



Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species

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ABSTRACT

There is a growing recognition of the important role of scale-dependent feedback for biogeomorphological landscape formation, where organisms locally improve survival and growth but at the same time negatively affect organisms at larger distance. However, little is known on how scale-dependent bio-geomorphic feedback is influenced by organism traits in combination with abiotic forcing. This was studied by measuring in a flume, the flow patterns around patches of three contrasting marsh species (*Spartina anglica*, *Puccinellia maritima* and *Salicornia procumbens*), using the flow acceleration around vegetation patches and deceleration within vegetation patches as quantitative proxy for the negative and positive feedback to the vegetation performance. The importance of external forcing was assessed by comparing three realistic current velocities: 0.1, 0.2 and 0.3 m s⁻¹. Our results showed that the dense clonal growth of stiff *Spartina anglica* shoots caused strongest flow deviations, irrespective of the applied current velocity. In contrast, the more sparsely growing, shorter stiff shoots of *Salicornia procumbens* induced much less flow deviation, allowing more water to pass through and over the vegetation canopy. The dense but highly flexible shoots of *Puccinellia maritima* caused strong flow deviations at low velocities, which diminished at higher velocities due to bending of the vegetation. Overall, these hydrodynamic results demonstrate that plant species traits interact with environmental conditions in creating scale-dependent feedbacks explaining why the effects of vegetation on landscape formation in saltmarshes are species specific.

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1. Introduction

In recent years it has become increasingly clear that two-way interactions between organisms and landscape-forming processes, also called bio-geomorphological (and sometimes ecohydrological) feedback, play a key role in the evolution of many landscapes (Corenblit et al., 2008; Murray et al., 2008; Reinhardt et al., 2010). These feedbacks imply that organisms modify the landscape, which in turn determines survival and growth of the organisms. Bio-geomorphic feedback processes are generally caused by so-called autogenic ecosystem engineers (cf. Jones et al., 1994), which are organisms that modify the abiotic environment via their physical structures (Jones et al., 1994, 1997; Reichman and Seabloom, 2002). The bio-geomorphic feedback between plants, water or air flow, and sediment transport has been identified as a major determinant of the larger scale landscape evolution in tidal marsh landscapes (D'Alpaos et al., 2007; Kirwan and Murray, 2007; Temmerman et al., 2007), alluvial floodplain rivers (Murray and Paola, 2003; Gurnell and Petts, 2006; Tal and Paola, 2007; Bertoldi et al.,

2009), fluvial hillslopes (Collins et al., 2004; Istanbuluoglu and Bras, 2005), and eolian dune landscapes (i.e., involving flow of air; Baas and Nield, 2007). In all these systems, plants exert friction to the flow, especially via their above-ground biomass which we refer to as shoots, thereby modifying flow-induced erosion and sedimentation, which feeds back to impact the survival and growth of plants.

The effects of ecosystem engineers can be scale dependent (Rietkerk and van de Koppel, 2008), such that locally, bio-geomorphic feedbacks improves the survival and growth of the ecosystem engineer (i.e., local positive feedback), while at a larger spatial scale survival and growth conditions get worse due to the negative effects of a second, inhibiting process (i.e., large-scale negative feedback). In the case of plant-flow-sediment feedbacks, the local positive feedback is achieved through flow reduction and sedimentation within vegetation patches (Bouma et al., 2007; Zong and Nepf, 2010; Vandenbruwaene et al., 2011), which leads there to improved plant growth (Van Wesenbeeck et al., 2008), while the long-distance negative feedback occurs through flow deviation, acceleration and erosion around vegetation patches (Rominger et al., 2010; Vandenbruwaene et al., 2011), leading to reduced plant growth just next to vegetation patches (Van Wesenbeeck et al., 2008). Here, positive and negative feedback effects are driven by

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the same process, modification of water flow and hydrodynamic sediment transport, rather than two separate processes. Therefore, the feedbacks can also be regarded as “distance dependent”. For generality, we maintain the term “scale-dependent”.

Scale-dependent feedbacks are proposed to explain self-organized regular pattern formation in a broad range of ecological communities (Rietkerk and van de Koppel, 2008). For example, scale-dependent bio-geomorphic feedback has been put forward to explain the formation of regular patterns of small hillocks and depressions on tidal flats induced by diatom–sediment interactions (Weerman et al., 2010), while vegetation–flow–sediment feedbacks have been found to form regularly-spaced drainage creeks in estuarine salt marshes (Temmerman et al., 2007), and ridge and slough systems in wetlands (Larsen and Harvey, 2010). Despite the possible generality as a framework for explaining bio-geomorphic interactions and landscape formation, little is known about how scale-dependent feedback (and thus landscape formation) is affected by the combination of organism traits and physical forcing driving landscape formation. These factors might, however, be expected to be highly important, as organism traits are known to affect a species ecosystem engineering capacity (Bouma et al., 2005a; Peralta et al., 2008; Bouma et al., 2010). Moreover, it was recently shown that the linkage between local positive feedbacks and long-distance negative feedbacks can be strongly dependent on the vegetation density in combination with physical forcing (Bouma et al., 2009).

Intertidal plant species offer a suitable model system to explore experimentally how organism traits and physical forcing affect scale-dependent feedbacks. Many saltmarsh species are well recognized ecosystem engineers in that their shoots interact with hydrodynamics and hence alter sediment dynamics (D'Alpaos et al., 2007; Kirwan and Murray, 2007; Temmerman et al., 2007; Mudd et al., 2010). Because of these engineering properties, scale-dependent feedback can be studied in a flume, using flow deceleration within the vegetation as proxy for the short-range positive feedback and flow acceleration around the vegetation as proxy for the long-distance negative feedback (Van Wesenbeeck et al., 2008; Vandenbruwaene et al., 2011). Also the large body of research on flow and sedimentation/scouring patterns around non-permeable flow-blocking structures in different arrangements (e.g., Melville, 1997; Melville and Chiew, 1999; Sumer et al., 2001; Oliveto and Hager, 2002; Sumer and Fredsoe, 2002; Ataie-Ashtiani and Beheshti, 2006) underlines the feasibility of studying scale-dependent feedback on porous vegetation patches in a flume.

Within NW Europe, three very different species dominate the pioneer vegetation that colonizes bare tidal flats: the clonally growing perennial species *Spartina anglica*, and *Puccinellia maritima*, and the annual *Salicornia procumbens*. The species differ markedly in their characteristics. While the stiff grass *Spartina* and the flexible *Puccinellia* generate dense stands, the stiff forb *Salicornia* creates a sparse vegetation of spaced-out individuals. It has been well recognized that dense patches of *Spartina* and *Puccinellia* can accumulate sediment (Castellanos et al., 1994; Sanchez et al., 2001; Langlois et al., 2003; van Hulzen et al., 2007). Recent experiments showed that *Spartina* stands indeed interact

in a scale-dependent way with water flow and sedimentation processes (Van Wesenbeeck et al., 2008; Bouma et al., 2009; Vandenbruwaene et al., 2011). For the two other pioneer species, this has not been studied yet, limiting our understanding of how species traits affect scale-dependent feedback between biology and geomorphology.

To elucidate the scale-dependent interaction between organism characteristics and physical processes, the flow patterns around 4 m-wide patches of three contrasting pioneer species, i.e. *Spartina anglica*, *Puccinellia maritima*, and *Salicornia procumbens*, were measured in a 16 m-wide flume. Flow deceleration within the vegetation and acceleration around the vegetation are used as proxies for short-range positive and long-distance negative feedbacks, respectively, as flow deceleration promotes sediment accretion and thereby plant survival and growth and flow acceleration enhances the risk of erosion by scouring and thereby reduces plant survival and growth (Van Wesenbeeck et al., 2008; Bouma et al., 2009). The importance of external forcing was assessed by subjecting the vegetation to three realistic current velocities. To illustrate the effect of shifting from emergence to submergence, the water depth was selected in such way that the flexible species (*Puccinellia*) could both be emergent and submerged based on its bending behavior, and the stiff species are just submerged (*Salicornia*) vs. clearly emergent (*Spartina*) (Table 1). Summarizing, the overall set-up was designed to highlight the effect of the organism traits shoot stiffness (stiff vs. flexible), vegetation density (dense vs. sparse) and stem height (submerged vs. emergent) on the strength of scale-dependent feedbacks and its dependence on hydrodynamic forcing.

2. Materials and methods

2.1. Plant material

In our study, three plant species that can be found as the dominant pioneer species in NW European saltmarshes (Fig. 1) were compared: the gramineae *Spartina anglica* Hubbard and *Puccinellia maritima* (Hudson) Parl, and the chenopodiaceae *Salicornia procumbens* (L.). Interestingly, these three species differ strongly in their growth strategies (Table 1): *Spartina anglica* is a densely-growing, tussock-forming clonal species with stiff shoots; *Puccinellia maritima* is a densely-growing, tussock-forming clonal species with flexible shoots; and *Salicornia procumbens* is an annual that forms more sparse vegetation patches consisting of stiff shoots. For simplicity, vegetation patches of *Salicornia* are also referred to as tussocks. As technical constraints (see Section 2.2) forced us to work with a single water depth, we selected a water depth that represented situations where the plants interact with the highest currents (Bouma et al., 2005b) and enabled us to illustrate the effect of shifting from emergent to submerged vegetation (Table 1): the stiff and tall *Spartina anglica* was emergent in all experiments, the stiff and much smaller *Salicornia procumbens* was entirely submerged, and the flexible *Puccinellia maritima* varied in submergence depth depending on the applied flow velocity and bending behavior of this vegetation (see Results). These differences in mechanical properties and spacing, in combination with the differences

Table 1
Description of various characteristics of the three vegetation types used in the flume experiment, and how this relates to the water depth used in the current flume experiment.

	<i>Spartina anglica</i>	<i>Salicornia procumbens</i>	<i>Puccinellia maritima</i>
Growth form	Perennial clonal tussocks	Annual sparse patches	Perennial clonal tussocks
Shoots properties	Stiff	Stiff	Flexible
Shoot density (stems m ⁻²)	658 ± 8 (n = 4)	189 ± 21 (n = 2)	6473 ± 3 (n = 2)
Standing biomass (g m ⁻²)	580 ± 49 (n = 4)	181 ± 14 (n = 2)	405 ± 41 (n = 2)
Mean stem height of (cm)	59 ± 1.8 (n = 100)	28 ± 0.3 (n = 150)	32 ± 0.9 (n = 150)
Position in 30 cm flume water	Emergent	Just submerged	Emergent in upright position and submerged when bended

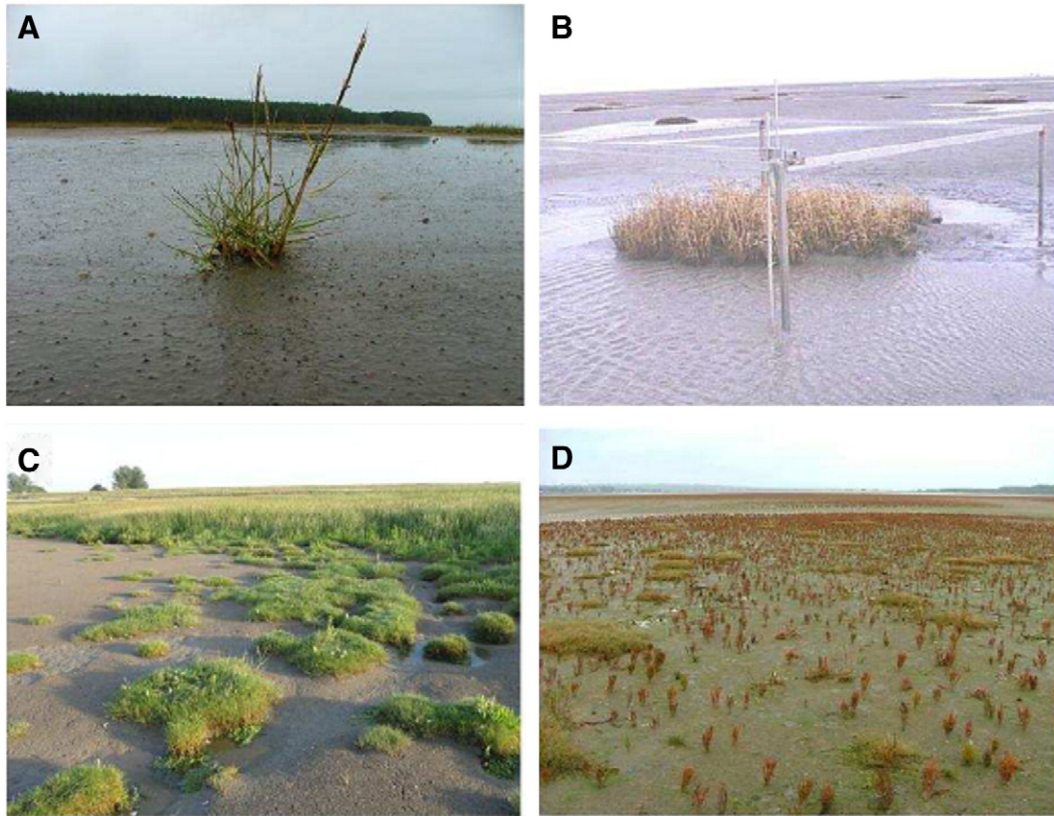


Fig. 1. Pictures of three contrasting pioneer species found in Western Europe: *Spartina anglica* develops from a single seedling (A) into dense clonal tussocks (B), with stiff shoots; *Puccinellia maritima* is a densely growing tussock-forming clonal species (C) with highly flexible shoots; *Salicornia procumbens* is a sparsely growing vegetation with stiff shoots (D). Pictures obtained with courtesy J. van Belzen.

in length and thereby emergence (Table 1) are expected to reveal how organism traits may alter interactions with tidal currents.

It is not always completely clear why the pioneer zone in different areas is dominated by one of these three plant species. In many areas like the Scheldt Estuary (SW-Netherlands) *Spartina* can reach a cover up to 90% in the majority of the low marshes. However, in other areas like the saltmarshes of the back-barrier islands of the Dutch Wadden Sea (N-Netherlands), *Spartina anglica* is nearly absent. This is probably due to a combination of the fact that the species reaches its northern distribution limit and grows less well on the sandier substrate that is available there. As a consequence, at those marshes the pioneer zone is dominated either by *Puccinellia maritima* and/or *Salicornia procumbens*. Similar patterns were observed on the Cefni marsh in Wales (pers. obs. T.J. Bouma) and have been described for the Mt. St. Michel in France, (Langlois et al., 2003).

For our flume experiment, we grew plants from seed in boxes (1 m long × 1 m wide × 0.15 m internal depth) that exactly fitted into holes in the flume bottom and could be lifted by a forklift truck. We combined boxes so that plant patches were 4 m wide (width perpendicular to incoming flow direction) and 2 m long (length parallel to incoming flow direction) (Fig. 2). The boxes were filled to the top with silty sand to provide a stable flat bed during all flume experiments. The sediment was selected because (i) all species will grow on it in natural ecosystems, although it is typically more representative for *Puccinellia maritima* and *Salicornia procumbens* than for *Spartina anglica*, which generally is more dominant on muddy sediments; (ii) previous experiments have shown that all species will grow vigorously and form healthy vegetation on this sediment, and (iii) this sediment type does not cause problems of silt deposition on the flume. Plant growth was optimized by supplying the plants with sufficient slow-release fertilizer and irrigation to take away any potential growth limitations. After the flume measurements, four plant boxes of every species were harvested

to determine the exact plant density and plant dimensions. The standard error on these measurements confirmed our visual observations that all boxes were highly uniform in shoot density, standing biomass and mean stem height (Table 1), due to the fact that plants were carefully grown from seed. The latter implies that shifting individual boxes from location would not have considerable effect on the result, which is important, as the costly nature of this kind of large-scale flume experiment makes it impossible to do true replicates. The vegetation densities used in the experiment fits within the normal densities as observed for *Spartina anglica* on sandy sediments (van Hulzen et al., 2007), and with local field counts for *Salicornia procumbens* (typically around 191 ± 15 ; $n = 15$) and *Puccinellia maritima* (typically between 6000 to 14,000 with an average of 9426 ± 1049 ; $n = 7$).

2.2. Large-scale flume experiments

The experiment was carried out in the so-called 'Vinjé' basin located at Deltares (Delft, The Netherlands; www.deltares.nl). The Vinjé basin is normally in use as a wave basin, but for the purpose of this experiment, it was reconfigured to give unidirectional flow. This flume had a test section 16 m wide × 26 m long × 0.5 m deep, with an elevated bottom of 0.2 m allowing a water depth of 0.3 m around the vegetation (Fig. 2; for details see Vandendbruwaene et al., 2011). The false bottom enabled the boxes with vegetation to be placed level with the floor (Fig. 2B). Within this test section, uniform uni-directional flow could be generated with velocities of 0.1, 0.2 and 0.3 m s⁻¹ by adjusting the discharge of the 6 pumps and setting the height of weirs at the upstream and downstream edge of the basin. The settings of the pumps and weirs were extensively tested before the start of the experiment, to ascertain a reproducible uni-form flow throughout the basin. The selected range of current velocities was based on long-term (several months) high-resolution (4 Hz) field measurements of flow velocity on a mudflat just in front of tidal marsh

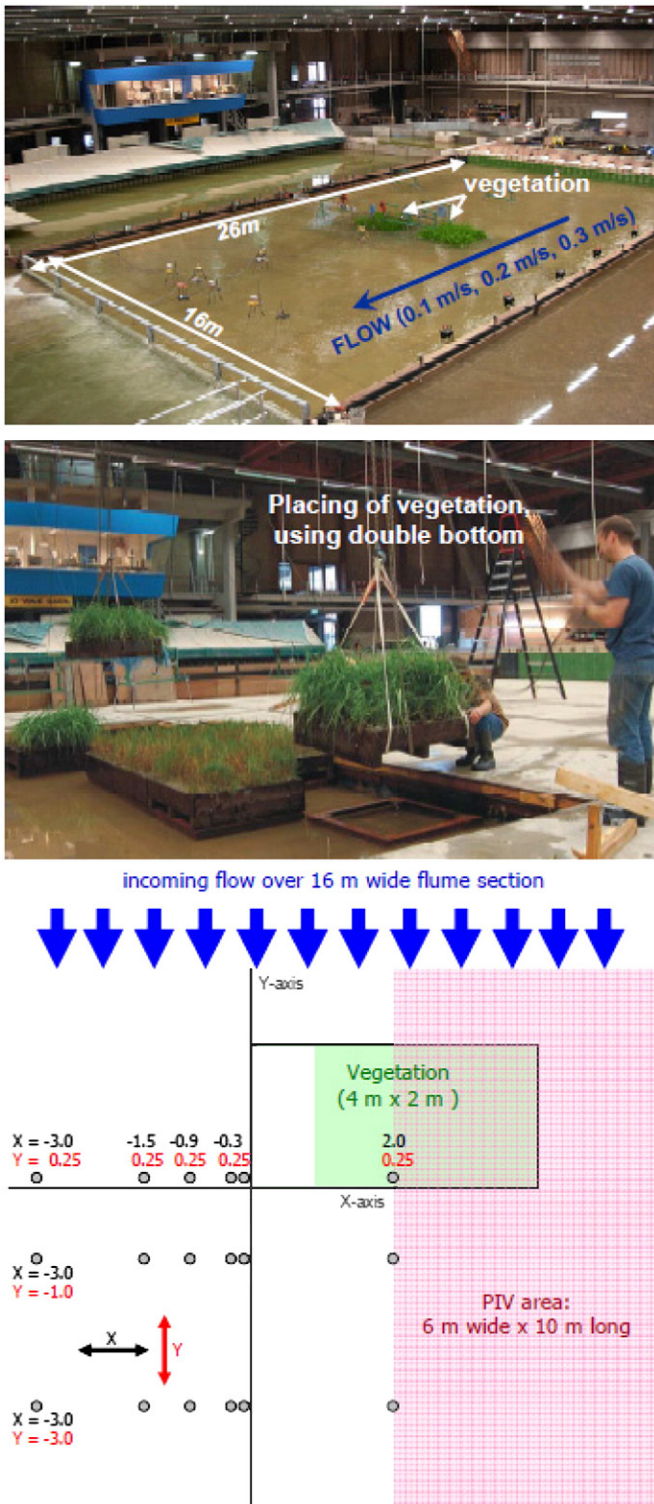


Fig. 2. Schematic representation of our flume measurements, with a picture of the flume in operation (A), a picture showing the placement of the vegetation (B) and a schematic drawing of the measuring lay-out (C). When showing the measuring lay-out, the exact locations of the electromagnetic flow meters (EMF-meters) in the flume are zoomed-in on (grey dots, which can be referred to by X,Y-coordinates in meters). As a result, the diagram only shows part of the total area for which PIV measurements were done.

vegetation in The Netherlands, showing that current velocities were proportional to the tidal amplitude, and could reach velocities up to slightly over 0.30 m s^{-1} (Bouma et al., 2005b). In tidal systems the water depth will vary over time and depend on the local tidal amplitude. However, technical limitations made it impossible to increase the water depth

during the experiments, given the height of the weirs and flume walls and the need for higher pumping capacities. Lowering the water depth was also not possible because of problems with air entering the huge pumps. Given the constraint that we could only use a single water depth, a water depth was selected that represented situations where the plants interact with the fastest currents (Bouma et al., 2005b), and that illustrate the effect of shifting from emergence to submergence (Table 1).

Current velocities and patterns at the water surface were measured using Particle Image Velocimetry measurement (PIV; see Section 2.3), and current velocities *within* the water column were measured with 8 electromagnetic flow meters (EMF-meters) at 0.125 m above the bottom surface, which was found to be representative for the depth-averaged current velocity in the flume (see Vandenbruwaene et al., 2011). To avoid disturbance by the EMF-meters on the PIV images, we assumed that flow around the tussocks was symmetrical, so that the PIV analysis and EMF measurements could be carried out separately on the two sides of the tussock (Fig. 2). After steady flow conditions were reached (i.e., always within 6 min after starting the pumps), we measured the flow during a 12-minute period with a frequency of 25 Hz, in order to obtain a long enough time-series for statistical analyses. Two upstream flow EMF-meters measured the incoming flow velocity as a reference and to check the proper working of the flume, while the other 6 EMF-meters were used to quantify the flow deceleration within the tussock ($X = 2 \text{ m}$; Fig. 2C) and flow acceleration next to the tussock along a cross-sectional transect ($X = -3.0, -1.5, -0.9, -0.3$, and -0.15 m ; Fig. 2C). For the highest incoming velocity (0.3 m s^{-1}), this cross-sectional transect of EMF-meters was deployed at 3 positions relative to the downstream vegetation edge: $Y = 0.25 \text{ m}$ indicates that velocities were measured 25 cm before the downstream end of the vegetation patch; $Y = -1$ and $Y = -3 \text{ m}$ indicate that velocities were measured 1 and 3 m downstream of the vegetation (Fig. 2C). For the other velocities (0.1 and 0.2 m s^{-1}), the cross-sectional transect of EMF-meters was only deployed at $Y = 0.25 \text{ m}$.

As the costly nature of this kind of large-scale flume experiment makes it impossible to do true replicates, we used the 12-minute 25 Hz velocities measurements after steady state flow conditions were reached to do some basic statistics. Analyses for autocorrelations within these velocity measurement showed that measurements taken 10 s apart were uncorrelated. Sub-sampling the whole data series with 10 s intervals allowed us to do an ANOVA on these uncorrelated velocity measurements. As all terms in these ANOVA's were significant, individual points could be compared by Tukey HSD post hoc testing. Doing this for all points showed that on average, differences between two relative flow rates were significant if larger than 0.08%. To maximize readability of the results, we only indicated an error bar of 0.08% to visualize significant differences.

2.3. Particle Image Velocimetry measurements

Particle Image Velocimetry (PIV) measurements were used to measure current velocities at the water surface over a larger spatial scale, by tracking over time the movement of particles floating with the water (for review, see Adrian, 2005 and references therein). A video camera was mounted about 15 m above the inner rectangle of the basin, perpendicular to the floor, to record flow images in an area of approx. $6 \text{ m} \times 10 \text{ m}$ (Fig. 2). The camera (Retiga 1300, monochrome with an 8 mm lens) had an acquisition velocity of 6 frames per second and an image resolution of 1280×1024 pixels, with a grey scale resolution of 12 bits. The camera was connected to a pc with image acquisition and processing software. For each experiment, a sequence of about 400 frames was recorded.

To measure flow with PIV, particles must be added to the water and made visible by providing proper illumination. Based on availability, two types of seeding were used: either low-density polyethylene (LDPE) particles with a diameter of 3 mm, a density of 920 kg m^{-3} and a

milky-white color or dried quinoa flakes that had a diameter of 2 mm and a white color. The particles were scattered over the surface area by three people from the overhead walkways. Illumination was provided by five 1 kW floodlights attached to the wooden sidewalls of the flume, mounted low above the water surface, so that the light was striking over the water surface. An aluminium plate was protruding from below each lamp, in order to avoid glare due to reflection. Two other floodlights were mounted on overhead walkways at about 10 m above the flume, with the light directed upwards to a white screen, providing a fairly even background illumination.

2.4. Particle Image Velocimetry processing

Due to the position of the low floodlights, certain areas at the edge of the PIV images were over-illuminated, causing an uneven background illumination that can interfere with the analysis. Prior to analysis, the raw pictures were therefore pre-processed, to remove these strongly illuminated areas (that were out of the zone of interest for analysis) and enhance the contrast in the remaining part of the image. This results in images with an even dark background and contrasting bright particles in the foreground. Subsequently, images were analyzed with a PIV software-package from La Vision®. The PIV algorithm is based on a two dimensional cross-correlation via fast Fourier transforms (FFT). In this study we chose an interrogation area of 32×32 pixels, with a 50% overlap, resulting in a spatial resolution of about 20×20 cm. To minimize errors in the vector field, all vectors which differed by two times the rms of the neighbors were deleted.

3. Results

Current velocity patterns at the water surface, showed clear differences between species (Fig. 3). Independent of the incoming current velocity, *Spartina* caused a major deviation of the water flow around the vegetation, visible as strongly accelerating flow next to the patch with strong velocity reduction within and behind the patch. This pattern was also supported with current velocity measurements made within the water column, at different distances next to the *Spartina* vegetation. These measurements showed strong flow acceleration next to the patch ($X = -0.9$ to -3 m; values significant larger than 1; Fig. 4 and Table 2), and a virtually blocked flow within ($X = 2$ m) and directly adjacent ($X = -0.15$ and -0.3 m) to the patch (i.e., values significant lower than 1; Fig. 4 and Table 2). Based on the data in Fig. 4, we calculated the scale-dependent feedback strength by taking the difference between the maximum observed relative acceleration adjacent to the tussock and the relative deceleration inside the vegetation. Averaging this scale-dependent feedback strength over the three incoming current velocities (0.1, 0.2 and 0.3 m s^{-1} ; Fig. 4) showed that *Spartina* generates a strong scale-dependent feedback (Fig. 5).

PIV measurements at the water surface, showed that the flow pattern of acceleration alongside the patches and flow blocking within the patches was maintained for a long distance behind the patch (Fig. 3). This pattern was confirmed by current velocity measurements within the water column (Fig. 6), which furthermore showed that the acceleration in current velocity gradually shifted outward (Table 2). That is, the peak velocity adjacent of the patch (i.e., $Y = 0.25$ m) was observed at X is -0.9 to -1.5 m lateral of the *Spartina* patch, whereas for Y is -1 and -3 m downstream, the peak velocity was observed at X is -1.5 m and -3 to -1.5 m, respectively (Fig. 6 and Table 2).

The *Salicornia* patches showed much less flow deviation at the water surface compared to the patches of *Spartina* (Fig. 3). That is, the PIV analyses indicated less acceleration adjacent to the *Salicornia* patches as compared to the *Spartina* patches, while above the *Salicornia* vegetation there is no flow deceleration but even flow acceleration. The latter is caused by the fact that the plants are just submerged (Table 1), so that some water is forced to flow over the vegetation at an increased velocity. Current velocity measurements within the water column showed that

between the submerged *Salicornia* plants ($X = 2$ m) flow indeed did slow down (values significant lower than 1; Fig. 4 and Table 2). However, at a velocity of 0.3 m s^{-1} this reduction was significant less than inside the denser *Spartina* patch whereas at a velocity of 0.1 m s^{-1} the flow reduction was stronger than inside the denser *Spartina* patch (Fig. 4 and Table 2). The clear upward shift of the *Salicornia* velocity curves with increasing externally-imposed velocities (Fig. 4 and Table 2) indicates that at higher imposed velocities, the relative importance of surface flow skimming over the canopy decreased and more transport occurred via the deeper water layers within the canopy. The combined effect of some flow going over the short *Salicornia* vegetation (Fig. 3) and some flow passing through the sparse *Salicornia* vegetation (Fig. 4), explains why there is significant less flow acceleration adjacent to *Salicornia* than *Spartina* patches (Figs. 3, 4 and Table 2). Averaged over the three incoming current velocities, *Salicornia* generated a significantly weaker scale-dependent feedback than *Spartina* (Fig. 5).

Looking behind the *Salicornia* vegetation patch, the PIV analyses showed that the water at the surface is decelerating (Fig. 3). The latter is probably due to turbulent mixing of the accelerated top layer passing over the vegetation with the more slowly moving bottom layers that passed through the vegetation. The velocity measurements within the water column showed no significant changes in current velocity going from the vegetation (i.e., $Y = 0.25$ m) to 1 and 3 m behind the vegetation (i.e., $Y = -1$ and -3 m in Fig. 6 and Table 2; except for $X = -1.5$ and $Y = -3$ where the velocity was higher than at $X = -1.5$ and $Y = 0.25$). The velocity pattern for *Salicornia*, with less acceleration next to the patch than observed for *Spartina*, is thus much more maintained over space than was observed for *Spartina* where the peak velocity shifted laterally.

Puccinellia showed an interesting response to current velocity, as revealed by flow patterns at the water surface. Whereas for *Spartina* and *Salicornia* patches, the flow patterns were relatively independent of the imposed current velocity, we saw for *Puccinellia* that at the lowest current of 0.1 m s^{-1} , all flow was virtually blocked by the vegetation, whereas at higher current velocities (0.2 and 0.3 m s^{-1}), the vegetation bent over so that part of the water could pass over the vegetation at an increased velocity (Fig. 3). As a result of the water passing over the bended vegetation, less flow acceleration adjacent to the vegetation is required. Thus, at low velocities, the PIV analyses of surface flow around a *Puccinellia* tussock resemble the PIV-pictures observed on emergent *Spartina*, but with increasing velocity the picture starts to increasingly resemble the PIV-pictures observed on submerged *Salicornia* patches. Within the water column, we saw a strong flow reduction (values significantly lower than 1) within ($X = 2$ m) and next to the patch ($X = -0.15$ and -0.3 m), whereas there was clear flow acceleration (values significantly larger than 1) further away from the patch ($X = -0.9$ to -3 m; Fig. 4 and Table 2).

Although both *Puccinellia* and *Spartina* generated a similar strong scale-dependent feedback averaged over the three incoming current velocities (Fig. 5), there is a major difference between these two species. The flow acceleration around *Puccinellia* reached the significant highest peak localized at -0.9 m next to the patch (Fig. 4 and Table 2), whereas the acceleration observed for *Spartina* is more laterally spread and lacks such strongly localized peak (Fig. 4 and Table 2). Looking at how the flow patterns within the water column are maintained at different locations behind the *Puccinellia* vegetation, similar as for *Spartina*, the acceleration next to the vegetation patch gradually shifted outward further downstream of the vegetation patch (Fig. 6). This caused the for *Puccinellia* pronounced peak in flow acceleration at X is -0.9 m to rapidly dissipate over a short downstream distance, whereas the flow acceleration at X is -1.5 and -3 m remained significant lower than for *Spartina* (Fig. 6 and Table 2). Overall, this suggests that the negative effects of a *Puccinellia* vegetation patch on plant establishment and growth will disappear over a relative short distance, and that the flexible shoots of *Puccinellia* are likely to induce a less strong negative feedback effect at the large scale than the stiff *Spartina* shoots.

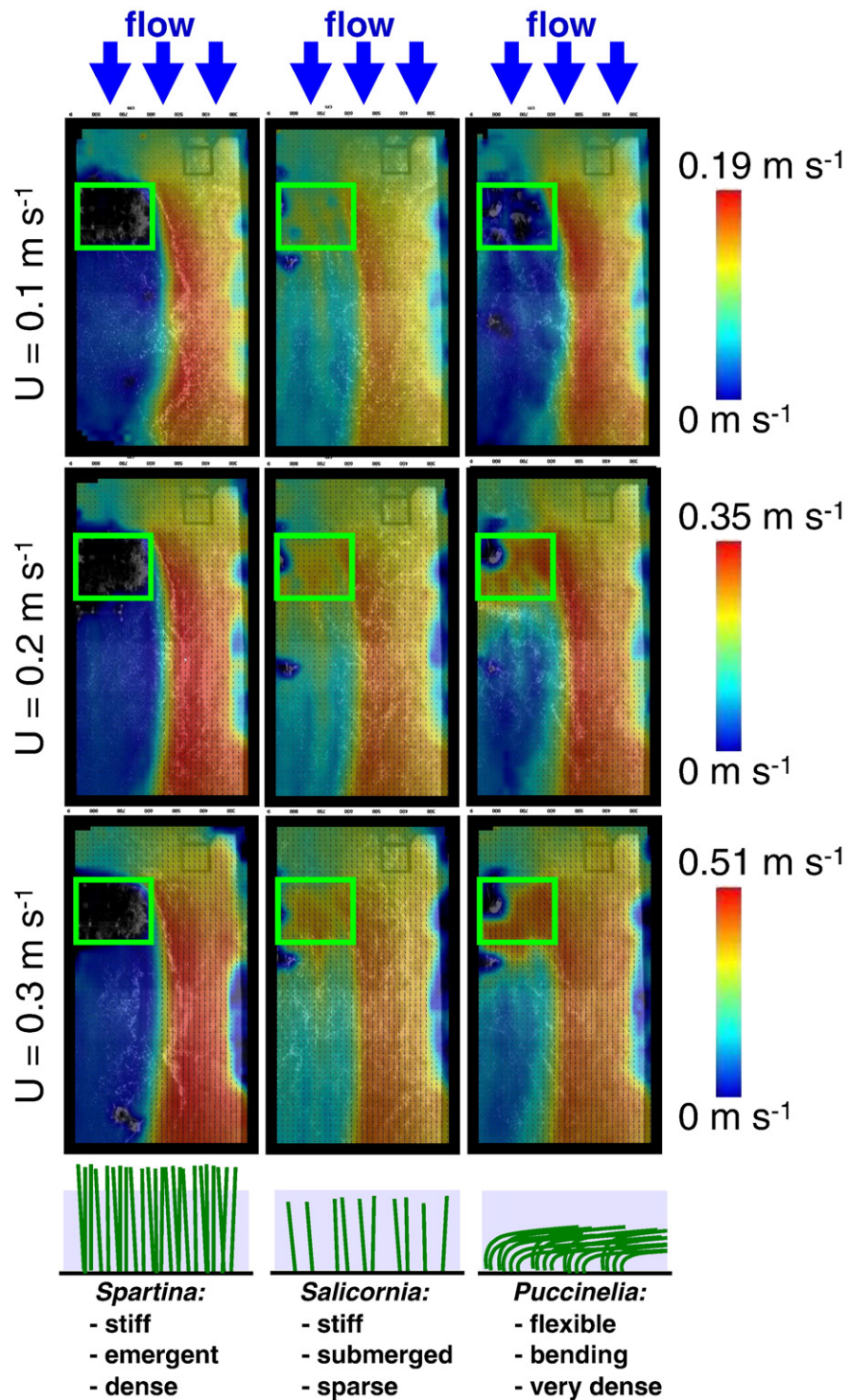


Fig. 3. Comparison of surface-level flow patterns between vegetation patches (indicated by green squares) of *Spartina anglica*, *Puccinellia maritima* and *Salicornia procumbens* as observed by PIV measurements (lay-out as indicated in Fig. 2). The arrows indicate the direction of the incoming current. The colors indicate current velocity, going from zero (blue) to a maximum value (red) of 0.19, 0.35 and 0.51 m s^{-1} for the 0.1, 0.2 and 0.3 m s^{-1} , treatments, respectively.

4. Discussion

Recent studies emphasize that scale-dependence of the interactions between organisms and physical processes is key in shaping ecological and geomorphological landscapes. However, little is known about how specific species traits affect such scale-dependent interaction, and how this depends on physical forcing. Here, we clearly demonstrate that traits such as shoot stiffness, shoot density and shoot length influence the intensity and scale of the interactions of organisms with their

environment. Independent of the species involved, deceleration of water flow within the vegetation and acceleration of flow around the vegetation was observed. However, the flow patterns differed markedly between plant species. *Spartina anglica*, a stiff, densely growing clonal species that was emergent during our flume experiment, revealed a strong scale-dependent effect on water flow, irrespective of the intensity of the flow. *Salicornia procumbens*, a stiff but sparsely growing annual that was just submerged during our flume experiment, induced a much less strong scale-dependent feedback due to some flow going over and

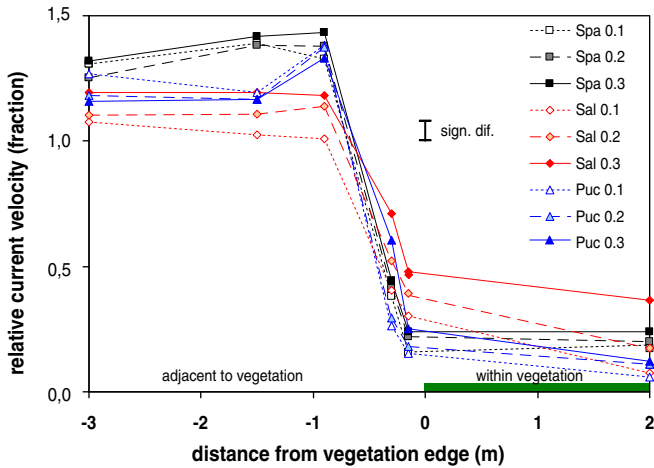


Fig. 4. Comparison of the effect of current velocity (0.1, 0.2 and 0.3 m s⁻¹; indicated as number behind species abbreviations) on flow patterns within (green line) and around vegetation patches of *Spartina anglica* (Spa), *Puccinellia maritima* (Puc) and *Salicornia procumbens* (Sal). Current velocity was measured within the water column (12.5 cm above the bottom) using an array of electromagnetic flow meters (EMF-meters) placed at different distances along the vegetation patch (i.e., Y-coordinate = 0.25 m; X-coordinates = -3, -1.5, -0.9, -0.3, -0.15 and 1 m; Fig. 2c). Velocities are always expressed relative to the incoming flow (i.e., 100% is 0.1 m s⁻¹ for Spa 0.1, Sal 0.1 and Puc 0.1; 100% is 0.2 m s⁻¹ for Spa 0.2, Sal 0.2 and Puc 0.2; 100% is 0.3 m s⁻¹ for Spa 0.3, Sal 0.3 and Puc 0.3). Differences between relative flow rates that are larger than 0.08% are significant (indicated as error bar in graph; for details see Section 2.2); standard errors are invisible as they are smaller than the symbol size.

some flow passing through the sparse vegetation. The flexible tuft grass *Puccinellia maritima* revealed a strong interaction with the intensity of the flow. Whereas a clear scale-dependent interaction was observed at low flow rates, this effect diminished as flow rates increased and caused the vegetation to bend. Moreover, this scale-dependent effect induced by *Puccinellia* was less persistent in space than the effect induced by the stiff *Spartina* shoots. From this, it is concluded that there is a strong interaction between species characteristics and flow regimes in determining bio-geomorphic interactions during early salt marsh development.

The results presented here are in line with earlier field studies showing flow attenuation inside vegetation (e.g., Leonard and Croft, 2006; Lightbody and Nepf, 2006; Neumeier and Amos, 2006) and small-scale

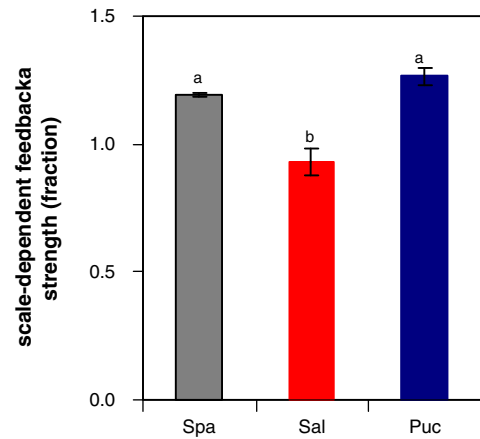


Fig. 5. Estimation of the strength of the scale-dependent feedback observed for *Spartina anglica* (Spa), *Puccinellia maritima* (Puc) and *Salicornia procumbens* (Sal). Scale-dependent feedback strength was calculated by taking the difference between the relative acceleration adjacent to the tussock and the deceleration inside the vegetation (Fig. 4) and averaging this number across the three incoming current velocities. Error bars indicate standard errors (n = 3); letters indicate significant differences based on an ANOVA test (p 0.05).

flume studies demonstrating flow deviation around vegetation patches (e.g., Van Wesenbeeck et al., 2008; Bouma et al., 2009; Zong and Nepf, 2010). This study extends on previous work by showing that the strength and spatial extent of scale-dependent feedbacks can be species specific. The latter may have important implications for the extent to which species growing under similar environmental forcing may be able to induce self-organized landscape formation, as modeled for *Spartina* marshes (Temmerman et al., 2007) and for freshwater wetlands (Larsen and Harvey, 2010). However, in the field current velocity and direction will change over time with changing tidal water depth, imposing a much broader range of settings than included in the present experiment, whereas here three contrasting marsh species for three realistic velocities were compared at a single water depth. Hence, extrapolation of present flume results to landscape-scale implications remains to be tested further. Examination of large-scale consequences of plant-growth strategies in different biotic environments can only be done by including species characteristics in bio-geomorphic models, which is currently still missing in state of the art models (Murray and Paola, 2003; Collins et al., 2004; Istanbuloglu and Bras, 2005; Baas and

Table 2

Averaged current velocities measured with the EMF-meters, expressed relative to the incoming velocity. To obtain uncorrelated measurements, we used 10 s sub-sampling from a 12 min 25 Hz measurement series. Statistical analyses indicated that differences between relative flow rates were significant if larger than 0.08% (for detailed explanation see Section 2.2).

Figure	Species	Velocity (m s ⁻¹)	Distance parallel to flow (Y) (m)	Distance to vegetation edge, perpendicular to flow (X)					
				-3m	-1.5m	-0.9m	-0.3m	-0.15m	2m
4	<i>Spartina anglica</i>	0.1	0.25	average ± SE	average ± SE	average ± SE	average ± SE	average ± SE	average ± SE
		0.2	0.25	1.31 ± 0.07	1.39 ± 0.06	1.33 ± 0.06	0.38 ± 0.05	0.16 ± 0.04	0.19 ± 0.02
		0.3	0.25	1.25 ± 0.06	1.38 ± 0.06	1.38 ± 0.05	0.41 ± 0.03	0.22 ± 0.04	0.20 ± 0.02
	<i>Salicornia europaea</i>	0.1	0.25	1.32 ± 0.06	1.42 ± 0.05	1.43 ± 0.05	0.44 ± 0.03	0.24 ± 0.03	0.24 ± 0.02
		0.2	0.25	1.08 ± 0.06	1.02 ± 0.06	1.01 ± 0.06	0.40 ± 0.06	0.30 ± 0.04	0.07 ± 0.03
		0.3	0.25	1.11 ± 0.06	1.11 ± 0.06	1.14 ± 0.06	0.52 ± 0.06	0.39 ± 0.04	0.18 ± 0.03
	<i>Puccinellia maritima</i>	0.1	0.25	1.20 ± 0.06	1.19 ± 0.06	1.18 ± 0.05	0.71 ± 0.10	0.48 ± 0.03	0.36 ± 0.03
		0.2	0.25	1.27 ± 0.08	1.19 ± 0.07	1.38 ± 0.10	0.26 ± 0.04	0.15 ± 0.03	0.06 ± 0.02
		0.3	0.25	1.18 ± 0.05	1.17 ± 0.06	1.37 ± 0.05	0.30 ± 0.04	0.18 ± 0.03	0.11 ± 0.02
6	<i>Spartina anglica</i>	0.3	0.25	1.16 ± 0.05	1.16 ± 0.05	1.33 ± 0.07	0.60 ± 0.21	0.25 ± 0.07	0.12 ± 0.02
		0.3	-1	1.23 ± 0.07	1.23 ± 0.06	1.25 ± 0.11	0.81 ± 0.17	0.57 ± 0.16	0.21 ± 0.16
		0.3	-3	1.32 ± 0.07	1.20 ± 0.06	1.22 ± 0.09	0.66 ± 0.14	0.53 ± 0.11	0.23 ± 0.08
	<i>Salicornia europaea</i>	0.3	0.25	1.40 ± 0.06	1.50 ± 0.06	1.31 ± 0.12	0.27 ± 0.05	0.14 ± 0.03	0.25 ± 0.02
		0.3	-1	1.48 ± 0.05	1.52 ± 0.06	1.23 ± 0.13	0.26 ± 0.07	0.13 ± 0.05	0.23 ± 0.04
		0.3	-3	1.20 ± 0.06	1.19 ± 0.06	1.18 ± 0.05	0.71 ± 0.10	0.48 ± 0.03	0.36 ± 0.03
	<i>Puccinellia maritima</i>	0.3	0.25	1.23 ± 0.06	1.24 ± 0.06	1.06 ± 0.08	0.73 ± 0.10	0.47 ± 0.07	0.34 ± 0.04
		0.3	-1	1.27 ± 0.05	1.29 ± 0.05	1.24 ± 0.08	0.70 ± 0.13	0.56 ± 0.10	0.31 ± 0.07
		0.3	-3	1.16 ± 0.05	1.16 ± 0.05	1.33 ± 0.07	0.60 ± 0.21	0.25 ± 0.07	0.12 ± 0.02

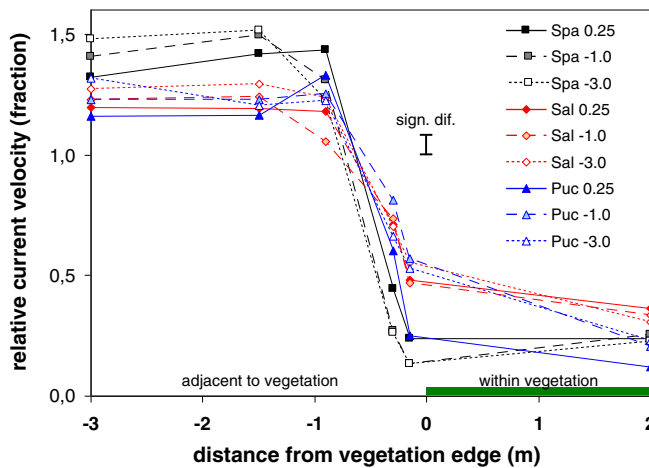


Fig. 6. Comparison of flow patterns within (green line) and around vegetation patches of *Spartina anglica* (Spa), *Puccinellia maritima* (Puc) and *Salicornia procumbens* (Sal) at different distances behind the vegetation (Y-coordinates = 0.25, -1.0 and -3.0 m; Fig. 2c). This Y-coordinate is indicated as number behind the species abbreviations. Current velocity was measured within the water column (12.5 cm above the bottom) using an array of electromagnetic flow meters (EMF-meters) placed at different distances along the vegetation patch (X-coordinates = -3, -1.5, -0.9, -0.3, -0.15 and 1 m; Fig. 2c). Velocities are always expressed relative to the incoming flow (i.e., 100% = 0.3 m s⁻¹). Differences between relative flow rates that are larger than 0.08% are significant (indicated as error bar in graph; for details see Section 2.2); standard errors are invisible as they are smaller than the symbol size.

Nield, 2007; D'Alpaos et al., 2007; Kirwan and Murray, 2007; Tal and Paola, 2007; Temmerman et al., 2007).

Current findings of a stronger scale-dependent feedback for *Spartina* (i.e., long-lived perennial landscape forming pioneer) than for *Salicornia* (i.e., short-lived annual opportunistic pioneer) seems to fit the known growth strategies for these species. That is, over time, the tall and dense *Spartina* will create an accreting vegetated platform intersected with deep, bare drainage channels (Temmerman et al., 2007). The increased elevation of the vegetated platform will provide better growing conditions to this species than the bare sediment that was originally colonized. However, over the long-term, the vegetated platform may become so high that *Spartina* will eventually be replaced by successional species in the sedimentary marshes as typically found in e.g. NW-Europe. For the sparse and short *Salicornia* we expect that a weaker scale-dependent feedback will cause less vegetation-induced sediment accretion, and hence little change in landscape elevation. Moreover, the disappearance of the annual *Salicornia* vegetation during winter will further prevent vegetation-induced sediment accretion. The lack of strong accretion implies that the area can be re-colonized over and over again by seed-dispersed individuals of *Salicornia*, unless external sedimentary processes have overriding effects. Having both annuals and per-annuals species in our comparison emphasizes that in addition to organism traits such as stiffness, density and vegetation height, future bio-geomorphic models should also put emphasis on the seasonal dynamics of plant growth.

A significant body of research points at the importance of scale-dependence of bio-geomorphic interactions in explaining the formation of spatial patterned landscapes in wetlands, intertidal flats, saltmarshes, and peat lands (Rietkerk and van de Koppel, 2008). This research purports scale dependence as a general framework for studying landscape formation in bio-geomorphic systems, especially in systems that concern transitions from bare to vegetated states via patchy intermediate structures and are, in part, dominated by accretion processes. Whereas the present study has focused on how organism traits affect the physical aspects of the scale-dependent feedbacks, it is equally important to obtain experimental evidence on plant growth responses to the bio-geomorphic feedback interactions to obtain in-depth understanding of the whole

system development (cf. Van Wesenbeeck et al., 2008). Integration of physical and ecological approaches is crucial to increase understanding in how physical constraints, such as flow direction and velocity and biological properties, such as density and organism traits, determine the scale, intensity, and isotropy of the resulting feedbacks. Ultimately, this will support the development of general theory of complexity for coupled ecological-geomorphological systems.

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