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FEATURE ARTICLE

Seagrass roots strongly reduce cliff erosion rates in sandy sediments

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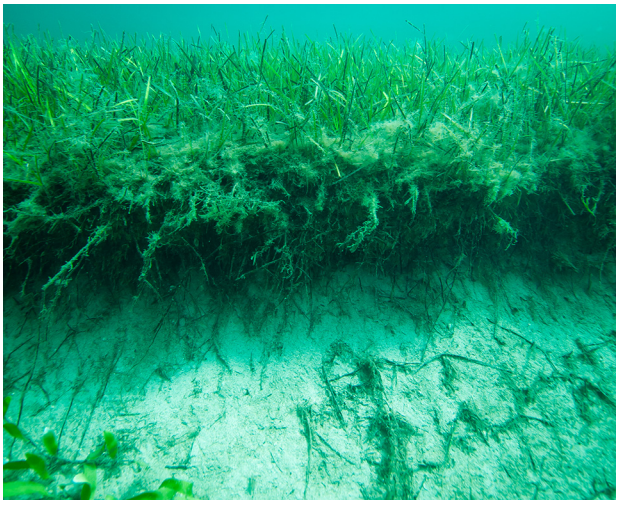
ABSTRACT: Vegetated coastal ecosystems such as saltmarshes, mangroves and seagrass beds are increasingly promoted as sustainable storm and flood defence solutions by reducing wave energy. Yet, there is still intense debate on the ability of root mats to mitigate erosion, with some studies arguing that the direct contribution of roots in preventing sediment erosion is minor, while others consider them of major importance. Here, we hypothesized that the contrasting findings on the role of seagrass root mats in preventing erosion may stem from differences in sediment type. To test this idea, we investigated how root mats of seagrass that thrives in both sandy and muddy sediments mitigate wave-induced cliff erosion using *Zostera marina* in manipulative flume experiments. Results demonstrate that roots are very effective in reducing cliff erosion rates in sandy sediments. Cliff erosion rates were reduced up to 70% in sandy sediment with high seagrass root biomass. In contrast, cliff erosion rates in cohesive muddy sediments were low and unaffected by seagrass roots. This highlights the important role of seagrass roots in erosion mitigation, which has been overlooked compared to the role of canopies, which has received more attention. We suggest that management strategies should be developed to enhance the stabilization of sandy sediment, such as (1) using species with high belowground biomass, (2) using fast-growing pioneer species and (3) applying temporary stabilising measures.



Cliff erosion in a seagrass meadow

Photo: Eduardo Infantes

KEY WORDS: Coastal erosion · Seagrass ecology · *Zostera marina* · Roots · Plant biomass · Wave exposure · Sediment dynamics · Coastal management · Restoration

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1. INTRODUCTION

Coastal vegetation, such as saltmarshes, mangroves and seagrass meadows, is present along the coasts of all continents except Antarctica. In these locations, coastal vegetation acts as a natural buffer zone between the land and the ocean, via the provision of key ecosystem services such as coastal protection and sediment stabilisation (Gedan et al. 2011, Ondiviela et al. 2014, Feagin et al. 2015, Sheehan & Ellison 2015, Silliman et al. 2019, Zhu et al. 2020). These ecosystem services are becoming increasingly important given the acceleration of sea level rise (Church & White 2006) and the associated synergistic impacts of increasing storm frequency and intensity on coastal areas (Easterling et al. 2000, Bender et al. 2010). Nearly 634 million people (~8% of the world's population) live in coastal areas that are less than 10 m above sea level (McGranahan et al. 2007), making them vulnerable to sea level rise and storm events. Hence, properly harnessing the coastal protection provided by coastal vegetation could be of critical importance for a substantial proportion of the population.

Salt marshes, mangroves and seagrass meadows can be very effective at attenuating waves and flow during storms (Mazda et al. 1997, Infantes et al. 2012, Möller et al. 2014, Zhu et al. 2020) but may be overwhelmed during extreme events such as tsunamis and storm surges (Feagin et al. 2010, Tsujimoto et al. 2016). However, apart from directly reducing hydrodynamic forces, coastal vegetation such as seagrass has an important function in raising the sediment surface and preventing erosion (Palinkas & Koch 2012, James et al. 2019, 2020). These effects on flow reduction within the canopy and sediment stabilisation have been mainly attributed to aboveground plant canopies where extensive studies have quantified these processes with currents (Ghisalberti & Nepf 2006, Lera et al. 2019), waves (e.g. Lowe et al. 2005, Luhar et al. 2010, 2017) and the resulting impacts on sediment stability (e.g. Ros et al. 2014, Marin-Diaz et al. 2020). Erosion of vegetation edges by lateral wave forces can form small cliffs, leading to the subsequent collapse of the sediment mass (van de Koppel et al. 2005, Bouma et al. 2016) suggesting that root mats could play a key role in mitigating the erosion rates along these cliffs. Roots have shown a positive role in reducing lateral erosion in saltmarshes (De Battisti et al. 2019), but the role of seagrass belowground root and rhizome mats still

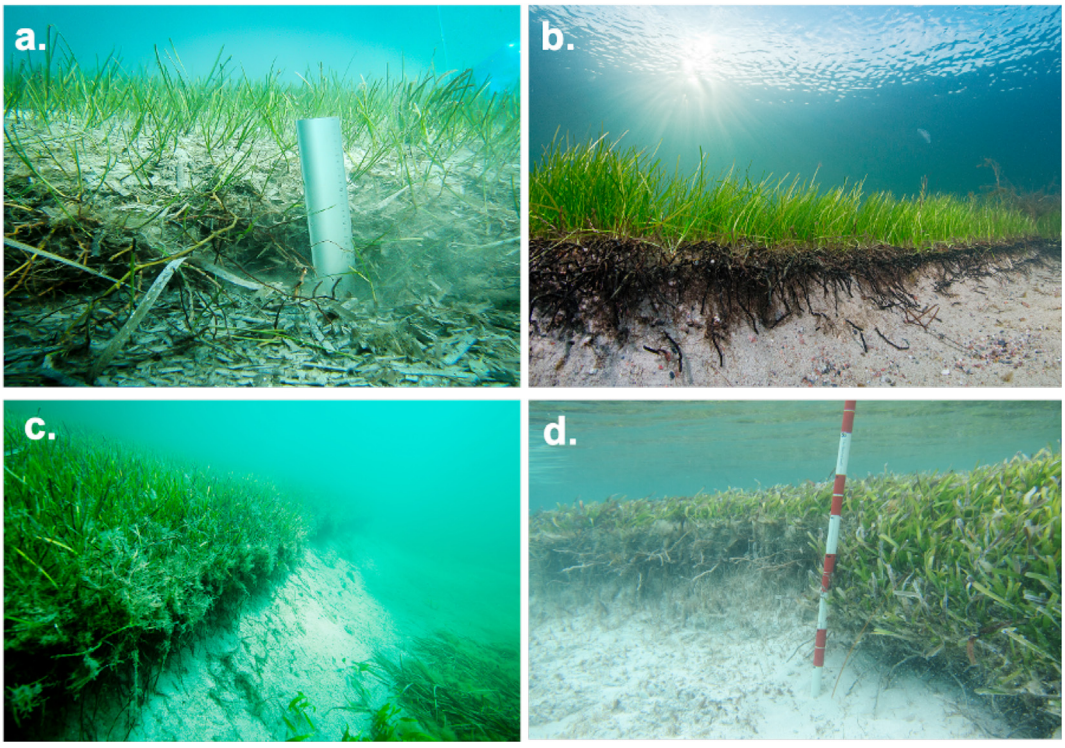

Fig. 1. Cliffs are a common phenomenon in seagrass beds; examples shown are (a) *Cymodocea nodosa* in the Mediterranean Sea, Mallorca, Spain, (b) *Zostera marina* in the Baltic Sea, Hanko, Finland, (c) *Posidonia oceanica* and *C. nodosa* in Mallorca, Spain, and (d) *Thalassia testudinum* in the Caribbean, St. Martin. Images: (a,c) E. Infantes, (b) P. Tuuri, (d) T. J. Bouma

remains overlooked. For example, the effect of seagrass on cliff erosion is largely unknown, even though cliffs are common in this ecosystem type (Fig. 1).

The role of coastal vegetation on foreshore stabilisation has been debated. For example, observational and experimental studies from sandy sediments suggest that root mats are vital in retaining substrate and preventing cliff erosion (Carter & Stone 1989, Logan et al. 1989, Sigren et al. 2014), while other studies have shown that seagrass root biomass in sandy sediment had no clear effect on cliff erosion (Twomey et al. 2021). In muddy environments such as salt marshes, the direct effect of vegetation on cliff erosion is more ambiguous. It has been stated that the direct contribution of saltmarsh vegetation in preventing sediment erosion is minor (Feagin et al. 2009), while other studies considered vegetation of major importance for coastal defence (Shepard et al. 2011, Wang et al. 2017, De Battisti et al. 2019, Silliman et al. 2019), especially by reducing erosion at sandy sites (Lo et al. 2017).

Here, we hypothesized that the contrasting findings on the role of root mats in preventing erosion may stem from differences in sediment type. In cohesive fine clay, which can bind particles together into larger mud flocs, the presence of root mats could play a minor role in cliff erosion, but this effect should be less evident in sandy sediment. We address the role of vegetation roots using seagrass meadows as a study system. Through manipulative flume experiments, we simulated cliff erosion to investigate how root mats of the seagrass *Zostera marina* in both sandy and cohesive muddy sediments mitigate wave-induced cliff erosion depending on sediment type.

2. MATERIALS AND METHODS

Eelgrass *Zostera marina* meadows are present in sandy and muddy sediments along the Swedish west coast. A range of sediment compositions and plant densities were collected in 2 subtidal meadows in the Gullmars Fjord: Bokevik (58° 14′ 56″ N, 11° 26′ 53″ E) and Gåsö (58° 13′ 52″ N, 11° 24′ 4″ E). Both locations have a microtidal range of 25 cm. Sediment cores with and without vegetation were collected at 0.5–6 m water depth, using scuba diving and snorkelling. The vegetated cores were sampled at least 5 m from the edges of the meadow. The cores were 30 cm long with a 12 cm diameter. After collection, the cores were carefully transported and kept in a 1500 l tank with seawater flow-through, until they were exposed to the erosion treatments within the following 48 h.

2.1. Sediment erosion using a wave flume

The impact of roots and rhizomes on sediment erosion rates was evaluated in a wave flume of 3.5 m length, 0.6 m width and 0.8 m depth (Fig. 2a). This wave flume is a further development of the wave mesocosm originally used by La Nafie et al. (2012), and closely resembles the wave flumes used by Lo et al. (2017) and Wang et al. (2017) and was described in detail in the methods paper of Infantes et al. (2021). In each trial, waves were generated via a pneumatic piston. The wave frequency was controlled by adjusting the piston stroke and speed. Waves were dampened using a fibre mat at the end of the wave flume. The water depth was set to 45 cm. Waves were recorded for 5 min using a pressure sensor (Druck, PT1830) with a sampling rate of 25 Hz. Orbital flow velocities were determined using an acoustic Doppler velocimeter (Nortek, Vectrino) with a sampling rate of 25 Hz, sampling volume of 7 mm and velocity range of 0.3 m s^{-1}. Flow velocities were measured for 5 min at 8 cm above the bed.

Sediment cores collected in the field were carefully transferred to a core holder structure located 2.5 m away from the wave pedal. Each sediment core was cut on one side to expose a flat sediment surface (20 cm long × 12 cm wide) to the flow (Fig. 2a). The remaining sediment from each core was used to characterize the sediment composition (see details below). To quantify the overall volume loss on each sediment core exposed to waves, photogrammetry (3D reconstructed images) was used as a non-invasive technique to avoid any possible contact with the sediment (cf. Wang et al. 2017). To build each 3D image, 30–50 photographs were taken from as many different angles as possible (Fig. 2b). Real dimensions and coordinates for the 3D images were obtained by placing 2 measuring tapes on the sides of the core holders. 3D images were reconstructed using the software program VisualSFM (Lo et al. 2017, Wang et al. 2017), which matches common patterns in images from different camera angles (Fig. 2c). All matches were translated into low-density point clouds which were then transformed into a high-density cloud using the software program CMVS (Y. Furukawa; https://github.com/pmoulon/CMVS-PMVS). The resulting 3D image was then transformed into x,y,z coordinates. Photographs of the sediment cores were taken using a camera with an underwater housing

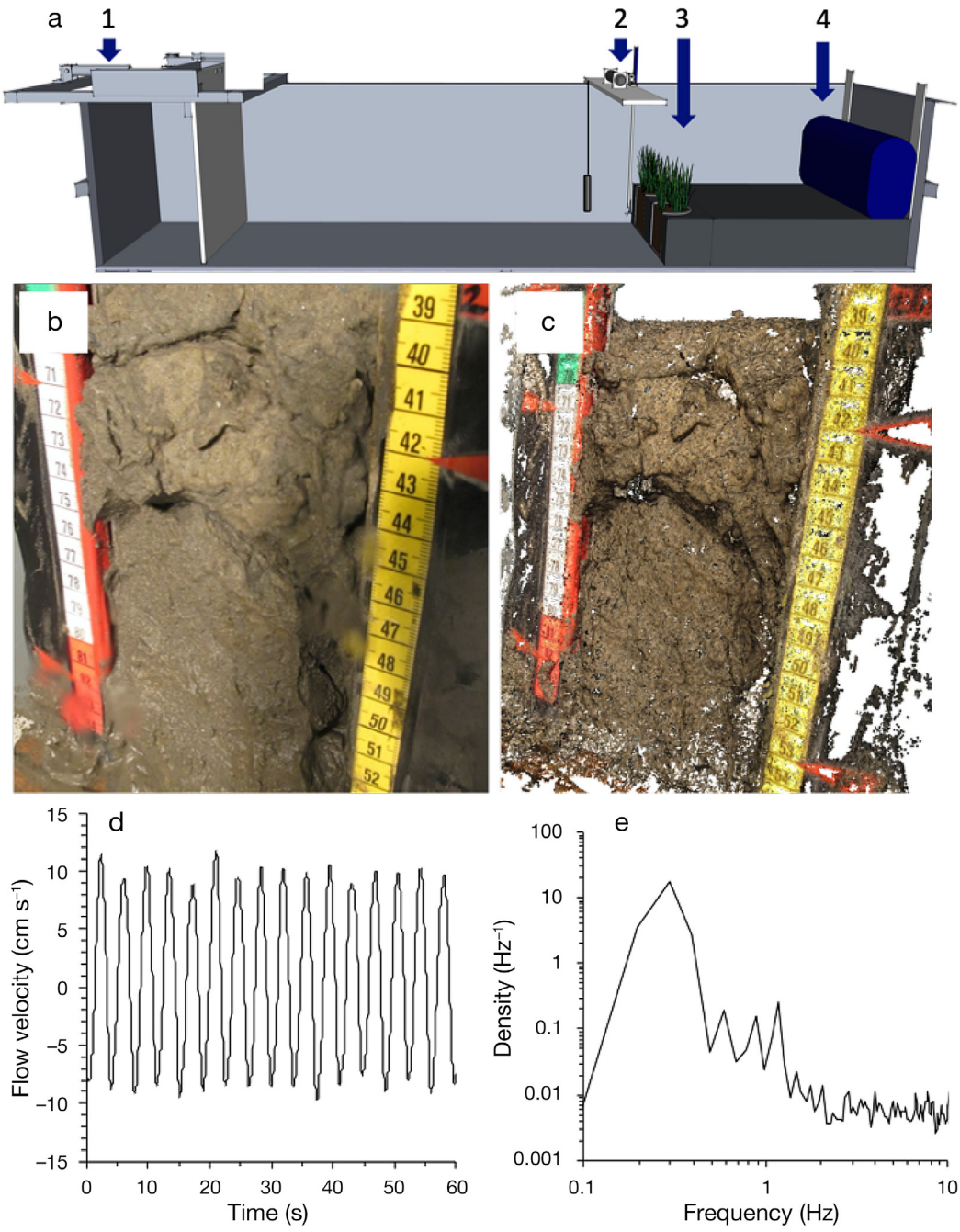

Fig. 2. Measurement of erosion rate of sediment exposed to waves. (a) Hydraulic wave flume, (b) area of exposed sediment and (c) 3D image reconstruction. Wave exposure is represented as (d) orbital flow velocities and (e) wave spectrum. The individual components of the wave flume in panel (a) are: (1) hydraulic wave generator, (2) flow meter to measure orbital velocities and pressure gauge to measure waves, (3) sediment core holder that mimics a cliff and (4) wave absorber to prevent reflections creating a standing wave. More details of the wave tanks are provided in Infantes et al. (2021)

(Canon, G11) and an underwater LED light (i-Torch, Venom 50). Images were pre-treated using Lightroom (Adobe) to remove wide-angle distortion and adjust contrast and exposure. The accuracy of this method for measuring erosion was tested by creating 3D reconstructions (n = 4) in which the volume loss was known (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m700p001_supp.pdf). These known volume losses were plotted against the estimated volume losses measured using the 3D reconstruction showing a high correlation coefficient (r^2 = 0.96, $p < 0.01$).

2.2. Cliff erosion measurements

The role of vegetation on sediment erosion was tested in 2 experiments: (1) effect of belowground biomass (BGB) on erosion of both sand and mud, and (2) effect of aboveground biomass (AGB) on erosion of sand plus BGB. Erosion rates were quantified by exposing intact sediment cores to orbital flow velocities ~10 cm s^{-1} (wave height of 4.4 cm and wave period of 3.4 s; Fig. 2d,e). These flow conditions represent the natural average wave conditions in the Gullmars Fjord generated by 8–16 km h^{-1} winds over a 10 km fetch (Dahl et al. 2020). The amount of sediment lost between the time steps was calculated with the 3D images and transformed into a volume. Sediment erosion rates (cm^3 h^{-1}) were calculated by dividing the volume of sediment lost (cm^3) by the time period that the core was exposed to waves in the flume (h). Two time periods were chosen for the trials (as explained later in this section). After each trial, the plant material present in and/or attached to the sediment core was carefully rinsed, and roots and rhizomes (i.e. BGB) were separated from the leaves (i.e. AGB). These separated vegetation fractions were dried at 60°C for 48 h to determine the dry weight (DW, g) of AGB and BGB.

First, to identify if erosion rates would differ with sediment type (sand/mud) and root biomass, erosion rates were estimated for a range of BGB growing in 2 contrasting sediments. Since the erosion rates were faster in sand than mud, sandy samples were exposed to waves for 4 h and sampled at 0, 1 and 4 h since wave exposure began, while muddy sediment was exposed to waves for 18 h and sampled at 0, 2, and 17–18 h since wave exposure began. Samples were separated into 3 BGB categories: high density (>160 g DW m^{-2}), medium density (30–160 g DW m^{-2}) and low density (<30 g DW m^{-2}). Spearman correlation coefficients (r^2) were calculated for the relationships between the erosion rates (cm^3 h^{-1}) and the amount of BGB (g) in the sediment core. Difference in erosion rates were tested for sandy sediment samples (n = 14) after 4 h of wave exposure and for the muddy samples (n = 10) after 17–18 h using a 1-way ANOVA (α = 0.05), with BGB biomass category as the independent variable and erosion rate as the dependent variable. Before analyses were performed, all data were tested for normality with a Shapiro-Wilk test (α = 0.05) and for homoscedasticity with Cochran's *C*-test using SPSS v.27. *A posteriori*, multiple comparisons were carried out with the Student-Newman-Keuls (SNK) procedure (Underwood 1996).

Second, to identify if erosion rates would differ in the presence or absence of AGB, a flume experiment was performed with sediment cores containing plants with intact leaves versus cut leaves. To reduce variability, all sediment cores had similar sediment type (sandy, 200–250 µm) and similar eelgrass BGB of 140–170 g DW m^{-2}, collected in Bokevik at 60–80 m water depth. Samples were exposed to waves in the flume for 4 h. Erosion rates for both treatments (n = 5) were assessed using a 1-way ANOVA (α = 0.05), with AGB presence as the independent variable and erosion rate as the dependent variable. All data were tested for normality with a Shapiro-Wilk test (α = 0.05) and for homoscedasticity with Cochran's *C*-test.

Sediment composition was characterized for each sediment core by taking samples from one vertical side of the core prior to the exposure to flow. Since one side needed to be removed to expose the sediment cylinder to the flow, the sediment extraction did not interfere with the erosion experiment. The organic content of the sediment after large biomass removal (roots and rhizomes) was calculated by loss on ignition, i.e. burning the samples at 450°C for 5 h and measuring the difference in sample weight before and after burning. The bulk density was calculated as the sediment DW in 25 cm^3. The water content was measured as the weight difference between wet and dry sediment (60°C for 48 h). The different grain size fractions were determined using a Mastersizer particle size analyzer (Malvern Instruments). Organic content (%), water content (%) and bulk density (mg cm^{-3}) are derived from averaging these sediment properties over the entire depth of the sediment core for each sample (Fig. S2). Sediment samples with median grain sizes (D_{50}) > 63 µm are defined as sand, while sediments with D_{50} < 63 µm are defined as cohesive mud composed of silt and clay.

3. RESULTS

BGB reduced sediment erosion by up to 70% in sandy sediment (Fig. 3a). In contrast, muddy sediments were much more resistant to erosion, and erosion rates were not significantly altered by the presence of root biomass. There was a strong significant negative correlation between the erosion rate and the quantity of roots and rhizomes in sand (Spearman, r = –0.81, p = 0.01), whereas for mud this correlation was not significant (r = –0.18, p = 0.54). Erosion rates in sand were reduced by 50 cm^3 h^{-1} per each increase of 100 g DW m^{-2} of BGB. Erosion rates were

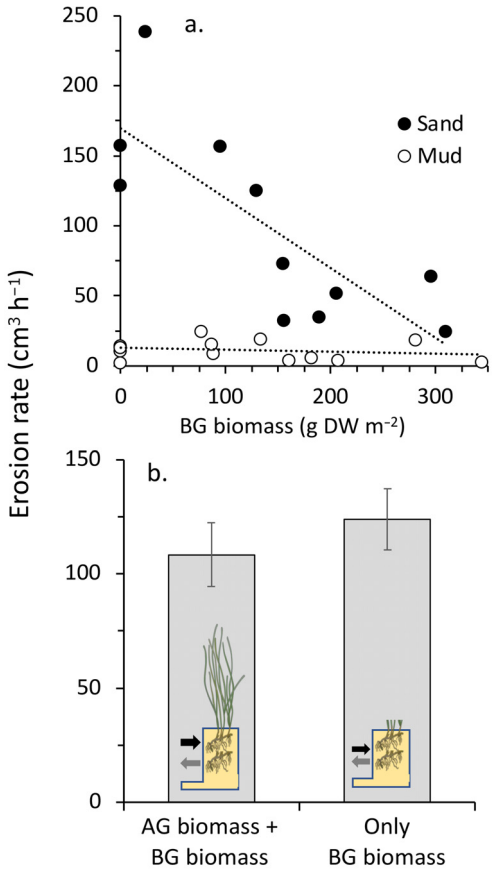

Fig. 3. (a) Correlation between erosion rates and belowground (BG) biomass (roots and rhizomes) for sand and mud sediment. Sandy sediments showed a significant correlation between the erosion rate and the amount of roots and rhizomes ($r^2 = 0.62$, $p < 0.01$), while this relation was not significant in muddy sediments ($r^2 = 0.04$). DW: dry weight. (b) Comparison in erosion rates for samples with aboveground (AG) biomass (seagrass leaves) + BG and samples with only BG after cutting the leaves. There were no significant differences between the erosion rates in sandy, muddy and all sediments combined

not significantly different for samples with or without AGB (Fig. 3b), in both sandy, muddy and all sediments combined, with sand sediment showing the strongest relation ($r = -0.33$, $p = 0.36$). The same applied to the relationship between erosion rate and the number of shoots ($r = -0.37$, $p = 0.29$ for sand) and between erosion rate and average root length ($r = -0.23$, $p = 0.53$ for sand).

Cliff erosion rates differed depending on the time that the sediment samples were exposed to waves (Fig. 4, Table 1). In sandy samples, the volume of sediment eroded differed significantly between the 3 BGB categories after 4 h of wave exposure (ANOVA, $F_2 = 21.9$, $p = 0.002$), while in muddy sediment the volume of sediment eroded was not significantly different even after 18 h (ANOVA, $F_5 = 0.67$, $p = 0.43$).

For all the sediment types (sand and mud), mean erosion rates expressed several clear relationships with sediment properties (Fig. 5). The rate of sediment erosion increased exponentially with both grain size ($r^2 = 0.67$, $p < 0.001$) and bulk density ($r^2 = 0.63$, $p < 0.001$). In contrast, erosion exponentially decreased with increasing sediment organic content ($r^2 = 0.72$, $p < 0.001$) and water content ($r^2 = 0.71$, $p < 0.001$). These results were expected, since sediment grain size and organic content are correlated with each other ($r^2 = 0.98$, $p < 0.0001$; Fig. S2a). In the same way, sediment bulk density and water content are also inversely correlated ($r^2 = 0.92$, $p < 0.0001$, Fig. S2b, Fig. 5). The large variability in erosion rate in sandy sediments (see data points for large grain size in Fig. 5a) could be explained solely by the density of vegetation BGB (Figs. 3a & 4a).

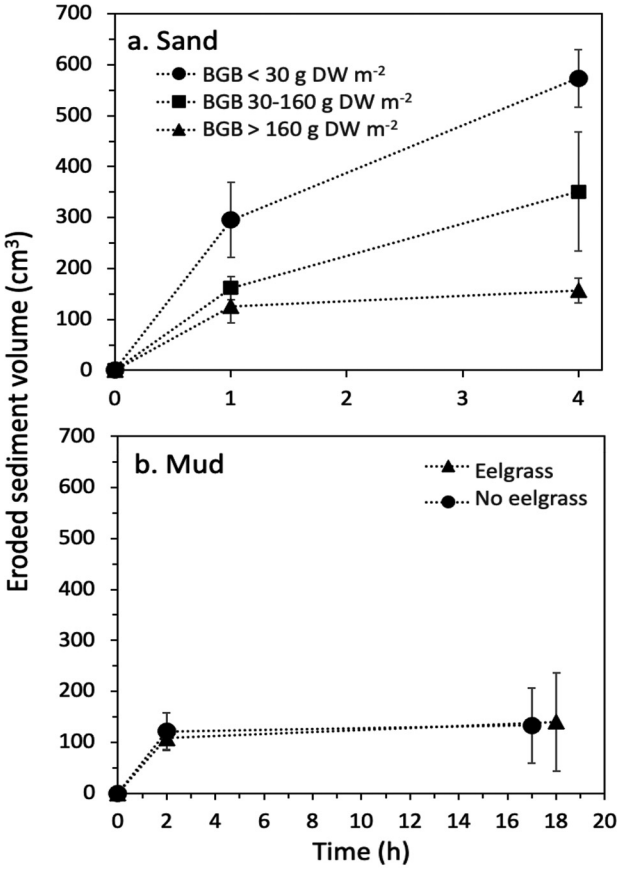

Fig. 4. Erosion in (a) sand and (b) mud sediments over a range of eelgrass densities. Sandy sediment samples are divided into 3 categories of belowground biomass (BGB): <30, 30–160 and >160 g dry weight (DW) m^{-2}. In contrast, muddy samples are divided into 2 categories (i.e. eelgrass vs. no eelgrass) due to low variation in erosion rates. Error bars represent mean ± SE

Table 1. Sediment samples categorised by sampling site. AG: aboveground; BG: belowground; DW: dry weight

Site	Depth (cm)	AG biomass (g DW m^{-2})	BG biomass (g DW m^{-2})	Water content (%)	Organic content (%)	Bulk density (mg cm^{-3})	Grain size D_{50} (µm)	Erosion (cm^3 h^{-1})
Bokevik shallow	25	9	122	16.40	0.39	1156.1	308.8	73
	25	15	149	16.74	0.47	1364.7	234.3	35
	30	3	74	18.29	0.42	1413.7	250.6	157
	30	0	0	15.82	0.51	1519.1	233.9	157
	30	6	123	18.84	0.51	1363.6	228.0	33
	30	0	162	18.21	0.81	1371.6	191.0	52
	40	7	18	11.68	0.49	1340.8	231.0	239
	40	0	0	17.17	0.54	1368.7	211.3	129
	40	4	102	13.93	0.59	1392.8	215.5	126
	55	5	233	11.65	0.55	1285.5	226.1	64
	60	8	309	10.67	0.56	1255.1	223.3	26
Bokevik deep	260	0	0	66.97	8.27	442.3	44.7	2
	260	7	68	67.22	8.67	374.6	37.5	16
	400	15	60	55.56	6.49	689.4	56.9	25
	400	20	222	58.49	6.94	661.2	58.3	19
	400	4	143	60.70	7.81	518.3	43.6	6
	400	0	105	60.50	8.31	520.6	40.1	19
	520	38	69	43.89	4.35	861.1	70.8	9
	520	0	0	64.61	8.73	427.6	32.3	13
Gåsö	35	0	0	18.46	2.85	1225.9	140.4	11
	50	0	0	38.53	7.30	1019.3	47.3	14
	60	62	163	80.28	10.23	436.0	32.9	4
	65	18	126	69.87	4.96	721.6	74.1	4
	70	72	271	71.92	9.60	662.3	34.2	3

4. DISCUSSION

Although cliff erosion is widely considered to be an important driver of coastal dynamics, the role of vegetation roots in mitigating this process remained unclear (Feagin et al. 2009, Silliman et al. 2019). This study shows that cliff erosion rates were increasingly reduced with increasing seagrass root biomass in sandy sediments, but that in contrast, erosion rates were unaffected by seagrass root biomass in cohesive muddy sediments (Fig. 6). By experimentally showing that the presence and quantity of seagrass roots is vital in mitigating cliff erosion, our results can explain earlier apparently contrasting findings (Feagin et al. 2009) that suggested that vegetation does not directly affect erosion rates.

In this study, we highlight how seagrass roots can increase sediment stabilisation in coastal areas. Sediment stabilisation is often acknowledged as an important ecosystem function of seagrasses (Hemminga & Duarte 2000, Ondiviela et al. 2014, James et al. 2019, 2020), but the relationship between seagrass roots and sediment stabilisation has remained understudied. Previous studies have mainly focussed on aboveground canopies, such as interactions between submerged vegetation and fluid dynamics (e.g. Lowe et al. 2005, Luhar et al. 2010) and the resulting impacts on sediment stability (e.g. Ros et al. 2014). We show a direct effect of the seagrass root mats, reducing cliff erosion of sandy sediments. Roots mechanically reinforce the sediment by transferring the shear stresses in the sediment to tensile resistance in the roots (Ziemer 1981). For example, Ziemer & Swanston (1977) suggested that roots add strength to the soil by vertically anchoring through the soil mass and by laterally tying the slope together across zones of weakness or instability. In salt marshes, roots and rhizomes enhance cohesion and tensile strength, resulting in higher shear strength (Micheli & Kirchner 2002, Turner 2011), and a loss of *Spartina* spp. BGB can reduce soil strength, which increases marsh erosion (Sheehan & Ellison 2015, Silliman et al. 2019). In line with present findings, this *Spartina* effect on erosion was found to be much more pronounced in sandy soils than in silty sediments (i.e. 70 versus 17% erosion reduction, Lo et al. 2017). In terrestrial systems, soil erosion was reduced with increasing root density (Li et al. 1991) and root hairs (De Baets et al. 2020). Our results also agree with Zhou & Shangguan (2005), who showed that the root surface area density (i.e. total root surface area divided by soil volume) appeared to be an important

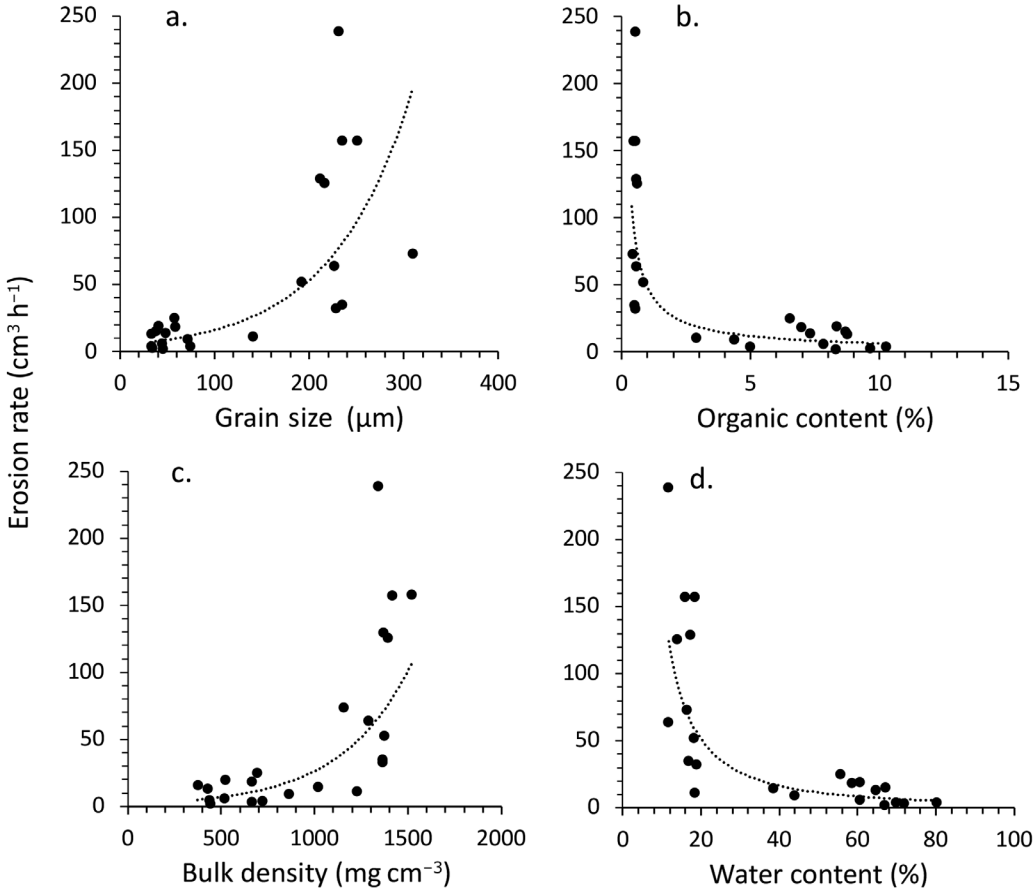

Fig. 5. Correlation between erosion rates and (unvegetated) sediment properties for all sediment types (sand and mud): (a) grain size, (b) organic content, (c) bulk density and (d) water content

variable in explaining observed cliff erosion rates. The presence of vesicular–arbuscular mycorrhizal fungi (AMF) on terrestrial ryegrass has been shown to reduce erosion from wind in sandy soils (Burri et al. 2013) by binding the sand grains, but the effect of AMF in seagrass roots is less clear. While fungal symbionts have been found in the seagrass *Posidonia oceanica* (Vohník et al. 2017) and *Zostera marina* (Ettinger & Eisen 2019), their role in sediment binding and erosion remains to be elucidated.

Sediment properties affect erodibility through changes in the size or quantity of sediment constituents, and include mean particle size, particle size distribution (e.g. clay content), bulk density and water content (Grabowski et al. 2011). In the present study, cliff erosion rates increased in sediments with grain sizes larger than 190 µm, organic content lower than 1%, water content lower than 20%, and bulk densities exceeding 1.1 g cm^{-3}. We found that BGB was the primary regulator of erosion rate in sediments with these properties. In contrast, erosion rates in muddy sediments were not affected by the presence of vegetation. This could be explained by the consolidation process of cohesive sediments in which fine particles are compacted over time and interstitial water is released (Torfs et al. 1996). Since the critical shear stress of sandy sediment increases with the addition of adhesive particles such

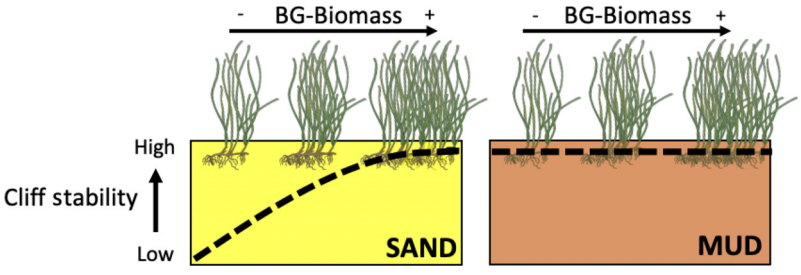

Fig. 6. Conceptual model representing the increase in cliff stability with belowground (BG) biomass in sandy sediment, but in cohesive muddy sediment, cliff stability is high, independent of BG biomass

as mud, the erosion rates would be also reduced (Mitchener & Torfs 1996). In this study, the magnitude of the sediment binding force in cohesive sediments seems to be similar to the presence of roots in non-cohesive sediment, resulting in low erosion rates compared to sandy non-cohesive sediment without roots.

Cliff erosion might be expected to differ between plant species since erosion rates could show contrasting effects depending on root sizes or root morphologies (Reubens et al. 2007). In terrestrial plants, fine roots (1–20 mm) are considered to provide greater improvement in soil fixation and slope reinforcement (Styczen & Morgan 1995, De Baets et al. 2007, Freschet & Roumet 2017), while coarse roots (>40 mm) are more important for slope stability (O'Loughlin & Watson 1979). In sand dunes, the more extensive root system of *Carex kobomugi* provides more effective stabilisation than *Ammophila breviligulata* (Charbonneau et al. 2016). It is well known that root architecture varies between seagrass species (Duarte et al. 1998, Kuo & den Hartog 2006). For example, seagrass root architecture varies greatly in size and shape, from very small-diameter roots (0.18 mm) of *Halodule uninervis*, to thick roots of *Posidonia oceanica* (1.8 mm) or *Enhalus acoroides* (3.5 mm) (Duarte et al. 1998, Kiswara et al. 2009, Infantes et al. 2011). Twomey et al. (2021) found no differences in root biomass on cliff erosion rates with *E. acoroides* since this species does not produce dense root mats. In our study, *Z. marina* had a thin average root diameter of 0.2 ± 0.1 mm, and the resistance to lateral erosion might differ in larger species. To confirm the generality of our results to other species and vegetation types, future work could involve repeating our analysis in vegetation subjected to other environmental conditions and/or possessing different root architectures or morphologies.

Seasonal root biomass variability might play an important role in sediment stabilisation. For example, shallow *Z. noltii* meadows in northern latitudes lose most leaves during winter, while maintaining the root structure in the sediment until temperatures rise again in spring and showing a strong sediment stability during winter (Suykerbuyk et al. 2016a). Intertidal hummocks of *Z. noltii* often remain visible during winter even without aboveground parts, in agreement with the erosion reduction by the root mats shown in our study. In contrast, erosion is enhanced when root mats disappear during winter, as in annual *Z. marina* patches (Bos et al. 2007).

Coastal engineering using natural solutions such as coastal vegetation is an attractive and potentially sustainable strategy for protecting coastlines (Temmerman et al. 2013, Bouma et al. 2014, James et al. 2019). Our study helps to clarify this strategy further by demonstrating that seagrass roots and rhizomes can be of great importance for controlling erosion in sandy sediments (Fig. 3a). Hence, coastal management of areas with sandy sediment could aim to use vegetation such as seagrass to enhance the stability of the sediment (cf. James et al. 2019), although initial plant establishment may require (temporary) sediment stabilising measures. Regardless of the sediment type, locally specific environmental factors such as erosion rates (Fonseca & Fisher 1986, Fonseca 1989) and turbidity (Ward et al. 1984, Gurbisz et al. 2016) always need to be considered, because both of these factors have a demonstrated impact on the success of both natural recovery and active restoration of seagrass meadows (Orth et al. 2012, Moksnes et al. 2018).

We show that muddy sediments have a high resistance to cliff erosion, with or without roots. Therefore, natural recovery of seagrass might be more likely to occur in relatively stable muddy sediments than in unstable sandy sediments, where light reduction by sediment resuspension can also prevent seagrass growth (van der Heide et al. 2007). For conservation management, this implies that areas with sandy sediment covered with seagrass should be highly protected since in these areas seagrasses may have an important function in erosion control. If restoration of vegetation is sought in unstable sandy sediments, methods which may improve restoration success could include:

(1) Using plants with high BGB to stabilise the sediment. Planting vegetation with such high BGB might be practically difficult, especially if large areas are aimed to be restored. An approach could be to plant species with high production of BGB (e.g. *Cymodocea nodosa* and *Z. noltii*) at the beginning of the growing season (late spring/summer) to allow development during the growing period (summer), to enhance resistance for the winter storm events.

(2) Using pioneer species at the start of the restoration programme. This is an alternative approach to (1), as pioneer species typically have low biomass (e.g. *Halodule* spp., *Halophila* spp.), but they are fast-growing and may colonise the upper sediment layers quickly with highly branching roots and rhizome systems (O'Brien et al. 2018).

(3) Using temporary stabilising measures to armour the sediment. For example, the application of shells (cockles) mixed with the sediment has been shown to be particularly useful for *Z. marina* and *Z. noltii* in intertidal habitats (van Katwijk & Hermus 2000, Suykerbuyk et al. 2016b). Recently, the addition of a

10 cm layer of sand-cap over muddy bottoms was shown to reduce sediment resuspension and potentially promote *Z. marina* growth (Flindt et al. 2022, Oncken et al. 2022). The addition of biodegradable structures designed to stabilise the top 5–10 cm sediment layer could be used temporarily until plants develop BGB and become established (Temmink et al. 2020, van der Heide et al. 2021). These structures, composed of biodegradable potato waste, are effective for salt marsh (*Spartina anglica* and *S. alterniflora*) and seagrass species (*Z. marina* and *Thalassia testudinum*) across temperate and tropical regions (op. cit.).

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