海草床沉积物有机碳研究综述

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摘要: 海草床具有重要的生态系统服务功能, 可以为海洋生物提供栖息地和食物来源, 同时还具有重要的碳储存功能, 海草床“蓝碳”功能日益受到学术界的重视, 据研究全球每年海草床的碳埋藏量高达$(2.7\sim4.4)\times10^7$ MgC。近年来, 由于人类活动的影响, 世界范围内海草床衰退严重, 导致海草床沉积物有机碳储量降低。本文综述了全球海草床沉积物有机碳的来源、组分、储量以及指示作用; 从物理、化学和生物三方面讨论了影响海草床碳储量的环境因素。最后提出了未来主要研究方向, 主要包括加强海草床碳通量普查, 分析全球气候变化背景下海草床沉积物有机碳的变化机制, 明确海草床碳储量流失速率, 研究海岸带工程对海草床沉积物有机碳的影响。评估海草床沉积物有机碳储量及变化机制可以为全球海洋蓝碳研究提供科学依据。

关键词: 海草床; 沉积物有机碳; 来源; 储量; 环境因素

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海草通常生活在潮间带和潮下带的浅水区域, 是一种广泛分布于热带以及温带海域的沉水性被子植物[1]。印度-太平洋区、热带大西洋区、温带北大西洋区、温带北太平洋区、温带南大洋区和地中海区为全球 6 个主要海草分布区[1], 共有 6 科 72 种海草[2]。热带地区海草种类较多[1], 热带印度-太平洋地区的海草种类多达 25 种, 而在温带北大西洋区, 仅有 5 种海草[3]。我国海草床主要有南海海草分布区和黄渤海海草分布区, 共有 10 属 22 种, 大约为全球海草种类的 30%[4-5]。全球海草床覆盖面积约为$(3\sim6)\times10^5$ km^2[6-7], 据估算其生态系统服务价值约为每年每公顷 34 000 美元[8]。海草生态系统具有极其复杂的结构, 可以提供多种生态功能[9], 为海洋生物提供栖息地[10-11]和食物来源[12]。海草床还具有重要的碳储存功能, 近年来, 海草床“蓝碳”功能越来越受到学术界的重视[13-16]。

海草是沿海生态系统中重要的碳汇[17], 可以通过光合作用吸收 CO_2[18]。通常情况下, 海草所固定的碳含量大于其代谢需要[19], 多余的有机碳大部分被运输到海草的根及根状茎, 最终通过环境作用将有机碳固存于沉积物中[20]。海草床可以通过释放生物质或者从凋落物释放溶解有机碳[21-22], 并通过水流作用输运到其他生态系统[23], 全球海草床年输出的溶解性有机碳高达$(1.6\sim3.3)\times10^8$ MgC[19], 约占全球海草净初级生产力的 46%[24]。Su 等对广西珍珠湾海草床及其周围沉积物有机碳储量进行分析, 发现海草床沉积物有机碳含量显著高于无海草区域[25]。海草碎屑具有大量稳定组分和高沉积速率, 沉积物中的厌氧环境不利于微生物的生长, 使得沉积物有机碳长期储存[17, 26-28]。全球海草床不到海洋总面积的 0.2%, 但全球海草床沉积物有机碳储量为 139.7 MgC/ha, 并且每年碳埋藏量为$(2.7\sim4.4)\times10^7$ MgC, 占到每年全球海洋碳汇的 10%~18%[7, 20, 29], 显著高于大部分陆地生态系统[30], 可以缓解全球气候变化及其带来的负面影响[31]。我国海草床每年碳汇量约为$(3.2\sim5.7)\times10^5$ MgC[32]。山东桑沟湾鳗草海草床生态系统每年总固碳量约为 290 MgC, 吸收碳的形式包括海草固碳、附生植物固碳、海草床捕获颗粒碳等, 其中, 海草固定的碳占到总固碳量的 46%, 为 54.35 MgC/ha[33]。通常温带地区海草床有机碳储量要高于热带地区,

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可能是因为热带地区海草可以为更多生物提供食物和更高的海草碎屑分解速率[34-35]。我国海南岛沿岸现存海草床面积约 48.646 7 km^2[36]，表层 5 cm 沉积物有机碳总储量为 40858.5 MgC，CO_2 吸附量为 (1.44± 0.03) MgC/ha，其中东水、抱才、黄龙、莺歌等 8 个海草床沉积物平均碳储量为 7.02 MgC/ha，总储量约为 1306.45 MgC[37-38]。本文根据海草床沉积物有机碳的相关研究，分别从海草床沉积物有机碳来源、组分以及储量进行综述，讨论影响海草床沉积物有机碳的主要环境因素，结果将为海草床沉积物有机碳相关研究提供科学依据。

1 海草床沉积物有机碳研究进展

1.1 沉积物有机碳来源

1.1.1 海洋沉积物有机碳来源

沉积物有机碳不仅是水体污染物迁移的重要媒介，还参与地球化学循环，对生物地球化学循环、沉积物演变等有重要的指示作用[39]。沉积物有机碳参数主要包括碳氮比、碳同位素等，储存着气候、环境变化的信息等[40-41]。对于海洋中沉积物来源，科学家一般采用碳氮比(C/N)、碳稳定同位素法($\delta^{13}C$)以及生物标志法(如脂类和木质素)等进行研究。研究发现陆源和海源有机碳具有一定差别，陆源 C/N 比大于 12，$\delta^{13}C$ 为–28‰～–25‰，海源 C/N 比值为 6~9，$\delta^{13}C$ 为–19‰～–12‰[42, 43]。Liu 等(2020) 采用碳氮稳定同位素法和碳氮比法对黄海南部表层沉积物进行研究，发现该地区沉积物有机碳来源组成为海洋、陆地及人为输入，且黄河三角洲北部沉积物有机质陆源贡献较高(>50%)，而在近海泥区有机质贡献主要来源于海洋(>70%)[44]。红树林生态系统的碳储存通常采用稳定同位素法和表层沉积物碳氮比方法进行研究[45]，红树林对来源于陆地的土壤矿物质有较好的沉降作用，在河流侵蚀率高的地区，红树林沉积物有机碳有三分之二来源于陆地[46]；而在侵蚀率低、河流输入少的环境下，红树林有机碳有三分之二来源于其本身[45]。Tanaka 等(2011)对珊瑚礁溶解有机碳研究，发现有机质是从底栖生物群落中释放的[47]。而珊瑚礁中几种有机质的来源主要包括珊瑚-虫黄藻共生群落[48-49]、海草[50]、底栖藻类[51]的释放以及细菌溶解沉积物有机质释放[52]。科学家还发现海源和陆源有机质中的溴元素(Br)存在显著差异[53-54]，相关研究采用溴与有机碳(Br/TOC)的关联，分析海源及陆源对沉积物有机碳的贡献[55-56]。通常湖泊地质、土壤、河床的 Br/TOC 比值为 0.02~2.8 mg Br/g TOC，而海岸带沉积物的 Br/TOC 要显著高于陆源沉积物，高达 7.6 mg Br/g TOC[57]。

1.1.2 海草床沉积物有机碳来源

海草床沉积物中的有机碳不仅来自于海草，还来源于陆生植物碎屑和海洋生物，如浮游植物、大型藻类、附生植物和底栖藻类[58-59]。天然碳同位素的差异是由于植物在进行光合作用的过程中对碳的吸收机制不同所引起的，由这种机制差异将植物分为 C3、C4 和 CAM 植物[60]，因此，可以通过其本身的同位素特征值($\delta^{13}C$ 和 $\delta^{15}N$)来测定沉积物有机碳的来源及不同植物的贡献[61-62]。有关研究发现，海草的 $\delta^{13}C$ 为–8.99‰，大型海藻为–13.61‰[63]。Liu 等利用碳稳定同位素方法对新村湾海草床有机碳来源进行分析，发现沉积物有机碳稳定同位素值介于–20.39‰～–7.39‰之间，并且从营养盐浓度相对较低的海草床到高营养盐海草床的沉积物中，大型海藻及附生藻类对沉积物有机碳的贡献增加了 16%，表明大型海藻及附生藻类对沉积物有机碳的贡献与营养盐浓度呈正相关[63]。但是，同位素法本身存在一定缺陷，海草与其他藻类可能存在 $\delta^{13}C$ 值重叠的情况[63-64]，导致分析结果偏差。Rahayu 等(2019)采用稳定同位素标记法及碳氮比分析，对印度尼西亚群岛的海草床研究发现：Barranglompo、Sarappokeke 和 Kapoposang 岛的海草床沉积物有机碳具有相似特征，并且来源于海草的有机碳占到了 75%[65]。但在同一研究中，Bauluang 岛与其他 3 个岛屿海草床沉积物有机碳主要来源不同，浮游植物对沉积物有机碳贡献最大，约为 44%。初级生产者合成的脂肪酸有一些是特定的，可以用于区分微藻[66]、大型海藻[67]、被子植物[68]以及原核生物[69]，通过脂肪酸标记法来确定初级生产者到初级消费者的食物链结构日益受到关注[70]，采用脂肪酸标记法与稳定同位素法联用以克服 $\delta^{13}C$ 重叠的问题[71-72]，不同植物的碳、氮稳定同位素特征值及特征脂肪酸详见表 1。海草叶片主要由多糖组成，其余物质主要为木质素、单宁和游离的脂所结合成的酚酸[73-74]。现有研究采用 PY-GC-MS 和 THM-GC-MS 两种热解技术对大洋波喜荡草进行有机质解析，发现海草不仅由碳水化合物及木质素组成，还主要由在维管植物中不常见的对羟基苯甲酸(p-HBA)类物质组成。同样，该区域海草床沉积物碎屑中主要由酚类物质 p-HBA 及碳水化合物组成，证实海草床沉积物碎屑主要来源于海草的根、茎、叶[75]。

表 1 海草、海藻及陆地植物碳、氮稳定同位素特征值及特征脂肪酸

Tab. 1 Characteristic stable isotope values of carbon and nitrogen and characteristic fatty acids in seagrasses, seaweeds, and land plants

来源	碳稳定同位素 $\delta^{13}C$	氮稳定同位素 $\delta^{15}N$	特征脂肪酸	文献来源
海草	–23‰ ~ –3‰	0 ~ 8‰	18: 2n-6; 18: 3n-3; 18: 3n-4; 18: 4n-3	[71, 76-78]
大型海藻	–16.8‰	7‰	16: 1n-7; 18: 1n-9; 20: 5n-3; 20: 4n-6; 16: 0; 14: 0	[71, 78-81]
浮游植物	–19.1‰ ~ –22‰	3.0‰ ~ 12.0‰		
附生藻类	–17.5‰	5.9‰		
陆地植物(C3 植物)	–22‰ ~ –33‰	7.8‰	LCFA 长链脂肪酸	[82-83]
陆地植物(C4 植物)	–9‰ ~ –16‰	6.5‰		

1.2 海草床沉积物有机碳分类

沉积物有机碳可以根据物理、化学、生物(微生物降解性)方法分组。沉积物有机碳分类方法详见表 2。粒度分组法自 20 世纪 60 年代开始出现，按照与有机碳结合的颗粒大小，可分为砂砾(53~2 000 μm)、粗粉粒(5~53 μm)、细粉粒(2~5 μm)、粗黏粒(0.2~2 μm)和黏粒(<0.2 μm)[84]。将有机碳按照密度分，可分为轻组碳和重组碳[85]。通过化学方法将沉积物有机碳分为活性有机碳(Labile organic carbon, LOC)和惰性有机碳(Recalcitrant organic carbon, ROC)，活性有机碳的生物活性高，矿化速率高而惰性有机碳则较低[86]。活性有机碳按照提取方式可以分为盐提取碳、水提取碳、氯仿提取碳、酸提取碳[87]。根据其溶解性和水解性又分为溶解有机碳(Dissolved organic carbon, DOC)、酸水解有机碳[86]。生物分组法通常将有机碳分为微生物量碳(Microbial biomass carbon, MBC)和可矿化碳。沉积物中的细菌、真菌、藻类等含有的碳称为微生物量碳[88]，那些可以被微生物分解且向大气中释放 CO_2 的有机碳称为可矿化碳[89]。多数研究中根据其矿化速率将其分为活性有机碳和惰性有机碳[90]，有机碳是否容易降解是区分活性有机碳和惰性有机碳的依据，有机碳矿化速率对沉积物有机碳来源变化响应迅速[91]。表示海草床有机碳活性的指标通常用微生物量碳和溶解有机碳[63, 92]。海草地下生物量含有相对较高的碳氮比值、生物可利用性较差，因此，海草床固定的碳一般为惰性有机碳[93]。

表 2 沉积物有机碳分类

Tab. 2 Sediment organic carbon classification

分类方法	名称		备注	文献来源
粒度	砂砾		53~2 000 μm	[84]
	粗粉粒		5~53 μm	
	细粉粒		2~5 μm	
	粗黏粒		0.2~2 μm	
	黏粒		<0.2 μm	
密度	轻组碳			[85]
	重组碳			
化学方法	活性有机碳	提取方式	酸提取碳	[87]
			氯仿提取碳	
			水提取碳	
			盐提取碳	
		水解方式	溶解有机碳	[86]
			酸水解有机碳	
		生物分组	微生物量碳	[88]
			可矿化有机碳	[89]
	惰性有机碳			[86, 90]

1.3 海草床沉积物有机碳储量

学术界将海草和海草床沉积物中的有机碳储量进行了量化研究(表 3)。估算海草床沉积物有机碳埋藏速率主要利用的是 ^{14}C 和 ^{210}Pb 测年技术或通过海草床年际生产力调查等方法[94]。国内外通用的海草床沉积物有机碳储量计算方法为：采集一定深度的沉积物样品，将其分为相同厚度的子样、测量容重、沉积物有机碳含量测定、沉积物有机碳密度计算、相同厚度子样有机碳储量计算、总样品有机碳储量计算。容重的测量是将一定深度的风干沉积物样本放入到固定体积的容器中，测定其质量，计算方法为：

表 3　全球海草床沉积物有机碳储量

Tab. 3　Organic carbon storage in seagrass sediments across the world

地点	海草种类	区域特征	采样深度/cm	海草床有机碳储量/($MgC\cdot ha^{-1}$)	文献来源
混合海草床					
全球			100	139.7	[29]
中国广西	卵叶喜盐草; 贝克喜盐草; 日本鳗草	潮间带	100	48.32	[103]
中国海南新村	海菖蒲; 泰来草	潮间带	30	4.53~11.25(6.80±1.03)	[104]
中国西沙群岛	卵叶喜盐草; 泰来草; 羽叶二药草; 圆叶丝粉草	宣德群岛	5	2.41±0.78	[37]
印度尼西亚 Spermonde Islands	海菖蒲; 泰来草; 毛叶喜盐草; 卵叶喜盐草; 圆叶丝粉草; 单脉二药草; 羽叶二药草; 针叶草	Barranglompo	20~55	18.8±4.1	[65]
		Bauluang	20~55	20.3±3.3	
		Sarappokeke	20~55	11.9±5.3	
		Kapoposang	20~55	32.1±13.4	
肯尼亚 Gazi Bay	全楔草; 海菖蒲; 圆叶丝粉草	海湾东部河流(红树林区)	100	117.85~544.65 (258.21±90.12)	[105]
	圆叶丝粉草; 齿叶丝粉草; 泰来草	海湾西部河流(人类活动区)	100	67.25~160.48 (106.66±21.36)	
苏格兰	鳗草; 诺氏鳗草	潮间带	50	50.69±26.69	[101]
美国 Florida Bay	龟裂泰来草; 莱氏二药草; 丝状针叶草	碳酸盐海草床	100	175.0±20.4	[97]
巴西东南部海岸	未公开	硅酸盐海草床	100	67.6±14.7	
单一海草床					
太平洋东部	鳗草	潮间带、潮下带	25	173.6±21	[100]
		潮间带、潮下带	100	69.4	
加拿大 British Columbia	鳗草	海草床内部	20	139.2±92.8	[106]
		海草床边缘	20	113.0±69.8	
		无海草覆盖	20	97.71±51.6	
		Choked Pass	20	18.5	
		McMullins North	20	514.7	
哥伦比亚 Caribbean	龟裂泰来草	海草、海藻、红树共生	100	241±118	[107]
太平洋西部	鳗草	潮间带、潮下带	25	234.3±12.2	[100]
			100	93.8	
中国广西北海 Shatian peninsula	贝克喜盐草	海草覆盖区域	60	19.00±0.90	[108]
		无海草区域	60	16.66±0.49	
澳大利亚	澳洲波喜荡草	河口	25	26.2~483.3	[98]
太平洋北部 San Quintín Bay	鳗草	潟湖口	10	8.2±0.1	[109]
			100	80.1±2.5	
		潟湖内	10	11.4±0.4	
			100	101.7±3.5	
太平洋西北部	鳗草	潮间带、潮下带	25	60~512.5 (181.1±15.4)	[110]
			100	75.2~2050.1 (651.2)	
大西洋东部	鳗草	潮间带、潮下带	25	138.4±24.1	[100]
			100	55.4	

续表

地点	海草种类	区域特征	采样深度/cm	海草床有机碳储量/($MgC\cdot ha^{-1}$)	文献来源
瑞典 Skagerrak coast	鳗草	水深 1.3~1.5 m、2.5~4 m (水动力暴露)	25	221.9±33.5	[111]
瑞典 Getevik	鳗草	深水区	50	396.5±21.4	[112]
		浅水区	50	346.5±15.4	
瑞典 Kristineberg		深水区	50	271.2±14.6	
		浅水区	50	105.3±10.8	
苏格兰	鳗草	潮间带	50	23.11 ± 8.17	[93]
	诺氏鳗草		50	68.90 ± 42.10	
大西洋西部	鳗草	潮间带、潮下带	25	134.9±19.4	[100]
			100	54.0	
大西洋西北部 New England	鳗草	海草覆盖	30	150~450 (283.2±41.6)	[113]
		无海草覆盖	30	10~550	
肯尼亚 Gazi Bay	圆叶丝粉草	海湾西部河流 (人类活动区)	100	97.57±7.74	[105]
美国弗吉尼亚州 South Bay	鳗草	海洋热浪发生前	5	39.9±2.9; 38.6±37	[114]
		海洋热浪发生后	5	57.1±2.7	
		海草床恢复初期	5	25.0±2.1	
		海草床恢复后	5	31.7±1.6	
地中海	鳗草	潮间带、潮下带	25	879.3±224.8	[100]
			100	357.1	
	大洋波喜荡草		25	483.7	[98]
	大洋波喜荡草		100	372.4±74.5	[29]
波罗的海	鳗草	潮间带、潮下带	25	57.8±4.3	[100]
			100	23.1	
波罗的海南部 波兰 Gdańsk 海湾	鳗草	Inner Puck Bay (水动力条件差、海草密度低)	10	22.8±1.16	[115]
		Outer Puck Bay (水动力条件强、海草密度低)	10	5.0±0.22	
		Gdańsk-Sopot (水动力条件强、海草密度高)	10	11.6±0.41	
黑海	鳗草	潮间带、潮下带	25	72.5±15.9	[100]
			100	29.0	

$$干容质量 = \frac{干质量}{体积}$$

使用元素分析仪测定沉积物中有机碳含量，计算一定深度下沉积物有机碳的密度，计算方法为:

沉积物有机碳密度=有机碳含量×干容质量.

一定深度沉积物有机碳储量的计算方法为:

沉积物有机碳储量=沉积物有机碳密度×沉积物子样厚度

通过对某一柱状样所有沉积物子样有机碳储量的总和，得到采样地区该深度下沉积物有机碳的总储量[95-96]。

1.3.1 不同地区海草床沉积物有机碳储量

地中海海草床沉积物有机碳储量较高，为 372.4 MgC/ha[29]; 佛罗里达湾的海草床沉积物有机碳略高于全球平均值(139.7MgC/ha)，约为 175.0 MgC/ha[97]; 而巴西南海岸、海南新村湾与宣德礁有机碳储量约为

67.6 MgC/ha，显著低于全球平均值；东亚、东南亚和澳大利亚海草床的沉积物有机碳储量约为全球平均水平的 25%[98-99]。不同地区同种海草之间的有机碳储量也存在显著差异，Röhr 等对温带鳗草海草床沉积物有机碳储量研究发现，地中海鳗草海草床沉积物有机碳储量高达 357.1 MgC/ha；太平洋东部和西部鳗草海草床沉积物有机碳储量分别为 69.4 MgC/ha 和 93.8 MgC/ha；大西洋东部和西部鳗草海草床沉积物有机碳与太平洋东部相近，分别为 55.4 MgC/ha 和 54.0 MgC/ha；而波罗的海鳗草海草床沉积物有机碳储量最低，仅为 23.1 MgC/ha[100]。

1.3.2 相近区域不同种类海草床沉积物有机碳储量

研究发现，相近区域不同海草种类的沉积物碳储量不同。例如，Lavery 等(2013)对澳大利亚不同种类海草床进行调查研究发现，澳洲波喜荡草的沉积物有机碳含量相对较高，卵叶喜盐草、牟氏鳗草、齿叶丝粉草和单脉二药草的沉积物有机碳含量相对较低，而泰来草和圆叶丝粉草等显著低于以上海草[98]。Potouroglou 等(2021)对英格兰海草床沉积物有机碳进行调查，牟氏鳗草海草床沉积物有机碳含量为 68.90±42.10 MgC/ha，要高于鳗草海草床(23.11±8.17) MgC/ha[101]。而对地中海区域的研究发现，大洋波喜荡草海草床沉积物有机碳含量相比于鳗草海草床相对较高[29, 100]。位于印度尼西亚群岛的 Kapoposang 岛和 Sarappokeke 岛海草床沉积物有机碳储量存在明显的差异，Sarappokeke 岛的海草优势种为圆叶丝粉草和单脉二药草，沉积物有机碳储量显著低于以海菖蒲和泰来草为优势种的 Kapoposang 岛[65, 102]。

2 海草床沉积物有机碳影响因素

2.1 物理因素

2.1.1 沉积物类型

沉积物类型可能会影响沉积物有机碳储量[116]。美国佛罗里达海草床沉积物有机碳储量显著高于巴西东南部海岸，这主要是因为佛罗里达与巴西东南部海岸沉积物类型分别为碳酸盐与硅酸盐[97]。钙化与沉积作用会加速碳酸盐沉积物的缺氧，增强有机碳的保存，并且当海草凋落物上覆盖矿物基质时，有机碳更难被分解[117, 118]。巴西东南部海岸缺乏钙化和碳酸钙的储备，使得有机碳的代谢与大气二氧化碳交换、碳酸盐流动之间存在直接联系[97]。

2.1.2 空间分布

海草床的水平属性(相对边缘的距离)是海草生态系统碳储量空间异质性的重要决定因素，研究发现，海草床边缘区域沉积物有机碳储量高于裸露沉积物约 3 倍，而海草床内部沉积物有机碳储量更要显著高于边缘[119]。大型海草沉积物有机碳储量要大于小型海草或无海草区域[120]，这主要是因为结构较大、埋藏较深的根茎组织可以对沉积物起到保护作用以保存有机碳和截获更多悬浮颗粒[121-123]，有效光照辐射是影响海草碳储存能力的关键因子，Collier 等研究发现生长在 2 m 水深的波状波喜荡草地上部分生物量(899 gDW/m^2)、地下部分生物量(1 028 gDW/m^2)以及海草密度(1 435 shoots/m^2)均显著高于 8 m 水深处海草(47 gDW/m^2; 43 gDW/m^2; 80 shoots/m^2)[123]。海草床沉积物有机碳储量与所在区域的深度呈现显著相关性，生长在 2~4 m 水深的波状波喜荡草海草床沉积物有机碳储量为生长于 6~8 m 水深区域的 4 倍，而位于水深 2 m 和 32 m 处的大洋波喜荡草海草床沉积物有机碳储量相差 10 倍以上[116]。

2.1.3 温度升高

全球气温升高会对海草床有机碳储量产生一定影响。全球温度升高将显著提高沉积物有机碳的矿化速率[124-125]。研究发现温度每上升 10 ℃，碳的矿化速率可提升 4.5 倍[124]。自养生物的呼吸速率要小于其吸收二氧化碳的速率，异养生物则相反[126]，温度升高的情况下，呼吸速率的增加量要显著高于二氧化碳的吸收速率[127-128]，气候变暖可能使得自养生态系统向异养生态系统转变，从而发生碳汇到碳源的转变[127]。海草生态系统的甲烷年排放量达 0.09~2.7 Tg，海草床沉积物甲烷的释放速率随着海水温度的升高而增加[129]。红海的海草生态系统已经在温度较高的夏季从自养状态向异养状态改变[130]。Burkholz 等研究发现，在温度从 25℃上升到 37 ℃的过程中，有海草覆盖区域的沉积物甲烷和二氧化碳释放速率为无海草覆盖区域的 10~100 倍，并且温度升高导致甲烷和二氧化碳通量显著增加[131]。另外，海洋沉积物微生物活性随着温度升高而增强，导致在较高的温度下沉积物有机碳水解和发酵速率都超过了正常条件[132]。

2.1.4 自然与人为扰动

台风伴随的强降雨会对沉积物表面造成明显的扰动[133-134]，降雨对沉积物造成的扰动为正常情况

下的 100 倍[135], 并且暴雨会导致沉积物中有机碳的氧化方式发生改变, 从而造成沉积物有机碳加速分解。Sampere 等对大陆边缘表层沉积物中有机质的木质素研究, 发现飓风过后来自海湾和沿海湿地的有机碳输入可能会迅速分解[136]。海平面上升会导致沿海地区沉积物有机碳大量释放到临近河口及开阔水域[137-138], 这可能会改变河口及开阔水域微生物群落及活性, 进一步造成沉积物有机碳降解。Aoki 等对美国弗吉尼亚州的鳗草海草床沉积物调查发现, 海洋热浪发生 3 年后沉积物有机碳含量下降近 20%, 海草密度下降 90%, 并且海草床衰退后沉积物有机碳的恢复呈现滞后性[114]。

人为的干扰也会造成海草床沉积物有机碳损失。例如, 疏浚工程、挖沙以及船只活动会引起海水沉积物扰动, 导致海水浑浊度升高, 从而危害海草生长[139-141]。海草床衰退导致海草床碳储存功能减弱, 使得原本存储于海草床中碳再次释放, 释放量高达$(1.5\sim9.0)\times10^7$ MgC[142]。船只搁浅所造成的有机碳损失量最高, 约为 57.1 MgC/ha[143]。海草床内频繁的滩涂渔业活动会扰动沉积物, 造成海草床沉积物有机碳储量降低[144]。海草床沉积物有机碳含量与沉积物深度呈显著负相关, Macreadie 等发现活性有机碳含量与沉积物深度呈显著负相关, 活性有机碳含量从表层的 43%下降至深层(80 cm)的 3%, 深层的有机碳暴露于空气中会显著增加微生物丰度, 加速有机碳矿化和周转, 表明沉积物的扰动会引起海草床有机碳减少[145]。Thorhaug 等对墨西哥近岸海草床进行调查, 发现人为干扰后海草床沉积物有机碳损失量平均值为(20.98 ± 7.14) MgC/ha, 并且在海草床修复工程中所恢复的有机碳平均值高达(20.96 ± 8.59) MgC/ha[143]。得克萨斯州 Predator 地区的海草床修复过程海草存活率高达 90.7%, 显著增加了当地海草覆盖度[146], 但该地区海草修复工程对有机碳的恢复效果并不显著, 其每年对沉积物有机碳的固定量仅为 0.5 MgC/ha[143]。学术界需要对海草床修复工程运行过程及后期可能对海草床碳通量产生的影响进行评估, 为政府平衡投入与收益间的关系提供依据。

2.2 化学因素

2.2.1 海洋酸化

海洋酸化可以引起海草生物量和密度增加, 从而加强其对有机碳的埋藏能力[147]。在温带以及热带的高二氧化碳区域, 都出现了海草密度以及生物量上升的情况[148]。但是, Apostolaki 等研究发现, 与较低的二氧化碳区域相比, 地中海中高二氧化碳区域海神草生物量反而减少[149]。Vizzini 等通过结合海草床植物以及沉积物性质对希腊 Milos 岛和意大利 Vulcano 岛的 2 个高二氧化碳区域进行调查, 发现 Vulcano 岛的海草生物量以及叶片面积减小, 可能会对沉积物表层有机碳的积累造成负面影响; 而在 Milos 岛, 虽然海草的生物量、叶面积均上升, 但是表层沉积物有机碳含量下降[150]。在较低 pH 值情况下, 细菌胞外酶活性增加, 加速高分子有机物向低分子有机物分解的过程, 可能降低海草床的碳储存能力[151, 152]。

2.2.2 富营养化

沿海水域的养分富集会降低海草床的碳汇能力[153]。营养盐浓度过高会导致海草氨中毒, 或者引起大型海藻爆发限制海草的光合作用[154-155], 降低海草生物量[156], 使得海草对沉积物有机碳的贡献减少[157]。营养盐浓度增高会影响浮游细菌的活动, 改变细菌群落, 加速溶解性有机碳的分解[158-159]。Liu 等发现, 当海草床处于高营养盐浓度环境下, 具有降解难降解化合物能力的微生物如酸微菌(Acidimicrobiia)、疣微菌(Verrucomicrobiales)以及微球菌(Micrococcales)的丰度增加, 从而减弱海草床长期固存有机碳的能力[44]。

2.3 生物因素

2.3.1 微生物因素

沉积物中有机碳长期储存的因素主要是因为厌氧环境不利于微生物生长以及海草碎屑不易分解[17, 26-28]。然而, 全球海草床每年的有机碳损失高达 2.99×10^8 MgC[29]。大量研究表明, 富营养化、全球变暖、植物入侵、人为干扰都会影响海草床中微生物群落特征[160-161], 微生物控制着关键的生物地球化学途径, 因此, 微生物活性和群落结构的变化会影响蓝碳的稳定性, 微生物的呼吸以及活性的增强会导致有机碳矿化速率提高, 从而加速碳的流失[162-164]。

2.3.2 底栖生物

小型底栖动物对沉积物的扰动会增加沉积物的孔隙度与含氧率, 并且小型底栖动物如线虫会释放粘液, 为细菌的生长发育创造条件[165], 显著提高微生物的丰度与活性[166-167]。大型底栖动物会通过

抑制或激活微生物基团来影响沉积物中微生物群落[168]。Lacoste 等发现，大型底栖动物对沉积物的扰动会造成细菌活性的增强，这可能会加速有机碳的降解[169]。

2.3.3 藻类爆发

由富营养化和全球气候变化协同影响下引起的附生藻类的大量繁殖会在一定程度上保护海草，并且增加海草床沉降悬浮颗粒物的能力[170-171]，但是附生藻类和大型海藻暴发，会通过与海草竞争营养盐、形成缺氧环境、影响光照等途径造成海草衰退[157]。由于海草床的加速减少，近岸海域更容易受到气流和波浪的影响，这会导致海草床中储存的有机碳大量减少[172]。当营养盐浓度升高时，大型海藻和附生藻类对沉积物有机碳的贡献短时间内会相对增加[27]，向水体中大量释放碳水化合物与氨基酸[173-174]，导致微生物所能利用有机碳的源发生改变[153]，引起海草床长期存储有机碳的能力降低。与海草相比，来源于附生藻类和大型海藻的有机碳更容易分解[175]，会在几天内被细菌迅速利用[176]，大量多糖及纤维素的加入，会引起沉积物中蔗糖酶与纤维素酶活性的显著上升[177]，增加原有有机碳的分解，导致海草床碳储量减少[178-179]。

3 展望

综上所述，国内外学术界对海草床沉积物有机碳来源、储量以及影响因素等方面已经展开了很多研究，但是相关研究仍有待加强。未来海草床沉积物有机碳研究应该在以下几个方面展开:

(1) 加强海草床碳通量普查和海草床调查。调查全国各海草床海草地上地下部分生物量和沉积物中有机碳的来源、组份及储量，明确全国海草床沉积物碳储存的基本情况。

(2) 分析全球气候变化背景下沉积物有机碳的变化机制。在全球气候变化背景下，研究海草床有机碳来源、组分，沉积物中微生物、酶活性变化等，明确海草床中有机碳的变化机制，为海草床沉积物有机碳的科学管理提供科学对策。

(3) 研究影响海草床碳储量的主要环境因素。对处于富营养化以及其它人类活动影响下的海草床沉积物进行碳储量的长期观测，利用野外操控实验和室内模拟实验，明确环境因素对沉积物有机碳储量的影响机制。

(4) 明确海草床修复工程对沉积物有机碳储存的长期响应，尤其是对海草床修复工程运行过程及后期对海草床碳通量的可能影响进行评估，分析海草床修复工程在碳汇方面的实际收益，为平衡海草床修复工程的投入与收益提供科学依据。

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Review of organic carbon in seagrass bed sediment

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Abstract: Seagrass beds provide important ecosystem services, such as supporting biodiversity and providing carbon storage. Several scientists have studied the carbon storage mechanisms of seagrass beds. The annual carbon sequestration of seagrass beds is $(2.7\sim4.4)\times10^7$ MgC. Recently, seagrass beds have declined worldwide due to human activities, resulting in organic carbon storage reduction in seagrass sediment. This paper reviewed the research advancements of sediment organic carbon in seagrass beds, including the sources, components, storage, and environmental indicators. The environmental variations affecting carbon storage in seagrass beds were discussed from the three aspects of physics, chemistry, and biology. Finally, the primary research directions for the future study were proposed, including strengthening the carbon flux survey of seagrass beds, exploring the mechanism of sediment organic carbon change due to global climate change, defining the rate of carbon storage loss in seagrass beds, and studying the impact of coastal zone engineering on sediment organic carbon. Evaluating carbon storage mechanisms will provide the scientific basis for the blue carbon study in the oceans globally.

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