Michael N. Githaiga*, Linda Gilpin, James G. Kairo and Mark Huxham Biomass and productivity of seagrasses in Africa

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Abstract: There is growing interest in carbon stocks and flows in seagrass ecosystems, but recent global reviews suggest a paucity of studies from Africa. This paper reviews work on seagrass productivity, biomass and sediment carbon in Africa. Most work was conducted in East Africa with a major geographical gap in West Africa. The mean above-ground, below-ground and total biomasses from all studies were 174.4, 474.6 and 514 g DW m⁻², respectively with a global range of 461–738 g DW m⁻². Mean annual production rate was 913 g DW m⁻² year¹ (global range 816–1012 g DW m⁻² year¹). No studies were found giving sediment organic carbon, demonstrating a major gap in seagrass blue carbon work. Given the small numbers of relevant papers and the large geographical areas left undescribed in Africa, any conclusions remain tentative and much remains to be done on seagrass studies in Africa.

Keywords: Africa; blue carbon; productivity; seagrasses.

Introduction

Understanding the role of vegetated coastal ecosystems in global carbon dynamics is a field of growing interest as knowledge of natural carbon sinks and flows can contribute to effective management of human impacts on the climate. Currently, our understanding of the roles of different ecosystems in the global carbon budget is limited by uncertainty about, and ignorance of, both individual ecosystems and their ecological connectivity. Vegetated coastal ecosystems that, in the past, have been relatively neglected have more recently received considerable attention following the "blue carbon" initiative, which established a clear distinction between the aquatic and terrestrial organic carbon sinks and helped to highlight the high relative efficiency of vegetated coastal sinks (Nellemann et al. 2009, http://the blue carbon initiative.org). Of the three key "blue carbon" habitats - salt marsh, mangrove and seagrass meadows - seagrasses are the most extensive but least studied. Available reviews of seagrass biomass and carbon flows globally (Duarte and Chiscano 1999, Fourgurean et al. 2012) reveal that the majority of studies have been done in Western Europe, the Mediterranean, the Caribbean, Australia and the American coasts. This is an indication of the relative paucity of information about seagrasses in African waters. Globally, seagrass ecosystems are estimated to store as much as 19.9 Pg of organic carbon and the oceans may bury an estimated 27.4 Tg C year¹ in seagrass meadows (Fourgurean et al. 2012). The average standing stock of seagrass is estimated at 460 g DW m² while the average production is 5.0 g DW m² day¹ (Duarte and Chiscano 1999). As these figures have been derived without much contribution from seagrass studies in Africa, estimates of the global seagrass carbon budget may change substantially if sequestration and storage rates in African systems are distinctive. Bearing in mind that seagrasses host a high species diversity globally (Short et al. 2007) and the fact that the role of seagrasses in carbon fluxes is acknowledged (Mateo et al. 2006), there is a need to understand variation in biomass and carbon storage across species and sites. The aim of the present study was to carry out a comprehensive assessment of all accessible literature on African seagrass species, to establish the current knowledge on biomass stocks and productivity, and to identify the geographic distribution of these data around Africa.

Materials and methods

Both the primary and gray literature were used. Four search engines – Google Scholar, Yahoo, Science Direct and ISI Web of Science – were used when looking for any available information on seagrass biomass and productivity studies in Africa up to the end of the year 2015. In addition, manual searches from libraries were done especially for the gray literature. Several researchers thought to have been involved in seagrass biomass and carbon studies in Africa were contacted to provide any available

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information. The search terms used were "seagrass" in combination with one of the following: "above-ground biomass", "below-ground biomass", "biomass stocks", "carbon burial", "productivity", "Africa", "target seagrass species" and "names of countries" along the African coasts. Where data on biomass and productivity were given as a range with no means reported, the mid-point was taken as an estimate of the mean from that study. In some cases, relevant information was not given in the text but could be reliably estimated from the figures. Data on biomass and productivity rates for different species at different sites were investigated and summarised.

Results

Of the over 300 abstracts initially found, 32 papers and eight reports or theses gave information on biomass

and/or productivity in Africa. Of these, 25 reported on seagrass biomass stocks alone while 15 reported entirely on productivity or a combination of biomass stocks and productivity. Six reports or theses were on biomass stocks and three on productivity, though one thesis reported on both biomass and productivity (Table 1). These peer reviewed papers, together with the reports and theses, come from studies carried out primarily on the Western Indian Ocean (WIO) coastline, especially in Kenya (Gazi Bay and around Mombasa), Tanzania (sites around Zanzibar Island), Mozambique (Inhaca Island), Aldabra Island in the Seychelles Republic, Mauritius and along the coast of South Africa. Other studies have been conducted at Sharm El-Moyia Bay along the Red Sea coastline of Egypt, Banc d' Arguin in N.W Mauritania and at some bays and lagoons such as Ghar El Melh Lagoon in Northern Tunisia and at Montazah Bay of Egypt on the southern Mediterranean Sea (Figure 1). Some studies

Table 1: Published papers, reports/theses on seagrass biomass and productivity studies around Africa.

Country	Biomass stocks		Productivity	
	Papers	Reports/theses	Papers	Reports/theses
Algeria			Semroud et al. 1990	
Egypt	Gab-Alla 2001			
	Mostara 1996			0.11. 4005
кепуа	Duarte et al. 1998	Gwada 2004	Duarte et al. 1996	Ochieng 1995
	Ochieng and Erftemeijer 1999		Hemminga et al. 1995	
	Kamermans et al. 2002		Ochieng and Erftemeijer 1999	
	Ochieng and Erftemeijer 2003		Uku and Björk 2005	
	Uku and Bjork 2005			
Libya			Pergent et al. 2002	
Mauritania	van der Laan and Wolff 2006		Vermaat et al. 1993	
	Vermaat et al. 1993		Van Lent et al. 1991	
Mauritius	Daby 2003			
Morocco		Bououarour et al. 2015		
		Boutahar et al. 2015		
Mozambique	Bandeira 1997	Larsson 2009	Bandeira 2002	Bandeira 2000
	Bandeira 2002		de Boer 2000	Larsson 2009
	de Boer 2000			
	Martins and Bandeira 2001			
	Paula et al. 2001			
Seychelles	Aleem 1984			
South Africa	Adams and Talbot 1992	Grindley 1976		
	Christie 1981			
	Hanekom and Baird 1988			
	Talbot and Bate 1987			
Tanzania	Eklöf et al. 2005	Mvungi 2011	Lyimo et al. 2006	
	Gullström et al. 2006			
	Kamermans et al. 2002			
	Lugendo et al. 2001			
	Lyimo et al. 2006			
	Lyimo et al. 2008			
Tunisia	Sghaier et al. 2011		Sghaier 2012	
	Sghaier 2012			



Figure 1: Sites along the coastline of the African continent where seagrasses biomass and productivity have been studied.

(unpublished) have recently been reported from Marcha Bay, Jbel Moussa Bay and the Atlantic coast of Morocco (Table 2). Data were available for 14 species, with biomass data available for 13 species (Table 2), while data on seagrass productivity were available for 10 species (Table 3). Most of the seagrass biomass studies considered mixed stands, but Thalassodendron ciliatum and Thalassia hemprichii were the most widely studied individual species, each having been a subject of research in nine out of the 35 locations where biomass studies were reported and in five and six locations, respectively, out of the 18 locations for productivity studies. Halodule wrightii, Cymodocea rotundata, Halophila stipulaceae and Halodule uninervis have been studied for biomass stocks in only one location each. Similarly, with the exception of T. hemprichii and T. ciliatum, a majority of the other species reported in productivity research were studied in only one location (Table 3). Thalassodendron ciliatum was the only species reported to have been studied for all the productivity indices (Table 3). Larger seagrass species such

as *T. hemprichii* and *T. ciliatum* recorded the highest per unit area biomass while smaller species, such as *H. wrightii*, recorded the lowest biomass. There was a large range in biomass between the highest and lowest species (Figure 2). The highest number of published biomass and productivity studies in Africa were carried out between 1996 and 2010 accounting for 65.6% of the total, while 62.5% of theses, reports or articles (unpublished or currently under peer review) have emerged between 2010 and 2015 (Figure 3).

Biomass of seagrasses in Africa

We obtained 47 data sets for both the above- and belowground biomass and 73 for total biomass contained within the 32 papers and eight reports or theses (Table 1). The total and the above-ground biomass data were each reported in 21 of the 40 papers, reports and theses while below-ground biomass was reported in 15 of those papers,

Country	Location	Latitude & Longitude	Species	Above-ground biomass (g DW m²)	Below-ground biomass (g DW m ⁻²)	Total biomass (g DW m²)	Reference
Egypt	Montazah Bay	31°12′N, 29°55′E	Cymodocea nodosa	287		1	Mostafa 1996
2	Sharm El Moyia Bay	27° 9′N, 34°3′E	Halophila Stipulaceae			270	Gab-Alla 2001
Kenya	Galu Bizzi	4°18'S, 39°32'E	Ihalassodendron ciliatum			40.6±40.6	Uku et al. 1996 Ulio et al. 1996
	DIANI	4°18'5, 10°32'E	Inalassoaenaron cillatum			2/9.3±9/.6	UKU ET AI. 1996
	Diani Cooli	4°18'5,10°32'E		57 - 5 / 7C		430 (33) 775 5 - 752 5	Kamermans et al. 2002
	חמבו	4 20 70 FC 4C 4C 4C	maassoaemanon cinatam	710°1 ⊤ 41	200.11222	0.20270.021	Uctilelig allu Frftemeiler 2003
	Chale lagoon	4° 25′S, 39°30′E	Thalassodendron ciliatum		243.4		Duarte et al. 1998
	Mombasa	4° 2′S, 39°41′E	Mixed			471.6±66.7	Kamermans et al. 2002
	Roka	1° 36′S, 39°12′E	Mixed			644 (7)	Kamermans et al. 2002
	Mombasa Marine	4° 2′S, 39°41′E	Mixed			760±96	Ochieng and
	Park						Erftemeijer 1999
	Nyali	4° 03′S, 39°43′E	Thalassodendron ciliatum–north	277.4±36.3	364.9±83.5		Gwada 2004
			East monsoon				
			<i> halassodendron ciliatum</i> –south Eset monecon	269.5±65	312.0±123		
	1111	1/C/00C 3/CV 0/				(22) 707	COC lo to community
	Nydii Maana	4 03 3, 39 43 E	MIXED			(55) 400	Namerinans et al. 2002
	Kenyatta	4° 00'5, 39°44'E 28 22/5 200550/F	Mixed			233 (33) 4 F 7 (22)	
	Vatariu	5- 25 5, 59-59 E				(66) /64 765	
Mauritania	banc d' Arguin	20° 35'N, 16°15'W	Mixed			555	Vermaat et al. 1993
			Mixed		255.0		van der Laan and Wolfe
							2006
Mauritius	Mon Choisy Bay	20° 17′S, 5733′W	Syringondium isoetifolium Halophila ovalis			129.3 102.5	Daby 2003
Morocco	Marcha lagoon	40° 39'N, 8°48'W	Cymodocea nodosa	8.02-61.2	10.8-235		Boutahar et al. 2015
	Atlantic coast	23° 30'N, 15°56'W	Zostera noltii	32-259	21-314		Bououarour et al. 2015
	Jbel Moussa Bay	30° 8′N, 5°21′W	Zostera noltii	3.08±1.12		7.72±1.38	
Mozambique	Inhaca	25° 58′S, 32°55′E	Thalassodendron ciliatum	355.2 ± 111.1	792.4±342.9	1148 (30)	Bandeira 1997
			<i>Zostera capensis</i> (summer)	15.7±4.5	173.4±47.5	190±51.2 (10)	de Boer 2000
			<i>Cymodocea serrulata</i> (summer)	34.1 ± 18.6	38.6±14.0	82.0±30.8 (10)	
			<i>Halodule wrightii</i> (summer)	16.0 ± 22.2	17.1 ± 14.5	22.2±21.7 (10)	
			Zostera capensis (winter)	25.7±8.0	198.9 ± 75	219.5±78.1 (10)	
			<i>Cymodocea serrulata</i> (winter)	17.6 ± 15.2	27.0±14.4	43.1±21.8 (10)	
			Halodule wrightii (winter)	6.9±5.5	18.1 ± 6.5	22.9±8.2 (10)	
	Inhaca (Northern	25° 58′S, 32°55′E	Thalassia hemprichii	154.4±22.7	633.0±163.5	787.4±233.8	Martins and Bandeira
	Bay)		Halodulo uniohtii			30 7+11 0	2001
			Halophila ovalis			0.6+0.4	
			Zostera capensis			4.8±2	
			Cymodocea rotundata			39.9 ± 18.7	
	Inhaca (Southern Bavi	25° 58′S, 32°55′E	Thalassia hemprichii	147.1±68.65	1729.7±495.25	1876±389.4	
	uay,						

Country	Location	Latitude & Longitude	Species	Above-ground biomass (g DW m ⁻²)	Below-ground biomass (g DW m ⁻²)	Total biomass (g DW m ^{.2})	Reference
			Halodule wrightii Halophila ovalis Zostera capensis Cvmodorea rotundata			0.9±0.7 0±0 0±0 4.5+4 3	
		25° 58′S, 32°55′E	opmooco.comore and the comore and th	50.1 - 170.7 14.2 - 291.1 7.9 - 51.3	0.04-1471.1 9.21-1307.6 66.0-195.5		Paula et al. 2001
Seychelles	Inhaca Aldabra Island	25° 58'S, 32°55'E 9° 41'S, 46°42′E	Thalassia hemprichii Halodule uninervis Halophila ovalis Mixed species Thalassia hemprichii	49.8±3.1		243 46.5 425 412.5	Larsson 2009 Aleem 1984
South Africa	Knysna estuary Langebaan lagoon	34° 05'S, 23°21'E 33° 01'S, 18°01'E	Thalassodendron ciliatum Syringondium isoetifolium Zostera capensis Zostera capensis	206 217		468 435	Grindley 1976 Christie 1981
	Swartkops estuary Kromme Estuary Kromme Estuary	33° 52'S, 25°38'E 34° 09'S, 24°51'E 34° 09'S, 24°51'E	Zostera capensis Zostera capensis (winter 1979) Zostera capensis (summer 1980)	105±44 55±21		75.8–124.7 244	Talbot and Bate 1987 Hanekom and Baird 1988 Adams and Talbot 1992
Tanzania	Chwaka Chwaka Chwaka	6° 10′S, 39°26′E 6° 10′S, 39°26′E 6° 10′S, 39°26′E	Thalassia hemprichii Thalassia hemprichii Enhalus acoroides Thalassodendron ciliatum Mixed	897.2±754.8 62–105	I	- 85 100 90	Kamermans et al. 2002 Eklöf et al. 2005 Gullström et al. 2006
	Chwaka Jambiani	6° 10′S, 39°26′E 6° 6′S, 39°32′E (With Saywood)	Enhalus acoroides Thalassia hemprichii Mixed Thalassia hemprichii	$76.4-105.1 (20) 61.8-99.1 (20) 94.5 (20) 90.4\pm16.1 (5)$	185±32.9 (5)	276±48.7 (5)	Gullström et al. 2008 Lyimo et al. 2006
	Chwaka	(Non Seaweed) 6° 10'S, 39°26'E (With Seaweed) (Non-Seaweed)	Thalassia hemprichii Thalassia hemprichii Thalassia hemprichii	609±71.5 (5) 108±23.8 (5) 175±19.0 (5)	2455±726 (5) 179±57.9 (5) 220±3.4 (5)	3063±715 (5) 286±81.5 (5) 393±18.7 (5)	
	Marumbi	(With Seaweed) (Non-Seaweed) 6° 13'S, 39°28'E (With Seaweed)	Enhalus acoroides Enhalus acoroides Thalassia hemprichii	177±85.5 (8) 199±54.5 (8) 465±183 (5)	563±272 (8) 415±114 (8) 90 4±129 (5)	740±358 (8) 614±98.9 (8) 1369±266 (5)	

Table 2 (continued)

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Country	Location	Latitude & Longitude	Species	Above-ground biomass (g DW m²)	Below-ground biomass (g DW m²)	Total biomass (g DW m ⁻²)	Reference
		(Non-Seaweed)	Thalassia hemprichii	301±42.1 (5)	442±66.9 (5)	742±81 (5)	
		(With Seaweed	Enhalus acoroides	$144\pm 63.0(8)$	810±356 (8)	953±418 (8)	
		(Non-Seaweed)	Enhalus acoroides	$143\pm57.5(8)$	512±207 (8)	655±264 (8)	
	Chwaka	6° 10′S, 39°26′E	Mixed			142.4–1652	Lyimo et al. 2008
		(With Seaweed)					
		(Non-Seaweed)				212.9–1829	
	Jambiani	6° 6′S, 39°32′E	Mixed			880.4-3467	
		(With Seaweed)					
		(Non-Seaweed)				203.4-3810	
	Kunduchi & Ocean	6° 40'S, 39°13'E	Mixed			0.25-135.29	Lugendo et al. 2001
	road						
	Ocean road	6° 45'S, 39° 20'E	Thalassia hemprichii	307.0±74.9	412.1±93.3		Mvungi 2011
			Cymodocea serrulata	202.7±69.6	267.7±147.9		
	Mji-mwema	6° 38′S, 39°40′E	Thalassia hemprichii	267.0±43.8	1177.4 ± 265.2		
			Cymodocea serrulata	352.2±141.7	737.2±260.8		
	Kiwengwa	5° 60'S, 39°23'E	Mixed			115 (30)	Kamermans et al. 2002
	Dongwe	6° 11′S, 39°32′E	Mixed			224 (21)	
Tunisia	Ghar El Melh	37° 09'N, 10°13'E	Cymodocea nodosa	97.3±51.4	264.7±69.2	327.7±86.1	Sghaier 2012
	Lagoon						
			Cymodocea nodosa	82.5±15.38	333.9±49.4	413.8±46	Sghaier et al. 2011
	Northern lagoon of	37° 14'N, 09° 56'E	Zostera noltii			79.75	Imen and Abdessalem
	Tunis						2015
NEM, North Ea	st Monsoon; SEM, South	ר East Monsoon. Value in	parenthesis (n) where available r	epresents the sample size. I	n some studies, the total	l biomass is not eq	ual to the sum of the
above-ground	and the below-ground d	lue to differences in the si	amples sizes but are captured as	reported in the studies.			
The four famili	es of seagrass and spec	ies studied on biomass aı	nd productivity in Africa; Hydroch	naritaceae [<i>Enhalus acoroide</i>	s (L.F) Royle, <i>Halophila n</i>	<i>ninor</i> (Zoll.) den Ha	ırtog, Halophila ovalis
(R.Br.) Hook f.,	Halophila stipulaceae (Forsk.) Aschers and Thala	<i>ıssia hemprichii</i> (Enhrenberg) As [,]	cherson]; Cymodoceae [<i>Cym</i>	odocea rotundata Ehrenb	o. et Hempx. et Asc	hers, <i>Cymodocea ser-</i>

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Table 2 (continued)

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rulata (R.Br.) Aschers. et Magnus, Cymodocea nodosa (Ucria) Aschers., Halodule uninervis (Forsk.) Aschers. in Bossier, Halodule wrightii Aschers., Syringondium isoetifolium (Aschers.) Dandy

and Thalassondendron ciliatium (Forsk.) den Hartog]; Zosteraceae (Zostera capensis Setchell, Zostera noltii); Posidonaceae [Posidonia oceanica (L.) Delile].

Country	Location	Latitude & longitude	Species	Season	Leaf growth (mm shoot ⁻¹ day ⁻¹)	Leaf production (g DW shoot ⁻¹ day ⁻¹)	Rhizome growth (mm day ⁻¹)	Total production (g DW m ⁻² day ⁻¹)	Reference
Algeria	Marsa	35° 51'N, 10°35'E	Posidonia oceanica				0.02		Semroud et al. 1990
	Tament foust		5				0.35		
Kenya	Gazi Bay	4° 25′S, 39°30′E	Thalassodendron					7.5	Hemminga et al. 1995
		4° 25′S, 39°30′E	Thalassodendron		20.7±0.8			4.43±2.7	Ochieng 1995
			ciliatum)
		4° 25′S, 39°30′E	Mixed species					2.4±0.6	Ochieng 1995
	Chale lagoon	4° 25′S, 39°30′E	Thalassodendron				0.4		Duarte et al. 1996
			ciliatum						
	Mombasa Marine park	4° 2′S, 39°41′E	Mixed species					8.2±2.8	Ochieng and Erftemeijer 1999
	Nyali	4° 03′S, 39°43′E	Thalassia	S.E	17.2±9.5	0.008±0.002		5.5±4.9 (30)	Uku and Björk 2005
			membricum	ЦN	28,5+4,1	0.008+0.006		5 3+0 5 (30)	
	Vipingo	3° 45′S, 39°50′E		S.E	17.1 ± 2.6	0.004 ± 0.001		2.4±1.04 (30)	
)			N.E	17.1 ± 2.8	0.004±0.002		3.3±1.1 (30)	
	Nyali	4° 03′S, 39°43′E	Thalassodendron	S.E	17.3 ± 1.6	0.005 ± 0.005		3.7±2.4 (30)	
			ciliatum						
				N.E	18.8 ± 5.9	0.006±0.003		3.1±1.8 (30)	
	Vipingo	3° 45′S, 39°50′E		S.E	12.4±5.7	0.005 ± 0.002		2.9±2.4 (30)	
				N.E	12.4±5.3	0.004 ± 0.001		1.8±1.6 (30)	
	Nyali	4° 03′S, 39°43′E	Cymodocea	S.E	12.8 ± 1.6	0.002 ± 0.0005		2.1±0.5 (30)	
			rotundata						
				N.E	14.9 ± 1.8	0.002 ± 0.0002		2.3±0.5 (30)	
	Vipingo	3° 45′S, 39°50′E		S.E	10.0 ± 9.1	0.001 ± 0.0006		2.0±1.1 (30)	
				N.E	11.7 ± 2.0	0.001 ± 0.0005		1.9±1.0 (30)	
Libya	Farwa lagoon	33° 05′N, 11°44′E					0.02-0.1		Pergent et al. 2002
Mauritania	Banc d' Arguin	20° 35′N, 16°15′W	Cymodocea					0.003	Van Lent et al. 1991
			nodosa						
			Zostera noltii		0.3				Vermaat et al. 1993
Mozambique	Inhaca Island	25° 58'S, 32°55'E	Thalassodendron		14.1–18.3				Bandeira 1997
			ciliatum						
			Thalassodendron		7.5–9.5				Bandeira 2000
			ciliatum						
			Zostera capensis	Summer	0.7 ± 1.4	0.03		0.18	de Boer 2000

Country	Location	Latitude & longitude	Species	Season	Leaf growth (mm shoot ⁻¹ day ⁻¹)	Leaf production (g DW shoot ^{.1} day ^{.1})	Rhizome growth (mm day¹)	Total production (g DW m ⁻² day ⁻¹)	Reference
			Zostera capensis	Winter	0.6 ± 1.1	0.02		0.18	
			Cymodocea	Summer	2.4±5.3	0.80		0.62	
			serrulata						
			Cymodocea	Winter	1.2 ± 1.5	0.46		0.20	
			serrulata						
			Halodule wrightii	Summer	1.5 ± 3.8	0.14		0.20	
				Winter	1.1 ± 2.0	0.08		0.08	
			Thalassia		10.4 ± 0.9	0.004		1.08 ± 0.06	Larsson 2009
			hemprichii						
South Africa	Kromme	34° 09′S, 24° 51′E	Zostera. capensis					0.93-1.98	Hanekom and Baird
	estuary								1988
Tanzania	Marumbi	6° 13′S, 39° 28′E	Thalassia hemprichii		13.4±4.7	0.004±0.002		1.97±0.89	Lyimo et al. 2006
	Chwaka	6° 10′S, 39° 26′E			17.1 ± 5.2	0.01 ± 0.01		1.86 ± 0.6	
	Jambiani	6° 6'S, 39° 32'E			15.8 ± 6.0	0.005±0.002		5.92 ± 2.33	
	Marumbi	6° 13′S, 39° 28′E			19.4±7.1	0.02 ± 0.01		2.05±0.9	
	Chwaka	6° 10'S, 39° 26'E	Enhalus acoroides		24.8±9.4	0.02 ± 0.01		2.77±1.6	
Tunisia	Ghar El Melh	37° 09′N, 10° 13′E	Cymodocea		3.35 (21)		1.2±1 (21)	1.42 (20)	Sghaier et al. 2011
	Lagoon		nodosa						
	Tabarka	36° 57′N, 8° 45′E	Zostera noltii				0.36		
	El Kantaoui	35° 51'N, 10° 35'E	Posidonia				0.14		Sghaier et al. 2013
			oceanica						

Table 3 (continued)



Figure 2: Mean $(\pm S.E)$ above-ground, below-ground and total biomass values for 13 seagrass species studied in Africa, pooled across all reported sites.

theses and reports. The total biomass for all species combined revealed large variation between sites (Table 2). The mean above- and below-ground biomasses for all species and across all sites were 174.4 and 474.6 g DW m⁻², respectively, representing an above- to below-ground biomass ratio of almost 1:3. The mean total biomass was 514.3 g DW m⁻². This was calculated from the data available on total biomass and not necessarily from the sum of above-ground and below-ground biomass as some studies did not record either the above-ground or the belowground biomass (Table 2). The highest total biomass was recorded for mixed seagrasses in a non-seaweed area at Jambiani in Zanzibar at 3063.3 g DW m⁻² whilst the lowest total biomass of 0.6 g DW m⁻² was recorded for Halophila ovalis at Northern Bay on Inhaca Island off Mozambique in the same study (Table 2). In terms of species, the highest biomass was recorded for Thalassia hemprichii at 1876 g DW m⁻² in Southern Bay of Inhaca Island, Mozambique (Table 2). Comparison of the means



Figure 3: Number of publications, reports/theses containing information on biomass and productivity of African seagrasses between 1976 and 2015.



Figure 4: Mean (±S.E) total biomass values for the seagrass species in different regions of Africa.

for the above-ground, below-ground and total biomasses for individual species reveal that the highest mean biomasses were found for T. hemprichii at 271.7 g DW m⁻². 817.8 g DW m⁻² and 928.0 g DW m⁻², respectively, while the lowest mean biomasses were for Halodule wrightii at 11.5 g DW m⁻², 17.6 g DW m⁻² and 19.2 g DW m⁻², respectively. In terms of the five regions where the seagrass data are available (Figure 4), the East African coast has the highest mean above-ground, below-ground and total biomass at 256.8, 587.1 and 778.1 g DW m⁻², respectively. The South Mediterranean seagrasses had below-ground and above-ground biomasses of 299.3 and 155.6 g DW m⁻², respectively, while the South Africa and the WIO Islands had means of 413.3 and 95.7 g DW m², respectively, for the same parameters. Data available from the North West African region show the lowest mean biomass for the three parameters with 61.06 g DW m⁻² for the above-ground biomass, 145.2 g DW m⁻² for the below-ground biomass and 159.4 g DW m⁻² for the total biomass (Figure 4).

Productivity rates of seagrasses in Africa

This review obtained 29 data sets on leaf growth rates, 24 on leaf production, seven on rhizome growth rates and 32 on total production (Table 3). The mean leaf growth rate was 12.4 mm shoot¹ day¹ while the mean leaf production was 0.07 g DW shoot¹ day¹. Rhizome growth rates were 0.36 mm day¹ while the mean total production was 2.5 g DW shoot¹ day¹. Lyimo et al. (2006) studied growth characteristics of Thalassia hemprichii and Enhalus acoroides at several sites in Zanzibar, where high growth rates in terms of leaf length and dry weight were observed for both species. In another study, Uku and Björk (2005) recorded higher growth rates for the same parameters for Thalassia hemprichii as compared to Cymodocea rotundata and Thalassodendron ciliatum at Nyali and Vipingo, Mombasa, Kenya. In Gazi Bay, Kenya, Hemminga et al. (1995) reported total productivity for T. ciliatum that was much higher than reported from other sites (Table 3). In another study of a monospecific stand of T. ciliatum at Gazi Bay, Ochieng (1995) recorded a mean shoot growth rate of 20.7 mm day¹ which was higher than the rate recorded in most of the other studies for the same species. The review for all species, whether growing in multispecific or pure stands, indicated that Zostera capensis and Cymodocea serrulata had the lowest shoot growth rates of <1 mm shoot¹ day¹ recorded at Inhaca Island, Mozambique (de Boer, 2000). Some seasonality is indicated for T. hemprichii with a maximum of 28.5 mm shoot¹ day¹ during the North East monsoon and 17.2 mm shoot¹ day¹ during the South East monsoon at Nyali in Mombasa (Uku and Björk 2005). Daily leaf production also differed between sites and species with a maximum of 0.01 g DW shoot¹ day¹ for T. hemprichii recorded at Chwaka in Zanzibar (Lvimo

et al. 2006). Lowest daily leaf production was 0.001 g DW shoot¹ day¹ for *Cymodocea rotundata* recorded at Vipingo in Mombasa (Uku and Björk 2005). The mean productivity rates for all species, where available, indicated that *T. hemprichii* had the highest total productivity rates while the lowest was in an eelgrass, *Zostera capensis* (Table 4). The mean leaf production per day for individual species was highest in *Cymodocea serrulata* while the lowest was in *C. rotundata*. Comparison of rhizome growth rates indicated highest rates in *Cymodocea nodosa* and lowest in *Posidonia oceanica*. The mean for total production was highest in mixed stands while the lowest was recorded in *Halophila ovalis* (Table 4).

Discussion and conclusion

This assessment of studies on seagrass biomass stocks and productivity around Africa found a limited number of papers and reports with most of them reporting from countries on the Western Indian Ocean coastline (Kenva, Tanzania, Mozambique, South Africa, Madagascar, Seychelles and Mauritius). A few studies have also been reported from the Red Sea coastline of Egypt, the north eastern part of the Atlantic coastline on the coast of Mauritania and Morocco and more recently some studies (unpublished), have emerged from the Mediterranean coastline of Tunisia. However, the limited number of studies demonstrates a paucity of information on the carbon budget and flows in Africa. Similar observations of a geographical bias in research on seagrass biomass stocks, with Africa particularly underrepresented, have been made in other reviews (Duarte and Chiscano 1999,

Table 4: Mean (±S.E) productivity values expressed as rates of leaf growth, leaf dry weight production, rhizome growth and total dry weight production for seagrass species based on all available data around the African coast.

Species	Leaf growth (mm shoot ⁻¹ day ⁻¹)	Leaf production (g DW shoot ⁻¹ day ⁻¹)	Rhizome growth (mm day ^{_1})	Total Production (g DW m ⁻² day ⁻¹)
Cymodocea nodosa	3.35±0		1.2±0	0.71±0.7
Cymodocea rotundata	12.35±1.0	0.002±0001		2.08±0.1
Cymodocea serrulata	1.8±0.6	0.63±0.17		0.41±0.2
Enhalus acoroides	24.8±0	0.02±0		2.77±0
Halophila ovalis	1.5±0	0.14±0		0.2±0
Posidonia oceanica			0.19±0.1	
Thalassia hemprichii	17.33±1.6	0.007±0.01		3.26±0.6
Thalassodendron ciliatum	15.18±1.6	0.05±0.01	0.4±0	3.90±0.7
Zostera capensis	0.8±0.2	0.04±001		0.47±0.3
Zostera noltii				0.004±0
Mixed				5.3±2.9

Fourqurean et al. 2012). Some of the seagrass studies in Africa concentrated on one biomass pool (above-ground or below-ground) while others focused on total biomass only (Table 2). An important observation in this review is that seagrass studies in Africa have ignored the sediment organic carbon, the most important part of the putative "blue carbon" sink provided by seagrasses, revealing a major gap in seagrass blue carbon work. Since the reviewed studies reported on only 14 out of a total of 34 species in the Tropical Atlantic, Tropical Indo-Pacific and South African flora, the current work suggests that the basic ecology, including productivity and standing stock, of many species remains largely unknown.

The available data from the seagrass biomass and productivity studies in Africa reveal that seagrasses allocate higher biomass to their below-ground than their above-ground components, with mean estimates for the above and below-ground biomasses of 174.4 g DW m² and 474.6 g DW m⁻², respectively. In a review of seagrass biomass from different studies globally, Duarte and Chiscano (1999) arrived at above- and below-ground mean biomasses of 223.9 g DW m⁻² and 237.4 g DW m⁻², respectively. These findings differ from the results of this study in which the above-ground biomass was only ~37% of the biomass below-ground. Though these results deviate from our findings, our results are consistent with other observations, such as the most recent review of a global dataset, that the below-ground component of seagrasses forms the largest proportion of the living seagrass biomass and may constitute about two thirds of the total biomass in seagrass meadows (Fourgurean et al. 2012). The similarity of above-ground and below-ground biomass estimates in Duarte and Chiscano (1999) was attributed to the fact that some seagrass biomass studies did not measure the below-ground biomass, which in some cases could account for 15-50% of the total production as observed in an earlier study (Duarte et al. 1998). Though grazing and mechanical damage inflicted by wave scouring and by human activities may not significantly affect seagrass productivity and biomass storage, it nevertheless impacts on the meadows leading to high turnover rates especially for the above-ground component.

The mean estimate for total seagrass biomass in this review of 514.3.4 g DW m⁻² is within the global range. The seagrasses of Abu Dhabi in the United Arab Emirates were estimated to contain a total biomass of 122.3 g DW m⁻² (Campbell et al. 2014). In a review of global seagrass carbon storage, the *Posidonia oceanica* of the Mediterranean Sea were found to have the highest biomass at 2144 g DW m⁻² while the mean biomass from the global seagrass data was estimated at 738.4 g DW m⁻² (Fourqurean

et al. 2012). While this global estimate is higher than our total African biomass estimate, this could be explained by the influence of the high biomass of *Posidonia oceanica* in other regions as well as the limited information on seagrass biomass from Africa in previous global estimates. In terms of the five regions along the coasts of Africa where seagrass research has been done, this study observed that the East African seagrasses had the highest biomass at 738.1 g DW m² compared to 370.8 g DW m² for the Southern Mediterranean where *Cymodocea nodosa* was the dominant species. No study was found from this southern part of the Mediterranean Sea containing information for *Posidonia oceanica*.

The review observed that higher biomass values occurred in larger species compared to the smaller species (Figure 2). This may suggest that larger species tend to develop higher below-ground biomass and hence have a higher capacity for biomass storage due to the relatively slow turnover of the below-ground materials (Duarte and Chiscano 1999). The current assessment of available data from Africa on seagrass biomass supports this view.

The current review arrived at a mean total production estimate of 912.5 g DW m⁻² year¹ against 1012 g DW m⁻² year¹ obtained in a previous seagrass biomass and production reassessment using a global data set (Duarte and Chiscano 1999) and an earlier one of 816 g DW m⁻² year⁻¹ (Duarte and Cebrián 1996). Seagrass beds with mixed species were found to have the highest total production, estimated at 1935 g DW m⁻² year¹, followed by Thalassodendron ciliatum at 1423 g DW m⁻² year¹, suggesting that some species do better when in association with others. Growth patterns for different species and variation in environment between sites could account for the differences in values observed. Some species may have the potential to accumulate biomass but this may be kept low by resource limitation or due to the heavy losses caused by physical disturbance (Duarte and Chiscano 1999). Biomass and productivity for some seagrass species was reported to exhibit seasonality which could be attributed to periodical fluctuations in abiotic factors such as irradiance, temperature and hydrological conditions (Uku and Björk 2005, de Boer 2000).

The estimates arrived at in this study may involve considerable errors, given the general paucity of studies, particularly for some seagrass species, and a lack of uniformity in the sampling methods used by different researchers. However, with the development of the Blue Carbon sampling manual by the International Blue Carbon Initiatives Scientific Working Group (Howard et al. 2014, http://the blue carbon initiative.org), and new emphasis on researchers adopting uniform sampling protocols, future research should produce more reliable and comparable estimates. Whilst the research gap revealed here may be similar to many other areas in which Africa is under-represented, seagrasses perhaps present a particular challenge for research in countries with relatively poor infrastructure and resources, since they may require expensive sampling work utilising specialised skills such as scuba diving.

Considering that the African coastline is extensive with large areas of seagrass cover, the spatial extent of study is very limited. The fact that this review did not find seagrass biomass studies from the West African coast, with the exception of Mauritania which is more to the North West coast, is another clear indication of the paucity of knowledge on seagrass biomass stocks in Africa. A majority of the studies have been done on the West Indian Ocean coastline mainly through funding by the West Indian Ocean Marine Sciences Association (WIOMSA) in partnership with the well-established research Institutions in the region or through partnership with institutions outside Africa. This signifies the importance of strengthening collaboration between institutions and the need for increased research funding if the knowledge gaps are to be filled. As the first review of seagrass biomass and productivity in Africa, we hope the current work will generate interest among the scientific community by identifying an important and missed opportunity for research. By contributing to a better understanding of the role of seagrass ecosystems in carbon budgets in Africa this may help to support the protection of these valuable ecosystems.

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