *et al.*, 1992; Saenger and Snedaker, 1993; Lee, 1995; Duarte *et al.*, 2005; Jennerjahn and Ittekkot, 2002] provided a basic set of data, which we supplemented with a significant amount of (mostly recent) new data from case studies. When data were only presented as figures in the original publications, these were digitized and the data extracted using PlotDigitizer

(<http://plotdigitizer.sourceforge.net/>). Estimates of carbon burial were taken from Twilley *et al.* [1992], Jennerjahn and Ittekkot [2002], and Duarte *et al.* [2005]. CO₂ fluxes from sediments are typically used as a proxy for benthic CO₂ mineralization, and we compiled data on benthic CO₂ fluxes from a variety of literature sources (see Table S2). Similarly, estimates of CO₂ exchange between mangrove creek surface waters and the atmosphere have been compiled (see Table S3). Moreover, we compiled a number of data sets on the distribution of dissolved organic and inorganic carbon (DOC and DIC) in mangrove creek waters, to provide a preliminary estimate of the relative importance of mangrove C export as dissolved inorganic carbon.

[8] Standard error propagation procedures were used to place uncertainties on our budget estimates; that is, standard deviations on budget components were propagated where possible. Since the area of mangrove cover (160,000 km²; based on FAO [2003]) and carbon concentrations in different tissues were taken as constants (i.e., with no uncertainty ascribed), some of the uncertainty estimates should be considered conservative.

3. Primary Production

[9] A total of 178 litter fall measurements were compiled. Previous studies have indicated that litter fall exhibits a pronounced geographical trend, with highest litter fall rates near the equator and decreasing with increasing latitude [e.g., Twilley *et al.*, 1992; Alongi, 2002]. Our extended data set confirms this trend (Figure 2; for full data, see Table S1), although it clearly shows more scatter than earlier compilations [Twilley *et al.*, 1992]. This is not surprising, since primary production is influenced by a range of other factors, e.g., nutrients such as N and P [e.g., Chen and Twilley, 1999; Feller *et al.*, 2002]. Using the same latitudinal zones as those used by the latter authors (i.e., 0–10°, 10–20°, 20–30°, and >30°), litter fall rates were found to be significantly higher in the 0–10° region ($10.4 \pm 4.6 \text{ t ha}^{-1} \text{ a}^{-1}$, $n = 53$) when compared to other latitudes, and significantly lower in the >30° latitudes ($4.7 \pm 2.1 \text{ t ha}^{-1} \text{ a}^{-1}$, $n = 16$). No significant differences were found between 10 and 20° ($9.1 \pm 3.4 \text{ t ha}^{-1} \text{ a}^{-1}$, $n = 47$) and 20–30° ($8.8 \pm 4.2 \text{ t ha}^{-1} \text{ a}^{-1}$, $n = 62$) latitudes (Figure 2). In order to scale these data to a global litter fall estimate, we assumed a global mangrove cover of 160,000 km² [FAO, 2003], and a latitudinal distribution similar to that presented by Twilley *et al.* [1992], i.e., we assumed that the loss of mangrove cover over the past decade was similar in each latitudinal region. This results in a global litter fall estimate of $156 \pm 45 \text{ Tg a}^{-1}$, equivalent to $68.4 \pm 19.7 \text{ Tg C a}^{-1}$ using a carbon content of 44% (the latter is based on a compilation of literature and our own unpublished data, 2002–2006). This estimate is $\sim 25 \text{ Tg C a}^{-1}$ lower than the most recent previous estimate [Jennerjahn and Ittekkot, 2002], which is largely due to a different areal extent used (160,000 km² in this study, versus 200,000 km² used by Jennerjahn and Ittekkot [2002]).

¹Auxiliary materials are available in the HTML. doi:10.1029/2007GB003052.

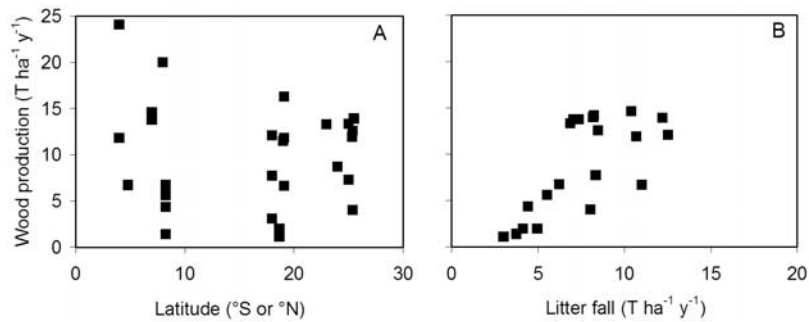


Figure 3. (a) Literature data on wood production plotted as a function of latitude and (b) relationship between litter fall rates and wood production, when simultaneously reported in the same source.

[10] Estimates of aboveground wood production are relatively scarce. *Twilley et al.* [1992] mentioned 11 measures of wood production and estimated the total global wood production at 160 Tg C a^{-1} (for a global area of $200,000 \text{ km}^2$). With 20 additional estimates of wood production (see Table 2 for data and sources), wood production estimates were found to range between 1.1 and $24.1 \text{ t ha}^{-1} \text{ a}^{-1}$, with no clear latitudinal trends in the still limited data set (Figure 3a). We compare two different approaches to estimate wood production by mangroves on a global scale: (1) On the basis of the average of all available wood production estimates ($10.0 \pm 5.6 \text{ t ha}^{-1} \text{ a}^{-1}$, $n = 31$), wood production can be estimated at $66.4 \pm 37.3 \text{ Tg C a}^{-1}$ (using a %C of 41.5%, based on a compilation of literature data) and, alternatively, (2) for a selection of these data where concurrent litter fall estimates are also available (Table 2 and Figure 3b), we estimate an average wood/litter production ratio of 1.03 ± 0.54 ($n = 23$). This ratio, which is within the range reported for other tropical forest ecosystems [*Malhi et al.*, 2004] can subsequently be used to convert global litter fall rates (see above paragraph, this section) to an estimated global wood production of $161 \pm 95 \text{ Tg a}^{-1}$, or $66.7 \pm 39.6 \text{ Tg C a}^{-1}$. Both estimates are very similar, but significantly lower than the previously mentioned estimate (160 Tg C a^{-1} [see *Twilley et al.*, 1992]), even when correcting for a 20% decrease in global area of mangroves (128 Tg C a^{-1}) that occurred between the two estimates. It should also be noted that the data on which our extrapolations are based are from studies measuring biomass increments over time, and that this approach does not consider processes such as natural gap formation and regeneration, which can result in significant natural biomass turnover [*Duke*, 2001].

[11] While belowground roots, pneumatophores and prop roots can form a substantial fraction of the total mangrove biomass [e.g., *Komiyama et al.*, 1987; *Mall et al.*, 1991], estimates of belowground production are even scarcer, which is undoubtedly due to the methodological difficulties involved. Of the four studies that have reported belowground root production estimates [*McKee and Faulkner*, 2000; *Gleason and Ewel*, 2002; *Sánchez*, 2005; E. Castañeda-Moya et al., unpublished data, 2002–2006], three were used for further analysis, since the rates presented by *Gleason and Ewel* [2002] referred only to the top 15 cm. Given the limited number of data ($n = 16$), we first compared these

root production estimates (all for mixed species assemblages) with concurrently reported litter fall rates, which resulted in a root/litter production ratio (in C equivalents) of 1.20 ± 0.76 ($n = 16$). Applying this ratio to our global litter fall rate, global root production can be estimated at $82.8 \pm 57.7 \text{ Tg C a}^{-1}$. Although this may appear to be high, our estimated root/litter production ratio for mangroves is considerably lower than ratios reported for productive terrestrial forest ecosystems (typically 2.2–2.5, see *Raich and Nadelhoffer* [1989]). This indicates that our root production estimate is likely to be conservative. The partitioning of biomass between belowground and aboveground biomass may also be dependent on nutrient availability, yet the precise impact of nutrient limitation or nutrient additions on belowground allocation and root turnover are not well understood [*Nadelhoffer*, 2000; *Hendricks et al.*, 2006] and to our knowledge, no studies have assessed such relationships in mangroves. Moreover, it must be stressed that because of the measurement approach (ingrowth of roots), the published root production estimates refer only to fine root production. Although fine roots may not always be the dominant root fraction in terms of biomass (e.g., *Komiyama et al.* [1987] and *Fiala and Hernandez* [1993]; depending on how fine roots are defined), they are considered the most active component and may therefore contribute more to NPP than coarse roots [*Clark et al.*, 2001b]. Coarse root production in mangroves has to our knowledge not been measured or estimated separately, and will require careful consideration of methodological issues, given the variety of different root structures formed by various mangrove types (e.g., stilt roots, cable roots, pneumatophores). Production of stilt roots by *Rhizophora* spp., however, is in most cases included in the existing estimates of wood production, since these are included in allometric relationships to estimate total aboveground biomass [e.g., see *Sherman et al.*, 2003].

[12] When comparing our estimated rates of litter, wood, and (fine) root production, it becomes evident that litter production only amounts to $\sim 32\%$ of the total mangrove NPP. A few reports have made a direct comparison of litter fall rates and total NPP, and indeed suggested that litter fall represents $\sim 30\%$ of the overall NPP [see *Alongi et al.*, 2005, and references therein]. These estimates match well with our global extrapolations, and hence, indicate that our numbers are realistic and likely to be valid within reason-

Table 2. Synthesis of Wood Production Data (and Litter Fall, if Available) in Mangroves^a

Site	Wood Production	Litter Fall	Wood/Litter Production	Reference
<i>0–10°S or °N</i>				
Malaysia	11.8			<i>Ong et al. [1979]^b</i>
Malaysia	24.1			<i>Ong et al. [1979]^b</i>
Phuket (Thailand)	20			<i>Christensen [1978]^b</i>
Malaysia	6.7	11	0.61	<i>Putz and Chan [1986]</i>
Java (Indonesia)	13.96	8.2	1.70	<i>Sukardjo and Yamada [1992]</i>
Java (Indonesia)	13.75	7.37	1.87	<i>Sukardjo and Yamada [1992]</i>
Java (Indonesia)	13.75	7.1	1.95	<i>Sukardjo and Yamada [1992]</i>
Java (Indonesia)	14.18	8.2	1.72	<i>Sukardjo and Yamada [1992]</i>
Java (Indonesia)	14.60	10.4	1.40	<i>Sukardjo and Yamada [1992]</i>
Kala Oya (Sri Lanka)	6.76	6.23	1.09	<i>Amarasinghe and Balasubramaniam [1992]</i>
Kala Oya (Sri Lanka)	5.62	5.52	1.02	<i>Amarasinghe and Balasubramaniam [1992]</i>
Erumathivu (Sri Lanka)	4.34	4.41	0.98	<i>Amarasinghe and Balasubramaniam [1992]</i>
Erumathivu (Sri Lanka)	1.40	3.74	0.37	<i>Amarasinghe and Balasubramaniam [1992]</i>
<i>10–20°S or °N</i>				
Puerto Rico	3.07			<i>Golley et al. [1962]^b</i>
Estero Pargo (Mexico)	7.72	8.34	0.93	<i>Day et al. [1987]^b</i>
Boca Chica (Mexico)	12.06	12.52	0.96	<i>Day et al. [1987]^b</i>
Hainan (China)	11.5			<i>Lin et al. [1990]^b</i>
Dominican Republic	16.3		0.58 ^c	<i>Sherman et al. [2003]</i>
Dominican Republic	11.8		0.58 ^c	<i>Sherman et al. [2003]</i>
Dominican Republic	6.6		0.58 ^c	<i>Sherman et al. [2003]</i>
Laguno de Terminos (Mexico)	1.96	4.96	0.40	<i>Day et al. [1996]</i>
Laguno de Terminos (Mexico)	1.11	3.01	0.37	<i>Day et al. [1996]</i>
Laguno de Terminos (Mexico)	1.99	4.14	0.48	<i>Day et al. [1996]</i>
<i>20–30°S or °N</i>				
Florida (United States)	13.9	12.2	1.14	<i>Ross et al. [2001]</i>
Fujian (China)	8.69			<i>Lin et al. [1985]^b</i>
Hong Kong	13.3	6.87	1.94	<i>Lee [1990]^b</i>
Florida (United States)	7.31			<i>Sell [1977]^b</i>
Florida (United States)	13.33			<i>Sell [1977]^b</i>
Shark River, Florida (United States)	12.57	8.46	1.49	<i>Ewe et al. [2006]</i> and E. Castañeda-Moya et al., unpublished data, 2002–2006
Shark River, Florida (United States)	4.01	8.03	0.50	<i>Ewe et al. [2006]</i> and E. Castañeda-Moya et al., unpublished data, 2002–2006
Shark River, Florida (United States)	11.90	10.68	1.11	<i>Ewe et al. [2006]</i> and E. Castañeda-Moya et al., unpublished data, 2002–2006

^aExpressed in $\text{t ha}^{-1} \text{a}^{-1}$. Data are sorted per latitudinal zone.

^bData previously compiled by *Twilley et al. [1992]*.

^cAverage value for wood/litter production mentioned by *Sherman et al. [2003]* for different vegetation types.

able limits. The overall global NPP of mangroves (using an areal extent of $160,000 \text{ km}^2$) can therefore be estimated at $\sim 218 \pm 72 \text{ Tg C a}^{-1}$, using the indirect approach described above for the wood production component.

[13] This estimate of NPP should be considered conservative, since (1) coarse root production data are not available and their contribution is therefore not included, (2) we do not account for direct herbivory in this context, although it represents a formal component of NPP (i.e., litter fall rates were not corrected for leaf damage or direct consumption, see further), and (3) a number of other components of NPP such as the exudation of dissolved organic carbon by roots [*Clark et al., 2001b*] are as yet unknown for any mangrove system.

4. Sinks of Mangrove Production

4.1. Organic Carbon Export

[14] Despite the longstanding debate on the role of mangrove forests in exporting organic carbon to the coastal

zone [e.g., *Lee, 1995; Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006*], the number of quantitative estimates remains very limited: we only found six and seven estimates for DOC and POC export, respectively, and 11 estimates for total organic carbon export (see Table 3). If the average rates of DOC export ($150 \pm 134 \text{ g C m}^{-2} \text{a}^{-1}$) and POC export ($137 \pm 172 \text{ g C m}^{-2} \text{a}^{-1}$) are combined, they are within the range of independent estimates for total organic carbon (TOC) export ($252 \pm 277 \text{ g C m}^{-2} \text{a}^{-1}$). Scaling these to a global level results in estimated exports of $44.6 \pm 30.5 \text{ Tg C a}^{-1}$ and $40.3 \pm 44.3 \text{ Tg C a}^{-1}$ based on the sum of DOC ($24 \pm 21 \text{ Tg C a}^{-1}$) and POC ($22 \pm 27 \text{ Tg C a}^{-1}$) export estimates or when scaling the TOC export rates, respectively. Although based on a small data set with significant shortcoming, our estimates are within the same range as previous global estimates, which are either partially based on the same data [*Twilley et al., 1992*] or were derived independently [*Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006*]. Note that these export estimates only refer to direct export of organic carbon, and do not include move-

Table 3. Summary of Literature Data on Particulate, Dissolved, and Total Organic Carbon (POC, DOC, and TOC) Export From Mangroves^a

Site/Country	POC Export	DOC Export	TOC Export	Data Source
Australia	420			<i>Boto and Bunt</i> [1981]
New Zealand	110			<i>Woodroffe</i> [1985]
Australia	340			<i>Robertson</i> [1986]
Hong Kong	2			<i>Lee</i> [1989]
Hong Kong	5			<i>Lee</i> [1990]
Zanzibar (Tanzania)	65	230	295	<i>Machiwa</i> [1999]
Florida (United States)	16	48	64	<i>Twilley</i> [1985]
Brazil		44		<i>Dittmar and Lara</i> [2001]
Florida (United States)		56		<i>Romigh et al.</i> [2006]
Brazil		144		<i>Dittmar and Lara</i> [2001], <i>Dittmar et al.</i> [2006]
Florida (United States)		381		<i>Davis et al.</i> [2001]
Malaysia			176	<i>Gong and Ong</i> [1990]
Florida (United States)			186	<i>Heald</i> [1969]
Florida (United States)			292	<i>Odum and Heald</i> [1972]
Florida (United States)			91	<i>Lugo and Snedaker</i> [1974]
Australia			332	<i>Woodroffe et al.</i> [1988]
Australia			-7	<i>Boto and Wellington</i> [1988]
Australia			994	<i>Alongi et al.</i> [1998]
Papua New Guinea			343	<i>Robertson and Alongi</i> [1995]
Florida (United States)			7.1	<i>Sutula et al.</i> [2003]

^aAdapted from *Lee* [1995] and updated with more recent data. Fluxes are expressed in $\text{g C m}^{-2} \text{a}^{-1}$.

ment of animal biomass dependent on mangrove-derived carbon, which has also been proposed as a potential mechanism for organic matter export [e.g., see *Lee*, 1995].

4.2. Burial

[15] Three different studies have estimated global organic carbon burial rates in mangrove systems, each using a different approach. *Twilley et al.* [1992] compiled the available data on organic carbon burial rates, while *Jennerjahn and Ittekkot* [2002] estimated global carbon burial rates on the basis of a number of assumptions, i.e., (1) that litter fall provides the dominant organic carbon input in the sediments, (2) a global litter fall of 92 Tg C a^{-1} , and (3) that 50% of the litter is exported and 25% mineralized. *Duarte et al.* [2005], on the basis of the data compiled by *Chmura et al.* [2003], presented both a bottom-up estimate (i.e., upscaling of carbon burial rates) and an estimate derived from global mangrove community mass balance. Despite the different approaches used, they all result in a very similar estimate at $\sim 23 \text{ Tg C a}^{-1}$. Since no significant new data are available, we have scaled this number to the surface area used here ($160,000 \text{ km}^2$), which results in a global organic carbon burial rate of 18.4 Tg C a^{-1} . Note that none of the literature sources provided an estimate of uncertainty on these global burial rates, hence no error was propagated in further calculations.

4.3. CO₂ Efflux as a Proxy for Mineralization

[16] Total mineralization in mangrove sediments has typically been estimated through measurements of CO₂ fluxes from sediments. Such data are available for a wide range of mangrove systems, and have been measured both under inundated conditions (i.e., as the increase in DIC through time in overlying water during sediment incubations, e.g., *Alongi et al.* [2004]) and exposed conditions (typically as gaseous CO₂ increase through time in a closed

or flowthrough benthic chamber, e.g., *Kristensen and Alongi* [2006]). Since the flux rates in our data set were not significantly different between exposed and inundated sediments ($p > 0.05$ and > 0.2 for light and dark conditions), data were pooled for further analysis (Figure 4). Dark fluxes from sediments range between 6 and $241 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, with an average of $61 \pm 46 \text{ mmol m}^{-2} \text{ d}^{-1}$ ($n = 82$). Under light conditions about half of the available flux data show a net CO₂ uptake (Figure 4), with an average influx of $-15 \pm 54 \text{ mmol m}^{-2} \text{ d}^{-1}$ ($n = 14$). These lower CO₂ fluxes result from CO₂ uptake during photosynthesis by benthic

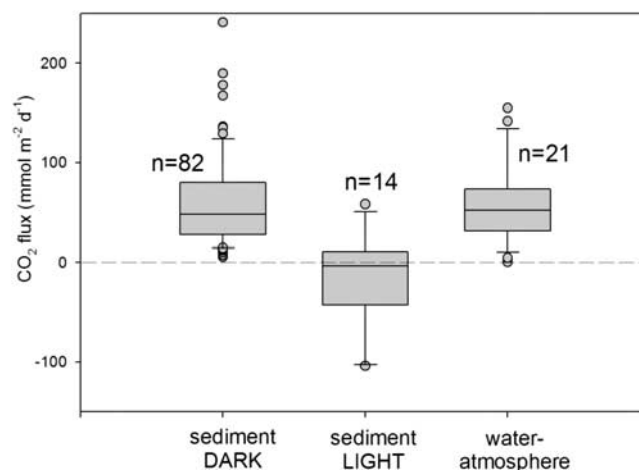


Figure 4. Boxplot compilation of available data on CO₂ fluxes from mangrove sediments (exposed and inundated, under dark and light conditions) and from the water column in mangrove-surrounding waters. Positive fluxes correspond to a CO₂ efflux, negative fluxes indicate net CO₂ uptake. Full data and data sources are presented by *Kristensen et al.* [2008].

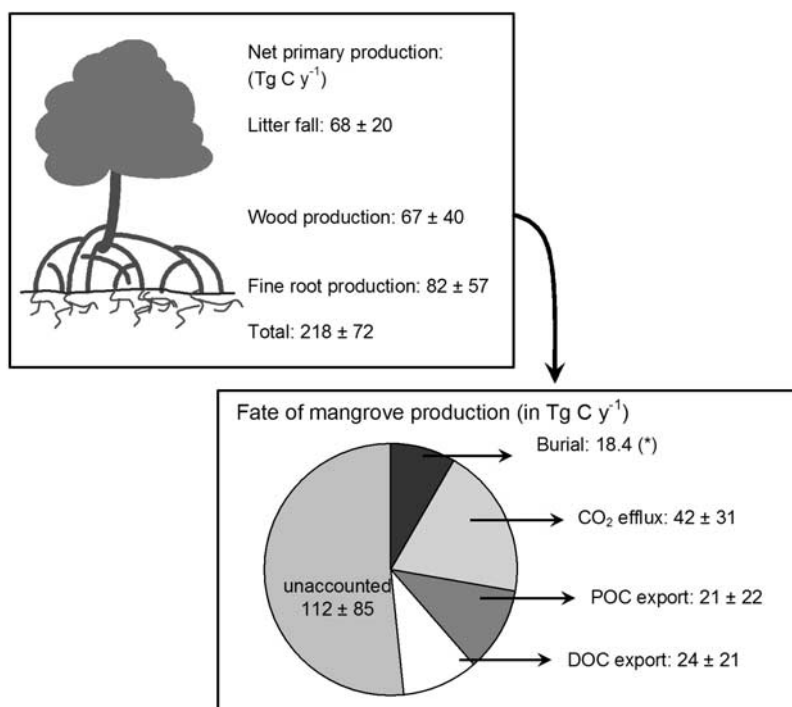


Figure 5. Synthesis of current literature estimates of the fate of mangrove production and a comparison with our estimates of total NPP. Asterisk in Figure 5, bottom, indicates no error estimate reported for organic carbon burial rates.

primary producers and should therefore not be taken into account since we are interested in assessing mineralization of mangrove-derived organic matter. Moreover, this light flux is based on a very limited data set and should be used with caution given the extreme variability in these data.

[17] Mangrove creek waters have consistently been found to show high CO₂ oversaturation, and hence, are a net source of CO₂ to the atmosphere, with average CO₂ flux estimates for a given system generally >20 mmol m⁻² d⁻¹ [Borges *et al.*, 2003]. We compiled 21 estimates on water-air CO₂ fluxes (see Table S2) with an overall average of 59 ± 52 mmol m⁻² d⁻¹. For most of these data, CO₂ fluxes were estimated on the basis of water column pCO₂ and gas transfer velocities estimated from field wind speed measurements (see Borges *et al.* [2003] for discussion).

[18] It must be stressed that these sediment and water column estimates relate only to net CO₂ fluxes, and not to overall mineralization rates (see discussion below, section 5.1). Upscaling CO₂ fluxes for sediments and the water column separately is somewhat problematic, since the surface areas to be used are not static in these intertidal systems. However, given the similar magnitude in CO₂ efflux from both sediments in the dark and water column, we estimated the overall CO₂ efflux from mangrove systems to be in the order of ~60 ± 45 mmol m⁻² d⁻¹. This results in a global estimate of 42 ± 31 Tg C a⁻¹.

5. Gaps in the Carbon Budget

[19] All the abovementioned estimates of organic carbon sinks (export, burial, and CO₂ efflux) together only accounted for ~45% of the estimated NPP (Figure 5), thus

leaving a surprisingly large part of the mangrove production unaccounted for (112 ± 85 Tg C a⁻¹, which is equivalent in magnitude to ~30–40% of the global riverine flux of organic carbon). Assuming that mangrove forests are in equilibrium and are currently not showing net biomass accumulation, this implies that either some sink components of the global mangrove C budget are severely underestimated, and/or that some quantitatively important pathways for mangrove-derived organic matter removal have been overlooked in previous budget studies. Although we must stress that the existing literature does not provide sufficient data to fill this gap, a closer look at several mechanisms and processes may explain and solve part of this discrepancy. In particular, the potential importance of export of mangrove carbon as dissolved inorganic carbon (DIC), the emission of CO₂ from sediments via burrows and along pneumatophores, and the consumption and respiration of organic matter by faunal communities will be discussed below, sections 5.1 and 5.2.

5.1. Mineralization and Export of Inorganic Carbon

[20] Mineralization is generally considered to be a major fate of plant production in coastal ecosystems [Duarte and Cebrián, 1996]. However, when based on sediment CO₂ fluxes, benthic mineralization only represents ~15% of the total mangrove NPP. For a number of reasons, however, these CO₂ emission rates are unlikely to serve as appropriate proxies for mineralization:

[21] 1. Core incubations typically use sediments which are free of pneumatophores and crab burrows. Recent data, however, indicate that these structures are important as vectors for enhancing CO₂ exchange, and add considerably

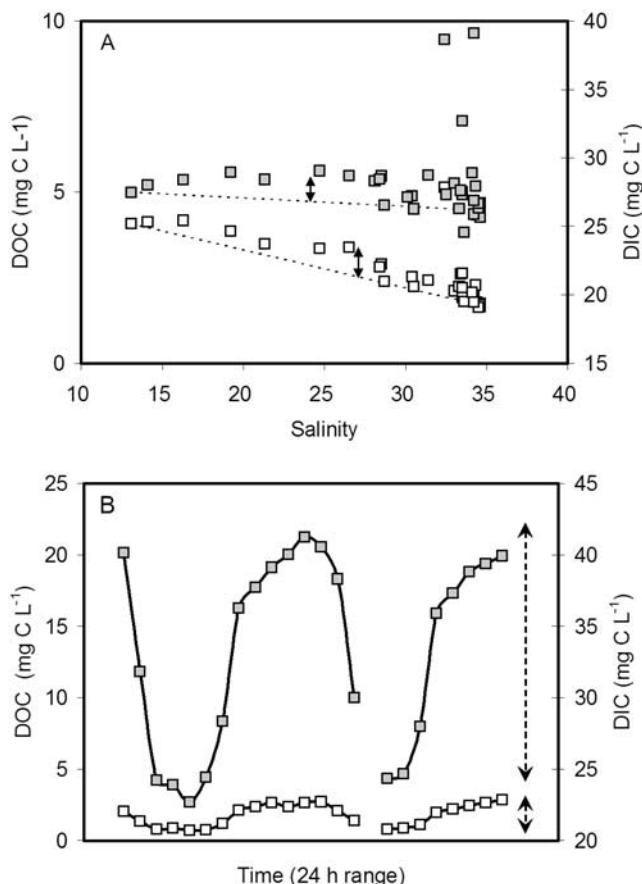


Figure 6. Examples of differences in DIC (gray symbols) and DOC (open symbols) inputs in mangrove creeks. (a) Nonconservative distributions of DIC and DOC in a tidal mangrove creek at Mtoni, Tanzania (S. Bouillon and A.V. Borges, unpublished data, 2005); note the different scales on the y axes. (b) Tidal variations in DIC and DOC in a mangrove creek in Ras Dege, Tanzania [Bouillon et al., 2007c]. Arrows in Figure 6, top, indicate the amount of “excess” DIC and DOC; in Figure 6, bottom, arrows indicate the range of variations in DIC and DOC.

to the total CO_2 flux from the sediment [Kristensen et al., 2008]. Crab burrows can be very complex, abundant, and deep structures, and thus greatly enhance the surface area of the sediment-air or sediment water interface where exchange of CO_2 or DIC can take place [Thongtham and Kristensen, 2003]. Similarly, CO_2 emission rates were found to be greatly enhanced when *Sonneratia* or *Avicennia* pneumatophores were included in the measurements, with CO_2 emission rates equivalent to $0.2\text{--}0.7\text{ mmol CO}_2\text{ d}^{-1}$ per individual pneumatophore (E. Kristensen, unpublished data, 2005).

[22] 2. An unknown part of CO_2 released from pneumatophores and rooted sediments might represent plant respiration rather than heterotrophic respiration (i.e., mineralization). Since our mangrove carbon budget is based on net primary production, the CO_2 release due to autotrophic respiration should not be included, but there are currently insufficient

data to estimate this contribution [Lovell et al., 2006]. This stresses the need for novel methodological approaches that allow quantitative estimates of the partitioning of measured CO_2 fluxes between autotrophic and heterotrophic respiration.

[23] 3. Lateral transport of DIC resulting from mineralization via pore water drainage is not taken into account using the standard approach used to estimate sediment mineralization: the latter is based on the assumption that efflux of carbon dioxide equates with depth-integrated mineralization. Mangrove pore waters are typically rich in total alkalinity and DIC [e.g., Ovalle et al., 1990; Bouillon et al., 2007a], indicating that buildup of inorganic carbon resulting from mineralization occurs. Lateral transport of DIC-enriched mangrove pore water to creeks thus results in an underestimation of mineralization rates if based on sediment-water carbon dioxide effluxes only. The impact of mineralization in intertidal sediments and subsequent lateral transfer on the DIC dynamics in mangrove creeks has been demonstrated in a number of studies [e.g., Ovalle et al., 1990; Borges et al., 2003; Bouillon et al., 2007c].

[24] In order to assess the potential magnitude of lateral CO_2 transport, we evaluated the water column concentrations of DIC and DOC along the salinity gradient in a number of mangrove systems. Because of lateral inputs into creek waters, DIC and DOC typically show a nonconservative pattern in the mangrove creek water column (see Figure 6). The relative amounts of “excess” DIC and DOC (ΔDIC and ΔDOC) can thus be considered proportional to their relative export rates, on the condition that the tidal variations in both parameters are similar, so that their overall relative fluxes are not influenced by the variations in flow rates during the tidal cycle [e.g., Dittmar and Lara, 2001]. We compiled data from several mangrove creeks in different regions (see Table 4), and calculated the amount of excess DOC and DIC for each of these data sets. This was based either on deviations from conservative mixing scenarios, or by comparing the amounts of DIC and DOC relative to reference concentrations at the outer boundary, i.e., where lowest DIC and DOC concentrations were found (see Figure 6). Although such data sets are only available from a limited number of sites ($n = 5$), the resulting calculations consistently show that ΔDIC exceeds ΔDOC , by a factor of $\sim 3\text{--}10$ (Table 4). Under the assumption that

Table 4. Overview of Ratios of Excess DIC to Excess DOC ($\Delta\text{DIC}/\Delta\text{DOC}$) in Different Mangrove Creeks^a

	$\Delta\text{DIC}/\Delta\text{DOC}$	Stdev	n	Source
Ca Mau (Vietnam)	6.6	2.9	26	S. Bouillon and A. V. Borges, unpublished data, 2005
Gazi (Kenya)	8.3	5.1	24	Bouillon et al. [2007b]
Ras Dege (Tanzania)	10.5	2.0	17	Bouillon et al. [2007c]
Mtoni (Tanzania)	8.8	6.7	19	S. Bouillon and A. V. Borges, unpublished data, 2005
Gaderu (India)	3.0	1.2	13	Bouillon et al. [2003]

^aThe n represents the number of data between end-members for each system for which ratios of excess DIC to excess DOC ($\Delta\text{DIC}/\Delta\text{DOC}$) could be determined. See text for details.

both originate mainly from the tidal exchange and therefore follow the same tidal variations [e.g., *Bouillon et al.*, 2007c], this implies that DIC export should exceed DOC export to the same degree. Assuming a global DOC export rate in the order of $24 \pm 21 \text{ Tg C a}^{-1}$ (see above, section 4.1), and using the available data on $\Delta\text{DIC}/\Delta\text{DOC}$ ratios, tidal DIC export would represent $178 \pm 165 \text{ Tg C a}^{-1}$. Other processes may obviously affect DIC and DOC pools after their export from the system boundaries (e.g., CO_2 efflux, mineralization or photodegradation of DOC), but data to assess this further are currently not available. It must be noted that the estimated tidal DIC export in principle includes the cumulated DIC released from mangrove sediments during tidal inundation, DIC released from permanently inundated sediments, and DIC from organic carbon degradation in the mangrove creek waters (which has seldom been measured). However, it does not include the sediment CO_2 emission during exposure or CO_2 exchange between the water column and atmosphere. Thus, although there are insufficient data to fully constrain CO_2 emission from sediments and tidal DIC export, our analysis clearly illustrates that sediment mineralization is likely to be much higher than suggested by standard CO_2 flux measurements alone. We thus suggest that a much larger fraction of mangrove production than previously anticipated may be mineralized and either emitted directly to the atmosphere, or exported as DIC to adjacent waters.

5.2. Secondary Production and Respiration by Fauna

[25] Although NPP formally includes biomass lost through direct feeding [*Clark et al.*, 2001b], we did not include this component in our budget estimates. The generally low levels of direct herbivory (typically <5%, e.g., *Robertson and Duke* [1987], *Lee* [1991], and *Saur et al.* [1999]) are unlikely to bias the overall budget considerations (see also section 3). It should be noted, however, that high levels of herbivory have been reported in a few cases (e.g., ~30% in the work of *Duke* [2002]). Particularly, the few available long-term measurements of leaf herbivory which take into account the consumption of entire leaves and abscission due to herbivory damage result in higher biomass loss than typically reported [*Burrows*, 2003].

[26] However, mangrove forests harbor a highly diverse and abundant invertebrate fauna (primarily crabs), which may rely directly or indirectly on carbon from mangroves. From a community perspective, the contribution of mangroves to invertebrates has been found to be less dominant than previously thought [e.g., *Bouillon et al.*, 2008]. Nevertheless, considering the high abundance of fauna, their overall impact on mangrove carbon turnover is considerable [see *Kristensen et al.*, 2008]. Individual species have been found to remove or consume a significant proportion of litter fall (most estimates range between 10 and 80%) in both Old World and New World mangrove systems [e.g., *McIvor and Smith*, 1995; *Lee*, 1998; *Proffitt and Devlin*, 2005]. Leaf litter retention by fauna can thus have a significant impact on organic matter dynamics and litter turnover, although the relative importance of fauna and geophysical processes (e.g., tidal inundation frequency or

river flow) on litter dynamics vary substantially among different mangrove settings [*Twilley et al.*, 1997].

[27] Quantitative estimates of carbon processing by the entire faunal community are scarce: the only detailed estimate available is that by *Koch and Wolff* [2002], who studied the energy balance of key species of epifauna in a Brazilian mangrove forest. For the high intertidal site in their study (where *Ucides cordatus*, a crab species known to feed substantially on mangrove material, was dominant), secondary production and respiration of key faunal species indicate a total assimilation rate equivalent to $15\text{--}20 \text{ mmol C m}^{-2} \text{ d}^{-1}$. Even for individual species, the few data available confirm the substantial role of mangrove fauna. Thus, *Thongtham and Kristensen* [2005] found that the assimilation (i.e., production + respiration) of the sesarmid crab *Neopisesarma versicolor* at a density of 5 ind. m^{-2} is equivalent to $\sim 40\text{--}60 \text{ mmol C m}^{-2} \text{ d}^{-1}$ in a Thai mangrove forest. When taking into account that faunal communities rely only partially on mangrove-derived carbon, these numbers stress the potential role of faunal production and respiration for the mangrove carbon budget. Reliable quantitative extrapolations on a global scale, however, require substantial research efforts to provide a broader database on the faunal impact.

6. Uncertainties in Budget Estimates and Source Characterization

[28] The large fraction of mangrove primary production that is unaccounted for in current budgets also warrants a critical inspection of the available literature estimates. All estimates have inherent uncertainties due to methodological issues, the limited amount of data on many of the potential carbon sinks, and the intrinsic variability within and between different mangrove systems regarding nutrient availability and relevant biogeochemical processes [e.g., *Twilley et al.*, 1997; *Rivera-Monroy et al.*, 2004; *Poret et al.*, 2007; *Kristensen et al.*, 2008]. An additional caveat in budgeting efforts is that with few exceptions [e.g., *Dittmar et al.*, 2001, 2006], most of the flux estimates refer to the total carbon pool, i.e., not taking into account that other potential carbon sources (e.g., riverine or marine inputs, photosynthetic and chemoautotrophic microbial production) may also contribute to the organic carbon flux measured. Such allochthonous sources have, however, been shown to contribute significantly to particulate and dissolved organic carbon pools, as well as microbial and faunal food webs [see *Bouillon et al.*, 2008].

[29] For the organic carbon export component (see section 4.1.), one of the main shortcomings is the relatively small number of well-documented studies and their high variability. Direct measurements of net carbon export require high-frequency sampling efforts coupled to knowledge on hydrodynamics, since the net result of import and export fluxes is often small compared to the gross fluxes [see also *Lee*, 2006]. Furthermore, the contribution of terrestrial and marine organic carbon to suspended and dissolved organic carbon can in some cases be substantial and would result in an overestimate of export of mangrove carbon if these are not considered.

[30] The three different burial estimates (see section 4.2) match remarkably well. Nevertheless, these may be partially skewed when the underlying data are based on direct estimates of sediment or carbon accumulation, since the potential contribution of nonmangrove sources may result in an overestimate of burial in the overall mangrove carbon budget. However, part of the underlying data is based on community mass balance budget [Duarte *et al.*, 2005], which may ignore the potentially important carbon storage fuelled by belowground production [e.g., Chen and Twilley, 1999; Middleton and McKee, 2001; Marchand *et al.*, 2003]. Recent evidence indeed suggests that belowground root accumulation contributes significantly to overall surface elevation changes in mangrove sediments [McKee *et al.*, 2007].

[31] The CO₂ emission data similarly reflect total CO₂ emission rather than CO₂ production linked to heterotrophic respiration fuelled by mangrove detritus. Some of the CO₂ may be attributed to root respiration and there is recent evidence that other carbon inputs may contribute substantially to mineralization, both in the upper sediment layers [Bouillon and Boschker, 2006] and on an ecosystem level [Bouillon *et al.*, 2007c]. With the data at hand, the bias caused by contributions of other carbon sources to the various sinks discussed here is difficult to constrain, yet this only adds to the conclusion that much of the mangrove production is unaccounted for in existing budget estimates.

7. Summary and Conclusions

[32] Despite the often cited role of mangroves in exporting organic carbon to adjacent waters, a reevaluation of the available data stresses the gaps in our knowledge on carbon cycling in these tropical coastal ecosystems. Net primary production by mangrove forests, assuming a global coverage of 160,000 km², was estimated at 218 ± 72 Tg C a⁻¹, with litter fall, wood and root production accounting for ~31, 31, and 38% of the overall production, respectively (Figure 5). The available literature estimates on carbon burial, organic carbon export and CO₂ emission from sediments and the water column are equivalent to ~45% of the mangrove production, leaving ~112 ± 85 Tg C a⁻¹ unaccounted for in current budgets. Our analysis suggests that tidal export of carbon as DIC is a quantitatively important pathway (178 ± 165 Tg C a⁻¹), and that CO₂ fluxes from intertidal sediments are likely significantly higher than currently assumed. These processes are of the same order of magnitude as the unaccounted carbon sink, and in view of the limited data available, there is a need for more detailed measurements of these processes in a range of different mangrove systems. Besides the need for more quantitative process studies, complementary approaches to determine the contribution of mangroves and other carbon sources to various fluxes and process rates are required to better constrain the major sinks of mangrove carbon.

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References

- Alongi, D. M. (2002), Present state and future of the world's mangrove forests, *Environ. Conserv.*, *29*, 331–349.
- Alongi, D. M., T. Ayukai, G. J. Brunskill, B. F. Clough, and E. Wolanski (1998), Sources, sinks, and export of organic carbon through a tropical, semi-enclosed delta (Hinchinbrook Channel, Australia), *Mangroves Salt Marshes*, *2*, 237–242.
- Alongi, D. M., A. Sasekumar, V. C. Chong, J. Pfitzner, L. A. Trott, F. Tirendi, P. Dixon, and G. J. Brunskill (2004), Sediment accumulation and organic material flux in a managed mangrove ecosystem: Estimates of land-ocean-atmosphere exchange in peninsular Malaysia, *Mar. Geol.*, *208*, 383–402.
- Alongi, D. M., B. F. Clough, and A. I. Robertson (2005), Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*, *Aquat. Bot.*, *82*, 121–131.
- Amarasinghe, M. D., and S. Balasubramaniam (1992), Net primary productivity of two mangrove stands on the northwestern coast of Sri Lanka, *Hydrobiologia*, *247*, 17–27.
- Baran, E., and J. Hambrey (1998), Mangrove conservation and coastal management in Southeast Asia: What impact on fishery resources?, *Mar. Pollut. Bull.*, *37*, 431–440.
- Barbier, E. B. (2000), Valuing the environment as input: Review of applications to mangrove-fishery linkages, *Ecol. Econ.*, *35*, 47–61.
- Borges, A. V., S. Djenidi, G. Lacroix, J. Théate, B. Delille, and M. Frankignoulle (2003), Atmospheric CO₂ flux from mangrove surrounding waters, *Geophys. Res. Lett.*, *30*(11), 1558, doi:10.1029/2003GL017143.
- Boto, K. G., and J. S. Bunt (1981), Tidal export of particulate organic matter from a northern Australian mangrove system, *Estuarine Coastal Shelf Sci.*, *13*, 247–255.
- Boto, K. G., and J. T. Wellington (1988), Seasonal variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated, mangrove waterway, *Mar. Ecol. Prog. Ser.*, *50*, 151–160.
- Bouillon, S., and H. T. S. Boschker (2006), Bacterial carbon sources in coastal sediments: A cross-system analysis based on stable isotope data of biomarkers, *Biogeosciences*, *3*, 175–185.
- Bouillon, S., M. Frankignoulle, F. Dehairs, B. Velimirov, A. Eiler, H. Etcheber, G. Abril, and A. V. Borges (2003), Inorganic and organic carbon biogeochemistry in the Gautami Godavari estuary (Andhra Pradesh, India) during pre-monsoon: The local impact of extensive mangrove forests, *Global Biogeochem. Cycles*, *17*(4), 1114, doi:10.1029/2002GB002026.
- Bouillon, S., F. Dehairs, L.-S. Schiettecatte, and A. V. Borges (2007a), Biogeochemistry of the Tana estuary and delta (northern Kenya), *Limnol. Oceanogr.*, *52*, 46–59.
- Bouillon, S., F. Dehairs, B. Velimirov, G. Abril, and A. V. Borges (2007b), Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi Bay, Kenya), *J. Geophys. Res.*, *112*, G02018, doi:10.1029/2006JG000325.
- Bouillon, S., J. J. Middelburg, F. Dehairs, A. V. Borges, G. Abril, M. R. Flindt, S. Ulomi, and E. Kristensen (2007c), Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine mangrove creek (Ras Dege, Tanzania), *Biogeosciences*, *4*, 311–322.
- Bouillon, S., R. Connolly, and S. Y. Lee (2008), Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies, *J. Sea Res.*, *59*, 44–58, doi:10.1016/j.seares.2007.05.001.
- Burrows, D. W. (2003), The role of insect leaf herbivory on the mangroves *Avicennia marina* and *Rhizophora stylosa*, Ph.D. thesis, 286 pp., James Cook University, Townsville, Queensland, Australia.
- Chen, R., and R. R. Twilley (1999), A simulation model of organic matter and nutrient accumulation in mangrove wetlands soils, *Biogeochemistry*, *44*, 93–118.
- Chmura, G. L., S. C. Anisfeld, D. R. Cahoon, and J. C. Lynch (2003), Global carbon sequestration in tidal, saline wetland soils, *Global Biogeochem. Cycles*, *17*(4), 1111, doi:10.1029/2002GB001917.

- Christensen, B. (1978), Biomass and primary production of *Rhizophora apiculata* in a mangrove forest in southern Thailand, *Aquat. Bot.*, *4*, 43–52.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chamber, J. R. Thomlinson, J. Ni, and E. A. Holland (2001a), Net primary production in tropical forests: An evaluation and synthesis of existing field data, *Ecol. Appl.*, *11*, 371–384.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, and J. Ni (2001b), Measuring net primary production in forests: Concepts and field methods, *Ecol. Appl.*, *11*, 356–370.
- Constanza, R., et al. (1997), The value of the world's ecosystem services and natural capital, *Ecol. Econ.*, *25*, 3–15.
- Davis, S. E., D. L. Childers, J. W. Day, D. T. Rudnick, and F. H. Sklar (2001), Wetland-water column exchanges of carbon, nitrogen, and phosphorus in a southern Everglades dwarf mangrove, *Estuaries*, *24*, 610–622.
- Day, J., W. Conner, F. Ley-Lou, R. Day, and A. Machado (1987), The productivity and composition of mangrove forests, Laguna de Terminos, Mexico, *Aquat. Bot.*, *27*, 267–284.
- Day, J. W., C. Coronado-Molina, F. R. Vera-Herrera, R. R. Twilley, V. H. Rivera-Monroy, H. Alvarez-Guillen, R. Day, and W. Conner (1996), A 7-year record of aboveground net primary production in a southeastern Mexican mangrove forest, *Aquat. Bot.*, *55*, 39–60.
- Diele, K., V. Koch, and U. Saint-Paul (2005), Population structure and catch composition of the exploited mangrove crab *Ucides cordatus* in the Caeté estuary, north Brazil: Indications of overfishing?, *Aquat. Living Resour.*, *18*, 169–178.
- Dittmar, T., and R. J. Lara (2001), Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River?: Evidence from long-term flux measurements, *Mar. Ecol. Prog. Ser.*, *213*, 67–77.
- Dittmar, T., R. J. Lara, and G. Kattner (2001), River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters, *Mar. Chem.*, *73*, 253–271.
- Dittmar, T., N. Hertkorn, G. Kattner, and R. J. Lara (2006), Mangroves, a major source of dissolved organic carbon to the oceans, *Global Biogeochem. Cycles*, *20*, GB1012, doi:10.1029/2005GB002570.
- Duarte, C. M., and J. Cebrián (1996), The Fate of marine autotrophic production, *Limnol. Oceanogr.*, *41*, 1758–1766.
- Duarte, C. M., J. J. Middelburg, and N. Caraco (2005), Major role of marine vegetation on the oceanic carbon cycle, *Biogeosciences*, *2*, 1–8.
- Duke, N. C. (2001), Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems, *Wetlands Ecol. Manage.*, *9*, 257–269.
- Duke, N. C. (2002), Sustained high levels of foliar herbivory of the mangrove *Rhizophora stylosa* by a moth larva *Doratifera stenosa* (Limacodidae) in north-eastern Australia, *Wetlands Ecol. Manage.*, *10*, 403–419.
- Ewe, S. M. L., E. E. Gaiser, D. L. Childers, D. Iwaniec, V. H. Rivera-Monroy, and R. R. Twilley (2006), Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida coastal Everglades, *Hydrobiologia*, *569*, 459–474.
- FAO (2003), *State of the World's Forests*, 151 pp., Food and Agric. Org. of the U.N., Rome.
- Feller, I. C., K. L. McKee, D. F. Whigham, and J. P. O'Neill (2002), Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest, *Biogeochemistry*, *62*, 145–175.
- Fiala, K., and L. Hernandez (1993), Root biomass of a mangrove forest in southwestern Cuba (Majana), *Ekologia Bratislava*, *12*, 15–30.
- Field, C. D. (1995), Impact of expected climate change on mangroves, *Hydrobiologia*, *295*, 75–81.
- Gattuso, J. P., M. Frankignoulle, and R. Wollast (1998), Carbon and carbonate metabolism in coastal aquatic ecosystems, *Annu. Rev. Ecol. Syst.*, *29*, 405–434.
- Gleason, S. M., and K. C. Ewel (2002), Organic matter dynamics on the forest floor of a Micronesian mangrove forest: An investigation of species composition shifts, *Biotropica*, *34*, 190–198.
- Golley, F. B., H. T. Odum, and A. F. Wilson (1962), The structure and metabolism of a Puerto Rico mangrove forest in May, *Ecology*, *43*, 9–19.
- Gong, W. K., and J. E. Ong (1990), Plant biomass and nutrient flux in a managed mangrove forest in Malaysia, *Estuarine Coastal Shelf Sci.*, *31*, 519–530.
- Heald, E. J. (1969), The production of organic detritus in a south Florida estuary, Ph.D. diss., Univ. of Miami, Coral Gables, Fla.
- Hendricks, J. J., R. L. Hendrick, C. A. Wilson, R. J. Mitchell, S. D. Pecot, and D. Guo (2006), Assessing the patterns and controls of fine root dynamics: An empirical test and methodological review, *J. Ecol.*, *94*, 40–57.
- Jennerjahn, T. C., and V. Ittekkot (2002), Relevance of mangroves for the production and deposition of organic matter along tropical continental margins, *Naturwissenschaften*, *89*, 23–30.
- Koch, V., and M. Wolff (2002), Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, north Brazil, *Mar. Ecol. Prog. Ser.*, *228*, 119–130.
- Komiyama, A., K. Ogino, S. Aksornkoae, and S. Sabhasri (1987), Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass, *J. Trop. Ecol.*, *3*, 97–108.
- Kristensen, E., and D. M. Alongi (2006), Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron and sulfur biogeochemistry in mangrove sediment, *Limnol. Oceanogr.*, *51*, 1557–1571.
- Kristensen, E., S. Bouillon, T. Dittmar, and C. Marchand (2008), Organic matter dynamics in mangrove ecosystems, *Aquat. Bot.*, doi:10.1016/j.aquabot.2007.12.005, in press.
- Lee, S. Y. (1989), Litter production and turnover of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal shrimp pond, *Estuarine Coastal Shelf Sci.*, *29*, 75–87.
- Lee, S. Y. (1990), Primary productivity and particulate organic matter flow in an estuarine mangrove-wetland in Hong Kong, *Mar. Biol.*, *106*, 453–463.
- Lee, S. Y. (1991), Herbivory as an ecological process in a *Kandelia candel* (Rhizophoraceae) mangal in Hong Kong, *J. Trop. Ecol.*, *7*, 337–348.
- Lee, S. Y. (1995), Mangrove outwelling: A review, *Hydrobiologia*, *295*, 203–212.
- Lee, S. Y. (1998), Ecological role of grapsid crabs in mangrove ecosystems: A review, *Mar. Freshwater Res.*, *49*, 335–343.
- Lee, S. Y. (2006), Exchange of organic matter and nutrients between mangroves and estuaries: Myths, methodological issues and missing links, *Int. J. Ecol. Environ. Sci.*, *31*, 163–176.
- Lin, P., C. Y. Lu, G. H. Lin, R. H. Chen, and L. Su (1985), The biomass and productivity of *Kandelia candel* community, *J. Xiamen Univ.*, *14*, 508–514.
- Lin, P., C. Y. Lu, G. L. Wang, and H. X. Chen (1990), Biomass and productivity of *Bruguiera sexangula* mangrove forest in Hainan Island, China, *J. Xiamen Univ.*, *29*, 209–213.
- Lovelock, C. E., R. W. Ruess, and I. Feller (2006), Fine root respiration in the mangrove *Rhizophora mangle* over variation in forest stature and nutrient availability, *Tree Physiol.*, *26*, 1601–1606.
- Lugo, A. E., and S. C. Snedaker (1974), The ecology of mangroves, *Annu. Rev. Ecol. Syst.*, *5*, 39–64.
- Machiwa, J. F. (1999), Lateral fluxes of organic carbon in a mangrove forest partly contaminated with sewage wastes, *Mangroves Salt Marshes*, *3*, 95–104.
- Mackenzie, F. T., A. Lerman, and A. J. Andersson (2004), Past and present of sediment and carbon biogeochemical cycling models, *Biogeosciences*, *1*, 11–32.
- Malhi, Y., and J. Grace (2000), Tropical forests and atmospheric carbon dioxide, *Trends Ecol. Evol.*, *15*, 332–337.
- Malhi, Y., et al. (2004), The above-ground coarse wood productivity of 104 Neotropical forest plots, *Global Change Biol.*, *10*, 563–591.
- Mall, L. P., V. P. Singh, and A. Garge (1991), Study of biomass, litter fall, litter decomposition and soil respiration in monogeneric mangrove and mixed mangrove forests of Andaman Islands, *Trop. Ecol.*, *32*, 144–152.
- Marchand, C., E. Lallier-Vergès, and F. Baltzer (2003), The composition of sedimentary organic matter in relation to the dynamic features of a mangrove-fringed coast in French Guiana, *Estuarine Coastal Shelf Sci.*, *56*, 119–130.
- McIvor, C. C., and T. J. and Smith (1995), Differences in the crab fauna of mangrove areas at a southwest Florida and a northeast Australia location: Implications for leaf litter processing, *Estuaries*, *18*, 591–597.
- McKee, K. L., and P. L. Faulkner (2000), Restoration of biogeochemical function in mangrove forests, *Restoration Ecol.*, *8*, 247–259.
- McKee, K. L., D. R. Cahoon, and I. C. Feller (2007), Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation, *Global Ecol. Biogeogr.*, *16*, 545–556.
- Middleton, B. A., and K. L. McKee (2001), Degradation of mangrove tissues and implications for peat formation in Belizean island forests, *J. Ecol.*, *89*, 818–828.
- Mumby, P. J., et al. (2004), Mangroves enhance the biomass of coral reef fish communities in the Caribbean, *Nature*, *427*, 533–536.
- Nadelhoffer, K. N. (2000), The potential effects of nitrogen deposition on fine-root production in forest ecosystems, *New Phytol.*, *147*, 131–139.

- Nordhaus, I., M. Wolff, and K. Diele (2006), Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil, *Estuarine Coastal Shelf Sci.*, *67*, 239–250.
- Odum, E. P. (1968), A research challenge: Evaluating the productivity of coastal and estuarine waters, in *Proceedings of the 2nd Sea Grant Conference*, edited by E. Keiffner, pp. 63–64, Univ. of Rhode Island, Kingston.
- Odum, W. E., and E. J. Heald (1972), Trophic analysis of an estuarine mangrove community, *Bull. Mar. Sci.*, *22*, 671–738.
- Ong, J. E., W. K. Gong, C. H. Wong, and G. Dhararajan (1979), Productivity of a managed mangrove forest in west Malaysia, in *Proceedings of the International Conference on Trends in Applied Biology in South East Asia*, edited by Y. M. Nor, pp. 274–284, Univ. Sains Malaysia, Penang.
- Ovalle, A. R. C., C. E. Rezende, L. D. Lacerda, and C. A. R. Silva (1990), Factors affecting the hydrochemistry of a mangrove tidal creek, Sepetiba Bay, Brazil, *Estuarine Coastal Shelf Sci.*, *31*, 639–650.
- Poret, N., R. R. Twilley, V. H. Rivera-Monroy, and C. Coronado-Molina (2007), Belowground decomposition of mangrove roots in Florida coastal Everglades, *Estuaries Coasts*, *30*, 491–496.
- Proffitt, C. E., and D. J. Devlin (2005), Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove litter degradation rates, *Mar. Ecol. Prog. Ser.*, *296*, 209–218.
- Putz, F. E., and H. T. Chan (1986), Tree growth, dynamics and productivity in a mature mangrove forest in Malaysia, *For. Ecol. Manage.*, *17*, 211–230.
- Raich, J. W., and K. J. Nadelhoffer (1989), Belowground carbon allocation in forest ecosystems: Global trends, *Ecology*, *70*, 1346–1354.
- Rivera-Monroy, V. H., L. A. Torres, N. Bahamon, F. Newmark, and R. R. Twilley (1999), The potential use of mangrove forests as nitrogen sinks of shrimp aquaculture pond effluents: The role of denitrification, *J. World Aquacult. Soc.*, *30*, 12–25.
- Rivera-Monroy, V. H., R. R. Twilley, E. Medina, E. B. Moser, L. Botero, A. M. Francisco, and E. Bullard (2004), Spatial variability in soil nutrients in disturbed riverine mangrove forests at different stages of regeneration in the San Juan River estuary, Venezuela, *Estuaries*, *27*, 44–57.
- Robertson, A. I. (1986), Leaf-burying crabs: Their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia, *J. Exp. Mar. Biol. Ecol.*, *102*, 237–248.
- Robertson, A. I., and D. M. Alongi (1995), Role of riverine mangrove forests in organic carbon export to the tropical coastal ocean: A preliminary mass balance for the Fly Delta (Papua New Guinea), *Geo Mar. Lett.*, *15*, 134–139.
- Robertson, A. I., and N. C. Duke (1987), Insect herbivory on mangrove leaves in North Queensland, *Austral Ecol.*, *12*, 1–7.
- Robertson, A. I., and M. J. Phillips (1995), Mangroves as filters of shrimp pond effluent: Predictions and biogeochemical research needs, *Hydrobiologia*, *295*, 311–321.
- Romigh, M. A., S. E. David, V. H. Rivera-Monroy, and R. R. Twilley (2006), Flux of organic carbon in a riverine mangrove wetland in the Florida coastal Everglades, *Hydrobiologia*, *569*, 505–516.
- Rönnbäck, P. (1999), The ecological basis for economic value of seafood production supported by mangrove ecosystems, *Ecol. Econ.*, *29*, 235–252.
- Ross, M. S., P. L. Ruiz, G. J. Telesnicki, and J. F. Meeder (2001), Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (U.S.A.), *Wetlands Ecol. Manage.*, *9*, 27–37.
- Saenger, P., and S. C. Snedaker (1993), Pantropical trends in mangrove aboveground biomass and annual litterfall, *Oecologia*, *96*, 293–299.
- Sánchez, B. G. (2005), Belowground productivity of mangrove forests in southwest Florida, Ph.D. thesis, 181 pp., Louisiana State Univ., Baton Rouge.
- Saur, E., D. Imbert, J. Etienne, and D. Mian (1999), Insect herbivory on mangrove leaves in Guadeloupe: Effects on biomass and mineral content, *Hydrobiologia*, *413*, 89–93.
- Schlünz, B., and R. R. Schneider (2000), Transport of terrestrial organic carbon to the oceans by rivers: Re-estimating flux- and burial rates, *Int. J. Earth Sci.*, *88*, 599–606.
- Sell, M. G. (1977), Modelling the response of mangrove ecosystem of herbicide spraying, hurricanes, nutrient enrichment and economic development, Ph.D. diss., Univ. of Florida, Gainesville.
- Sherman, R. E., T. J. Fahey, and P. Martinez (2003), Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic, *Ecosystems*, *6*, 384.
- Smith, T. J., K. G. Boto, S. D. Frusher, and R. L. Giddins (1991), Keystone species and mangrove forest dynamics: The influence of burrowing by crabs on soil nutrient status and forest productivity, *Estuarine Coastal Shelf Sci.*, *33*, 419–432.
- Sukardjo, S., and I. Yamada (1992), Biomass and productivity of a *Rhizophora mucronata* Lamarck plantation in Tritih, Central Java, Indonesia, *For. Ecol. Manage.*, *49*, 195–209.
- Sutula, M., B. Perez, E. Reyes, D. Childers, S. Davis, J. Day, D. Rudnick, and F. Sklar (2003), Factors affecting spatial and temporal variability in material exchange between the southern Everglades wetlands and Florida Bay (USA), *Estuarine Coastal Shelf Sci.*, *57*, 757–781.
- Thongtham, N., and E. Kristensen (2003), Physical and chemical characteristics of mangrove crab (*Neopisesarma versicolor*) burrows in the Bangrong mangrove forest, Phuket, Thailand; with emphasis on behavioural response to changing environmental conditions, *Vie Milieu*, *53*, 141–151.
- Thongtham, N., and E. Kristensen (2005), Carbon and nitrogen balance of leaf-eating sesamid crabs (*Neopisesarma versicolor*) offered different food sources, *Estuarine Coastal Shelf Sci.*, *65*, 213–222.
- Twilley, R. R. (1985), The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary, *Estuarine Coastal Shelf Sci.*, *20*, 543–557.
- Twilley, R. R., A. E. Lugo, and C. Patterson-Zucca (1986), Litter production and turnover in basin mangrove forests in southwest Florida, *Ecology*, *67*, 670–683.
- Twilley, R. R., R. H. Chen, and T. Hargis (1992), Carbon sinks in mangrove forests and their implications to the carbon budget of tropical coastal ecosystems, *Water Air Soil Pollut.*, *64*, 265–288.
- Twilley, R. R., M. Poro, V. H. Garcia, V. H. Rivera-Monroy, R. Zambrano, and A. Boderó (1997), Litter dynamics in riverine mangrove forests in the Guayas River Estuary, Ecuador, *Oecologia*, *111*, 109–122.
- Valiela, I., J. L. Bowen, and J. K. York (2001), Mangrove forests: One of the world's threatened major tropical environments, *Bioscience*, *51*, 807–815.
- Vermaat, J. E., and U. Thampanya (2006), Mangroves mitigate tsunami damage: A further response, *Estuarine Coastal Shelf Sci.*, *69*, 1–3.
- Woodroffe, C. D. (1985), Studies of a mangrove basin, Tuff Crater, New Zealand: II. Comparison of volumetric and velocity-area methods of estimating tidal flux, *Estuarine Coastal Shelf Sci.*, *20*, 431–445.
- Woodroffe, C. D., K. N. Bardsley, P. J. Ward, and J. R. Hanley (1988), Production of mangrove litter in a macrotidal embayment, Darwin Harbour, N.T., Australia, *Estuarine Coastal Shelf Sci.*, *26*, 581–598.

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