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RESEARCH ARTICLE

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Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development

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Key Points:

- Algal mats create elevated and strengthened sediment ridges on tidal flats, possibly promoting the establishment of marsh plants
- In a self-reinforcing cycle, algae grow better on elevated ridges and stabilize the sediment, which increases relative sediment elevation
- This study shows that it may be crucial to consider biogeophysical interactions in order to predict the formation of new ecosystems

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Ecosystem establishment under adverse geophysical conditions is often studied within the “windows of opportunity” framework, identifying disturbance-free periods (e.g., calm wave climate) where species can overcome establishment thresholds. However, the role of biogeophysical interactions in this framework is less well understood. The establishment of saltmarsh vegetation on tidal flats, for example, is limited by abiotic factors such as hydrodynamics, sediment stability and drainage. On tidal flats, raised sediment ridges colonized by algal mats (*Vaucheria sp.*) appear to accommodate high densities of plant seedlings. Such ridges were previously found to have higher sediment strength than substratum without algae. Here, we investigate whether these measurements can be explained by geophysical factors only, or that biological (*Vaucheria*-induced) processes influence tidal marsh establishment by forming stabilized bedforms. We performed two experiments under controlled mesocosm conditions, to test the hypotheses that (a) *Vaucheria* grows better on elevated topographic relief, that (b) the binding force of their algal filaments increases sediment strength, and that (c) *Vaucheria* consequently creates elevated topographic relief that further facilitates algal growth. Our experimental results confirm the existence of this algal-induced biogeomorphic feedback cycle. These findings imply that benthic algae like *Vaucheria* may contribute significantly to tidal marsh formation by creating elevated and stabilized substratum. This suggests biogeophysical feedbacks can “widen” the windows of opportunity for further ecosystem establishment. Our results could be useful for the design of managed realignment projects aimed at restoring the unique ecosystem services of coastal wetlands, such as habitat biodiversity, carbon sequestration potential and nature-based flood defense.

Plain Language Summary Densely populated coastlines are exposed to flood risks due to sea-level rise and storms. Tidal marshes, sandy or muddy coastal plains colonized by plants, form a natural buffer zone that reduces flood risks. However, tidal marshes only form when plants manage to establish on unvegetated coastal plains known as tidal flats. Waves and currents wash away young plants and inundation by salt water limits plant growth. Hence, firmer sediment and higher sediment elevation are geophysical factors that increase plant survival. However, the biological processes affecting plant establishment are less well understood. In the field, we found plants concentrated on elevated sediment hummocks colonized by *Vaucheria* algal mats. We performed laboratory experiments, simulating tidal flat conditions, to investigate the role of these algae. We found that *Vaucheria* algae grow better on elevated hummocks and that hair-like algal filaments strengthen the sediment. We showed that sediment strengthening by *Vaucheria* creates elevated sediment hummocks, thus self-reinforcing algal growth. Our findings imply that, despite being small, algae like *Vaucheria* may promote marsh establishment by creating stable and elevated surfaces. Marsh restoration efforts could benefit from our results, ultimately increasing the natural value and flood-protection capacity of these important coastal ecosystems.

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1. Introduction

Coastal wetlands, which are found worldwide and provide valuable ecosystem services (e.g., Arkema et al., 2013; Barbier et al., 2008; Temmerman et al., 2013; Zhu et al., 2020), are under increased anthropogenic pressure (e.g., Kirwan & Megonigal, 2013). Vegetation growing in wetlands such as salt and freshwater

marshes and mangroves attenuate waves (e.g., Möller et al., 2014; Willemsen et al., 2020), buffer storm surges (e.g., Loder et al., 2009; Stark et al., 2016; Temmerman et al., 2012) and reduce dike breaches when occurring (Zhu et al., 2020), thereby providing a natural coastal protection for the densely populated hinterlands. In addition, wetlands are a significant carbon sink (e.g., Chmura et al., 2003) and provide habitat to numerous species (e.g., Gedan et al., 2009). However, wetland ecosystems are at risk of drowning due to sea-level rise (e.g., Arkema et al., 2013; Best et al., 2018; Crosby et al., 2016; Kirwan & Megonigal, 2013; Vinent et al., 2021) and narrowing due to sea-level rise in combination with intensified storminess (Zhu et al., 2020), while their natural resilience is impeded by anthropogenic stressors (e.g., Gedan et al., 2009). Worldwide efforts are therefore undertaken to protect natural wetlands, as well as to restore and create new wetlands by managed coastal realignment and promoting vegetation colonization (e.g., Fivash et al., 2020; Lawrence et al., 2018; Mossman et al., 2012; Wolters et al., 2005).

Several factors, however, impede the establishment and further colonization of vegetation on bare tidal flats. In disturbed environments, such as wave-exposed coastal ecosystems, vegetation establishment relies on a narrow window of opportunity, within which seeds and seedlings can settle and develop roots to prevent being washed away (Balke et al., 2011). These windows of opportunity are opened when (hydrodynamic) disturbances become weaker or less frequent (e.g., Balke et al., 2014) or when grazing pressure is reduced (Hughes et al., 2000). Therefore, plants are more likely to establish in more stable sediment (e.g., Balke et al., 2011, 2013; Bouma et al., 2016; Cao et al., 2018), at elevated topographic relief (e.g., Bouma et al., 2016; Fivash et al., 2020; Lawrence et al., 2018; Mossman et al., 2020; Xie et al., 2019) and in wave-attenuating convex-shaped foreshores (e.g., Hu et al., 2015). Both the formation of stable and elevated sedimentary bedforms (e.g., Allen, 1987; Carling et al., 2009; McCave & Geiser, 1979), as well as factors that “keep windows of opportunity closed” (e.g., Romme et al., 1998) have traditionally been studied from a dominantly geophysical viewpoint. Despite mounting evidence for the important role of organisms in the creation and stabilization of raised bedforms (e.g., de Boer, 1981; Friend et al., 2008; Noffke, 1999; van de Vijssel et al., 2020; Weerman et al., 2011), the possibility that biota could in this way widen the windows of opportunity for further ecosystem establishment remains poorly studied. Deeper insight into the (physical and biological) processes that affect windows of opportunity might ultimately improve the success of wetland restoration projects.

Observations on tidal flats suggest that vegetation establishment is facilitated on elevated sedimentary ridges colonized by mats of the filamentous algae *Vaucheria sp.* (Figure 1). These algae can form dense networks of filaments that trap sediment (Black, 1933; Skowroński et al., 1998) and grow centimeters through overlying sediment (Gallagher & Humm, 1981), forming thick felt-like mats (Gallagher & Humm, 1981; Simons, 1975; Wilcox, 2012). Algal spores can establish across the entire mudflat (van de Vijssel et al., 2020), but developed *Vaucheria* mats are mostly found on elevated hummocks/ridges whose sediment stability is higher than that of the surrounding bare mudflat (Paterson, 1994; van de Vijssel et al., 2020; Webber, 1967). However, most of these findings come from observations and measurements under natural field conditions, rather than controlled experimental conditions. Hence, it remains unclear whether *Vaucheria* merely follow the pre-existing landscape topography by growing better on elevated relief, where the sediment is better drained and hence more stable (e.g., Carling et al., 2009; Gouleau et al., 2000; O'Brien et al., 2000; Williams et al., 2008), or that these organisms play an active role in the formation of stabilized bedforms and might thus be an important biogeomorphic process to consider in the development of vegetated wetlands.

Many coastal wetland species have been found to induce biogeomorphic feedbacks that shape their environment (e.g., Corenblit et al., 2007), often through interaction with other organisms (e.g., Passarelli et al., 2014). For example, plants are known to reduce flow speeds and trap sediment with their above-ground biomass (e.g., Bouma et al., 2013; Neumeier & Ciavola, 2004) and reinforce the substratum with their roots (e.g., Mariotti et al., 2016; Murray & Paola, 2003), whereas microbial biofilms increase erosion thresholds (e.g., Paterson et al., 2000) by excreting glue-like extracellular polymeric substances, or EPS (e.g., Neumann et al., 1970; Stal, 2010). Local biotic sediment stabilization creates topographic elevations (e.g., Temmerman et al., 2007; Weerman et al., 2010). On top of these elevations, plants are better oxygenated (e.g., Fivash et al., 2020) and the EPS excreted by biofilms is less diluted by water (e.g., Blanchard et al., 2000; Paterson et al., 2000; Weerman et al., 2010), which further stimulates biotic growth and thus induces a closed biogeomorphic feedback loop. The same feedbacks have a negative effect at somewhat further distance,

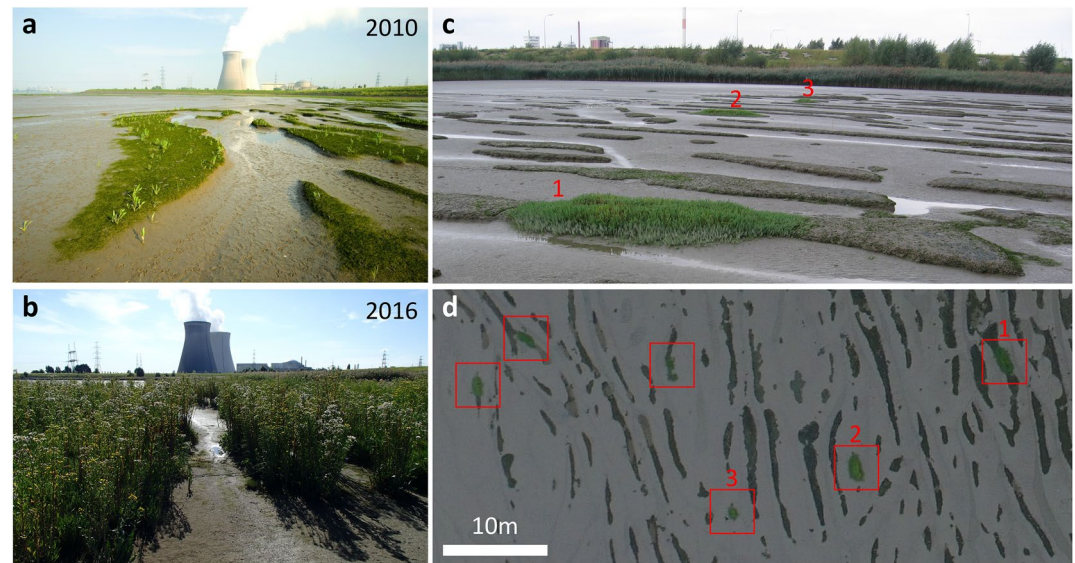


Figure 1. On tidal flats, halophytic vegetation appears to establish preferably on algal mat-covered, elevated surfaces. (a) Establishment of vegetation seedlings (*Aster tripolium*) on elevated and *Vaucheria*-covered ridges (photo © Vilda/ Yves Adams). Photo taken around 2010 at the intertidal flat of Paardenschor (51.334521°N, 4.251750°E), Schelde estuary, Belgium. (b) In 2016, the vegetation seedlings in photo (a) have developed into dense vegetation tussocks. The selective growth of vegetation on the elevated algal-covered ridges at this same field location can also be seen in aerial image time series shown (van de Vijssel et al., 2020). (c) Three examples of vegetation tussocks (*Glaux maritima*) growing on top of sedimentary ridges covered by macroalgal mats (*Vaucheria* sp.). Photo taken at the intertidal flat of Ketenisse (51.284931°N, 4.311964°E), Schelde estuary, Belgium. (d) Aerial photo of the same location as photo (c), emphasizing several examples, including the three from (c), of vegetation tussocks growing on elongated, algal-covered ridges. Algal mats are visible in dark green colors; vegetation in brighter green.

where flow deflection and acceleration around the biotically stabilized hummocks/ridges scours out hollows or channels, in which inundation and shear stress are higher (e.g., Temmerman et al., 2007; Weerman et al., 2010). Although filamentous algae like *Vaucheria* are notably different from plants and microbial biofilms, in the sense that they do not have roots nor excrete large amounts of EPS, field observations suggest that these algae might induce similar biogeomorphic feedbacks (van de Vijssel et al., 2020). If such algal-induced feedbacks indeed exist, they could explain the observed algal-covered bedforms (Figure 1) and their apparent facilitative influence on marsh development.

Here, we conduct two controlled mesocosm experiments to test the hypothesis that *Vaucheria* grows better on elevated topographic relief (Experiment 1), and that the algae increase sediment strength (resistance to deformation, a proxy for sediment consolidation and erosion resistance [Williams et al., 2008]) and thereby relative sediment elevation (Experiment 2), which would enhance algal growth and thereby close the feedback loop needed for biogeomorphic landscape formation. In the first experiment, we cultivated *Vaucheria* on sediment surfaces with elevated topographic relief (hummocks), no topographic relief (flat surfaces) and lowered topographic relief (hollows). In the second experiment, we cultivated *Vaucheria* on sediment to measure its effect on sediment strength (i.e., measured as compressive deformability, which is inversely related to strength) and surface elevation of the sediment. Both experiments were performed under controlled mesocosm conditions that simulate sheltered intertidal field conditions.

2. Materials and Methods

2.1. Experiment 1: Effect of Sediment Topographic Relief on Algal Growth

2.1.1. Aim and Outline of the Experiment

The objective of this experiment was to test the hypothesis that *Vaucheria* mats grow better on elevated topographic relief (hummock) than on sedimentary substratum without relief (flat), and better on flat

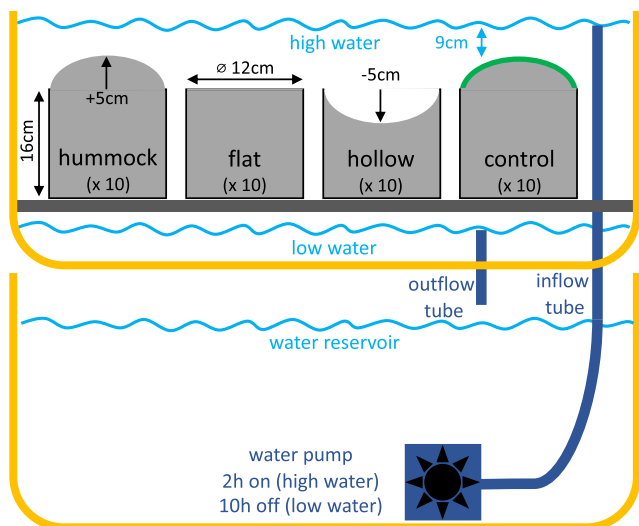


Figure 2. Schematic setup for Experiment 1. Three sediment topography types are illustrated (hummock, flat, hollow). The positive control has sub-surface algal spores that are expected to grow, as to verify that growth conditions are sufficient in the experimental setup. Each type has 10 replicates, distributed randomly and placed within a single mesocosm. The PVC-pots filled with sediment are placed in the upper tidal mesocosm, which is connected to a mesocosm below (the water reservoir). The pots are placed such that they are emerged during “low water” and submerged during “high water”, simulating intertidal conditions.

topography than in local depressions (hollow). To this end, *Vaucheria* algal mats were cultivated under controlled conditions in a mesocosm, mimicking algal growth conditions on intertidal flats. Algae were grown on sedimentary substrata with different topographic profiles (hummock, flat, hollow, control), with 10 replicates per treatment and in a single mesocosm to avoid pseudoreplication. After several weeks, sediment samples were taken to measure the chlorophyll-a and organic carbon content, which was used as a measure of algal growth.

2.1.2. Mesocosm Setup to Simulate Intertidal Conditions

Algae were cultivated in a tidal mesocosm in order to reproduce the growth conditions experienced by *Vaucheria* in the field. The mesocosm consisted of two tanks (open at the top; inner dimensions 112 × 94 cm wide, 59 cm high) that were placed on top of each other and connected with tubes (Figure 2). The experiment was carried out in the upper tank, which was flooded and drained periodically to mimic intertidal conditions; excess water was stored in the lower tank (for details see Cao et al., 2018). A water pump regulated flooding and drainage, such that the upper tank had 2 hr of high water and 10 hr of low water, roughly equal to the inundation time that *Vaucheria* typically experiences on tidal flats (Van den Bergh et al., 2005). TL-tubes mounted above the upper tank, spanning the entire width of the tank to provide a homogeneous light field, and connected to a timer mimicked a 14 hr day, 10 hr night cycle. In the upper tank, light intensity was about 250 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, in accordance with similar mesocosm experiments (Bouma et al., 2016). The mesocosm was set up in a climate room under a consistent temperature of 18°C.

In order to guarantee that *Vaucheria* algal spores were abundantly present in the mesocosm at the onset of Experiment 1, this experiment was carried out in a mesocosm that had previously been used for the long-term (ca. 2 years) cultivation of *Vaucheria* (here referred to as the preparatory phase). Experiment 1 was initiated shortly after the preparatory phase was finished; the tank water from the preparatory phase (containing ample algal spores) was kept in the tanks. This tank water had originally (ca. 2 years ago) been taken from the Oosterschelde estuary in front of the research institute (NIOZ, Yerseke, The Netherlands). Both in the preparatory phase and in Experiment 1, the salinity was kept roughly at 5–10 ppt by regularly adding tap water to compensate for evaporation losses and minor leaks. During the preparatory phase, additional nutrients had been added (60 g of Osmocote slow release fertilizer, suspended in the tank water in a stocking). After 3 months into Experiment 1, the old nutrients were replaced by a new supply.

2.1.3. Preparation of Sediment and Topographic Relief

Algae were cultivated on the surface of 40 pots filled with sediment. The pots consist of PVC tubes, 12 cm in diameter, 16 cm high and closed off with a lid at the bottom. The sediment was collected at the mudflat of Paardenschor (51.334236°N, 4.252603°E). The pots and sediment from the preparatory phase were re-used for Experiment 1; sediment from the deepest layers was homogenized and used to create the surface topography of Experiment 1, hence excluding all living benthos or previously formed algal mats (see Supporting Information S1 for details). With this sediment, 10 PVC pots were modelled with a smooth sediment mound, with the crest protruding about 5 cm above the top edge of the PVC pots; this is the “hummock” topography (Figure 2). For 10 other PVC pots, the homogenized sediment was used to fill the pot exactly until the PVC-edge; that is, the surface was smooth and horizontal; this is the “flat” topography. In 10 other pots, the homogenized sediment was used to create (without compressing the sediment too much) a smoothly depressed surface, 5 cm at the deepest point, that is, the “hollow” topography. The 10 remaining pots from the preparatory phase served as “positive controls” to verify that the experimental conditions for algal growth were sufficient: *Vaucheria* mats were “pulled off” these 10 remaining pots, leaving a sediment hummock with algal filaments below the surface. All pots were placed on a raised platform such that they

were both completely emerged during the low water phase and completely submerged (top of the PVC-pots about 9 cm below the high water mark) during the high water phase. The pots were placed in the tank in a randomized configuration to exclude the effect of any non-uniform mesocosm conditions (e.g., lighting).

2.1.4. Sediment Sampling to Quantify Algal Biomass

To quantify algal growth on each of the types of topographic relief, Experiment 1 was ended after almost 9 months (264 days) of algal cultivation. To quantify algal biomass, sediment samples were taken with plastic syringes (inner diameter 35 mm) with a cut-off tip. In the center of the pot surfaces, the upper 5 cm (ca. 50 mL) was sampled. This sampling depth was an approximation, as the sediment was highly cohesive, such that the sampled cores inevitably deformed upon sampling or sometimes would not fully detach from the surrounding sediment in the pot. However, it can be assumed that the algal filaments did not reach deeper than 5 cm, such that the uncertainty in sampling depth could be corrected for (as explained hereafter). The samples were weighed, frozen at -80°C , freeze-dried and weighed again to calculate dry bulk densities and to prepare the samples for further analysis.

2.1.5. Analyzing Chlorophyll-a and Organic Carbon Content as Proxy for Algal Biomass

For the chlorophyll-a analysis, samples were kept in the dark at -80°C until the actual analysis. The samples were homogenized and sieved with a 1 mm sieve to remove any shell and animal material, after which they were kept in the dark under lab temperature. Under illuminated lab conditions, subsamples of 1g were taken to extract the pigments. The subsamples were blended in a Bullet Blender (Next Advance), which was cooled to 4°C with dry ice and where glass beads (6 g, 1 mm diameter) had been added. The samples were blended for 15 min at speed 12 after addition of 5 mL acetone (90%); hereafter this treatment was repeated once more. After extraction, the supernatant was centrifuged (in the dark) at 1,500 rpm for 5 min. A Specord 210 spectrophotometer was then used to measure absorption. The equation of Ritchie (2006) was used to calculate chlorophyll-a concentration ($\mu\text{g/g}$). This concentration was multiplied by the dry weight of the entire sample and divided by the sampled surface area to obtain chlorophyll-a mass per area. Although it has been reported that *Vaucheria* filaments can penetrate 4–6 cm into the sediment (Gallagher & Humm, 1981), we here assume that most algal biomass was concentrated well within the upper 5 cm. Under this assumption, which should be verified in future experiments by analyzing the pigment content of deeper layers, chlorophyll-a mass per surface area is a measure for algal biomass that is independent of the exact sampling depth. After chlorophyll-a analysis, the full (freeze-dried, homogenized and sieved) sediment samples were used to analyze the organic carbon content. Between the moment of chlorophyll-a extraction and organic carbon measurement, the samples were stored in the dark under room temperature. Subsamples of 10–15 mg were taken, which were put in a silver cup. Inorganic carbon was removed by adding 10 μL of 30% HCl to each subsample; this treatment was repeated with 10–20 μL of 30% HCl until the reaction (bubbling) had stopped. The samples were placed on a heating plate at 50°C and the temperature was increased to 120°C . After 15 min, the samples were taken off the heating plate until they had cooled down. Again, 10 μL of 30% HCl was added to ensure the removal of all inorganic carbon. The samples were placed on the heating plate for 1 hr to dry. The subsamples were then rolled into small balls. Using an autosampler, the samples were introduced into a combustion tube, where combustion took place under the influence of oxygen and the catalysts Cr_2O_3 and AgCo_3O_4 . The combustion gases CO_2 , N_2 , N_xO_y , H_2O and the excess O_2 were led through a heated quartz tube filled with copper wire. All nitrogen oxides were here reduced to N_2 . Water was absorbed on magnesium perchlorate. N_2 and CO_2 were separated in a gas chromatographer on a Haysep-Q column (Thermo element analyzer, Flash, 2000) and finally detected with a Thermal Conductivity Detector. Data acquisition and analysis was then performed using the software EAGER-200 (Carlo Erba Instruments). Similarly to chlorophyll-a, we here assumed that organic carbon content related to *Vaucheria* biomass was concentrated within the upper 5 cm. For organic carbon, density-by-weight was also multiplied by the dry weight of the total sample and divided by the sampled surface area to calculate total organic carbon mass per area, as a measure of algal biomass.

2.1.6. Statistical Testing of the Effect of Topographic Relief on Algal Growth

The measured chlorophyll-a values (i.e., total mass per area) were grouped per substratum type (hummock, flat, hollow, control). Homogeneity of variance across groups was tested with Levene's test. A linear model (one-way ANOVA) was fitted to explain chlorophyll-a as a function of substratum. The Shapiro-Wilk test

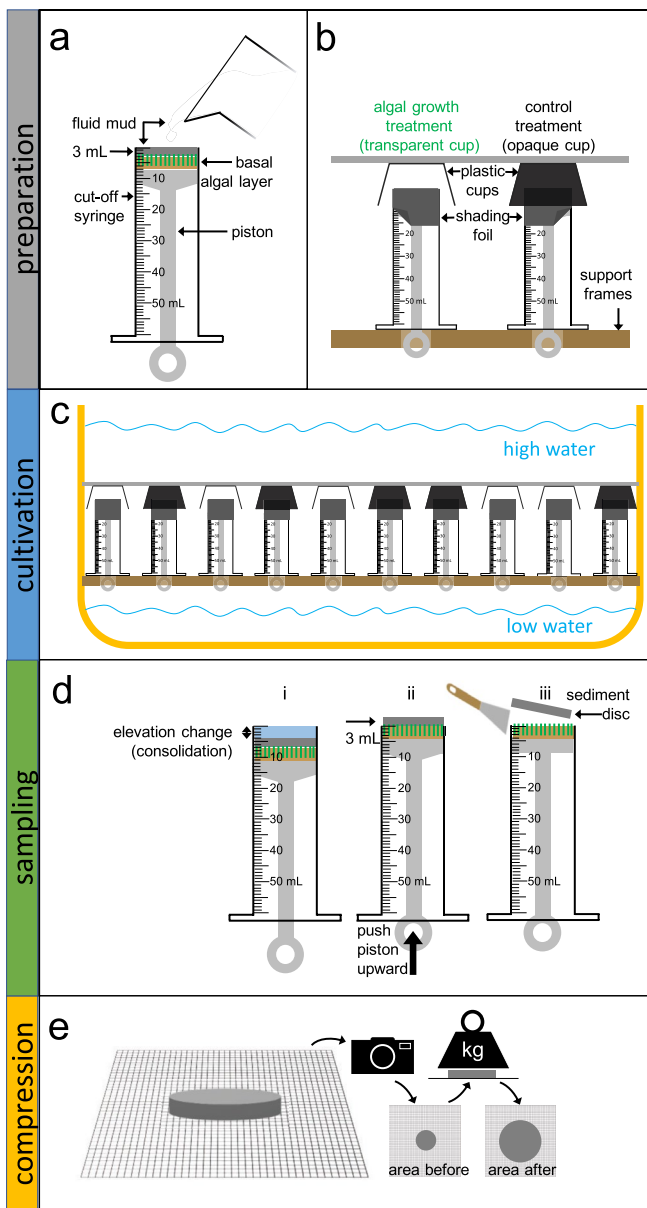


Figure 3. Schematic representation of the experimental setup and procedure in Experiment 2, that is, to study the effect of algal growth on sediment relative elevation and sediment strength. *Vaucheria* algae and sediment are placed in an experimental setup (a, b) immersed in a mesocosm that mimics intertidal growth conditions (c). At specific time intervals, sediment discs are sampled (d) to quantify algal biomass, relative sediment elevation and sediment water content. The resistance of sediment discs against compressive deformation (e) is used as a measure of sediment strength.

of normality was applied to the residuals of the linear model. For chlorophyll-a, homoscedasticity and normality were satisfied, justifying the use of ANOVA. A post-hoc test (Tukey HSD, 95% family-wise confidence level) was applied to the ANOVA results to test which group means differed significantly from each other. The same procedure was applied to the organic carbon values (i.e., total mass per area), grouped per substratum type. These values were homoscedastic but did not have normally distributed residuals. The original data (x) was therefore logarithmically transformed,

$$y = \log_{10}(x), \quad (1)$$

to obtain transformed data (y) that was both homoscedastic and normally distributed. Hence, the ANOVA and post-hoc analyses were done on the transformed data.

2.2. Experiment 2: Effect of Algae on Sediment Strength and Relative Elevation

2.2.1. Aim and Outline of the Experiment

Experiment 2 was designed to test whether *Vaucheria* algae (a) increase sediment strength and (b) increase relative sediment elevation. To this end, a controlled mesocosm setup (simulating intertidal conditions) was designed in which the filaments of a previously grown *Vaucheria* mat could grow through a layer of deposited sediment, to see how this affected sediment strength and elevation. After 0, 2, 4 and 10 weeks, biomass (chlorophyll-a content), relative elevation of the sediment surface (subsidence rate, sediment water content) and sediment strength were measured. Thin slices of this sediment were then compressively deformed and the degree of deformation was quantified as a measure inversely related to sediment strength. The effect of algal growth on sediment strength and relative elevation was determined by comparing with control sediment that had been shaded to prevent algal growth.

2.2.2. Mesocosm Setup to Accommodate Algal Mats and Deposited Sediment

Experiment 2 was designed in such a way that a large number of treatments/replicates could be used, while using limited mesocosm space. To this end, the setup of Experiment 2 (Figure 3) consisted of a large number of plastic syringes (inner diameter 29.2 mm) with cut-off tips, mounted with the open side upwards in a supporting frame that fitted into the upper tidal mesocosm tank of a two-tank setup similar to that of Experiment 1 (Figure 2). Further details are given in the Supporting Information S1. Each of these syringes would accommodate a small patch of *Vaucheria* mat on top of which a layer of sediment would be deposited (as explained in the next section). For the control treatments, in which algal growth was prevented, the light was blocked out by mounting black plastic cups over these syringes. To correct for the effect of placing these

shading cups, similar but transparent cups were mounted over the other half of the syringes, such that light was not blocked out there and the algae could grow well. Shading and non-shading cups were randomly distributed across the frame. At the onset of the experiment, the experimental frame was placed in the upper tank of a mesocosm setup similar to that of Experiment 1. Water salinity fluctuated between 12–14 PSU, syringes were fully submerged during high water and fully emerged during low water (2 hr high, 10 hr low water) and nutrients were added in the same way as during the preparatory phase of Experiment

1. The experimental setup was continuously illuminated without a day-night cycle, with a light intensity (LI-COR LI-250 Light Meter, 10 measurements just above the shading cups) of (mean \pm standard error) $268 \pm 18 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The mesocosm was placed in a climate room with constant temperature of 18°C .

2.2.3. Preparation of Algal Mats and Deposited Sediment and Start of the Experiment

Vaucheria algal mats were cultivated in a tidal mesocosm prior to the onset of the experiment, as explained in detail in the Supporting Information S1. Once thick felt-like algal mats had developed after 10.5 weeks, discs of 30 mm in diameter were cut out of the mats and the underlying sediment substratum. These basal algal layers were placed in the syringes and the algal filaments were gently flattened to create a smooth surface. Each syringe piston was adjusted in height such that the top of each basal algal layer was at 3 mL (4.4 mm) below the syringe edge. Very poorly consolidated sediment (“fluid mud”) was collected from the field, defaunated and deposited on top of the *Vaucheria* mats to fill up the upper 3 mL in each syringe (as explained in more detail in the Supporting Information S1). This is the onset of Experiment 2. The syringes meant for the first measurement timestep (t_0) were sampled directly at the start of Experiment 2. One set of nine syringes was used to account for both “algal” and “control” samples at t_0 , because there was no physical difference in sediment properties between the treatments at the onset of Experiment 2. With the remaining syringes and shading cups placed in the mesocosm, Experiment 2 was run for 10 weeks. One third of the syringes in the frame was “harvested” for analysis after 2 weeks (t_1), one third after 4 weeks (t_2) and one third after 10 weeks (t_3), as explained in the next section.

2.2.4. Quantifying the Effect of Algal Growth on Sediment Strength and Elevation

For each subsequent timestep (t_1 , t_2 and t_3), 18 syringes (9 algal, 9 control) were used to quantify water content and chlorophyll-a content. The syringe pistons were pushed upwards and the top 3 mL of each sediment core was cut off and stored in a container. For algal-overgrown sediment cores, the top of the sediment core (i.e., sediment, interwoven by filaments) was estimated after gently flattening the protruding algal filaments; the top of the sediment core was then considered to be slightly below this flattened algal surface, as explained in detail in the Supporting Information S1. The sediment discs were weighed, frozen at -80°C , freeze-dried and weighed again to compute water content, that is,

$$\text{water content} = 100\% \times (m_w - m_d) / m_w \quad (2)$$

with wet sample weight m_w and dry sample weight m_d . The same methodology as in Experiment 1 was followed to quantify the chlorophyll-a content of these sediment discs.

At each harvest, a different set of syringes (9 for algal and 9 for control treatment at t_{1-3} , 9 for the identical algal/control treatment at t_0) was used to quantify the effect of algal growth on sediment strength, by measuring how much sediment deformed when it was compressed. Given the destructive nature of this test, different samples had to be used than the ones used to quantify biomass and water content. To cut off the upper 3 mL sediment discs, the same method was followed as for the syringes used to quantify chlorophyll-a and water content. However, for the current syringes, the height difference between the top of the sediment core and the syringe edge was also measured, to quantify the change in sediment surface elevation since the onset (t_0) of Experiment 2 (see Supporting Information S2.4 in Supporting Information S1 for details). Since the t_0 measurements were performed almost directly after the 3 mL layer of fluid mud was deposited, the sampled sediment discs of t_0 practically had the same physical properties as the fluid mud before it was exposed to experimental treatment. Each sediment disc was put on a “test surface”, consisting of a sheet of plasticized millimeter-paper placed on a table. The sediment disc was compressed by applying incrementally increasing weights (first 0 kg, secondly 1.67 kg, thirdly 3.37 kg, fourthly 5.77 kg). Further details are given in the Supporting Information S1. Photos were made in topview, before and after each “load step” to quantify the deformation of each sediment disc. In MATLAB (Mathworks, Inc.), these photos were converted to color intensity matrices. The red color channel was used to distinguish the sediment disc from the surrounding test surface. A median filter (3×3 pixels) was used to remove noise. The pixels classified as sediment disc were counted to calculate the surface area (in top view) of each disc. The surface area at each load step was divided by the surface area of the unloaded disc, to obtain a deformation ratio (i.e., unloaded

discs had a deformation ratio of 1). Only the deformation ratio at the final load step (5.77 kg) was used for statistical analyses (discussed hereafter).

2.2.5. Statistically Testing the Effect of Algal Growth on Sediment Strength and Elevation

At each harvest (t_0 – t_3), four variables were measured: water content, surface elevation change, chlorophyll-a content and sediment deformation ratio. Each harvest had 9 replicates per treatment (algal, control). To test whether the two factors, algal growth and time until harvest, had a significant influence on either of the four variables, all data (per variable separately) were grouped by *Vaucheria* treatment and by time. Homogeneity of variance across these 4×2 groups was tested (Levene). For each variable separately, a linear model with interactions was fit through the data (sorted per group). Normality of the residuals of the linear model was tested (Shapiro-Wilk). For the deformation ratio, the data was neither homoscedastic nor normally distributed. The variance appeared largest for intermediate values of the deformation ratio, suggesting that there was a physical upper and lower bound to the deformation ratio. Therefore, the deformation ratios (x) were normalized to obtain proportion values y , that is,

$$y = (x - x_{\min}) / (x_{\max} - x_{\min}), \quad (3)$$

where x_{\min} and x_{\max} were the minimum and maximum deformation ratios encountered in the entire dataset. An arcsine-transformation (e.g., Crawley, 2015) was then applied to the proportion data y , that is,

$$z = \arcsin(y^{1/2}) \quad (4)$$

to satisfy homoscedasticity and normality. For the elevation change data, the t_0 measurements were not included because these were (by default) chosen to be zero. Of the remaining data set, 3 data points were classified as outliers (further than 5 times the standard error away from the mean) and were removed; after which transformation (Equations 3 and 4) were applied. For the water content data, the data from t_0 was included but duplicate datapoints (resulting from using the same syringes for algal and control treatments at t_0) were discarded; the remaining data set was then log-transformed, according to Equation 1. For these three variables (deformation ratio, elevation change, water content), a two-way ANOVA was applied to the linear model of the transformed (homoscedastic and normal) data. A Tukey HSD post-hoc test (95% family-wise confidence level) was applied to the ANOVA results to see which group means were significantly different. For the chlorophyll-a data, the duplicate datapoints at t_0 (i.e., identical values for algal and control treatment) were discarded. As no suitable data transformation could be found to obtain normally distributed and homoscedastic data, a non-parametric test (Kruskal-Wallis rank sum test) was performed, with the combination of time and *Vaucheria* treatment considered as the only factor. Post-hoc pairwise comparisons were done using Dunn's test with Bonferroni correction and a 5% significance level.

3. Results

3.1. Experiment 1: Effect of Sediment Topographic Relief on Algal Growth

We found that *Vaucheria* grew better on sediment with raised topographic relief (hummocks) than on sediment without relief (flat surfaces) or with lowered relief (hollows) (Figure 4). Visually, hummocks were covered in a denser and more healthy-looking, green and felt-like algal mat (Figure 4g) compared to sparser and more patchy cover on flat and hollow surfaces (Figures 4e and 4f). On flat and hollow sediment surfaces, algal cover on the slightly elevated outer rim (against the PVC tube) was typically denser than in the lower-lying center of the pot surface. Positive controls were visually comparable to the hummocks (Figure 4h). These observations were confirmed quantitatively, that is, sedimentary relief significantly affected chlorophyll-a density (ANOVA, $p < 0.001$) and log-transformed organic carbon density (ANOVA, $p < 0.01$). The chlorophyll-a density (Figure 4i) on hollow surfaces (mean \pm standard error: 1.26 ± 0.06 g/m²) was significantly lower (Tukey HSD, $p < 0.01$) than on hummocky (1.74 ± 0.11 g/m²) and control surfaces (1.76 ± 0.12 g/m²). Chlorophyll-a density on flat surfaces (1.25 ± 0.05 g/m²) was significantly lower ($p < 0.01$) than on hummocky and control surfaces. The other pairwise differences were not found to be statistically different (Tukey HSD, $p > 0.05$), including the difference between hummock and control, which showed that algal growth conditions in the experimental setup were sufficiently good. The measured organic

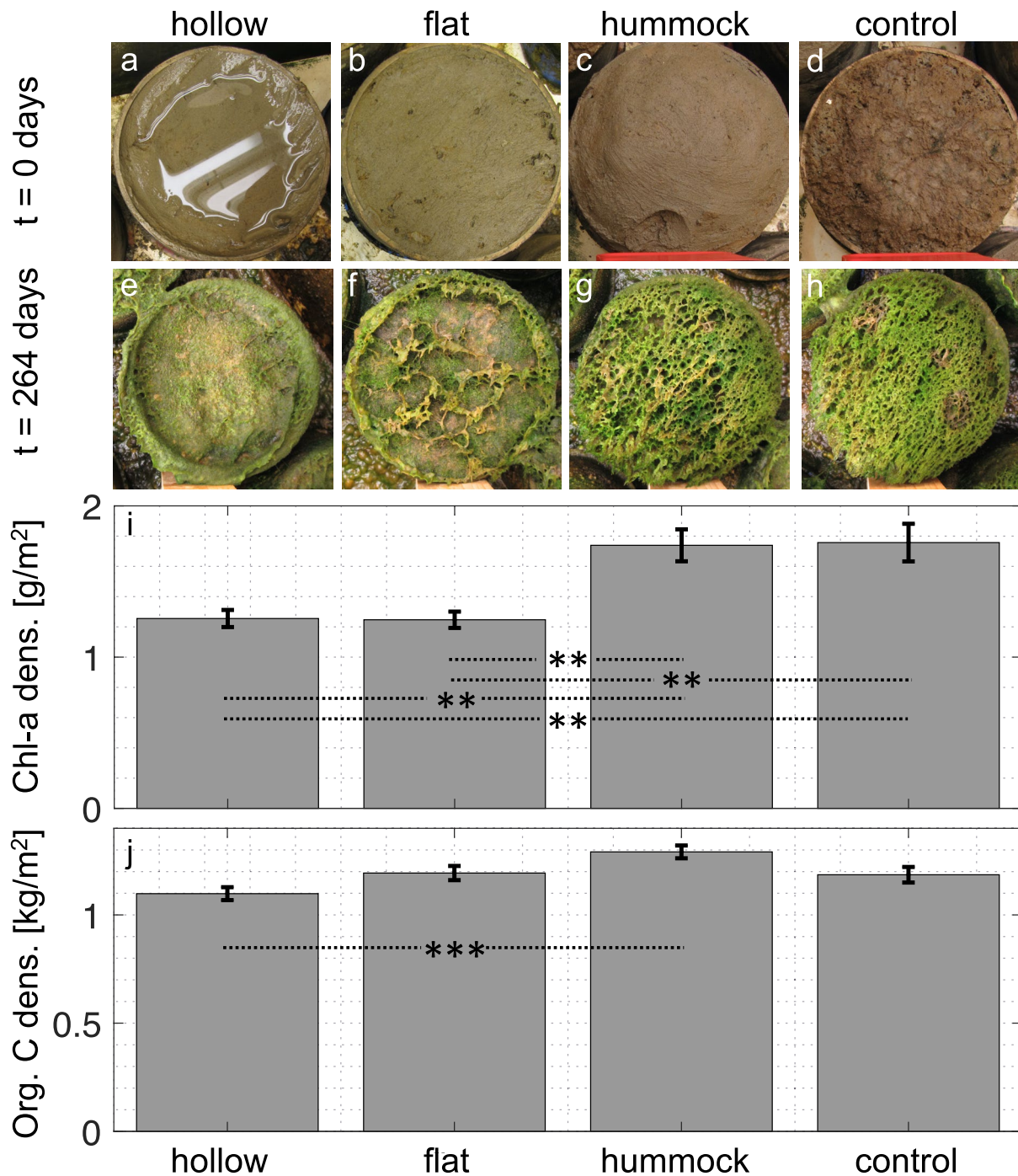


Figure 4. The effect of sediment surface topography on algal (*Vaucheria*) growth (a–d) Examples of the sedimentary surface per “sediment pot”, at the start of the experiment. Color of the hummock sediment appears different from flat/hollow; this is due to light refraction and/or the photo’s white balance. Hollows/flat/hummock treatments initially consisted of the same type of sediment. Control was similar to hummock but initially had *Vaucheria* filaments present below the sediment surface, to test if experiment growth conditions were sufficient (e–h) Examples of the sedimentary surface at the end of the experiment, that is, after ~8.5 months of algal growth. Quantitative test results are shown of the effect of surface topography on chlorophyll-a density (i) and organic carbon density (j), both after 264 days, sampled in the upper ca. 5 cm of each sediment pot (10 replicates per treatment). Mean values \pm standard errors shown; *p*-values of Tukey HSD pairwise comparisons indicated: ***p* < 0.01; ****p* < 0.001. No pairwise comparison indicated: *p* > 0.05.

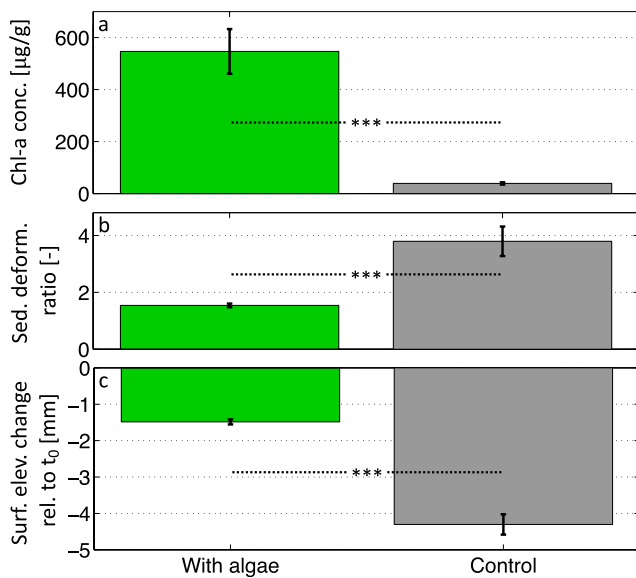


Figure 5. The effect of *Vaucheria* on sediment strength and elevation, at the end of the experiment, that is, after 10 weeks of algal growth. Mean \pm standard errors are shown, both for sediment where algal growth was promoted (illuminated sediment) and control sediment, where algal growth was inhibited (shaded sediment). (a) Chlorophyll-a concentration (as measure of algal growth), (b) sediment deformation ratio (inversely proportional to sediment strength, and (c) sediment surface elevation change (for algal-covered discs, the protruding algal filaments were gently flattened; the “sediment surface” was then considered to be slightly below this flattened algal surface) relative to the start of the experiment. For all variables, the differences between algal-colonized and control sediment are statistically significant (Tukey HSD, $p < 0.001$). For full set of data, see Figure 6, and for full statistical analysis, see Table S1 in Supporting Information S1.

carbon density (Figure 4j) was $1098 \pm 30 \text{ g/m}^2$ for hollow, $1193 \pm 33 \text{ g/m}^2$ for flat, $1291 \pm 30 \text{ g/m}^2$ for hummocky and $1186 \pm 36 \text{ g/m}^2$ for control surfaces. Only the difference in organic carbon density between hummocks and hollows was found to be statistically significant (Tukey HSD, $p < 0.001$). All three measures, that is, visual, chlorophyll-a and organic carbon, are in line with the hypothesis that elevated relief improves the growth conditions of *Vaucheria* mats.

3.2. Experiment 2: Effect of Algal Growth on Sediment Strength

Algal growth was found to significantly increase sediment strength (Figure 5). After 10 weeks, sediment colonized by *Vaucheria* was noticeably less deformable than shaded control sediment where algal growth had been prevented. Visually, sediment discs colonized by algae appeared to be rather coherent when load was applied, apart from the expulsion of some water (Figure S3a and b in Supporting Information S1). Shaded sedimentary discs, on the other hand, already started falling apart when they were placed on the test surface (Figure S3c in Supporting Information S1) and strongly deformed upon compression (Figure S3d in Supporting Information S1). Quantitative analyses confirmed these observations. After 10 weeks of cultivation, the chlorophyll-a concentration in algal-colonized sediment had increased to $546.9 \pm 86.0 \text{ µg/g}$ (mean \pm standard error), compared to $39.0 \pm 4.5 \text{ µg/g}$ in control sediment (Figure 5a). Algal-colonized sediment had a deformation ratio of 1.54 ± 0.06 , compared to 3.80 ± 0.52 for shaded control sediment (Figure 5b). A difference in relative surface elevation was also noticeable, that is, the surface elevation of algal-colonized substratum had decreased by $1.49 \pm 0.07 \text{ mm}$ compared to the onset of the experiment, whereas the surface elevation of shaded substratum had decreased $4.30 \pm 0.28 \text{ mm}$. Two-way ANOVA's indicated that the two factors, time and *Vaucheria* treatment, interacted significantly (deformation ratio: $df = 3$, F -value = 5.3, $p < 0.01$; elevation change: $df = 2$, F -value = 17.8, $p < 0.001$; water content: $df = 2$, F -value = 32.4, $p < 0.001$). In the next section, the temporal development of

algal growth and its effects on sediment strength, relative elevation and water content will therefore be treated in more detail. For now, these results show that colonization by *Vaucheria* algae significantly increases sediment strength.

3.3. Experiment 2: Effect of Sediment Strength and Algal Growth on Topographic Relief

Algal colonization, sediment strength and topographic relief are closely interacting. This becomes apparent when considering how sedimentary properties changed over the first 4 weeks of the experiment. In the first 2 weeks, significant (Table S1 in Supporting Information S1) algal growth was measured in non-shaded sediment but not in shaded control sediment (Figure 6a). Rapid consolidation (Figure 6c) and an increase in sediment strength (Figure 6b) were measured both for algal-colonized and control sediments and the water content of control sediment dropped significantly (Figure 6d). Although sediment properties were not found to change with statistically significant magnitude (Table S1 in Supporting Information S1) between 2 and 4 weeks, the algal-covered substratum had subsided significantly less than control sediment after 4 weeks. Thus, in the first 4 weeks of the experiment, shaded control sediments rapidly subsided and were strengthened due to self-weight consolidation, whereas sediment strengthening of *Vaucheria*-colonized sediment resulted from the binding force of algal filaments. As these algal filaments limited sediment subsidence, after 4 weeks the algal-covered sediment had similar strength as control sediment, but a higher relative surface elevation.

Whereas the effect of algal growth on sediment strength and topographic relief remained rather subtle during the first 4 weeks of Experiment 2, it became much more apparent after these 4 weeks. A thick felt-like

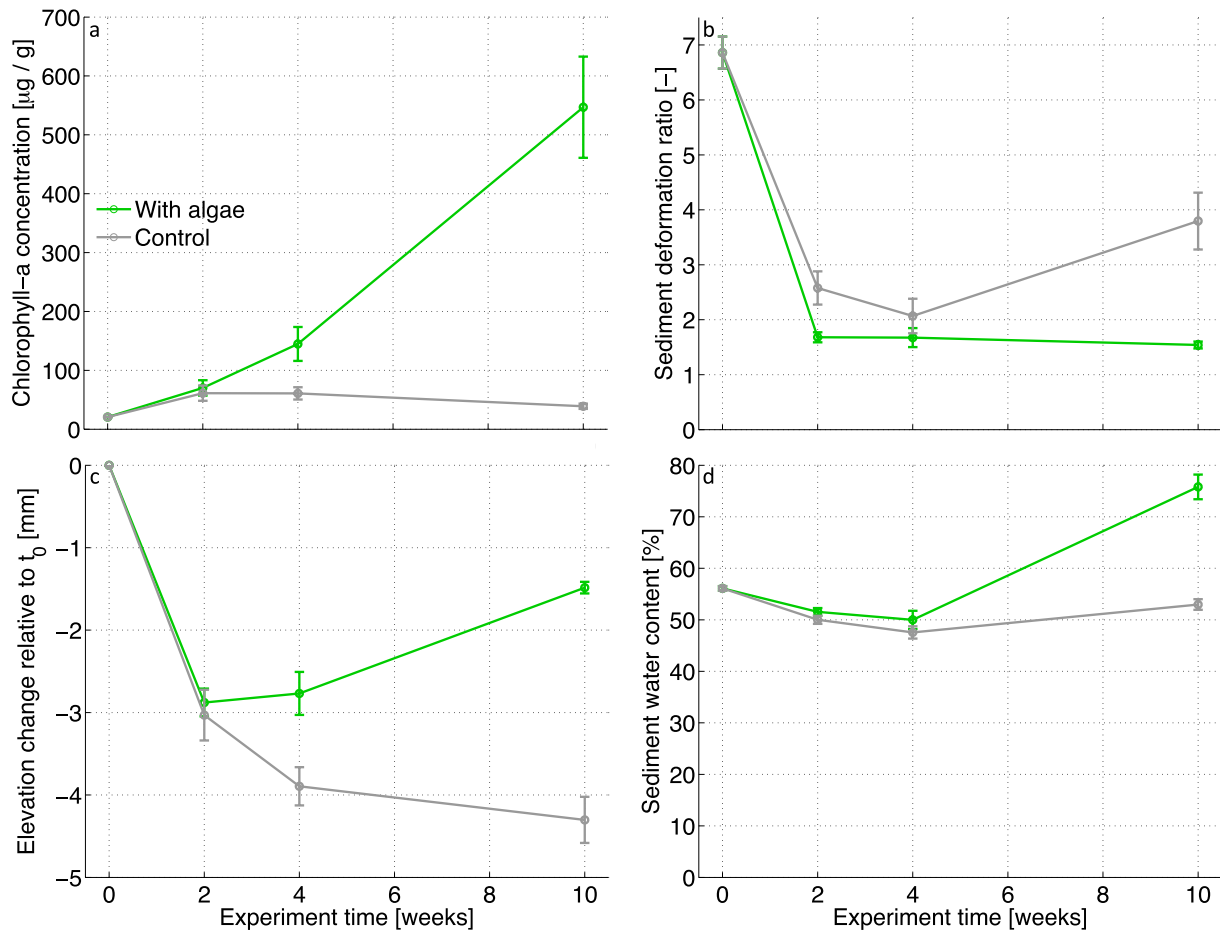


Figure 6. Changes in sediment variables. (a) Chlorophyll-a concentration, (b) sediment deformability (inversely related to sediment strength), (c) surface elevation change relative to the start of the experiment and (d) water content in the sediment, after 0, 2, 4 and 10 weeks. Mean values \pm standard errors are shown. Note that, as sediment could not be reused after analysis, the measurements after 0, 2, 4 and 10 weeks were all performed on different sets of samples. The statistical significance of the pairwise comparisons between group means is given in the Table S1 in Supporting Information S1.

algal mat had formed after 10 weeks (Figure 6a), which had a high water content (Figure 6d) and lead to an increase in surface elevation (Figure 6c). Algal-covered sediment had already reached its maximal resistance to sediment deformation earlier on (Figure 6b). However, shaded control sediment continued to subside, which caused a stagnant layer of water to remain in the syringe, on top of the sediment. Control sediment hence became saturated with water, which counteracted the previously strengthening effect of consolidation. Thus, the interactions between algal growth, sediment strength and substratum relief were found to result in strongly contrasting states, characterized either by mat accretion and biotic sediment armoring, or by waterlogging and increased sediment deformability.

4. Discussion

Biogeomorphic feedbacks originating from the interaction between physical and biological processes play an important role in shaping coastal wetlands. Whereas the landscape-shaping importance of plant-induced feedbacks is widely acknowledged, these plants require stable and well-drained sedimentary substrata to become established on tidal flats in the first place. In the field, plant seedlings seem to establish in high densities on elevated sedimentary ridges covered by algal mats composed of the filamentous species *Vaucheria* (Figure 1). However, the formation of such bedforms and the role of algae therein remains poorly understood. Our controlled mesocosm experiments revealed that *Vaucheria* induces a biogeomorphic feedback loop. This feedback cycle (Figure 7) consists of (a) improved algal growth on elevated sedimentary surfaces, compared to flat or depressed surfaces, (b) sediment binding by algal filaments, leading to increased

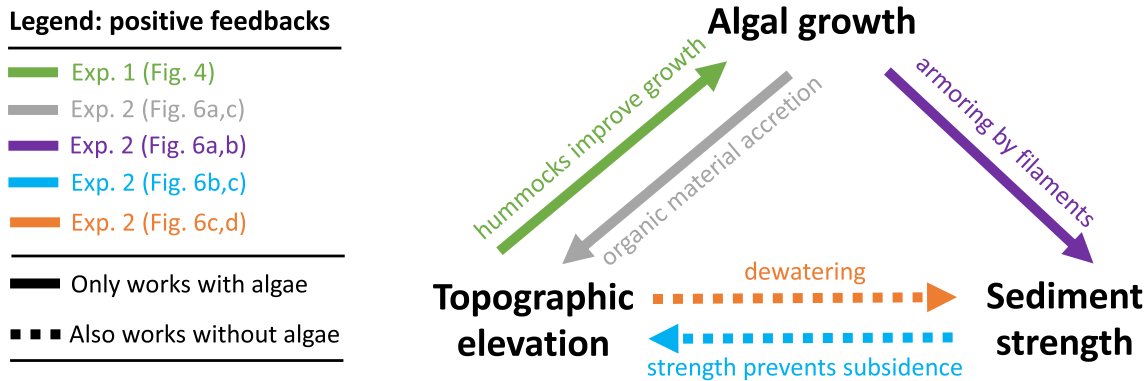


Figure 7. Overview of the algal-induced, biogeomorphic feedback loops found in our two experiments. Each arrow indicates a positive (reinforcing) interaction between algal growth, sediment strength and topographic elevation. Arrow colors indicate the Experiment (1 or 2) from which the interaction can be concluded and the associated figure in this study. Solid lines indicate interactions that are induced by the presence of *Vaucheria* algae; dashed lines indicate interactions that can also take place when algae are absent.

resistance to deformation, and (c) vertical mat build-up in combination with reduced subsidence of biotically strengthened soil, causing algal-covered substratum to have higher relative elevation than shaded control substratum, which in turn improves algal growth and closes the feedback loop. Our study thus shows that *Vaucheria* plays an active role in shaping elevated, algal-covered ridges with high sediment strength on tidal flats. Previous studies have shown how raised bedforms and increased sediment stability facilitate seedling establishment. As our field observations suggest (Figure 1), sediment-stabilizing organisms like *Vaucheria* might thus play a pioneering role in the biogeomorphic development of (vegetated) coastal ecosystems by actively forming stabilized and well-drained substrata.

4.1. Elevated Topographic Relief Enhances Algal Growth

Our results indicate that *Vaucheria* grows better on raised sedimentary relief. In the field, these algal mats typically only grow on elevated hummocks or ridges and not on flat or lowered topographic surfaces, despite the global presence of algal spores (van de Vijssel et al., 2020). Although this patterning could result from random hydrodynamic disturbances of the algal mat (e.g., Noffke, 1999), our findings support the idea that sediment stabilizing biota actively promote ridge formation to improve their own growth conditions (e.g., Bouma et al., 2005; Fivash et al., 2020; Weerman et al., 2010). Previous studies have shown that pore space occupation by water in poorly drained sediments limits soil oxygenation and hence hinders seedling establishment (Fivash et al., 2020, 2021; Lawrence et al., 2018; Mendelssohn & Seneca, 1980; Mossman et al., 2020; Xie et al., 2019). Enhanced drainage and oxygenation of hummock sediments therefore seems a possible explanation for the enhanced *Vaucheria* growth that we measured on hummocks, although this requires more study. As *Vaucheria* does not produce large amounts of EPS, it is not likely that EPS dissolution in waterlogged hollows—which can explain the absence of microbial biofilms in hollows (e.g., Blanchard et al., 2000; Paterson et al., 2000; Weerman et al., 2010) – plays a role in *Vaucheria* patterning. The positive effect of topographic relief on algal growth that we found in our experiment is expected to be even stronger in the field, because (a) our setup does not account for the higher shear stresses in hollows or channels (e.g., Temmerman et al., 2007; Weerman et al., 2010; Williams et al., 2008), (b) hollows or channels in the field can be significantly deeper than in our experimental setup (e.g., Carling et al., 2009; Gouleau et al., 2000), and (c) the stagnant water in our experimental hollows gradually disappeared through infiltration during the low water phase. Nevertheless, we found a significant effect on algal growth which emphasizes the importance of hummock formation as a biogeomorphic pioneering strategy for many sediment-stabilizing organisms in coastal wetlands.

4.2. Algal Growth Enhances Sediment Strength and Elevated Topographic Relief

Our experiments clearly show that colonization by *Vaucheria* leads to increased resistance to sediment deformation and gives the substratum a higher relative elevation than non-colonized sediment. Resistance

to deformation is similar to penetration resistance, which has been used as a proxy for sediment compaction and erosion resistance (van de Vijssel et al., 2020; Williams et al., 2008), here referred to as “sediment strength”. *Vaucheria* raises the topographic relief relative to shaded control sediment by vertically building a thick organic mat. In the field, *Vaucheria* also enhances sediment accretion (Black, 1933; Gallagher & Humm, 1981; Skowroński et al., 1998; Webber, 1967), which will further increase the elevation difference between mat-covered and bare substrata. Raised topography, in turn, facilitates algal growth, closing the feedback loop (Figure 7). Our results furthermore show that *Vaucheria* filaments provide internal sediment coherence, hence preventing soil subsidence as well as compressive deformation, which are measures of self-weight consolidation (e.g., Zhou et al., 2016) and soil slumping (e.g., Mariotti et al., 2016; Murray & Paola, 2003), respectively. Hence, despite the simple filamentous architecture of *Vaucheria*, its biogeomorphic properties are more similar to root binding effect of plants (e.g., Mariotti et al., 2016; Murray & Paola, 2003; Pestrone, 1969) rather than the surficial “skin layer protection” (e.g., de Brouwer et al., 2000; Le Hir et al., 2007) provided by microbial biofilms. As soil strength highly affects landscape development (e.g., Garofalo, 1980; Perron et al., 2008, 2012; van de Vijssel, 2021), our findings highlight the biogeomorphic importance of benthic algae like *Vaucheria*.

4.3. Abiotic Feedback between Sediment Strength and Elevation

Apart from the biogeomorphic feedback cycle highlighted in our study, the experimental results also point at an additional, abiotic feedback loop between water drainage and sediment stability (Figure 7). In our experiments, the sediment rapidly consolidates in the absence of algal cover, which leads to the expulsion of pore water (e.g., Zhou et al., 2016) and hence an increase in soil strength. However, when soil subsidence continues too long in our experimental setup, water gets trapped below the edge of the sediment-containing syringe edge, such that the sediment becomes saturated with water and loses strength. Although this process is in part a result of the experimental design, it illustrates the positive feedback between drainage, sediment stability and relative sediment elevation that has been well-known from the field as well (e.g., Blanchard et al., 2000; Gouleau et al., 2000; Williams et al., 2008). Our findings hence show that the geomorphic and biogeomorphic feedback loops are very similar, but that biostabilization of elevated topography amplifies these feedbacks, similar to what was found for microbial biofilms (e.g., Blanchard et al., 2000; Lanuru et al., 2007; Williams et al., 2008; Weerman et al., 2010). Moreover, our study implies that *Vaucheria* widens the range of environmental conditions under which topography-forming feedbacks can be induced, because the sediment-binding effect of *Vaucheria* filaments allows these feedbacks to be triggered even when strong topographic diffusion (e.g., due to poor sediment consolidation) would impede the abiotic feedback cycle (Perron et al., 2009, 2012; van de Vijssel, 2021).

4.4. Self-Organization due to the Algal Feedbacks

Our findings indicate that the same feedback cycle can either have “positive” effects on algal growth, hence creating algal-covered and strengthened sedimentary hummocks, or have “negative effect”, creating bare hollows with weakened soil. In coastal wetlands, the often regularly spaced alternation between biotically-stabilized hummocks/ridges and bare hollows/channels has previously been ascribed to this same two-way action of one and the same biogeomorphic feedback (e.g., Temmerman et al., 2007; van de Vijssel et al., 2020; Weerman et al., 2010). These so-called scale-dependent feedbacks have been shown to give rise to self-organized pattern formation in various ecosystems (e.g., Klausmeier, 1999; Meinhardt, 2003; Rietkerk & van de Koppel, 2008; Tarnita et al., 2017; van de Vijssel, 2021). Self-organization strongly impacts the functioning and resilience of these ecosystems and can give rise to catastrophic state shifts (e.g., Bastiaansen et al., 2018; Liu et al., 2012, Liu, Weerman, et al., 2014; Liu, Herman, et al., 2014; Rietkerk et al., 2002; van de Koppel et al., 2005; Weerman et al., 2010, 2012). It is therefore essential to better understand the self-organization of *Vaucheria*-induced, patterned landscapes (van de Vijssel et al., 2020). A first step could be the development of a mathematical model, for example, in line with the model developed for microbial biofilm patterns (Weerman et al., 2010).

4.5. Algae as Pioneers in Coastal Wetland Development

Windows of opportunity for coastal wetland establishment are often linked to periods of reduced physical disturbance (e.g., Balke et al., 2014) and to the capacity of the key ecosystem species to cope with disturbances (e.g., Balke et al., 2011, 2013; Bouma et al., 2016; Cao et al., 2018; Fivash et al., 2020; Hu et al., 2015). However, our findings imply that biological processes also play an essential part in the windows of opportunity framework, as biota can actively “widen” the windows of opportunity for ecosystem establishment. We found that *Vaucheria* stabilizes the sediment, thereby reducing the intensity of disturbances and possibly facilitating plant establishment (e.g., Balke et al., 2011, 2013; Bouma et al., 2016; Cao et al., 2018). These algae moreover generate an elevated surface on which plant seedlings may grow faster due to better soil drainage and thus enhanced oxygenation (e.g., Fivash et al., 2020). On raised topography, seedlings may moreover be less exposed to hydrodynamic stress (e.g., Temmerman et al., 2007), which reduces the duration and frequency at which seedlings are exposed to disturbances. These properties, in combination with *Vaucheria*'s fast lateral expansion (Van den Neucker et al., 2007) and tolerance to a wide range of salinities (Simons, 1975), makes this algal species a potential ecosystem engineer (e.g., Jones et al., 1994) that can “prepare” the landscape for further ecosystem development. Observations of apparent seedling concentration on algal-covered ridges (Figure 1) and earlier reports of co-existence between *Vaucheria* and marsh plants (e.g., Simons, 1975; Van den Neucker et al., 2007) seem to support this notion, but quantitative measurements are required to confirm this idea. Artificially triggering the algal-induced biogeomorphic feedbacks identified in our study, e.g., by creating topographic relief to enhance soil drainage and, with that, increase sediment strength (Blanchard et al., 2000; Gouleau et al., 2000; Williams et al., 2008) and promote soil oxygenation (Fivash et al., 2020, 2021; Xie et al., 2019), could help to increase the success of wetland restoration projects (e.g., Lawrence et al., 2018; Mossman et al., 2012; Oosterlee et al., 2019). The inoculation or transplantation of *Vaucheria* patches on bare tidal flat could also be considered, but this possibility should be preceded by careful analysis of the potential negative effects of the introduction of a new (possibly invasive) species to the wetland ecosystem. Ultimately, this study might contribute to a nature-based protection of our densely populated coastal lowlands against global change (e.g., Arkema et al., 2013; Barbier et al., 2008; Temmerman et al., 2013; Zhu et al., 2020).

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All raw and processed data supporting this study are available at <https://doi.org/10.25850/nioz/7b.b.ub>.

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