Seagrass roots strongly reduce cliff erosion rates in sandy sediments

Eduardo Infantes1,2,*, Selwyn Hoeks1,2, Matthew P. Adams3,4,5, Tjisse van der Heide6,7, Marieke M. van Katwijk8, Tjeerd J. Bouma2,9

1Department of Biological and Environmental Sciences, University of Gothenburg, 45178 Kristineberg, Sweden
2Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ), 4401 NT Yerseke, the Netherlands
3School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD 4000, Australia
4Centre for Data Science, Queensland University of Technology, Brisbane, QLD 4000, Australia
5School of Chemical Engineering, The University of Queensland, St Lucia, QLD 4072, Australia
6Department of Coastal Systems, Royal Netherlands Institute for Sea Research (NIOZ), 1790 AB Den Burg, The Netherlands
7Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9747 AG Groningen, The Netherlands
8Department of Environmental Science, Radboud University, 6525 AJ Nijmegen, The Netherlands
9Faculty of Geosciences, Department of Physical Geography, Utrecht University, 3508 TC Utrecht, The Netherlands

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 pio-

*Corresponding author: eduardo.infantes@gu.se

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

© The authors 2022. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.
Publisher: Inter-Research · www.int-res.com
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 x 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

---

**Infantes et al.: Seagrass roots reduce cliff erosion**
(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.intres.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 relationship 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. 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
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).
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 D₅₀ (μm) | Erosion (cm³ h⁻¹) |
|---------------|------------|-----------------------|-----------------------|-------------------|---------------------|------------------------|---------------------|------------------|
| Bokevik shallow | 25         | 9                     | 122                   | 16.40             | 0.39                | 1156.1                 | 44.7                | 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                | 679.4                  | 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             | 0.56                | 1255.1                 | 223.3               | 26               |
|               | 50         | 0                     | 0                     | 18.46             | 0.56                | 1255.1                 | 223.3               | 26               |
|               | 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
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* (Ettlinger & 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. 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.](image1)

![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.](image2)
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 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 (Tem-merman 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.).

**Acknowledgements**. We thank FORMAS (grant Dnr. 2019-01192) and Stiftelsen Längmanska Kulturfonden. The contribution by M.P.A. was funded by the Royal Swedish Academy of Sciences and an Australian Research Council Discovery Early Career Researcher Award DE200100683. Thanks to the staff of Kristineberg Research Station for providing their facilities and staff at NIOZ who constructed the flume.

**LITERATURE CITED**

- Bender MA, Knutson TR, Tuleya RE, Sirutis JJ, Vecchi GA, Garner ST, Held IM (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327:454−458
- Bos A, Bouma TJ, Dekort G, van Katwijk MM (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. Estuar Coast Shelf Sci 74:344−348
- Bouma TJ, van Belzen J, Balke T, Zhu Z and others (2014) Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: opportunities & steps to take. Coast Eng 87:147−157
- Bouma TJ, van Belzen J, Balke T, van Dalen J and others (2016) Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics. Limnol Oceanogr 61:2261−2275
- Burri K, Gromke C, Graf F (2013) Mycorrhizal fungi protect the soil from wind erosion: a wind tunnel study. Land Degrad Dev 24:385–392
- Carter RWG, Stone GW (1989) Mechanisms associated with the erosion of sand dune cliffs, Magilligan, Northern Ireland. Earth Surf Process Landf 14:1−10
- Charbonneau BR, Wnek JP, Langley JA, Lee G, Balsamo RA (2016) Above vs. belowground plant biomass along a barrier island: implications for dune stabilization. J Environ Manag 182:126−133
- Church JA, White NJ (2006) A 20th century acceleration in global sea-level rise. Geophys Res Lett 33:L01602
- Dahl M, Asplund ME, Deyanova D, Franco JN and others (2020) High seasonal variability in sediment carbon stocks of cold-temperate seagrass meadows. J Geophys Res Biogeosci 125:e2019GC005430
- De Baets S, Poesen J, Knappen A, Galindo P (2007) Impact of root architecture on the erosion-reducing potential of roots during concentrated flow. Earth Surf Process Landf 32:1323−1345
- De Baets S, Denbigh TDG, Smyth KM, Eldridge BM and others (2020) Micro-scale interactions between *Arabidopsis* root hairs and soil particles influence soil erosion. Commun Biol 3:164
- De Battisti D, Fowler MS, Jenkins SR, Skov MW and others (2019) Intraspecific root trait variability along environmental gradients affects salt marsh resistance to lateral erosion. Front Ecol Evol 7:150
- Duarte CM, Merino M, Agawin NSR, Uri J and others (1998) Root production and belowground seagrass biomass. Mar Ecol Prog Ser 171:97−108
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mears L. (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068−2074
- Ettinger CL, Eisen JA (2019) Characterization of the myco-biome of the seagrass, *Zostera marina*, reveals putative associations with marine chytrids. Front Microbiol 10:2476
- Feagin RA, Lozada-Bernard SM, Ravens TM, Möller I, Yeager KM, Baird AH (2009) Does vegetation prevent wave erosion of salt marsh edges? Proc Natl Acad Sci USA 106:10109−10113
- Feagin RA, Mukherjee N, Shanker K, Baird AH and others (2010) Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. Conserv Lett 3:1−11
- Feagin RA, Figlus J, Zinnert JC, Sigren J and others (2015) Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. Front Ecol Environ 13:203−210
- Flindt MR, Oncken NS, Kuusemäe K, Lange T and others (2022) Sand-capping stabilizes muddy sediment and improves benthic light conditions in eutrophic estuaries: laboratory verification and the potential for recovery of eelgrass (*Zostera marina*). J Sea Res 181:102177
- Fonseca MS (1989) Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. Estuar Coast Shelf Sci 29:501−507
- Fonseca MS, Fisher JS (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar Ecol Prog Ser 29:15−22
- Freschet GT, Roumet C (2017) Sampling roots to capture plant and soil functions. Funct Ecol 31:1506−1518
- Gedan KB, Kirwan ML, Wolanski E, Barbier EB, Silliman BR (2016) Above vs. belowground plant biomass along environmental gradients affects salt marsh resistance to lateral erosion. Front Ecol Evol 7:150
- Ghisalberti M, Nepf H (2006) The structure of the shear layer in flows over rigid and flexible canopies. Environ Fluid Mech 6:277−301
- Grabowski RC, Droppo IG, Wharton G (2011) Erodibility of cohesive sediment: the importance of sediment properties. Earth Sci Rev 105:101−120
- Gurbisz C, Kemp WM, Sanford LP, Orth RJ (2016) Mechanisms of storm-related loss and resilience in a large submerged plant bed. Estuar Coasts 39:951−966
- Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge
- Infantes E, Orfila A, Bouma TJ, Simarro G, Terrados J (2011) *Posidonia oceanica* and *Cymodocea nodosa* seedling tolerance to wave exposure. Limnol Oceanogr 56:2223−2232
- Infantes E, Orfila A, Simarro G, Terrados J, Luhar M, Nepf H (2012) Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. Mar Ecol Prog Ser 456:63−72
- Infantes E, Smit JC, Tamarit E, Bouma TJ (2021) Making realistic wave climates in low-cost wave mesocosms: a
new tool for experimental ecology and biogeomorphology. Limnol Oceanogr Methods 19:317–330

James RK, Silva R, van Tussenbroek BI, Escudero-Castillo M and others (2019) Maintaining tropical beaches with seagrass and algae: a promising alternative to engineering solutions. Bioscience 69:136–142

James RK, Christianen MJA, van Katwijk MM, de Smit JC, Bakker ES, Herman PMJ, Bouma TJ (2020) Seagrass coastal protection services reduced by invasive species expansion and megaherbivore grazing. J Ecol 108: 2025–2037

Kiswara W, Behnke N, van Avesaath P, Huiskes AL, Erftemeijer PLA, Bouma TJ (2009) Root architecture of six tropical seagrass species, growing in three contrasting habitats in Indonesian waters. Aquat Bot 90:235–245

Kuo J, den Hartog C (2006) Seagrass morphology, anatomy, and ultrastructure. In: Larkum AWD (ed) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, p 51–87

La Nafie YA, de los Santos CB, Brun FG, van Katwijk MM, Bouma TJ (2012) Waves and high nutrient loads jointly decrease survival and separately affect morphological and biomechanical properties in the seagrass Zostera noltii. Limnol Oceanogr 57:1664–1672

Lera S, Nardin W, Sanford LP, Palinkas CM, Guercio R (2019) The role of submerged aquatic vegetation on the development of river mouth bars. Earth Surf Process Landfl 44:1494–1506

Li Y, Zhu XM, Tian JY (1991) Effectiveness of plant roots to increase the anti-scorability of soil on the loess plateau. Chin Sci Bull 36:2071–2082

Lo VB, Bouma TJ, van Belzen J, van Colen C, Airolid L (2017) Interactive effects of vegetation and sediment properties on erosion of salt marshes in the Northern Adriatic Sea. Mar Environ Res 131:32–42

Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. Aust J Plant Physiol 16:141–146

Lowe RJ, Koseff JR, Monismith SG (2005) Oscillatory flow through submerged canopies: 1. Velocity structure. J Geophys Res 110:C10016

Luhar M, Coutu S, Infantes E, Fox S, Nepf H (2010) Wave-induced velocities inside a model seagrass bed. J Geophys Res 115:C12005

Luhar M, Infantes E, Nepf H (2017) Seagrass blade motion under waves and its impact on wave decay. J Geophys Res Oceans 122:3736–3752

Marin-Diaz B, Bouma TJ, Infantes E (2020) Role of eelgrass on bed-load transport and sediment resuspension under oscillatory flow. Limnol Oceanogr 65:426–436

Mazda Y, Magi M, Motohiko K, Nguyen P (1997) Mangroves as a coastal protection from waves in the Tong King delta, Vietnam. Mangroves Salt Marshes 1:127–135

McGranahan G, Balk D, Anderson B (2007) The rising tide: assessing the risks of climate change and human settlement in low elevation coastal zones. Environ Urbaniz 19:17–37

Micheli ER, Kirchner JW (2002) Effects of wet meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. Earth Surf Process Landfl 27:687–697

Mitchener H, Torfs H (1996) Erosion of mud/sand mixtures. Coast Eng 29:1–25

Moksnes PO, Eriander L, Infantes E, Holmer M (2018) Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish west coast. Estuaries Coasts 41:1712–1731

Möller I, Kudella M, Rupprecht F, Spencer T and others (2014) Wave attenuation over coastal salt marshes under storm surge conditions. Nat Geosci 7:727–731

O’Brien KR, Waycott M, Maxwell P, Kendrick GA and others (2018) Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Mar Pollut Bull 134:166–176

O’Loughlin C, Watson A (1979) Root-wood strength deterioration in radiata pine after clearfelling. NZ J For Sci 9: 284–293

Oncken NS, Lange T, Kristensen T, Quintana CO, Steinfurth RC, Flindt MR (2022) Sand-capping—a large-scale approach to restore organic-enriched estuarine sediments. Mar Environ Res 173:105534

Onndiviela B, Losada LJ, Lara JL, Maza M, Galván C, Bouma TJ, van Belzen J (2014) The role of seagrasses in coastal protection in a changing climate. Coast Eng 87:158–168

Orth RJ, Moore KA, Marion SR, Wilcox DJ, Parrish DB (2012) Seed addition facilitates eelgrass recovery in a coastal bay system. Mar Ecol Prog Ser 448:177–195

Palinkas CM, Koch EW (2012) Sediment accumulation rates and submersed aquatic vegetation (SAV) distributions in the mesohaline Chesapeake Bay, USA. Estuaries Coasts 35:1416–1431

Reubens B, Poesen J, Danjon F, Geudens G, Muys B (2007) The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. Trees (Berti) 21:385–402

Ros À, Colomer J, Serra T, Pujol D, Soler M, Casamitjana X (2014) Experimental observations on sediment resuspension within submerged model canopies under oscillatory flow. Cont Shelf Res 91:220–231

Sheehan MR, Ellison JC (2015) Tidal marsh erosion and accretion trends following invasive species removal, Tamar Estuary, Tasmania. Estuar Coast Shelf Sci 164:46–55

Shepard CC, Crain CM, Beck MW (2011) The protective role of coastal marshes: a systematic review and meta-analysis. PLOS ONE 6:e27374

Siggren J, Figlus J, Armitage A (2014) Coastal sand dunes and dune vegetation: Restoration, erosion, and storm protection. Shore Beach 82:5–12

Silliman BR, He Q, Angelini C, Smith CS and others (2019) Field experiments and meta-analysis reveal wetland vegetation as a crucial element in the coastal protection paradigm. Curr Biol 29:1800–1806

Styczyn C, Morgan R (1995) Engineering properties of vegetation. In: Morgan RPC, Rickson RJ (eds) Slope stabilization and erosion control: a bioengineering approach. E. & F.N. Spon, London, p 5–58

Suykerbuyk W, Bouma TJ, Gover LL, Giesen K and others (2016a) Surviving in changing seascapes: sediment dynamics as bottleneck for long-term seagrass presence. Ecosystems 19:296–310

Suykerbuyk W, Governs LL, Bouma TJ, Giesen WB and others (2016b) Unpredictability in seagrass restoration: analysing the role of positive feedback and environmental stress on Zostera noltii transplants. J Appl Ecol 53:774–784

Temmeerman S, Meire P, Bouma TJ, Herman PMJ, Ysebaert T, De Vriend HJ (2013) Ecosystem-based coastal defence in the face of global change. Nature 504:79–83

Temminck RJM, Christianen MJA, Fivash GS, Angelini C and others (2020) Mimicry of emergent traits amplifies coastal restoration success. Nat Commun 11:3668
