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Quantitative study of sediment contribution by epiphytic coralline red algae in seagrass meadows in Shark Bay, Western Australia

D. I. Walker[1], Wm. J. Woelkerling[2]

[1] Department of Botany and Centre for Water Research, University of Western Australia, Nedlands, 6009 Western Australia
[2] Department of Botany, La Trobe University, Bundoora, 3083 Victoria, Australia

ABSTRACT: Calcium carbonate on leaves and within leaf clusters of the seagrass *Amphibolis antarctica*, resulting from the growth of epiphytic coralline red algae, was used to calculate the rate of accumulation and rate of deposition of $CaCO_3$ for a range of sites of different salinities in Shark Bay, Western Australia. Up to 200 g m^{-2} or 200 tonnes km^{-2} of $CaCO_3$ occurred on leaves and stems; up to 40 % of the dry weight of seagrass leaves was due to $CaCO_3$. Significant decreases in the amount of $CaCO_3$ present were observed with increasing salinity. Calcification rates of up to 0.2 mg (leaf cluster)$^{-1}$ h^{-1} were measured using alkalinity changes. Based on the distribution of $CaCO_3$ within leaf clusters and previous measurements of leaf turnover, $CaCO_3$ deposition on seagrass leaves could account for an increase in depth of sediment of 0.5 mm yr^{-1}; this is comparable with geological calculations of the composition and rate of accumulation of sediment banks in Shark Bay.

INTRODUCTION

The contribution of coralline algal epiphytes to sediment accumulation by seagrass meadows is largely unknown. Extensive populations of these algae have been recorded on a number of seagrass species e.g. *Thalassia testudinum* (Humm 1964), *Amphibolis antarctica* (Bramwell & Woelkerling 1984), and *Zostera marina* (Cullinane et al. 1985). The suggestion that this contribution is significant to sediment accumulation has been made in the geological literature. James & MacIntyre (1985), referring to the Florida mud banks, stated that 'plants that leave little or no trace in the fossil record have played a significant role in the formation and preservation of these accumulations'. Humm (1964) commented that *Melobesia* may make a significant contribution to calcareous sediments on *Thalassia* flats. However, only one published study has quantified this process (Land 1970).

Thick calcium carbonate accumulations have been documented for a variety of systems. Some good examples occur in Shark Bay, Western Australia (Fig. 1), which is a 13 000 km^2, semi-enclosed basin, with a strong hypersalinity gradient (36 to 70 ‰) and well-developed sediment banks up to 10 m thick (Hagan & Logan 1974) and extensive seagrass meadows which dominate the benthos (Walker et al. 1988). Examination of sediment cores reveals that 15 to 20 % of the particles are coralline algal fragments (Davies 1970). Harlin et al. (1985) documented the occurrence of coralline algal epiphytes on the leaves of *Amphibolis antarctica*, the dominant seagrass species, and noted their contribution to seagrass ecosystems and possible significance to the sediments, but they did not estimate the magnitude of this contribution. This amount of calcium carbonate produced is dependent on availability of new substrata for colonisation in the form of new leaf production. Rates of leaf production by *A. antarctica* in Shark Bay may be rapid, a new leaf occurring every 7 to 10 d (Walker 1985).

Shark Bay was therefore a suitable location to quantify the seagrass epiphyte contribution to the accumulation of sediment for comparison with geological records.

METHODS

Sites. The sites used (Fig. 1) were those previously utilised by Walker (1985) and Harlin et al. (1985). Salinities were measured *in situ* using a Hamon Temperature-Salinity Bridge. Individual seagrass stems

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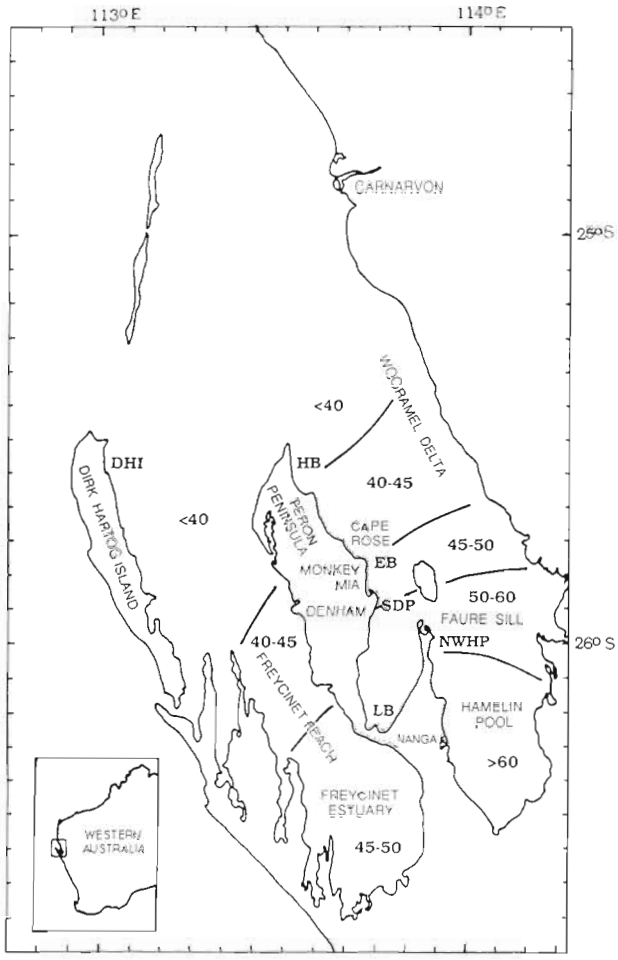

Fig. 1. Shark Bay showing salinity (‰) and collection sites

bearing leaf clusters were collected over an area of approximately 400 m^2 using SCUBA or snorkelling. These were used for identification of major coralline epiphytes and for calculation of calcium carbonate distribution within each leaf cluster. In addition, several randomly selected plants were placed in a large bin filled with seawater from the site and transported back to shore for use in calcification rate experiments. Seawater was also collected for use in the incubations. Six quadrat (0.04 m^2) samples (Walker 1985) were taken for measurement of seagrass calcareous biomass.

Measurement of calcium carbonate fraction. Fresh material was sorted in the field within a few hours of collection, and frozen. Quadrat samples were separated into leaves and stems, and 25 leaf clusters separated into individual leaves, numbered from the smallest, and hence the youngest, at the centre of each leaf cluster, to the outermost, oldest leaves. On return to the laboratory, the material was dried to constant weight at 105 °C, weighed, and ground using a hammer mill. A known weight of sample was ashed (600 °C, 1 h) to remove the organic fraction and reweighed. The ash was acidified (10 ml, 0.2 M HCl) and, when dissolution was complete, the solution titrated against 0.1 M NaOH and the weight of calcium carbonate in the original sample calculated. The method was tested with known proportions of calcium carbonate and glucose, and the results obtained were within 5 % of the known value.

Calcification experiments. Leaf clusters were utilised for measurements of instantaneous calcification rates using the alkalinity method of Smith & Kinsey (1978). Two incubations were performed for each salinity. Two leaf clusters were removed from freshly collected seagrass stems and placed in a sealed chamber which had been filled with seawater from the collection site, circulated using a magnetic stirrer pump. A water jacket surrounded this chamber to maintain a constant temperature. The incubations were carried out under natural light. Photon fluence rates were measured with a Licor quantum sensor, checked every few minutes and, if necessary, adjusted using neutral density screens. All incubations were run for 1 h at 16 °C (approximately ambient water temperature *in situ*) and at 1100 µmol m^{-2} s^{-1}. Replicate water samples were taken both at the start and finish of the incubation, filtered into weighed bottles containing a known weight of 0.010 N HCl, shaken well, and sealed. This volume of acid gave pH values in the range of 3 to 3.5. The samples were kept cool in the dark until return to Perth where they were reweighed, at a known temperature, and pH values measured using a Ross electrode connected to a digital mV meter (precision = 0.00035 pH units). These values were then entered into a computer programme to calculate alkalinity changes (C. Simpson pers. comm., based on the models of Smith & Kinsey [1978] and adapted for the prevailing conditions in Shark Bay). Replicates differing by more than 10 % were discarded.

Calculations of rates of calcium carbonate accumulation. Rates of calcium carbonate accumulation were then calculated on an areal basis, using the 3 different and independent methods of measurement, i.e. standing stock estimates, leaf accumulation data and alkalinity results, for comparison between methods and with the geological records of bank accumulation.

RESULTS

Community composition

Amphibolis antarctica leaves were dominated by plants of the coralline red algal genera *Fosliella* and *Pneophyllum*, with occasional individuals of the related genus *Melobesia*. All species produce applanate, calcified thalli, less than 100 µm thick, which spread over

the leaf surface with time, often becoming confluent with adjacent individuals. Foraminifera and gastropods were sometimes present on leaf clusters, but tended to drop off on collection. In addition to some encrusting coralline red algae, the seagrass stems had abundant epiphytic bryozoans and filamentous, non-calcareous algae.

Standing stock results

Higher proportions of calcareous epiphytes occurred on leaves than on stems (range, 1.2:1 to 3.3:1; mean, 1.6:1) (Fig. 2). However, the stems are older than the leaf material and have had longer to accumulate

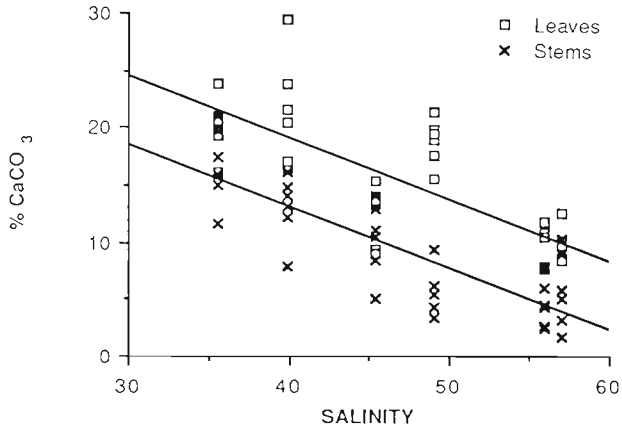

Fig. 2. *Amphibolis antarctica*. Percentage of $CaCO_3$ of dry weight of stems and leaves with increasing salinity. Leaf % $CaCO_3$ = 40.515 − 0.534 × Salinity (r = 0.75). Stem % $CaCO_3$ = 34.825 − 0.540 × Salinity (r = 0.82)

material (Walker 1985). This difference between leaves and stems may be related to the greater surface area:volume (and hence weight) ratio of the leaves, and the greater abundance of encrusting Corallinaceae. Leaf surfaces may also be better environments for calcification, as there are greater rates of water flow over the leaves than within the canopy (Fonseca & Kenworthy 1987). Smith & Kinsey (1976) attributed differences in calcification rate between reef areas to variations in water motion. There may also be more competitive interactions on the stems between the abundant non-calcareous filamentous algae (Kendrick et al. 1988) and the encrusting calcareous algae.

There was a significant linear decrease in the percentage of calcium carbonate of stems ($r = 0.82$; $p < 0.001$; $n = 36$) and leaves ($r = 0.75$; $p < 0.001$; $n = 36$) with increasing salinity (Fig. 2). This corresponds to the decrease in cover by epiphytic Corallinaceae recorded by Harlin et al. (1985).

The weight of calcium carbonate borne on the seagrass on an areal basis (Fig. 3) reaches a maximum of over 100 g m^{-2} on both stems and leaves, a total of over 200 g m^{-2} or 200 tonnes km^{-2}. The mean total value for all sites was 117 g m^{-2}. No data are available for seagrasses from other regions for comparison.

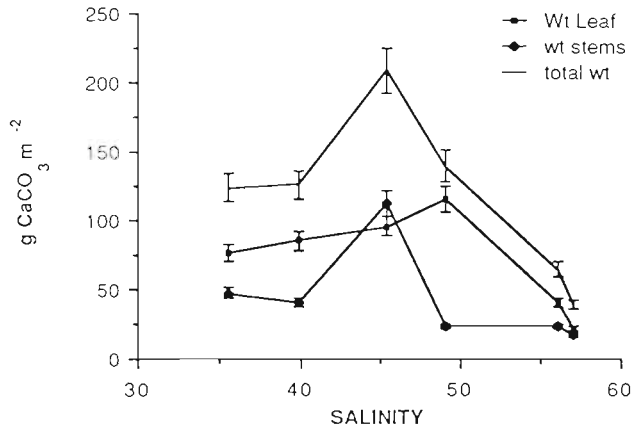

Fig. 3. Standing stock of epiphytic $CaCO_3$ along the salinity gradient. (Mean ± SE; n = 6)

A preliminary value for calcium carbonate production can be estimated by converting these values of standing stock to an annual estimate, using a ratio of annual production to biomass based on the leaf turnover results of Walker (1985) and the seasonal data of Walker & McComb (1988) (Table 1).

Distribution and accumulation within leaf clusters

At all sites, the smallest, youngest leaves had a very low $CaCO_3$ fraction, which increased with increasing size of the leaves, as they became encrusted with calcareous epiphytes (Fig. 4). Once the leaves reached their maximum length, the accumulation slowed, presumably as all available surface was colonised. There was decreasing calcium carbonate deposition with increasing salinity.

The highest proportion of $CaCO_3$ on the oldest leaves

Table 1. Estimation of annual calcium carbonate production based on standing crop data from quadrat analyses

Salinity (‰)	Leaf $CaCO_3$ (g m^{-2})	Annual productivity/biomass ratio (yr^{-1})	g $CaCO_3$ m^{-2} yr^{-1}
35.6	76.5	2.54	194
40.0	85.7	3.45	296
45.3	96.1	5.48	526
49.0	115.2	3.64	419
55.9	40.8	2.47	101
57.0	21.8	2.29	50

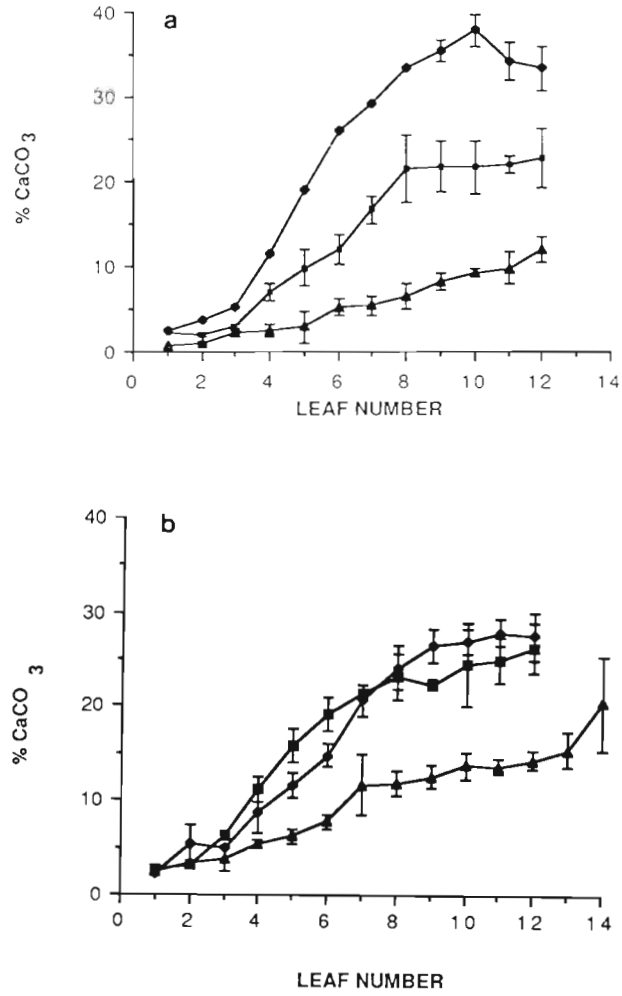

Fig. 4. *Amphibolis antarctica*. Distribution of $CaCO_3$ within leaf clusters at all sites (Fig. 1). (a) (◆) Dirk Hartog Island, DHI, 35.6 ‰; (■) Eastern Bluff, EB, 45.3 ‰; (▲) Lharidon Bight, LB, 55.9 ‰. (Means ± SE; n = 4). (b) (◆) Herald Bight, HB, 40.0 ‰; (■) Dubaut Point, DP, 49.0 ‰; (▲) northwest Hamelin Pool, NWHP, 57.0 ‰. (Means ± SE; n = 4)

occurred at the site with the lowest salinity (35.6 ‰) where the maximum was on Leaf No. 10 which had 37.9 % (SE 1.9 %) of the leaf dry weight as $CaCO_3$, whereas at 56 ‰, the maximum was 12.0 % (SE 0.7 %) for Leaf No. 12, approximately one-third of that for the low salinity site (Fig. 4). At sites of intermediate salinities there were intermediate proportions of $CaCO_3$.

The distribution of carbonate within leaf clusters can be used to calculate the rate of $CaCO_3$ accumulation on leaves. For each salinity, the age of each leaf number was determined from previous measurements of leaf turnover (Walker 1985) and from this, the rate of deposition of $CaCO_3$ per leaf was calculated based on Fig. 4. These results were then multiplied by the total number of leaf clusters per unit area, and leaf production per leaf cluster (Walker 1985), to give an annual estimate of 30 to 300 g m^{-2} yr^{-1} (Table 2). The weight of sediment was converted to a depth accumulation assuming all material was trapped *in situ* and there was no dissolution, and a mean bulk sediment density of 1.35 g cm^{-3} (Land 1970). Maximum values of 0.25 mm yr^{-1} were obtained (Table 3).

Although many assumptions are involved, an estimation was made of calcium carbonate deposited by these processes over geological time by utilising the time since the last major rise in sea-level, which inundated the basin (ca 5000 yr ago; Read 1974). A range of values up to 2.0 m depth of sediment accumulated were obtained (Table 3).

Rates of calcification from alkalinity incubations

Calcification rates of up to 0.2 mg (leaf cluster)$^{-1}$ h^{-1} were obtained. Calcification rates decreased with increasing salinity. Calcification was assumed to be light dependent (Pentecost 1978), and a 12 h day length used in calculations of annual calcification (Table 3). This estimate of annual calcification will be an approximation, as incubations were performed in winter, and thus the calculated annual calcification rates may well be conservative. However, the results do provide another method of assessing the contribution of calcifying organisms to the accumulation of sediment. These data are of the same order of magnitude as those obtained by analysing quadrat or leaf accumulation data (Table 3).

Table 2. Estimation of annual calcium carbonate production based on leaf accumulation data

Salinity (‰)	mg $CaCO_3$ $leaf^{-1}$	Leaf clusters m^{-2}	Leaf prod. (leaf cluster)$^{-1}$ d^{-1}	$CaCO_3$ (mg m^{-2} d^{-1})	$CaCO_3$ (g m^{-2} yr^{-1})
35.6	1.60	2900	0.074	341	124
40.0	1.10	1760	0.172	333	122
45.3	0.78	5030	0.220	858	313
49.0	0.91	4680	0.157	667	244
55.9	0.24	2450	0.129	76	28
57.0	0.54	2090	0.088	100	36

Table 3. Comparison of estimates of calcium carbonate production by the 3 different methods

Salinity (‰)	$CaCO_3$ production ($g\ m^{-2} yr^{-1}$)			Potential depth of sediment ($mm\ yr^{-1}$)			Potential accumulation of sediment ($cm\ 5000 yr^{-1}$)		
	Quadrat	Leaf accumulation	Alkalinity	Quadrat	Leaf accumulation	Alkalinity	Quadrat	Leaf accumulation	Alkalinity
35.6	194	124	279	0.144	0.092	0.207	72	46	103
40.0	296	122		0.219	0.090		109	45	
45.3	526	313	295	0.389	0.232	0.219	195	116	110
49.0	419	244		0.310	0.180		155	90	
55.9	101	28	140	0.075	0.021	0.103	37	10.5	51
57.0	50	36	35	0.037	0.027	0.026	18	13.5	13

DISCUSSION

Seagrasses are regarded as significant in coastal ecosystems, but discussion of their role in sedimentation has been largely confined to their role in trapping and binding sediment (Scoffin 1970). The results reported here demonstrate the potential magnitude of the contribution of calcareous epiphytes on seagrasses to sediment supply.

This process has been significant in the formation of the bank structures of Shark Bay. Sediment cores have been documented to contain up to 30 % coralline algal fragments, although the range is more usually 15 to 20 % (Davies 1970). Thus in an accumulation of sediment under seagrass on the Woramel delta, which reaches the maximum thickness of 10 m, the coralline algal component would account for 1.5 to 2.0 m; this corresponds to the values of 1.0 to 2.0 m obtained in this study. Of course, not all the sediment produced by epiphyte calcification and leaf shedding will necessarily be trapped by the seagrass meadows, and some sedimentary material produced outside the seagrass meadows will also be accumulated.

These epiphytic calcareous algae are 'sedentary' and the scale of their contribution to sediment production is a direct result of similar timespans of seagrass leaf age and coralline algal growth rates, and the dependence of the epiphytes on the availability of new substrata. Although other larger organisms which live on and around *Amphibolis antarctica* (including foraminifera, bryozoans, tube worms, bivalves and gastropods) also contribute to the sediments, these are 'independent' of the rate of new leaf production. It is the continuous production of new leaves, a 'conveyor belt' for settlement by calcareous organisms and deposition of calcium carbonate, which is the mechanism which makes the seagrasses important to the formation of sediment, and of the structures (Davies 1970, Read 1974) resulting from the binding and trapping of these sediments.

The rates of calcium carbonate production obtained here (up to 500 g $m^{-2} yr^{-1}$) are higher than those reported by Land (1970) who estimated that 40 to 180 g $m^{-2} yr^{-1}$ were produced by epibionts on *Thalassia testudinum*, although he suggested that these values were low, as they were based on one measurement of regrowth of clipped shoots. He also extrapolated his estimates of sediment accumulation to 3 to 13 cm in 1000 yr or 15 to 65 cm in 5000 yr, indicating that there are similar scales of processes for different seagrass species of very different morphologies under different environmental conditions.

Our results, and those of Harlin et al. (1985) suggest that high salinity, or other factors correlated with this salinity gradient, lead to reduced production by calcareous algae. The decrease in cover of Corallinaceae on the leaves of *Amphibolis antarctica* with increasing salinity (Harlin et al. 1985) was matched by a decrease in calcium carbonate. This may indicate that the biological process of sediment accumulation has been self limiting: as the banks accumulated under the seagrasses over geological time, they restricted the circulation of oceanic seawater, leading to the development of the hypersalinity gradient.

Smith & Atkinson (1983) calculated the rate of calcium carbonate production, based on oceanographic measurements, for their carbon and phosphorus budget for the Shark Bay ecosystem. Their result of

Table 4. Calculation of total calcium carbonate production in Shark Bay

Salinity (‰)	Seagrass area (km^2)	Calcification rate ($g\ m^{-2} yr^{-1}$)	$CaCO_3$ produced ($10^9\ g\ yr^{-1}$)
35–40	596	200	119
40–45	603	300	181
45–50	909	350	318
50–55	222	200	44
55–60	95	50	5
60+	2	0	0
Total	2427		667
Whole bay	7768	117	907

3.2 mmol $m^{-2} d^{-1}$ (0.32 g $m^{-2} d^{-1}$ or 117 g $m^{-2} yr^{-1}$) corresponds well with the results obtained in this study, but a more accurate comparison may be made by calculating total calcification using these data, total seagrass areas (Walker unpubl.) and data from Smith & Atkinson (1983) on a whole bay basis (Table 4), giving results of the same order of magnitude and suggesting that this process may account for about 70 % of the total calcification in Shark Bay. Smith & Atkinson (1983) suggested that calcium carbonate production was even throughout the Bay, but that progressive restriction had slowed the rates of production, which corresponds to the observations made here.

Other seagrasses, particularly those with larger strap-like leaves, have potential to contribute to sediments. *Thalassia testudinum* has already been mentioned as a contributor to sediments in the Caribbean (see also Swinchatt 1965, Lynts 1966), and sediment banks accumulate under *Posidonia* meadows elsewhere on the southwest and south coasts of Australia (McComb et al. 1981) and under *Posidonia oceanica* beds in the Mediterranean, where the sediment banks are up to 6 m thick (Molinier & Picard 1952). Large *Zostera* meadows in the northern hemisphere may also have similar potential for production of calcium carbonate.

Further, the geological literature contains many descriptions of ancient crinoid and phylloid algal carbonate banks, significant as oil-bearing deposits, as well as more recent deposits (Read 1974). The latter are analogous to the seagrass banks in Shark Bay, and may therefore have accumulated beneath seagrasses which have themselves left no trace in the geological record.

These results demonstrate that calcium carbonate production by epiphytes on *Amphibolis antarctica* is significant in the deposition and accumulation of sediment. Although this mechanism has not been adequately documented for other seagrasses in different environments, it is probably of more widespread significance. The scale of the process in Shark Bay suggests that this contribution to the sediments may be an important role for seagrasses in coastal ecosystems.

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