

Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows

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[1] The metabolic rates of seagrass communities were synthesized on the basis of a data set on seagrass community metabolism containing 403 individual estimates derived from a total of 155 different sites. Gross primary production (GPP) rates (mean \pm SE = 224.9 ± 11.1 mmol O₂ m⁻² d⁻¹) tended to be significantly higher than the corresponding respiration (R) rates (mean \pm SE = 187.6 ± 10.1 mmol O₂ m⁻² d⁻¹), indicating that seagrass meadows tend to be autotrophic ecosystems, reflected in a positive mean net community production (NCP 27.2 ± 5.8 mmol O₂ m⁻² d⁻¹) and a mean P/R ratio above 1 (1.55 ± 0.13). Tropical seagrass meadows tended to support higher metabolic rates and somewhat lower NCP than temperate ones. The P/R ratio tended to increase with increasing GPP, exceeding, on average, the value of 1 indicative of metabolic balance for communities supporting a GPP greater than 186 mmol O₂ m⁻² d⁻¹, on average. The global NCP of seagrass meadows ranged (95% confidence limits of mean values) from 20.73 to 50.69 Tg C yr⁻¹ considering a low global seagrass area of 300,000 km² and 41.47 to 101.39 Tg C yr⁻¹ when a high estimate of global seagrass area of 600,000 km² was considered. The global loss of 29% of the seagrass area represents, therefore, a major loss of intense natural carbon sinks in the biosphere.

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1. Introduction

[2] Seagrass meadows are ecosystems conformed by one or more marine angiosperm species present in shallow coastal areas around all continents, except Antarctica [Hemminga and Duarte, 2000]. Seagrass meadows rank among the most productive ecosystems on Earth [Zieman and Wetzel, 1980; Duarte and Chiscano, 1999], with the total primary production of the community contributed almost equally by the angiosperms themselves and the epiphytes and macroalgae they support [Hemminga and

Duarte, 2000]. The abundance and activity of heterotrophs are also greatly enhanced in seagrass meadows [Hemminga and Duarte, 2000], which support high community respiration rates [Middelburg *et al.*, 2005].

[3] Yet, a large fraction (81.4%, on average [Duarte and Cebrián, 1996]) of their production is not consumed by herbivores. Seagrass tissues have relatively high C:N:P ratios and are, therefore, relatively recalcitrant and decompose slowly [Enríquez *et al.*, 1993]. In addition, a significant fraction of seagrass production is laid in the sediments, as roots and rhizome material, where this material is often preserved over long, exceeding millenary, time scales [Mateo *et al.*, 1997]. Hence, a significant fraction of the gross production of seagrass meadows is not used by the heterotrophs, driving seagrass ecosystems to be autotrophic communities [Duarte and Cebrián, 1996; Gattuso *et al.*, 1998]. Indeed, available analyses, based on community carbon budgets [Duarte and Cebrián, 1996], community metabolism measurements [Gattuso *et al.*, 1998], and estimates of carbon burial capacity [Duarte *et al.*, 2005], show that seagrass communities tend to be net autotrophic, acting therefore as net CO₂ sinks in the biosphere. Yet, seagrass, along with other vegetated coastal habitats, are ignored altogether in global carbon budgets despite early evidence showing that marine macrophytes act as global carbon sinks [Smith, 1981]. We submit that the reason for this neglect

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was the result of insufficient empirical evidence, with most of the estimates derived from a couple of dozens of seagrass meadows [Smith, 1981; Duarte and Cebrián, 1996; Gattuso et al., 1998; Duarte et al., 2005], associated with a charisma deficit that rendered these ecosystems uninteresting to the wider public and the scientific community [Duarte et al., 2008].

[4] Evidence that increased loss rates of seagrass ecosystems globally [Orth et al., 2006; Waycott et al., 2009] may be weakening the carbon sink capacity of the biosphere [Nellemann et al., 2009] have prompted growing interest in the role of seagrass meadows as carbon sinks. In fact, many studies examining the community metabolism of seagrass meadows have been published since seagrass metabolic rates were first reviewed [Smith, 1981; Duarte and Cebrián, 1996; Gattuso et al., 1998]. Here we review and synthesize available information and derive patterns on the community metabolism of seagrass meadows, as described by the gross primary production (GPP), respiration (R), and net community production (NCP), and P/R of the communities. We do so as a step to assess their potential role as carbon sinks, thereby allowing this component of the carbon cycle to be incorporated into global carbon budgets, as well as to evaluate the possible loss of this capacity associated with the current global decline of seagrass meadows.

2. Methods

[5] We searched the available literature (including graduate student dissertations) for estimates of GPP, R, NCP and P/R of seagrass meadows from studies completed since 1956 (see Data Set S1 for the complete database).¹ We amended the resulting database with four unpublished studies (E. Gacia et al., 2006, C. Barrón, 2000, J. W. Fourqurean, 2006, and Silva and Santos, 2005) of metabolism from our own work as well as that of our colleagues.

[6] Not all studies reported all three metabolic rates, so we calculated the missing values, where possible by solving the mass balance equation $NCP = GPP - R$, which was necessary for 20% of the NCP estimates. We also calculated the corresponding P/R ratios as GPP/R , since we are interested in the P/R ratio of the community, not that of the seagrasses alone, and the overall P/R ratio of the community is provided by the GPP/R ratio. For those studies that reported rates in units other than $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, we converted the raw data to these units. For the studies that reported fluxes in terms of mass or moles of carbon, we assumed, following Kirk [1983], $PQ = RQ = 1$ unless the authors of a study explicitly used another value for PQ or RQ. The photosynthetic quotient (PQ, moles O_2 : moles CO_2) should theoretically be between 1.0 and 1.3, depending on the physiological state of the plant cells and the amount of photorespiration. PQ has been estimated as 1.2 for submerged aquatic plants [Westlake, 1963] and 1.27 for *Potamogeton* sp. [Kemp et al., 1986], but measurements of PQ for seagrasses are few. Ziegler and Benner [1998] surveyed the literature for simultaneous measurements of O_2 evolu-

tion and DIC uptake in macrophyte dominated systems and report a range of PQ from 1.03 to 1.30. Ziegler and Benner [1998] also reported the respiratory quotient for seagrass communities (i.e., moles CO_2 : moles O_2) from seagrass-dominated ecosystems of between 0.8 and 1.14. These PQ and RQ ratios refer to seagrass physiology, but many other processes, including carbonate production and dissolution and sulphate reduction affect the apparent stoichiometry between net community production based on dissolved inorganic carbon budgets and those based on oxygen. Indeed, Barrón et al. [2006] report $NCP_{\text{DIC}}: NCP_{\text{O}_2}$ ratios to range from 0.3 to 4.8 for a *P. oceanica* meadow, and Ziegler and Benner [1998] report that of a *T. testudium* meadow in Laguna Madre (Texas) to range from 0.6 to 6.8. Hence, the PQ and RQ value of 1.0, as assumed here for simplicity, is consistent with estimates reported for seagrass meadows.

[7] Carbon-based and oxygen-based estimates of seagrass community metabolism meet different challenges. Oxygen-based estimates may underestimate community respiration when anaerobic pathways, such as sulphate reduction, are important. However, the products of anaerobic respiratory pathways are largely reoxidized when diffusing across the sediment-water interface so that oxygen consumption does capture, through the oxidation of the reduced products, most anaerobic respiration as well [Heip et al., 1995]. Oxygen-based approaches may underestimate community respiration in ecosystems with terrigenous sediments where iron can precipitate sulfide as pyrite, which may result in the underestimation of respiration rates when using oxygen-based methods equivalent to about 25% of the anaerobic respiration [Heip et al., 1995]. In contrast, carbon-based measurements are also subject to uncertainty derived from changes in alkalinity along the day resulting, from instance from sulphate reduction, as well as interference from the substantial carbonate production and dissolution rates affecting carbon budgets of seagrass meadows [Barrón et al., 2006]. Hence, both methods are subject to interference that contribute to the error in the individual estimates reviewed here.

[8] For studies that reported rates on an hourly rather than a daily basis, we assumed that reported daytime respiration rates could be applied over a 24 h day and that the mean GPP rates applied for a 12 h photoperiod unless the original authors used a different photoperiod. We report in the data set the general methods utilized in the source literature. The two most common methods derived metabolic rates from changes in oxygen concentrations in incubation chambers [Penhale, 1977] and diel oxygen concentration curves [Odum, 1956] obtained in the field, but other methods like CO_2 and ^{14}C uptake and laboratory incubations of sediment cores containing seagrass were also used by some of the literature sources. For studies that reported more than one estimate of metabolic rates, we retained each estimate presented in the study as a data point for analysis. Each seagrass meadow was assigned to the community type defined by the corresponding seagrass biogeographical province [Hemminga and Duarte, 2000].

[9] We used Wilcoxon ranked sign test on paired estimates of GPP and R to test for the significance of the tendency for seagrass meadows toward autotrophy or

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GB003793.

Table 1. Mean \pm SE, Range and Number of Observations and Sites for Gross Primary Production, Community Respiration, Net Community Production, and the P/R Ratio of Seagrass Communities, as Well as Those for Temperate and Tropical Seagrass Meadows^a

	Mean	Standard Error	Minimum	Maximum	N Observations	N Sites	F	p
<i>Whole Data Set</i>								
GPP (mmol O ₂ m ⁻² d ⁻¹)	224.85	11.07	0.40	1296.88	354	141		
R (mmol O ₂ m ⁻² d ⁻¹)	187.61	10.10	0.63	1046.88	326	116		
NCP (mmol O ₂ m ⁻² d ⁻¹)	27.19	5.80	-477.28	531.63	358	123		
P/R	1.55	0.13	0.03	37.77	319	111		
<i>Temperate/Tropical Comparison</i>								
GPP (mmol O ₂ m ⁻² d ⁻¹)								
Temperate	165.52	14.21	5.89	794.65	112	41	13.78	0.0002
Tropical	252.30	14.47	0.40	1296.88	242	100		
R (mmol O ₂ m ⁻² d ⁻¹)								
Temperate	129.76	10.49	12.28	606.00	111	40	17.82	<0.0001
Tropical	217.48	13.90	0.63	1046.88	215	76		
NCP (mmol O ₂ m ⁻² d ⁻¹)								
Temperate	33.47	8.03	-209.25	531.63	127	45		ns
Tropical	23.73	7.83	-477.28	484.20	231	78		
P/R								
Temperate	1.44	0.09	0.12	6.28	109	38		ns
Tropical	1.61	0.19	0.03	37.77	210	73		

^aAlso shown are results (F statistic and p value) of ANOVA testing for differences in these rates between temperate and tropical seagrass meadows.

heterotrophy. Differences in GPP, R and NCP between temperate and tropical seagrass meadows were assessed by means of Analysis of Variance (ANOVA). We log-transformed variables when required for statistical analyses and used model II principal component regression analysis to examine the relationship between metabolic rates, as these are measured with comparable error. The threshold biomass for seagrass meadows to be, on average, autotrophic, was calculated by first establishing, by solving the model II regression equation between the P/R ratio and GPP, the average GPP at P/R = 1 ($GPP_{P/R=1}$), and then calculating the seagrass biomass at which GPP equals $GPP_{P/R=1}$ from the mean ratio of GPP to aboveground seagrass biomass.

3. Results

[10] The data set compiled on seagrass community metabolism (Data Set S1) contained 403 individual estimates,

about 20 times more than those used in past assessments [Smith, 1981; Duarte and Cebrián, 1996; Gattuso *et al.*, 1998], derived from a total of 155 different sites, dominated by monospecific meadows (72.6%), from 50 sources (Table 1 and Text S1). Most (67.2%) of the records were derived from subtropical and tropical meadows, where a large fraction of the global seagrass area is found [Green and Short, 2003], and the Mediterranean Sea (27.8% of records, Figures 1 and 2). In contrast, we were unable to find any record of community metabolism for seagrass meadows in the North Pacific and the coasts of Central and South America, South Africa, New Zealand and the West Pacific (Figures 1 and 2).

[11] GPP rates (Mean \pm SE = 224.9 ± 11.1 mmol O₂ m⁻² d⁻¹) tended to be significantly higher (Wilcoxon ranked sign test, $p < 0.0001$) than the corresponding R rates (Mean \pm SE = 187.6 ± 10.1 mmol O₂ m⁻² d⁻¹), indicating that seagrass meadows tend to be autotrophic ecosystems,

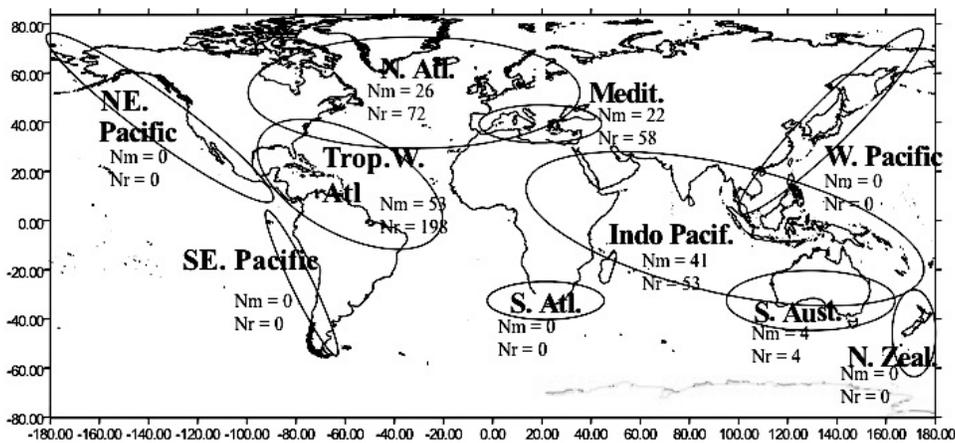


Figure 1. Map showing the distribution of number of sites (Nm) and records (Nr) in different biogeographic regions worldwide.

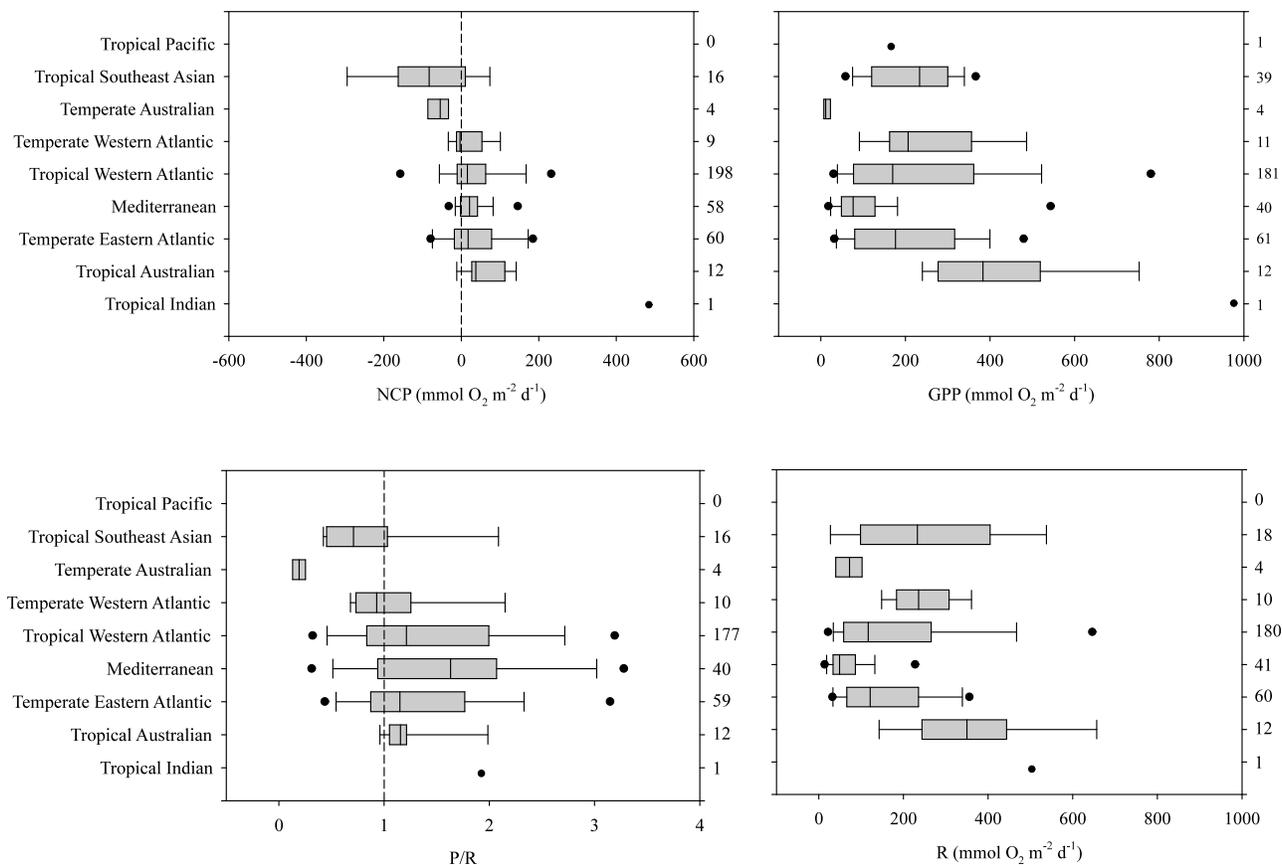


Figure 2. Box plots showing the distribution of NCP, GPP, R and P/R of seagrass meadows across different community types. Boxes encompass the central 50% quantile; the line within the box represents the median, the whiskers extend to the 10% and 90% quantiles of the distribution, and the points represent the 5% and 95% quantiles of the distribution. Whenever $N \leq 2$, the data are just shown as data points. Numbers along the right vertical axis show the number of records in each category.

reflected in a positive mean NCP ($27.2 \pm 5.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and a mean P/R ratio above 1 (1.55 ± 0.13 , Table 1). Indeed, two thirds of the records on seagrass metabolism indicated net autotrophy (63%).

[12] Tropical seagrass meadows tended to support higher metabolic rates, and somewhat lower, but not significantly (ANOVA, $p > 0.05$), NCP than temperate ones (Table 1). The examination of the metabolic rates revealed significant differences in GPP, R and NCP across biogeographic domains and species (ANOVA, $p < 0.0001$, for both comparisons, Figure 2). Metabolic rates measured in tropical meadows in the Indian Ocean and Australian were higher than other community types (Figure 2). GPP measured in meadows dominated *Ruppia maritima*, *Syringodium isoetifolium* and *Halodule uninervis*, considered pioneer, fast growing species [Hemminga and Duarte, 2000], had the highest median GPP, and, together with *Thalassia hemprichii*, the highest R (Figure 3). *Enhalus acoroides*, *Ruppia maritima*, and *Syringodium filiforme* had the highest median NCP (Figure 3).

[13] There was a strong, positive relationship between R and GPP in seagrass communities (Figure 4), showing that highly productive meadows also supported high community

respiration rates. The P/R ratio tended to increase with increasing GPP (Figure 5), exceeding, on average, $P/R = 1$ indicative of metabolic balance when GPP exceeded $186 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Figure 5). However, there was considerable variability in the relationship between the P/R ratio and GPP (for comparison, see insert in Figure 5).

4. Discussion

[14] The results presented confirm, on the basis of a much larger data set than used in the past [Smith, 1981; Duarte and Cebrián, 1996; Gattuso et al., 1998], that seagrass meadows support a broad range of metabolic rates and tend to be autotrophic and act, therefore, as CO_2 sinks in the ecosystem. This is consistent with reports of undersaturation of dissolved CO_2 in waters overlying seagrass beds driving an air-sea flux [Frankignoulle, 1988; Gazeau et al., 2005]. The overall mean NCP derived here ($9.9 \pm 2.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$) is well below those reported, on the basis of a much smaller data set, in the past ($42 \text{ mol C m}^{-2} \text{ yr}^{-1}$ [Smith, 1981]; $37 \text{ mol C m}^{-2} \text{ yr}^{-1}$ [Gattuso et al., 1998]), suggesting that earlier accounts were biased toward highly autotrophic meadows. In fact, our results suggest that these

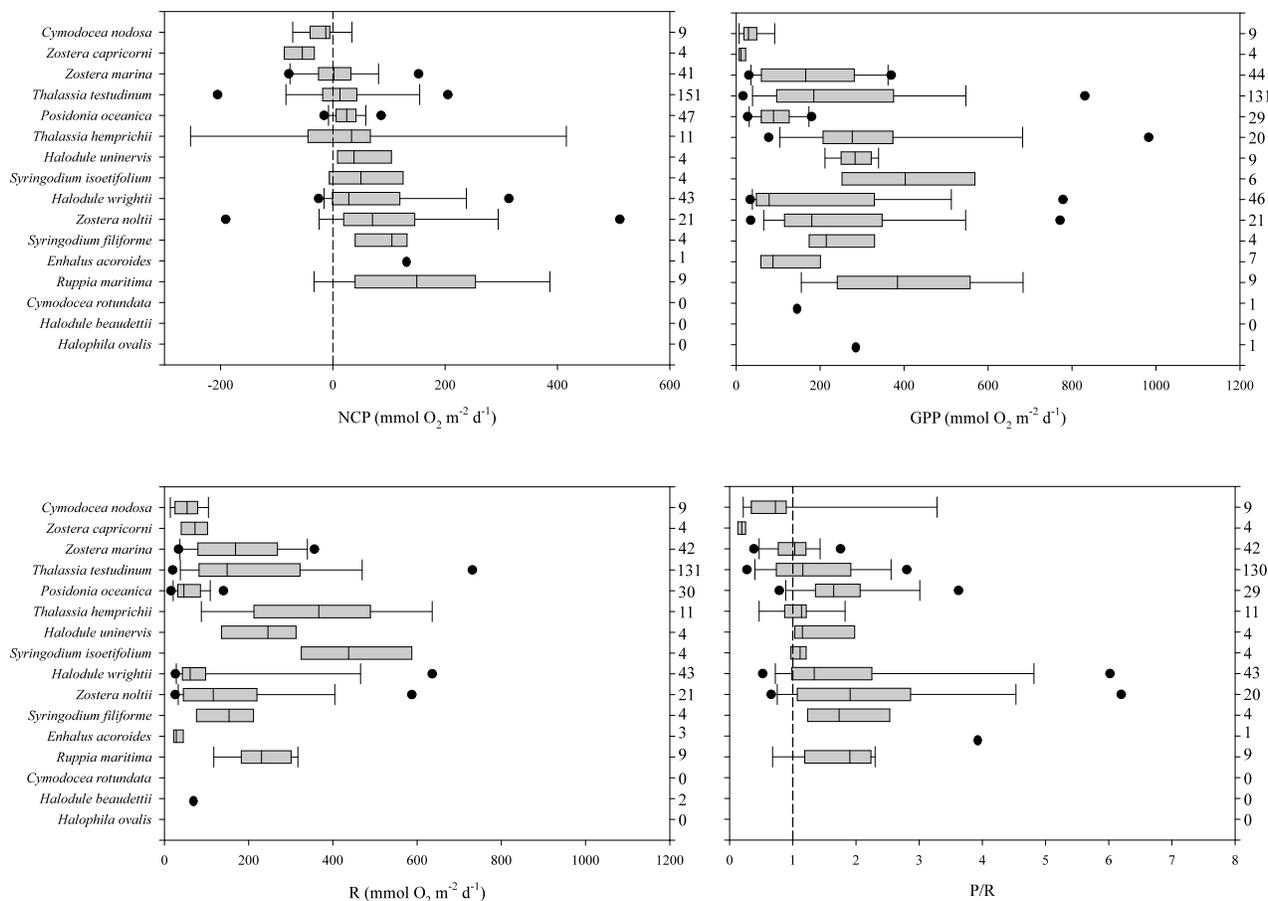


Figure 3. Box plots showing the distribution of NCP, GPP, R and P/R of seagrass meadows across different dominant species. Boxes encompass the central 50% quantile; the line within the box represents the median, the whiskers extend to the 10% and 90% quantiles of the distribution, and the points represent the 5% and 95% quantiles of the distribution. Whenever $N \leq 2$, the data are just shown as data points. Numbers along the right vertical axis show the number of records in each category.

differences in mean global NCP estimates are dependent on the geographical spread of the data, as we found large, significant differences in metabolic rates among community types and species. In particular, there is a considerable gap of reports of seagrass community metabolism in the Southern Hemisphere, contributing only 17 records and 8 meadows to the database compiled here (4.2% and 5.1%, respectively), as the only records available are those derived for Australia and Fiji. Hence, even though the present database is much expanded relative to earlier efforts at assessing seagrass metabolism, a global mean value providing a reliable basis to calculate the global sink capacity of seagrasses, requires that present imbalances in the geographic spread of the data available be addressed. Efforts should target meadows in the Southern Hemisphere as well as those in major but yet poorly explored seagrass regions, such as SE Asia.

[15] The results presented suggest that there is a threshold GPP of $186 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, on average, above which seagrass communities tend to act as CO_2 sinks, with the meadows acting as CO_2 sources at lower production values. The mean ratio of GPP to aboveground seagrass biomass,

specific GPP, derived from our database is $4.45 \pm 0.79 \text{ mmol O}_2 \text{ g DW}^{-1} \text{ d}^{-1}$. Therefore, seagrass meadows with an average aboveground biomass in excess of 41 g DW m^{-2} should be autotrophic and act as net CO_2 sinks (Table 2). Indeed, the average threshold biomass for seagrass meadows to be autotrophic, 41 g DW m^{-2} , is much lower than the mean aboveground seagrass biomass of $223.9 \pm 17.5 \text{ g DW m}^{-2}$ reported by Duarte and Chiscano [1999], suggesting that most seagrass meadows are autotrophic. There were, however, major species-specific differences in the ratio of GPP to aboveground seagrass biomass (ANOVA, $F = 12.76$, $p < 0.001$) suggesting that this threshold GPP must be met, on average, in meadows with aboveground biomass ranging from about 20 g DW m^{-2} , for species developing highly productive communities (e.g., *Thalassia hemprichii*, *Halodule wrightii*, *Ruppia maritima*) to a biomass up to 735 g DW m^{-2} for less productive Mediterranean *Posidonia oceanica* meadows (Table 2).

[16] The estimate of mean NCP derived here ($9.9 \pm 2.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$) corresponds closely with the mean C burial of $6.9 \text{ mmol C m}^{-2} \text{ yr}^{-1}$, independently estimated in

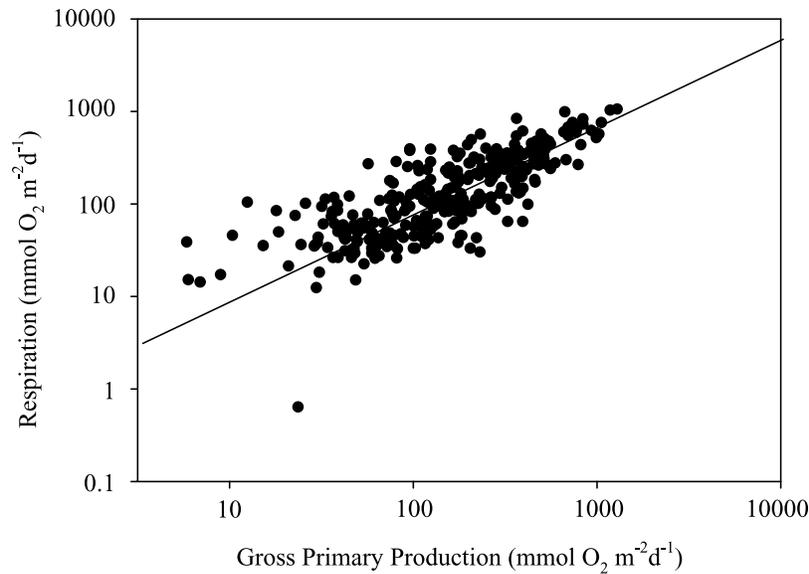


Figure 4. The relationship between respiration (R) and gross community production (GPP) in seagrass meadows. The solid line represented the fitted model II regression equation, $\log_{10} R \text{ (mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}) = 0.14 + 0.90 (\pm 0.03) \log_{10} \text{ GPP (mmol O}_2 \text{ m}^{-2} \text{ d}^{-1})$, ($R^2 = 0.60$, $p < 0.0001$).

seagrass sediments [Duarte *et al.*, 2005], showing good agreement between metabolic estimates of the C sink capacity of seagrass meadows and those derived from ecosystem C budgets and sediment C budgets [Duarte *et al.*, 2005]. The NCP of seagrass ecosystems can be compared with that of other ecosystems considered to be important C sinks, such as wetlands and the Amazonian rain forest. The average NCP of seagrasses (Table 3) is well above (>5 times) the average C sink capacity of North American wetlands ($0.19 \text{ t C ha}^{-1} \text{ yr}^{-1}$ [Brigham *et al.*, 2006]). Indeed,

the top 10% seagrass meadows in terms of their carbon sink capacity in our data set support NCP in excess of $6.7 \text{ t C ha}^{-1} \text{ yr}^{-1}$ (Table 3), well above that of undisturbed Amazonian forests ($1.02 \text{ t C ha}^{-1} \text{ yr}^{-1}$ [Grace *et al.*, 1995]), considered to be the strongest carbon sinks on land.

[17] The global NCP of seagrass ecosystems can be calculated by scaling up the estimates derived from this analysis to their global extent. Even though based on a much expanded ($N = 403$) data set, the estimates available do not represent a random sample, and the estimates of mean sea-

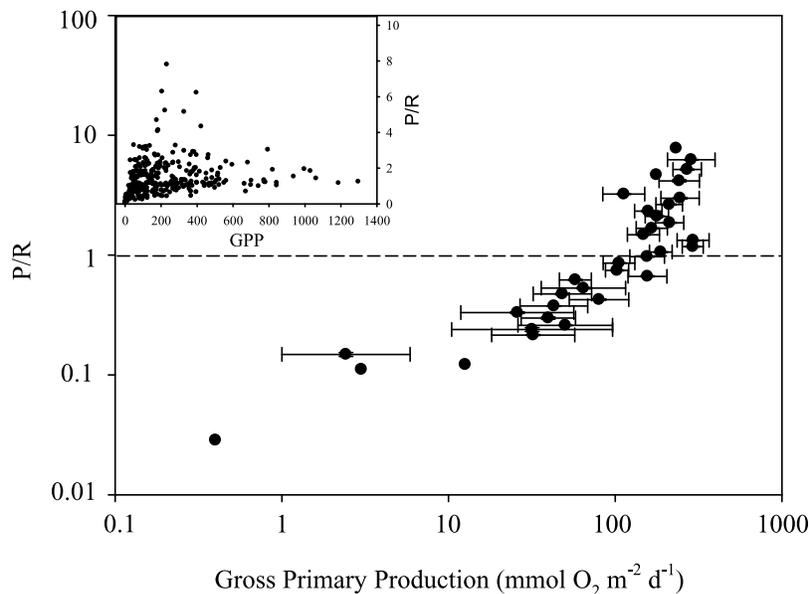


Figure 5. The relationship between the average (\pm SE) P/R ratio and the mean GPP within bins of $0.2 \log_{10}$ P/R units. The insert shows the relationship between individual estimates of P/R and GPP.

grass NCP derived here may contain biases if the major underrepresented areas happen to deviate greatly from the mean value presented here. For instance, the only record of NCP available for *Enhalus acoroides*, a dominant species in shallow, Indo-Pacific seagrass meadows, supports a fivefold greater NCP than the mean value for all species in the data set. In addition, there is considerable uncertainty as to the global extent of seagrass meadows, resulting from the existence of key regions certainly supporting extensive seagrass meadows that have not yet been charted (e.g., Indonesia and Pacific archipelagos), and the continuing loss of seagrass area [Orth et al., 2006; Waycott et al., 2009]. We, thus, assumed a low estimate of global seagrass extent of 300,000 km² [Duarte et al., 2005] and a high estimate of 600,000 km² [Charpy-Roubaud and Sournia, 1990]. The resulting estimates of the global NCP of seagrass meadows range (95% confidence limits of mean values) from 20.73 to 50.69 Tg C yr⁻¹ assuming the low estimate of global seagrass area and 41.47 to 101.39 Tg C yr⁻¹ when the high estimate of the global seagrass area is considered (Table 3). These are conservative estimates of net C flux in seagrass ecosystems, as these estimates do not include the capacity of seagrass meadows to trap allochthonous water column particles [e.g., Hendriks et al., 2008] and bury them in the sediment, which has been shown to contribute as much as 50% of the carbon buried in seagrass sediments [Gacia et al., 2002]. In addition, a significant fraction of seagrass NCP (as much as 25%) is exported to adjacent beach ecosystems [Heck et al., 2008], where it accumulates and can be buried in dune formations, so that not all NCP remains in the seagrass meadows. Seagrass meadows occupy a narrow strip of a few kilometers wide around the coastline, well below 0.1% of the ocean surface. Yet, they play an important role as net carbon sinks in the biosphere.

[18] Current estimates indicate that at least 29% of the global seagrass area has been lost globally [Waycott et al., 2009], implying that close to 1/3 of the associated carbon

Table 2. Number of Estimates, Mean \pm SE Gross Primary Production to Aboveground Seagrass Biomass Ratio for Meadows Dominated by Different Seagrass Species and for the Overall Data Set, Along With the Estimated Biomass for GPP to Exceed the Threshold Value of 186 mmol O₂ m⁻² d⁻¹, Above Which Seagrass Meadows Tend to Be Autotrophic^a

Dominant Species	N	Specific GPP (mmol O ₂ g DW ⁻¹ d ⁻¹)	Threshold Biomass (g DW m ⁻²)
<i>Cymodocea nodosa</i>	8	0.91 \pm 0.57	203.5
<i>Cymodocea rotundata</i>	1	2.78	67.0
<i>Enhalus acoroides</i>	3	0.94 \pm 0.25	198.2
<i>Halodule uninervis</i>	8	3.17 \pm 1.02	58.8
<i>Halodule wrightii</i>	41	8.53 \pm 1.89	21.8
<i>Halophila ovalis</i>	1	12.86	14.5
<i>Posidonia oceanica</i>	29	0.25 \pm 0.04	735.3
<i>Ruppia maritima</i>	5	8.08 \pm 1.70	23.0
<i>Syringodium filiforme</i>	4	4.24 \pm 1.62	43.9
<i>Syringodium isoetifolium</i>	4	5.82 \pm 2.39	32.0
<i>Thalassia hemprichii</i>	19	9.95 \pm 7.25	18.7
<i>Thalassia testudinum</i>	29	1.82 \pm 0.21	102.2
<i>Zostera marina</i>	35	2.01 \pm 0.52	92.7
Overall	215	4.45 \pm 0.79	41.8

^aThresholds were calculated as the ratio of 186 and the specific GPP rate.

Table 3. Estimates of the Metabolic C Sink Capacity of Seagrass Meadows, in t C ha⁻¹ yr⁻¹ and the Global Estimate of the Seagrass Metabolic Inorganic C Sink Capacity^a

Estimates	NCP (t C ha ⁻¹ yr ⁻¹)	Low Global Extent (km ²)	Tg C yr ⁻¹	High Global Extent (km ²)	Tg C yr ⁻¹
Mean	1.19	300,000	35.71	600,000	71.43
Upper 95 c.l. of mean	1.69	300,000	50.69	600,000	101.39
Lower 95 c.l. of mean	0.69	300,000	20.73	600,000	41.47
Upper 90% c.l.	6.73	300,000	201.96	600,000	403.92
Maximum	23.28				

^aThe estimates were derived using the mean NCP and its 90% confidence limits, the upper 90% quantile and the maximum NCP in the data set. Global estimates are derived using a low (300,000 km² [Duarte et al., 2005]) and high (600,000 km² [Charpy-Roubaud and Sournia, 1990]) global seagrass extent; c.l., confidence limits. Note: multiply tons C ha⁻¹ yr⁻¹ by 3.66 to calculate tons CO₂ ha⁻¹ yr⁻¹.

sink capacity of seagrass meadows has been lost. In fact, the loss of carbon sink capacity is probably greater, since seagrass meadows lose biomass and gross primary production well before they are extirpated, so that extant seagrass meadows are also expected to have lost sink capacity relative to undisturbed seagrass meadows. Efforts to stop seagrass loss and to recover lost seagrass area will, therefore, contribute to rebuild some of the lost seagrass carbon sink capacity and help, therefore, mitigate climate change [Nellemann et al., 2009].

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References

- Barrón, C., C. M. Duarte, M. Frankignoulle, and A. V. Borges (2006), Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (*Posidonia oceanica*) meadow, *Estuaries Coasts*, 29, 417–426.
- Brigham, S. D., et al. (2006), The carbon balance of North American wetlands, *Wetlands*, 26, 889–916, doi:10.1672/0277-5212(2006)26[889:TCBONA]2.0.CO;2.
- Charpy-Roubaud, C., and A. Sournia (1990), The comparative estimation of phytoplanktonic and microphytobenthic production in the oceans, *Mar. Microb. Food Webs*, 4, 31–57.
- Duarte, C. M., and J. Cebrián (1996), The fate of marine autotrophic production, *Limnol. Oceanogr.*, 41(8), 1758–1766, doi:10.4319/lo.1996.41.8.1758.
- Duarte, C. M., and C. L. Chiscano (1999), Seagrass biomass and production: A reassessment, *Aquat. Bot.*, 65(1–4), 159–174, doi:10.1016/S0304-3770(99)00038-8.
- Duarte, C. M., et al. (2005), Major role of marine vegetation on the oceanic carbon cycle, *Biogeosciences*, 2(1), 1–8, doi:10.5194/bg-2-1-2005.
- Duarte, C. M., et al. (2008), The charisma of coastal ecosystems: Addressing the imbalance, *Estuaries Coasts*, 31, 233–238, doi:10.1007/s12237-008-9038-7.
- Enríquez, S., et al. (1993), Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content, *Oecologia*, 94, 457–471, doi:10.1007/BF00566960.
- Frankignoulle, M. (1988), Field measurements of air-sea CO₂ exchange, *Limnol. Oceanogr.*, 33(3), 313–322, doi:10.4319/lo.1988.33.3.0313.
- Gacia, E., et al. (2002), Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow, *Limnol. Oceanogr.*, 47(1), 23–32, doi:10.4319/lo.2002.47.1.0023.

- Gattuso, J.-P., et al. (1998), Carbon and carbonate metabolism in coastal aquatic ecosystems, *Annu. Rev. Ecol. Syst.*, 29, 405–434, doi:10.1146/annurev.ecolsys.29.1.405.
- Gazeau, F., et al. (2005), Whole-system metabolism and CO₂ fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean), *Biogeosciences*, 2(1), 43–60, doi:10.5194/bg-2-43-2005.
- Grace, J. J., et al. (1995), Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993, *Science*, 270, 778–780, doi:10.1126/science.270.5237.778.
- Green, E. P., and F. T. Short (Eds.) (2003), *World Atlas of Seagrasses*, 298 pp., Univ. of Calif. Press, Berkeley, Calif.
- Heck, K., Jr., et al. (2008), Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers, *Ecosystems*, 11(7), 1198–1210, doi:10.1007/s10021-008-9155-y.
- Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg, and K. Soetaert (1995), Production and consumption of biological particles in temperate tidal estuaries, *Oceanogr. Mar. Biol. Annu. Rev.*, 33, 1–149.
- Hemminga, M., and C. M. Duarte (2000), *Seagrass Ecology*, 322 pp., Cambridge Univ. Press, Cambridge, U. K., doi:10.1017/CBO9780511525551.
- Hendriks, I. E., et al. (2008), Experimental assessment and modeling evaluation of the effects of seagrass (*P. oceanica*) on flow and particle trapping, *Mar. Ecol. Prog. Ser.*, 356, 163–173, doi:10.3354/meps07316.
- Kemp, W. M., M. R. Lewis, and T. W. Jones (1986), Comparison of methods for measuring production by the submersed macrophyte, *Potamogeton perfoliatus* L., *Limnol. Oceanogr.*, 31, 1322–1334, doi:10.4319/lo.1986.31.6.1322.
- Kirk, J. T. O. (1983), *Light and Photosynthesis in Aquatic Ecosystems*, 401 pp., Cambridge Univ. Press, Cambridge, U. K.
- Mateo, M. A., et al. (1997), Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*, *Estuar. Coast. Shelf Sci.*, 44, 103–110.
- Middelburg, J. J., et al. (2005), Respiration in coastal benthic communities, in *Respiration in Aquatic Ecosystems*, edited by P. A. del Giorgio and P. J. leB. Williams, pp. 206–224, Oxford Univ. Press, Oxford, U. K., ISBN:0-19-852709-8.
- Nellemann, C., et al. (Eds.) (2009) *Blue Carbon. A Rapid Response Assessment*, 80 pp., U. N. Environ. Programme, GRID-Arendal, Birkeland Trykkeri AS, Birkeland, Norway.
- Odum, H. T. (1956), Primary production in flowing waters, *Limnol. Oceanogr.*, 1, 102–117, doi:10.4319/lo.1956.1.2.0102.
- Orth, R. J., et al. (2006), A global crisis for seagrass ecosystems, *BioScience*, 56(12), 987–996, doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.
- Penhale, P. A. (1977), Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community, *J. Exp. Mar. Biol. Ecol.*, 26, 211–224, doi:10.1016/0022-0981(77)90109-5.
- Smith, S. V. (1981), Marine macrophytes as a global carbon sink, *Science*, 211, 838–840, doi:10.1126/science.211.4484.838.
- Waycott, M., et al. (2009), Accelerating loss of seagrasses across the globe threatens coastal ecosystems, *Proc. Natl. Acad. of Sci. USA*, 106, 12,377–12,381, doi:10.1073/pnas.0905620106.
- Westlake, D. F. (1963), Comparisons of plants productivity, *Biol. Rev. Camb. Philos. Soc.*, 38, 385–425, doi:10.1111/j.1469-185X.1963.tb00788.x.
- Ziegler, S., and R. Benner (1998), Ecosystem metabolism in a subtropical, seagrass-dominated lagoon, *Mar. Ecol. Prog. Ser.*, 173, 1–12, doi:10.3354/meps173001.
- Zieman, J. C., and R. G. Wetzel (1980) Productivity in seagrasses: Methods and rates, in *Handbook of Seagrass Biology: An Ecosystem Perspective*, pp. 87–116, edited by R. C. Phillips and C. P. McRoy, Garland STPM Press, New York.

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