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Thresholds and shifts
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Chapter 2

Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems?

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Abstract

Complexity theory highlights scale-dependent feedback mechanisms as an explanation for regular spatial patterning in ecosystems. To what extent scale-dependent feedback clarifies spatial structure in more complex, non-regular systems remains unexplored so far. We report on a scale-dependent feedback process generating patchy landscapes at the interface of intertidal flats and salt marshes. Here, vegetation was characterized by *Spartina anglica* tussocks, surrounded by erosion gullies. Field surveys revealed that larger tussocks have deeper gullies, suggesting that gully erosion is caused by increased water flow around tussocks. This was confirmed by flume experiments. Transplantation of small clumps of *Spartina* revealed that the growth of *Spartina* transplants compared to transplant growth on bare sediment was higher within *Spartina* tussocks, but lower in the gully just outside *Spartina* tussocks, providing clear evidence of scale-dependent feedback. Our results emphasize that scale-dependent feedback is a more general explanation for spatial complexity in ecosystems than previously considered.

Introduction

What determines the spatial structure of ecosystems? This simple question addresses one of the most complex issues in ecology for over a century now. For long it has been assumed that underlying abiotic variability explains spatial patterns of species distribution, either directly (Clements 1916; Tilman 1982), or indirectly by dictating the strength of biological interactions along gradients, such as the rocky intertidal (Menge 1976; Bertness 1998). Although this theory is valid for many ecosystems, it fails to explain the occurrence of spatial patterning within ecosystems with little underlying abiotic heterogeneity.

Recently, a body of theory has emerged emphasizing the presence of heterogeneous species distribution in systems with little variety in environmental background conditions, such as regular vegetation patterning in arid zones (Klausmeier 1999; Couteron & Lejeune 2001; von Hardenberg *et al.* 2001), vegetation patterning in boreal and temperate bogs (Rietkerk *et al.* 2004b), and regular patterning of mussels on intertidal flats (van de Koppel *et al.* 2005). These studies propose that a scale-dependent feedback between localized facilitation and large-scale inhibition induces spatial self-organization, and explains the observed spatial structure. In arid systems, for example, infiltration of water is locally enhanced by plant presence, while on landscape scales competition for water between plants is the dominant process explaining observed vegetation patterns (Couteron & Lejeune 2001; Rietkerk *et al.* 2002). So far, scale-dependent feedback mechanisms have mostly been linked to regular patterns, such as banded, spotted or labyrinth structures (Rietkerk *et al.* 2004a). This is consistent with the activator-inhibitor principle that was originally introduced by Turing (1952) and which is considered the basis of scale-dependent theory (Rietkerk *et al.* 2004a). It is still unknown whether scale-dependent feedbacks also play a role in structuring systems that have more complex non-regular spatial patterning and, thus, whether the concept is more generally applicable.

In stressful environments, such as coastal ecosystems, habitat modification is an important mechanism by which many species are known to improve the living conditions for themselves and for other species. A good example of this is attenuation of wave and current stresses by the cordgrass *Spartina anglica* in salt-marsh pioneer zones, a mechanism that is known to facilitate other species (Bruno 2000; van de Koppel *et al.* 2006), but also has beneficial effects on *Spartina* itself (Bouma *et al.* 2005b). Reduced hydrodynamics within the vegetation increase sedimentation, leading to higher soil elevation in *Spartina* vegetation (Yapp *et al.* 1917; Ranwell 1964; Castellanos *et al.* 1994; Cahoon *et al.* 1996). Increased soil elevation shortens inundation time, increases aeration and lowers salinity, improving conditions for plant growth. This constitutes a positive feedback between the density and size of *Spartina* and its growth potential (Wilson & Agnew 1992). However, despite local positive feedback within patches, negative effects may occur on larger scales, just outside the patches. Small gullies, that are observed just outside *Spartina* patches (Figure 2.1A), indicate that current velocities may be increased around *Spartina* tus-
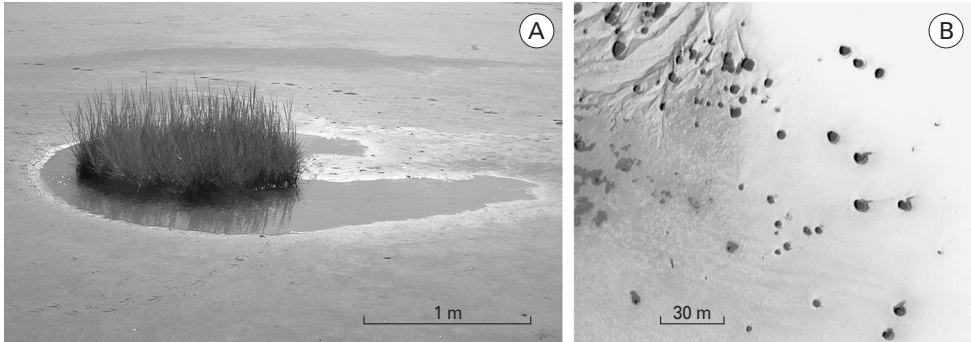
Figure 2.1. (A) Typical example of an elevated tussock with erosion gullies on the side on intertidal flat in the Westerschelde. (B) Aerial photograph representing a 600 by 600 m area of an intertidal flat in the Westerschelde. Black patches are vegetation in a matrix of bare sediment (white-gray). Gray patches on the left of the picture are microphytobenthos.
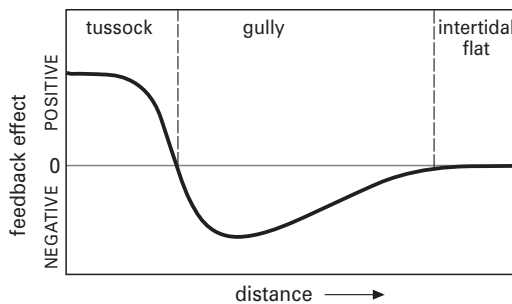

Figure 2.2. Schematic representation of expected feedback effects at different distances from tussock centre. Dashed line represents zero feedback effect. If the black line rises above the dotted line feedback effects are positive, below the dashed line feedback effects are negative. The variable distance refers to distance from the tussocks' center.

socks, leading to erosion of the gullies and possibly preventing tussocks from expanding laterally. Hence, divergence of flow may induce a scale-dependent feedback determining the patchy structure of pioneer salt-marsh vegetation (Figure 2.1B).

Here we ask the question if scale-dependent feedbacks might affect ecosystem structure in a system without regular patterning. We hypothesize that feedback effects on plant growth are scale-dependent; effects are positive within vegetation patches but negative just outside, relative to plant growth on bare sediment (Figure 2.2). These hypotheses were tested by exploration of aerial photographs to investigate whether distribution of *Spartina* tussocks was random or regular, by executing flume studies to explore relationships between physical stress and feedbacks effects, and by transplanting experiments in the field to assess influence of feedbacks effects on vegetation development under natural conditions. We discuss the implications of

our results as indicative for the importance of scale-dependent feedbacks in complex, non-patterned ecosystems.

Methods

Field site

Pioneer salt-marsh vegetation consisting of *Spartina anglica* is, in early stages of salt-marsh development, characterized by a patchy vegetation structure (Figure 2.1B). Although under ideal growth conditions a homogeneous vegetation cover will develop, there is growing evidence that vegetation expansion can be inhibited by interactions with abiotic processes, such as nutrient availability and hydrodynamics (Hemminga *et al.* 1998). This might explain the sometimes stable appearance of *Spartina* tussocks over periods of more than ten years.

To examine whether scale-dependent feedback processes might retard tussock expansion field experiments were conducted on the Plaat van Walsoorden (N 51° 22, 6', E 4° 04, 7') in the Westerschelde, The Netherlands. This is an intertidal flat of approximately 2 kilometers width with patchy distributed tussocks of the English Cordgrass, *Spartina anglica* (Figure 2.1B). Although some erosion and expansion of tussocks was recorded, tussocks generally have been present for over ten years (unpublished data). Most tussocks are characterized by a dome-shaped appearance and by erosion gullies running along their edges (Figure 2.1A). Transitions between tussocks and surrounding sediment are sharp and sometimes tussock edges seem vulnerable to erosion because of their slightly elevated position.

Pattern analysis of aerial photographs

To determine if tussock distribution in salt-marsh pioneer zones was random, clustered, dispersed or regular, we examined tussock distribution by calculating Ripley's K (Ripley 1977) from aerial photographs from the same intertidal flat where we executed experiments. Photographs were selected based on their clarity and absence of benthic macro algae, allowing us to easily extract vegetation from the surrounding sediment using color information from red and blue bands. Photographs from 2004 were selected, which were the most recent ones that were usable and were between 500 and 700 meters in width and length. This way there was no interference with edges of the flat, with areas without vegetation or with areas with other vegetation types. The photographs were scanned and middle points of all vegetation patches were determined using Matlab, Version 7.1. Ripley's K was calculated using R, version 2.2.1. Inter-tussock distances were used to calculate K(d), which compares distances between neighboring tussocks with random values and uses this to obtain a measure for spatial distribution of point data for different inter-tussock distances. 100 Monte Carlo iterations were used to calculate the 95% confidence intervals for spatial randomness. Instead of K(d) the more robust function L(t) was plotted (L(t)= $\sqrt{K(d)/\pi}$). L(t)-values represent the number of points that are expected to be found at certain distances if point data are randomly distributed (based on Poisson distribu-

tion). L(t)-values that rise above the upper confidence limit imply that for these specific inter-tussock distances more points are found than would be expected based on a Poisson distribution, pointing at clustering of point data. L(t)-values below the lower confidence limit indicate a dispersed distribution as the number of points encountered for that specific inter-tussock distance are less than expected. L(t)-values that stay between the confidence intervals imply randomness.

Field surveys of mound volume and gully depth
We investigated if any relationship exists between the volume of a tussock and the depth of erosion gullies along the tussock edges by measuring gully depth and tussock volume of 13 tussocks in the field. To obtain an estimate of tussock volume we measured tussock surface area and height of the mound in the field and multiplied these parameters. Tussock size was determined by measuring the diameter in both North-South and East-West direction. Tussock mound elevation and gully depth were calculated by measuring soil height in the middle of the tussock and then measuring the deepest point of the gully and a point at 5 meters distance from the tussock center. Height in the middle of the mound was measured only once, but the elevation of the gully and 5 meter from the tussock were measured in all four wind directions: North, East, South, and West. To obtain the height of the mound we calculated the average altitude of the four points at 5 meter distance North, East, South and West from the mound and subtracted this average from the altitude of the mound middle. For calculating gully depth mean elevation of the gully was subtracted from the mean altitude at 5 meters. The resulting four gully depth values for each tussock were averaged for all 13 tussocks. Finally, mound volume and gully depth were correlated using Statistica, Version 7.1.

Flume experiments
We examined whether scale-dependent effects were caused by hydrodynamic forces in a flume study. To test whether scale-dependent effects varied with changing physical stress the effects of current velocity and water height on tussock border erosion were measured. A flume is an artificial channel used for studying the flow of fluids. In the test section, objects such as vegetation can be placed to study the effects of the object on hydrodynamics. Our measurements were done in a racetrack flume at the NIOO-CEME in Yerseke. This flume has a total length of 17.5 m and a volume of about 10 m^3. Current velocity can be regulated between 0 and 0.6 m s^{-1} respectively. The test section of the flume is 0.6 meter wide and 2 meters long. For further details on this flume system see Van Duren *et al.* (2006). For our flume study, we used vegetation densities representative of *Spartina* densities in the field (1600 shoot per m^2) on mixed sandy silt sediments. *Spartina* was grown from seed. Seeds were obtained from *Spartina anglica* in the field six months earlier (September/October) and stored in salt water at 7 °C. For germination seeds were rinsed with fresh water and put in a warm, moist and light place. Small seedlings were planted in trays that fitted the flume test section widthwise (0.6 m), but were shorter than the test section length-

wise (tray 1.0 m compared to test section of 2.0 m). In these trays seedlings were grown to adult *Spartina* plants (average plant height was comparable to natural *Spartina* plants under salt conditions), while being watered with a mixture of fresh and salt water to mimic field conditions. Finally, half of the tray was filled with vegetation (0.3 meter wide and 1 meter long), so that vegetation bordered one side of the flume while filling half of the test section. The other half consisted of bare sediment. For the flume experiment, trays were put in the middle of the test section, leaving 0.5 m open space on each end of the tray. This allowed us to remove front and back plates of the tray, fill the remainders of the test section with sediment that was similar to the sediment used in the trays (comparable to sandy silt) and make soils in the complete test section level with the flume bottom. All this was done to prevent the front and back plates of the tray from interfering with occurring erosion.

To detect if erosion was caused by diversion of current stress to tussock borders, as the tussock acts as a barrier for water flow, erosion was measured after running the flume with six different water heights (12, 15, 17, 20, 22.5, 25 cm), but with a constant flow velocity of 0.3 m s^{-1} for 30 minutes. Data from flume studies were only used to obtain a qualitative understanding of ongoing processes, as increased current velocities alongside vegetation patches will differ quantitatively from currents in the field, where lateral water movement is not restricted by the width of the flume channel. However, velocities that were imposed in the flume are representative for velocities observed in the field (Bouma *et al.* 2005a). To determine the influence of current velocities with incoming tides on tussock border erosion, we used six different flow velocities (0.2, 0.23, 0.25, 0.27, 0.3, 0.4 m s^{-1}) with a constant water height of 12 cm. After running the flume with a unidirectional flow, erosion was measured manually. This was done by laying out a grid of 120 cm in the x-direction and 60 cm in the y-direction measuring sediment height with a measuring stick every 5 centimeters. After each measurement sediment was restored by adding (and removing) sediment where necessary. Two multiple regression analyses were performed in Statistica, with eroded volume as the dependent variable in both and water height and current velocity as independent variables respectively.

Transplanting experiments
The presence of a scale-dependent feedback in the field was established by executing transplanting experiments. To test whether growth of *Spartina* was affected by erosion in a scale-dependent way, we planted small *Spartina* clumps (15-20 stems) at various distances from the center of tussocks in the field. Transplant units were obtained from a single *Spartina* tussock growing at the same field site. To determine if *Spartina* tussocks facilitate growth of con-specifics within a tussock, transplants were planted inside existing tussocks (0 meter). To test whether plants have lower survival next to tussocks a second clump of vegetation was planted just next to existing tussocks in the gully (0.5 meter). As a control, the last piece of vegetation was planted outside the influence area of the tussock (4 meter). To eliminate effects of competition for light we added a treatment of clumps that were transplanted inside

tussocks into small areas where aboveground biomass of other plants was repeatedly removed up to 20 cm from the transplant. All treatments were repeated twelve times in different randomly chosen tussocks. Transplant success was monitored every two months by scoring presence/absence of transplanted units, measuring diameter, counting stems and measuring height of five random stems of each transplant. After 14 months all transplants were harvested. Biomass was dried in an oven at 50 degrees Celcius for 48 hours and weighed afterwards. Analysis of variance was applied, with competition treatments nested in the 0 distance class, to determine if variances in biomass of transplants were explained by distance from the tussock. Post hoc comparisons were done using a Tukey HSD test.

Results

Extracting middle points for all tussocks from the four aerial photographs resulted in a point pattern (Figure 2.3A) that was used to calculate L(t) for inter-tussock distances using Ripley's K-test for determining randomness of spatial point data (Figure 2.3B). Inter-tussock distances that form a wave around the confidence intervals expose a regular pattern. Although not all trends are similar, L(t)-values derived from photograph 2 lie completely in between the confidence intervals (Figure 2.3B2), pointing at a random tussock distribution. L(t) values in Figure 2.3B1 and 2.3B3 rise slightly above the upper-confidence limit, pointing at clustering of tussocks. In figure 2.3B3 clustering only occurs for inter-tussock distances above 50 m and below 300 meter. Above 300 meter L(t) values are in between the confidence intervals again. Hence, our analysis did not provide any evidence for regularity in tussock distribution.

Our field survey of tussock surface area, mound height and gully depth shows a significant positive correlation between tussock volume and depth of the erosion gullies next to the tussock ($R^2 = 0.32$, $P < 0.05$). So, tussocks with large volumes are surrounded by deeper gullies. Our flume studies, testing if erosion next to tussocks could be linked with current velocity and water height, showed a positive linear relationship between current velocity and eroded volume (Figure 2.4A: $R^2 = 0.86$, $P < 0.01$). This implies that faster water flow generates deeper erosion gullies alongside tussocks. Furthermore, these erosion gullies are mainly generated with low water levels; our flume study revealed a perfect negative linear relation between border erosion and height of the water column (Figure 2.4B: $R^2 = 0.96$, $P < 0.001$).

Biomass of transplants in the field fluctuated with distance from the naturally present tussocks. Significant effects of distance from the original tussock on transplant performance were detected (Figure 2.5: nested-ANOVA, $F_{1,44} = 30.49$, $P < 0.001$). Average biomass was highest inside the tussock, whereas lowest biomass was recorded in the 0.5 meter class, just next to the original tussock. This class differed significantly from all other classes (Figure 2.5: Tukey HSD test, $P < 0.001$). Transplants in this class stand in the erosion gully, that is waterlogged, which probably
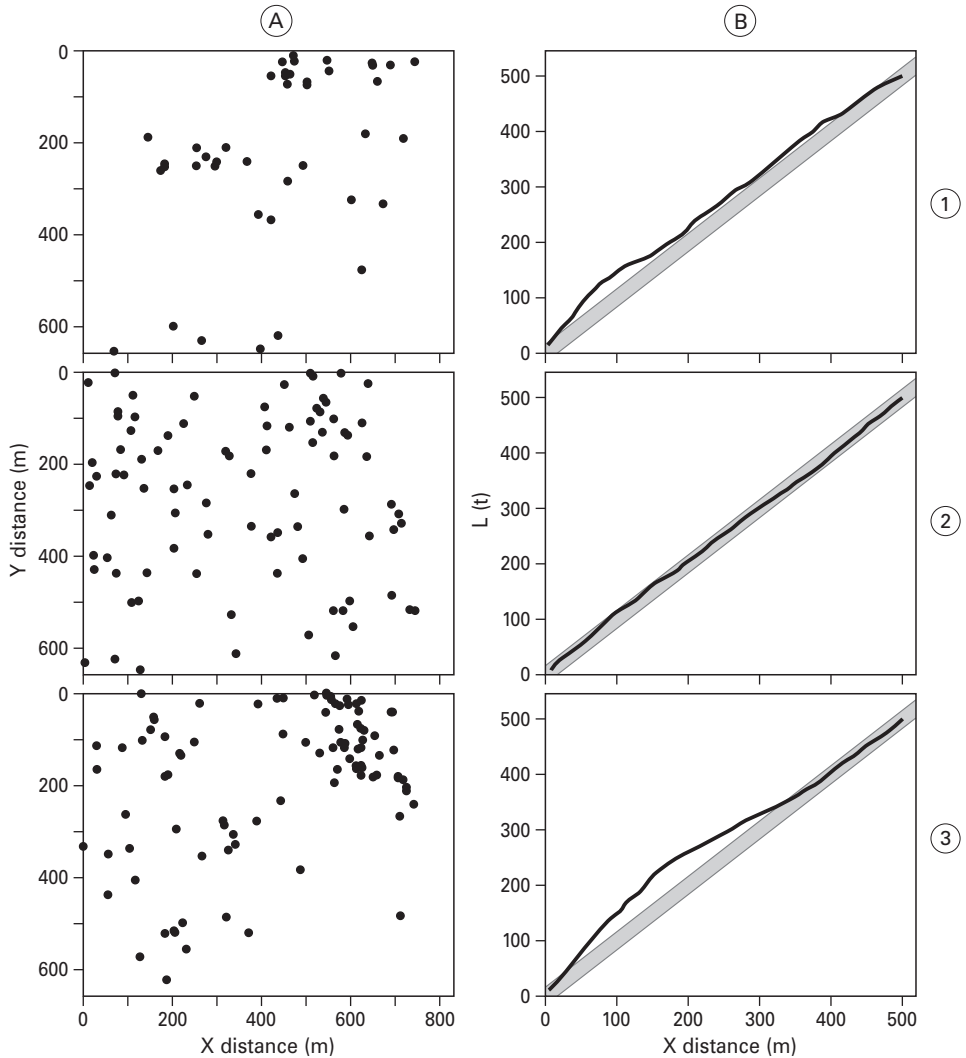
Figure 2.3. (A) Point patterns derived from aerial photographs which were used to calculate (B) L (t) values for inter-tussock distances using Ripley's K-test for determining randomness of spatial point data. Dotted lines represent confidence intervals (95%) and solid lines represent L(t) values. If the solid line rises above the upper confidence limit points are clustered, if it goes below the lower confidence limit points are showing a regular pattern. If L(t) values are in between both confidence limits points are randomly distributed.

caused their mortality. The transplants at 4 meters from the tussocks perform better than those at 0.5 m from the tussock but worse than transplants within the tussock (Figure 2.5). No significant effect of above ground competition on tussock performance was encountered for the transplants in distance class 0 (Figure 2.5: nested-ANOVA, $F_{2,44} = 1.66$, $P = 0.21$). The 0 m class without competition, differed only
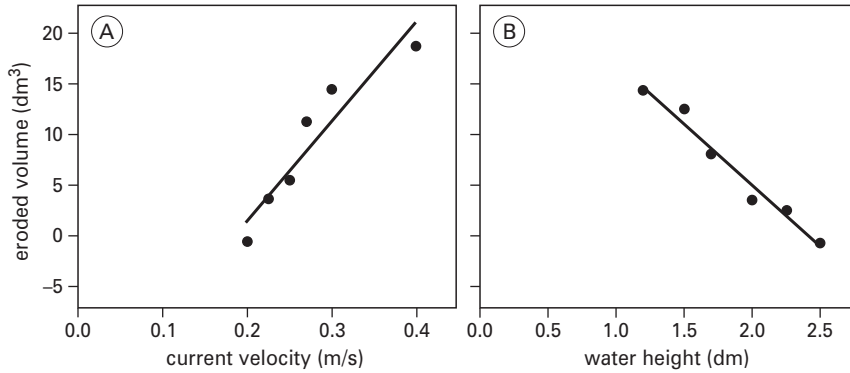
Figure 2.4. Correlation of the eroded volume next to *Spartina* vegetation with (A) current velocity (R^2=0.86), and (B) water height (R^2=0.96), in a race-track flume.
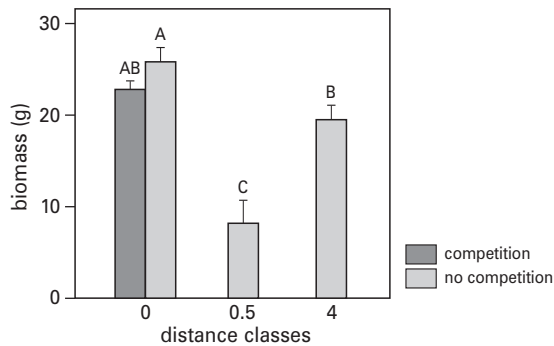

Figure 2.5. Average biomass (dry weight) of transplanted vegetation units per distance class (0, 0.5 and 4). In the 0 category competition and without competition treatments are depicted. Letters indicate significant differences (Tukey test) and bars represent standard errors (+1 SE).

marginally from the furthest distance class of 4 meter (Figure 2.5: Tukey HSD test, *P* = 0.05). The 0 m class with competition did not differ significantly from this class (Figure 2.5: Tukey HSD test, *P* = 0.53).

Discussion

The results of our study reveal that scale-dependent feedback processes, previously described exclusively in systems with regular spatial patterns, can also be an important cause of spatial structure in systems with a more random distribution of vegetation. In salt-marsh pioneer zones, tussocks divert stresses imposed by water currents, resulting in sedimentation and improved growth within the tussocks, but also

in erosion and deprived growth conditions next to tussocks. Tussocks with larger volumes were found to have deeper erosion gullies and flume experiments showed that deeper erosion gullies are created by larger current velocities. In the field, survival and growth of transplanted *Spartina* units was severely suppressed inside erosion gullies. Despite of clear evidence for the presence of a scale-dependent feedback in our system, analysis of aerial photographs revealed that tussock distribution was either random or close to random, and little evidence of regularity was found. Hence, our study indicates that scale-dependent feedback mechanisms can be an important cause of spatial structure, even in systems that lack the regular patterns that are typically linked to scale-dependent feedback.

Most examples in literature, linking regular patterning to scale-dependent feedbacks, originate from systems under close to relatively homogeneous underlying (abiotic) conditions (Klausmeier 1999 (arid systems); see Rietkerk *et al.* 2004b (peatlands); van de Koppel *et al.* 2005 (musselbeds); but also see van de Koppel *et al.* 2006 for scale-dependent feedback influencing community structure along abiotic gradient). In salt-marsh pioneer zones, the main abiotic force, being hydrodynamic stress, is particularly variable in space and time, which might be a possible cause for the generation of irregular patterns. Hence, the presence of scale-dependent feedbacks in these more heterogeneous systems might lead to development of complex spatial structures. A recent modeling study emphasized that the presence of vegetation fixated dynamic creek structures on intertidal flat, resulting in formation of unvegetated tidal channels and a vegetated platform (Temmerman *et al.* 2007). Here, similar to our results, spatial structure (creek formation) was proposed to result from scale-dependent effect of plant growth on sedimentation. Our combined findings strongly suggest that scale-dependent interactions between plant growth and hydrodynamics play a key role in the formation of the extensive networks of creeks and gullies that are typical for salt marshes (Allen 2000), implying that scale-dependent feedbacks on small scales can possibly influence complex structures at larger scales.

Scarcity of resources is generally stressed as an important condition for the formation of regular patterns, generated by scale-dependent feedbacks (von Hardenberg *et al.* 2001; Lejeune *et al.* 2002; Rietkerk *et al.* 2002). In our study scale-dependent feedback is caused by diversion of physical stress at small scale within tussocks, which inevitably results in magnification of physical stress at larger scales, outside of the tussocks. This is illustrated by our flume study that shows that, in particularly at low water levels, strong erosion is observed along tussock borders. Hence, scale-dependent feedback can not only arise from the redistribution of scarce resources but may also have other underlying processes such as divergence of physical stresses. These seemingly different processes have in common that local stress is reduced (larger availability of nutrients or water, reduction of current velocities), resulting inevitably in enhanced stresses on larger scales (smaller availability of nutrients or water, increased current velocities). Hence, our study highlights a new class of scale-dependent feedback, broadening their generality as a cause of spatial complexity in ecosystems.

Scale-dependent feedbacks are density dependent processes, where scale-dependent positive and negative effects fluctuate with density or biomass, as was found in arid vegetation or in mussel beds (Rietkerk *et al.* 2002; van de Koppel *et al.* 2005). In salt-marsh pioneer zones feedback effects vary with volume of the mound (this study), but have also been shown to vary with stem density (van Hulzen *et al.* 2007). Higher shoot densities inside tussocks cause more sedimentation inside the tussock but deeper erosion gullies next to the tussock. Effects of scale-dependent feedbacks differ with varying physical stress. In arid vegetation the amount of rainfall, which logically is the main stressor, determines the final vegetation pattern and the vulnerability of the system to sudden and catastrophic shifts (Klausmeier 1999; Rietkerk *et al.* 2004a). Similarly, in salt-marsh systems, stress levels depend on current velocities, and high current velocities were found to generate strong erosion patterns around tussocks. Hence, our experiments, combined with other data (van Hulzen *et al.* 2007), emphasize the feedback nature of plant-current interactions: effects become stronger with increased density and higher flow velocity.

Concluding, we demonstrated the presence of scale-dependent feedbacks, between vegetation and current velocity, in salt-marsh pioneer zones where *Spartina* tussocks are patchily distributed on the intertidal flat. In these zones, tussocks were distributed in a random or slightly clustered fashion, implying that occurrence of scale-dependent feedbacks in ecosystems is not necessarily limited to systems with regular spatial patterns. Moreover, the physical stressor is current velocity, suggesting that scale-dependent feedbacks may act through a wider range of potential mechanisms than previously thought. These findings suggest that scale-dependent feedbacks might be a widely applicable mechanism causing spatial complexity in a broad range of ecosystems.