

Self-Organization and Vegetation Collapse in Salt Marsh Ecosystems

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ABSTRACT: Complexity theory predicts that local feedback processes may strongly affect the organization of ecosystems on larger spatial scales. Whether complexity leads to increased resilience and stability or to increased vulnerability and criticality remains one of the dominant questions in ecology. We present a combined theoretical and empirical study of complex dynamics in mineralogenic salt marsh ecosystems that emerge from a positive feedback between clay accumulation and plant growth. Positive feedback induces self-organizing within the ecosystem, which buffers for the strong physical gradient that characterizes the marine-terrestrial boundary, and improves plant growth along the gradient. However, as a consequence of these self-organizing properties, salt marshes approach a critical state as the edge of the salt marsh and the adjacent intertidal flat becomes increasingly steep and vulnerable to wave attack. Disturbance caused, for instance, by a storm may induce a cascade of vegetation collapse and severe erosion on the cliff edge, leading to salt marsh destruction. Our study shows that on short timescales, self-organization improves the functioning of salt marsh ecosystems. On long timescales, however, self-organization may lead to destruction of salt marsh vegetation.

Keywords: emergence, positive feedback, salt marsh development, self-organization.

The study of complexity in ecosystems has been recognized as one of the frontiers of ecology (Thompson et al. 2001). Many ecosystems exhibit remarkable complexity in both structure and dynamics, which has repeatedly frustrated attempts to predict the response of ecosystems to human interference (Scheffer et al. 2001). Complexity within ecosystems, however, has also been recognized as the basis for the adaptive capacity of ecosystems to future changes on both regional and global scales (Levin 1998, 1999, 2002). A key property of complex systems is emergence, where properties of the ecosystem at large spatial scales result from feedback interactions between components occurring at smaller scales (Holland 1995; Levin 1998). These emergent properties result from the capacity of systems to self-organize (Ulanowicz 1979; Levin 1998; Rietkerk et al. 2002).

Complexity theory has successfully been applied to diverse and structurally complex ecosystems such as coral reefs, rainforests, and rocky shore communities (Wootton 2001; Plotkin et al. 2002; Mistr and Bercovici 2003). The application of complexity principles to relatively simple ecosystems has been limited. In this article, we apply complexity concepts to salt marsh ecosystems. Salt marshes typically have low plant diversity and a simple trophic structure relative to coral reefs or rainforests (Olff et al. 1997). However, unlike many other ecosystems, many mineralogenic salt marshes do not develop toward homeostasis. Early developmental stages, characterized by accumulation of clay (Olff et al. 1997; van Wijnen and Bakker 2001; Temmerman et al. 2003), are followed by a degenerative phase in which erosion at the edge, in the form of retreating cliffs, removes both the vegetation and the accumulated sediment (Gray 1972; Van Eerd 1985; Pringle 1995; Olff et al. 1997; Allen 2000). Cliff erosion has been described for a wide range of European and North American salt marshes and has been attributed to sea level rise, changes in position of estuarine channels, or increased shipping (Gray 1972; Dijkema 1987; Allen 1989, 2000; Shaw et al. 1993; Pringle 1995; Kirchner and Ehlers 1998; Adam 2002). Other studies regard marsh erosion as an intrinsic characteristic of salt marshes, in-

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evitably occurring once the marsh has built up sufficiently (Yapp et al. 1917; Dijkema 1997; Allen 2000). On some locations, pioneer vegetation reestablished on the exposed sediment, leading to cyclic dynamics in salt marshes (Yapp et al. 1917; Gray 1972; Pringle 1995), and on several locations, a multitude of cliff remnants have been found (see Allen 2000 for a review on salt marsh morphodynamics).

Salt marshes develop at the boundary of the terrestrial and marine biome and are characterized by a strong gradient in physical stresses imposed by the sea water (Olff et al. 1997). As a consequence, plant growth in salt marshes is characterized by positive, facilitative interaction, both among individuals (Bertness and Hacker 1994) and among species (Bertness and Shumway 1993; Bertness and Yeh 1994; Shumway and Bertness 1994). Many salt marsh plants strongly increase the deposition of clay, prevent sediment erosion by both waves and water currents (Yapp et al. 1917; Castellanos et al. 1994; Esselink et al. 1998; Sanchez et al. 2001), and ameliorate salinity levels (Bertness and Hacker 1994; Hacker and Bertness 1995; Srivastava and Jefferies 1995*b*). This in turn benefits the growth of the vegetation because salt stress and tidal currents are reduced by the increased elevation of the sediment relative to the average water level (Bertness et al. 1992; Srivastava and Jefferies 1995*a*). Hence, salt marsh plants typically experience positive feedback between increased plant growth and improved edaphic conditions (Srivastava and Jefferies 1996).

Recent studies emphasize that positive feedback can strongly affect the functioning of ecosystems (Rietkerk and Van de Koppel 1997; Van de Koppel et al. 1997; Scheffer et al. 2001). Positive feedback may induce complex behavioral responses in which small changes in environmental conditions may lead to a dramatic response of the ecosystem (May 1977; Scheffer et al. 1993, 2001). In this article, we show by means of a combined theoretical and empirical investigation that the complex temporal dynamics of mineralogenic salt marshes may emerge from a positive feedback between clay accumulation and plant growth. We investigate the consequences of this feedback for the functioning of salt marsh ecosystems and relate our findings to current concepts on the relation between organization, complexity, and criticality in ecosystems.

A Model of Salt Marsh Development

Model Description

Salt marshes are found at the boundary of the terrestrial and marine biomes. The physical habitat in which salt marshes occur is characterized by a gradient of tidal in-

undation by sea water. At the landward side, tidal currents are low, and a thick sediment layer is formed even in the absence of vegetation. At the seaward side, tidal currents are more severe, and there is a high exposure to wind-driven waves. As a consequence, the sediment is typically found at greater depth relative to the average water level. To study the effect of plant-sediment feedback on salt marsh development along this boundary, we made a one-dimensional model describing the changes in the thickness of the sediment layer S_x and in plant standing crop P_x along a gradient in current-induced shear stress that characterizes the salt marsh environment. Net sedimentation is determined by the balance of deposition and erosion by water flow and wave action. Changes in plant standing crop are determined by growth; mortality caused by, for instance, senescence or grazing; and damage from the waves. For simplicity, we assume that water flow has little effect on plant growth or mortality. A model that satisfies the above description would follow the general structure

$$\begin{aligned}\frac{dS_x}{dt} &= \text{deposition} - \text{flow erosion} - \text{wave erosion}, \\ \frac{dP_x}{dt} &= \text{growth} - \text{mortality} - \text{wave damage}.\end{aligned}\quad (1)$$

Deposition, flow erosion, plant growth, and mortality are dependent on the thickness of the sediment layer and plant standing crop. Wave-induced sediment erosion and plant losses, however, are also influenced by the slope of the sediment layer because wave action is focused when the slope increases (Riis and Hawes 2003).

In this article, we use a specific example of system (1) that includes the interactive effects of vegetation on sediment dynamics and vice versa. The balance of sedimentation and erosion is described as

$$\begin{aligned}\frac{\partial S_x}{\partial t} &= I_{\max} \left(1 - \frac{S_x}{K_s} \right) - e_{\max} \frac{a}{a + P_x} \tau(x) S_x \\ &\quad - d_s \frac{b}{b + P_x} \frac{\partial S_x}{\partial x}.\end{aligned}\quad (2a)$$

In this model, net deposition decreases from the maximal deposition rate I_{\max} at $S_x = 0$ to zero at $S_x = K_s$, where K_s is the maximal sediment elevation, set by the mean high water level (Temmerman et al. 2003). Sediment erosion by water flow has its maximal value e_{\max} at low plant density, and it decreases with plant density as determined by constant a . The effects of water flow are given by the standardized bottom shear stress $\tau(x)$, which is 1 at the

seaward edge and 0 at the landward edge of the salt marsh. Sediment erosion by waves is a function of the slope of the sediment $\partial S/\partial x$, multiplied by a conversion coefficient d_s . Again, erosion is a decreasing function of plant density, determined by constant b . The model formulations used for sediment deposition and erosion are qualitatively in accordance with empirical formulas describing a decrease of deposition rate with sediment height and with distance from the marsh edge (Temmerman et al. 2003; references herein). An overview of model parameters is given in table A1 in the appendix.

The dynamics of the vegetation are described by the following equation:

$$\frac{\partial P_x}{\partial t} = r \left(1 - \frac{P_x}{K_p} \right) \frac{S_x}{c + S_x} P_x - dP_x - d_p \frac{\partial S}{\partial x} P_x. \quad (2b)$$

Here, density dependence of plant growth is described by the logistic equation, where r is the intrinsic growth rate and K_p is maximal plant standing crop. Logistic growth is multiplied by the term $S_x/(c + S_x)$ to include the effects of sediment elevation on plant growth, where c is a half-saturation constant. The constant d represents plant mortality due to senescence. Specific plant mortality due to wave damage is assumed to be a linear function of the slope in sediment elevation $\partial S/\partial x$ and the conversion constant d_p .

Model Predictions

We used the model to analyze the consequences of the positive feedback between plant growth and sediment accumulation on the spatial development of the salt marsh. The model predicts a rapid development of the salt marsh in the first years after establishment of the vegetation (fig. 1A). No development is predicted at the exposed side of the transect because conditions are too adverse for plant growth. Below a threshold bottom shear stress, vegetation can establish and sediment elevation increases due to the positive effect of vegetation on sediment accumulation. Deposition is predicted to be highest at the exposed side of the salt marsh due to the low initial sediment height, and therefore a salt marsh platform develops, which in part compensates for the more steep sediment profile that exists in the absence of vegetation (fig. 1A, *dotted line*).

As a consequence of the formation of the platform, the model develops toward an equilibrium characterized by strongly sloping sediment at the edge of the vegetated and unvegetated part of the gradient. This edge is sensitive to disturbances that remove vegetation and/or sediment at the lower section of the salt marsh. The disturbance may

instigate local vegetation collapse due to focused wave action, in turn leading to severe erosion of exposed sediment, and a salt marsh cliff develops (fig. 1B). Instead of returning to equilibrium, the edge retreats landward in a cascade of local vegetation collapse and strong erosion of sediment, maintaining a steep cliff. In front of the cliff, vegetation is predicted to recover. When the newly established vegetation approaches the cliff, cliff retreat is arrested.

The complex dynamics predicted by the model can be understood if we analyze a slightly simplified version of equation (2a), in which $d_s = 0$. This model allows for analytical investigation of threshold behavior while still predicting qualitatively similar dynamics compared with the full model. An important assumption in the model is that wave damage on plants increases with the slope of the sediment because of higher and longer exposure. However, because of the nonlinear feedback relation between plant growth and sediment accumulation, equilibrium plant standing crop does not decrease monotonically with increasing sediment slope (fig. 2A). Instead, a foldlike relation is found. The shape of this curve implies that above a threshold slope, no vegetation can persist, and an irreversible vegetation collapse is predicted once the sediment slope is increased beyond this threshold (May 1973; Scheffer et al. 1993, 2001). The threshold slope is a function of the erosive stress imposed by the currents. As a consequence, the value of this threshold depends on the position along the gradient (fig. 2B, *dotted line*), increasing from the seaward to the landward end of the gradient. At the start of the simulated developmental sequence, sediment slope is highest near the landward edge of the simulated transect. As sediment accumulates, the maximum slope moves toward the seaward side of the gradient and approaches the critical threshold as was predicted analytically from equations (2a) and (2b). Disturbances that cause the sediment slope to exceed the threshold will lead to local vegetation collapse. Vegetation collapse in turn leads to strong erosion of accumulated sediment maintaining a steep slope, and leading to continued retreat of the salt marsh cliff.

We assessed the sensitivity of the model predictions to changes in key environmental variables: sediment availability and wave energy input. In figure 3, a parameter plane is presented that depicts the qualitative effect of the maximal deposition rate (I_{\max}) and wave erosion (d_s) constants on salt marsh dynamics. The analysis revealed three zones with principally different transient behavior. Cliff erosion occurred only at high deposition rate and low wave action. In this region of the parameter plane, a steep salt marsh edge develops that is vulnerable to disturbances. As a consequence, disturbances may invoke a spatial runaway reaction, which destroys part of the

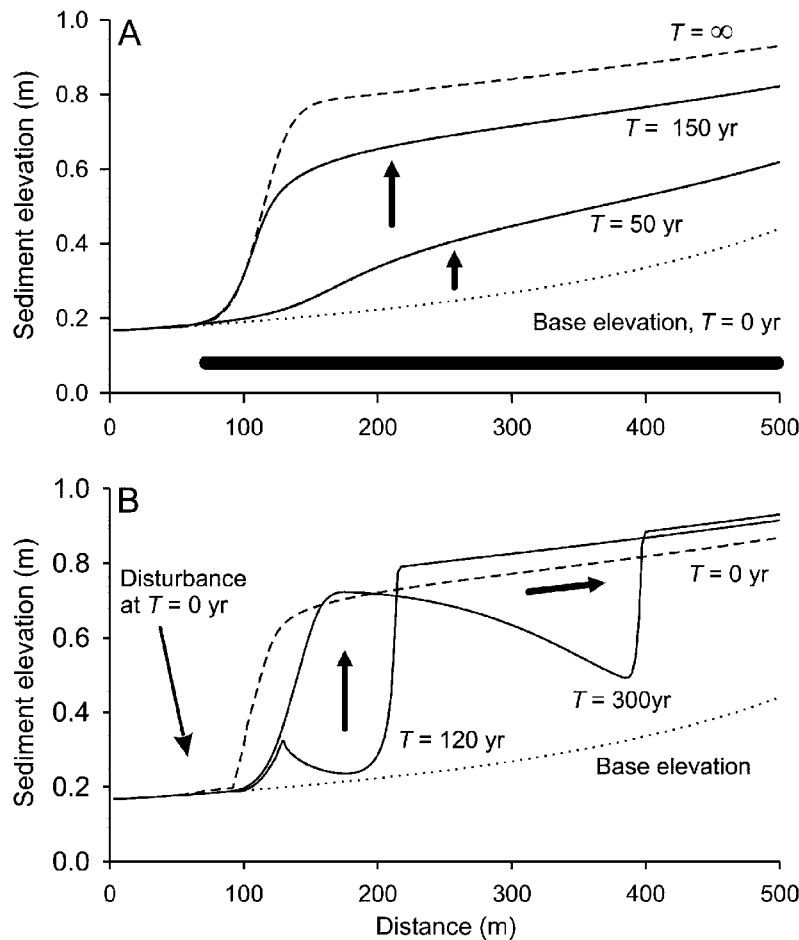


Figure 1: Predicted temporal development of the salt marsh by a model of a positive plant-sediment feedback, along a transect from the land to the seaward edge of the salt marsh. Graphs depict sediment elevation as a function of the distance along the transect. A represents the initial development of a salt marsh from an unvegetated tidal flat. B represents the development following a disturbance (at $T = 200$ years in A) that has created a gap in the vegetation, as indicated by the thin arrow. Note the retreat of the marsh and the simultaneous recovery in front of the cliff. Thick black arrows indicate direction of change. The thick black line in A represents the range where vegetation establishes. Parameter values: $I_{\max} = 0.01$; $K_s = 1$; $e_{\max} = 0.05$; $\tau = 1-0$ along the transect; $a = 50$; $d_s = 2$; $b = 20$; $r = 4$; $K = 1,000$; $d = 0.6$; $c = 1$; $d_p = 30$.

salt marsh. If wave energy levels are high, no steep sediment slope develops, and the effects of disturbances remain local. The distinction between the two types of transients remains arbitrary, and in between the two regions, a zone can be identified where disturbances lead to small, short-duration cliffs (fig. 3, *gray area*). If both the sediment input is low and wave energy levels are high, no vegetation can survive.

Interpretation of Model Results

The results of our analysis reveals conceptually important aspects in salt marsh development. Positive feedback between plant growth and sediment accumulation leads to

self-organization in salt marshes, in which elevational differences and the accompanying differences in salt stress and erosional loss are greatly reduced. Hence, positive feedback allows the ecosystem to buffer the effects of variation in physical conditions, and they underlie its ability to function as a complex adaptive system (Levin 1998). As an inevitable consequence, however, a strong gradient in sediment elevation develops over a short range at the edge of the salt marsh and the adjacent intertidal flat. Wave action, which spreads out over a long distance in an unvegetated tidal flat, is focused at this boundary. As the system develops, it approaches a critical threshold. The closer the marsh gets to this threshold, the more vulnerable it becomes to disturbances, which

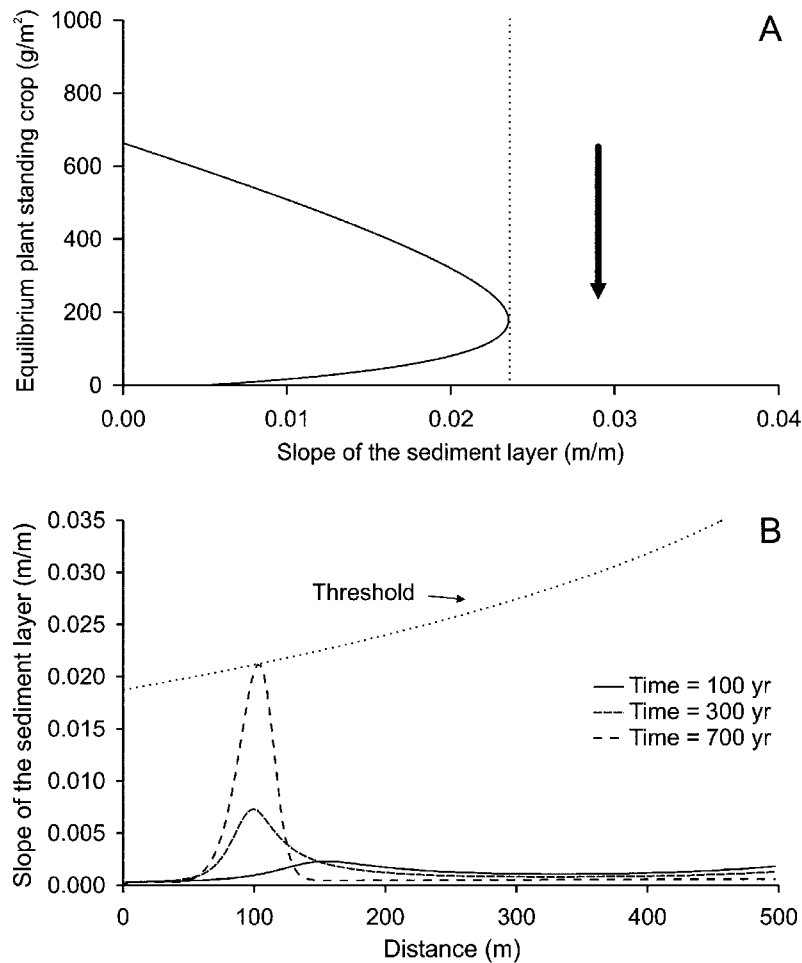


Figure 2: A, Relation between equilibrium plant standing crop and the slope of the sediment at a particular point along the gradient. The curve shows that, at that particular point, vegetation is not able to withstand a slope that exceeds ~ 0.028 m/m, as depicted by the dotted line. As a consequence, a collapse of vegetation is expected once the slope of the sediment exceeds this threshold value. B, Slope of the salt marsh along the salt marsh transect, during salt marsh development (fig. 1A). The upper dotted line represents the threshold slope, above which vegetation cannot persist. The slope of the vegetation is found to increase in time at the seaward edge of the salt marsh, approaching the threshold slope value. Parameters as in figure 1, apart from $d_s = 0$ in A and B and $\tau = 0.5$ in A.

may result in cascading vegetation losses and collapse of the salt marsh ecosystem.

Empirical Support

Our model analysis makes a number of predictions with regard to the development of salt marsh ecosystems. These predictions can be verified in field studies. Salt marsh dynamics occur at large spatial and temporal scales and are determined by a multitude of causal factors. For these reasons, direct experimental testing of predictions using strong inference methods is difficult. We follow the adaptive inference methodology, which aims to produce a body of indirect evidence to support a particular line of argu-

ments (Holling and Allen 2002). As a consequence, our study will not produce definitive evidence that verifies our model, and more research will be required to demonstrate the validity of our model in mineralogenic salt marsh ecosystems.

First, the model predicts that during early salt marsh morphogenesis, the interaction between sedimentation and plant growth decreases the initial slope of the sediment, creating a salt marsh plateau. As a consequence, the edge of the plateau with the tidal flat becomes increasingly steep. Second, the model predicts that cliff erosion and regrowth of vegetation in front of a salt marsh cliff may occur simultaneously, indicating that the continuing retreat of this salt marsh cliff is an autono-

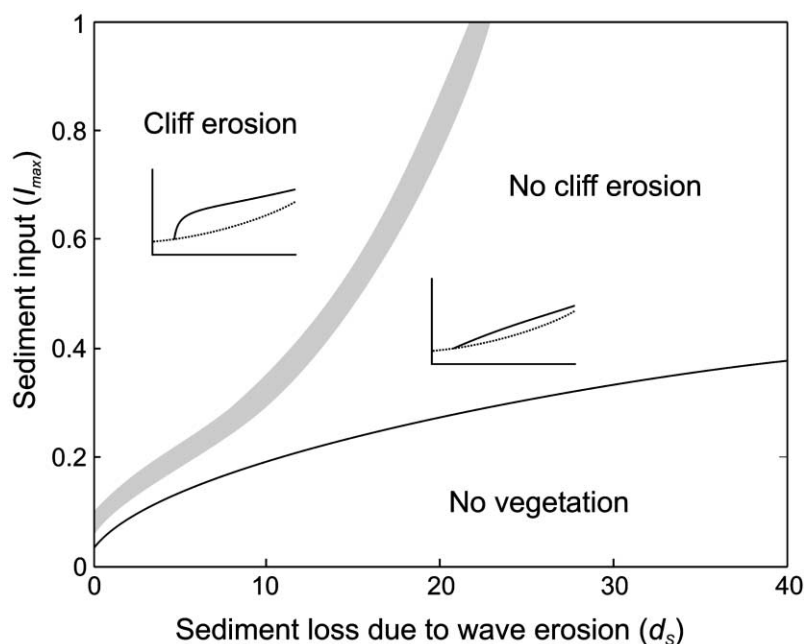


Figure 3: Parameter plane portraying the effects of sediment deposition rate and average wave energy on the transient dynamics of the salt marsh model. The three zones depict parameter combinations with a similar transient behavior. The gray zone depicts a range in between the cliff erosion and no cliff erosion zones, where the classification in either category is difficult because it depends on arbitrary threshold values. The inlay figures represent the general shape of the marsh, similar to figure 1.

mous process and not solely the consequence of external conditions. We investigated these predictions using databases on salt marsh development on the back-barrier salt marsh of Schiermonnikoog and on the foreland salt marshes in the Westerschelde estuary, both in the Netherlands.

Increasing Slope of the Salt Marsh Edge

We analyzed an extensive database on sediment elevation of a chronosequence reflecting 100 years of salt marsh development on the barrier island of Schiermonnikoog, the Netherlands (53°29'N, 6°17'E). Salt marsh develops to the south of a dune ridge that forms the northern edge of the island (Olff et al. 1997). Because the island is slowly extending eastward, a chronosequence of marshes of different age was created, covering more than 100 years of marsh development. During salt marsh development, silty sediment is deposited on top of the sand bank that was present before marsh development started. A sharp boundary is found between the original sand layer and the deposited clay (hereafter referred to as base elevation), enabling quick measurement of the amount of sediment deposited during salt marsh development (van Wijnen and Bakker 2001). The elevation of the sed-

iment and the base elevation of the clay-sand edge was measured along 33 transects in north to south direction, covering about 80 years of salt marsh development. The age of the sediment layer was estimated using aerial photographs. We used only transects on sediment younger than 60 years because sediments older than 60 years were too fragmented. Transects were pooled in classes of 10 years to avoid artifacts due to uncertainty in age estimation. We fitted a nonlinear “breakpoint” model consisting of two linear submodels to the data. The first section of the curve was dubbed the edge slope, whereas the second section reflects the decrease in thickness of the clay layer on the salt marsh plateau.

In all transects, the clay layer was found to increase strongly when moving from the seaward edge inland and then to decrease toward zero near the dunes (fig. 4). Furthermore, the average thickness of the clay layer increased with age of the salt marsh (multiple regression: $r^2 = 0.43$, $P < .001$; not shown in figure). In agreement with model predictions, the slope of the clay layer at the seaward edge was found to increase with age (linear regression: $r^2 = 0.83$, $P = .012$; figs. 4 [*dashed line*], 5A), whereas it decreased on the plateau (linear regression: $r^2 = 0.90$, $P = .004$; figs. 4 [*dotted line*], 5B). The increasingly negative slope of the plateau compensates for the positive

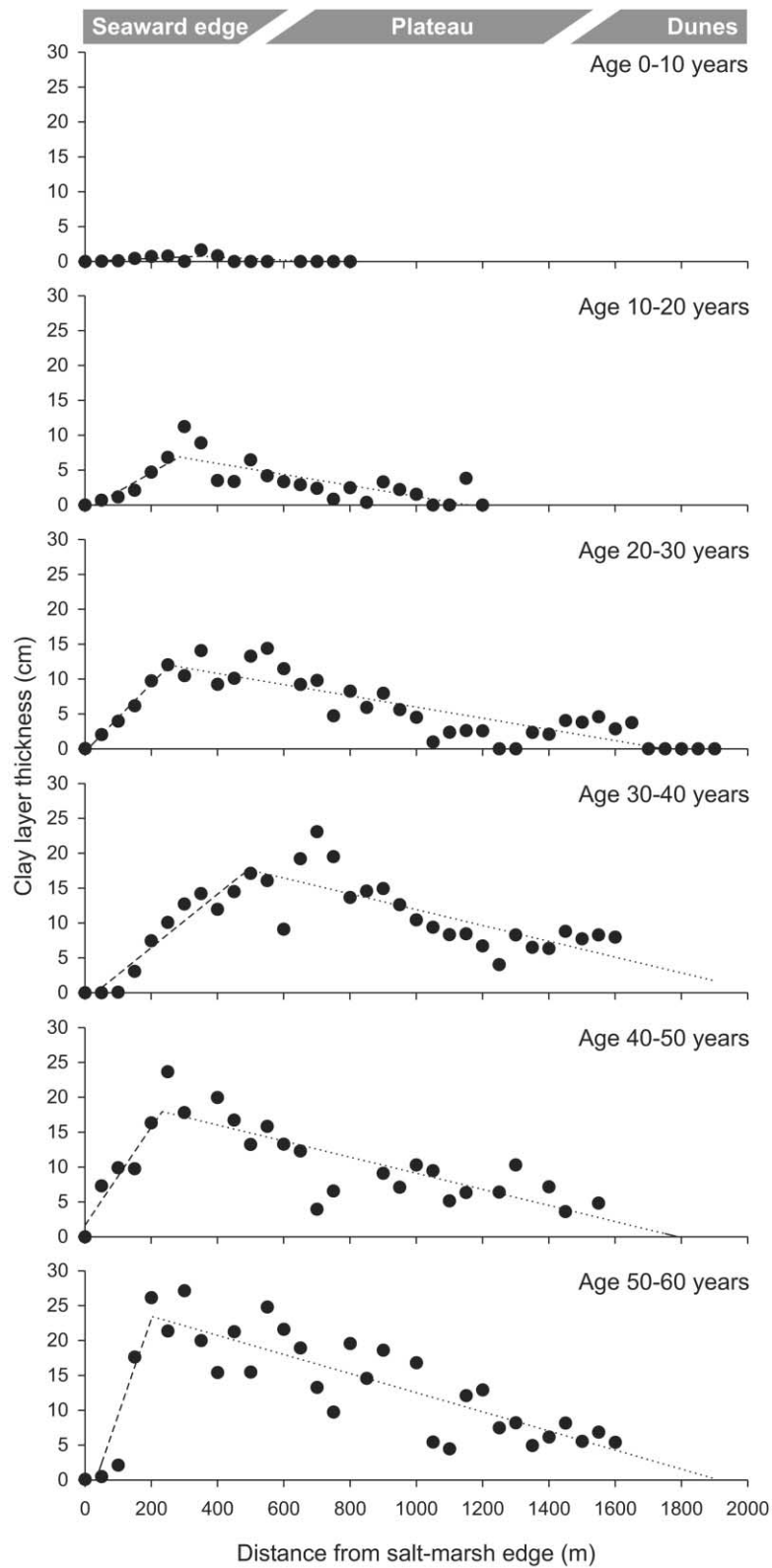


Figure 4: Thickness of the clay layer versus the distance along transects from the seaward (*left*) to the landward edge (*right*) of the salt marsh, along a 60-year chronosequence on the island of Schiermonnikoog, the Netherlands. Lines represent a fit of a linear breakpoint model. The dashed line represents the slope of the clay layer at the seaward edge; the dotted line represents the slope of the clay layer on the plateau.

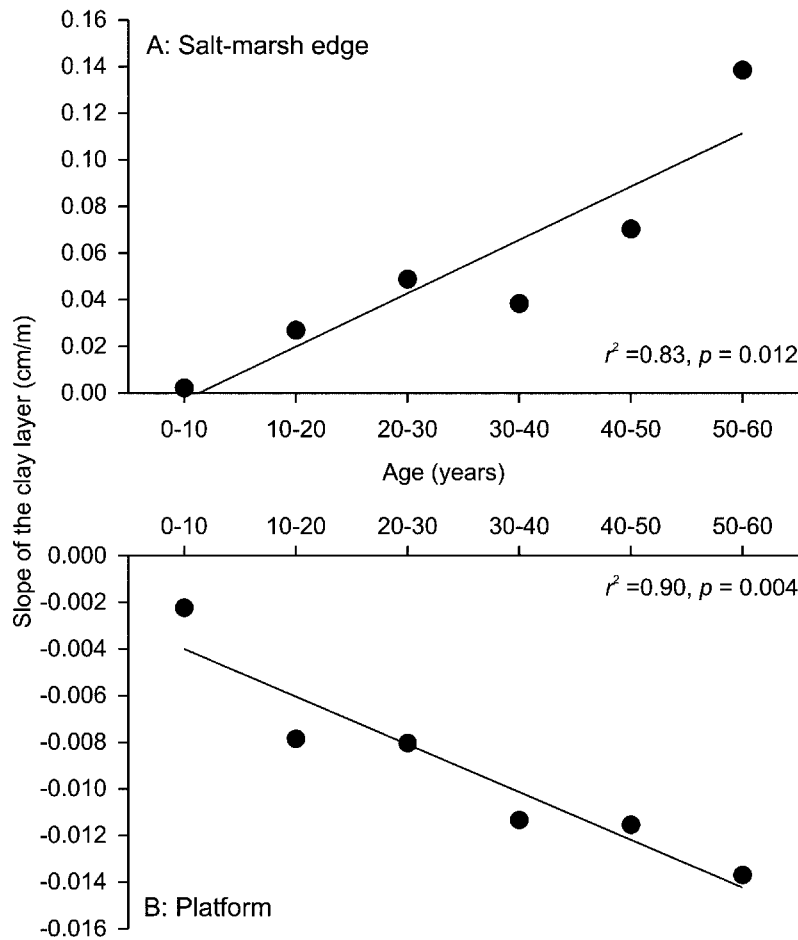


Figure 5: Relation between the slope of the clay layer on the seaward edge (A; the left side of the model fits in fig. 3) and on the plateau (B; the right side of the model fits in fig. 3) and the age of the salt marsh.

slope of the underlying sand base, which is about 75 cm/km. Hence, in agreement with the model, we found that during salt marsh development, the elevational gradient that characterizes the salt marsh is buffered by sedimentation on the plateau, while the seaward edge of the plateau becomes increasingly steep.

Simultaneous Cliff Erosion and Regrowth

We investigated a database of remote sensing images of the Paulinapolder (51°21'N, 3°43'E) and Hellegatpolder (51°21'N, 3°57'E) foreland salt marshes in the Westerschelde estuary in the southwest of the Netherlands. The salt marsh edge in both systems is dominated to a large extent by pioneer *Spartina anglica* stands but also exhibits actively eroding cliffs. We investigated the model predic-

tion that cliff erosion may occur simultaneously with vegetation establishment and expansion in front of the cliff. We studied changes in the cover of vegetation using false-color aerial photographs of 1982 and 1998. In both salt marshes (fig. 6), we found that patches of pioneer vegetation were expanding while, at the same time, erosion at the cliff continued behind these patches. Field observations revealed that the cliffs depicted in figure 6B and 6C are continuing to erode, which falsifies the alternative explanation that erosion and regrowth of vegetation had occurred in sequence (J. van de Koppel, personal observation; fig. 6D). Hence, cliff erosion and regrowth of vegetation occurred simultaneously in both salt marshes, suggesting that internal processes rather than external forcing such as increased exposure or currents causes the continued retreat of salt marsh edge. This is in agreement with

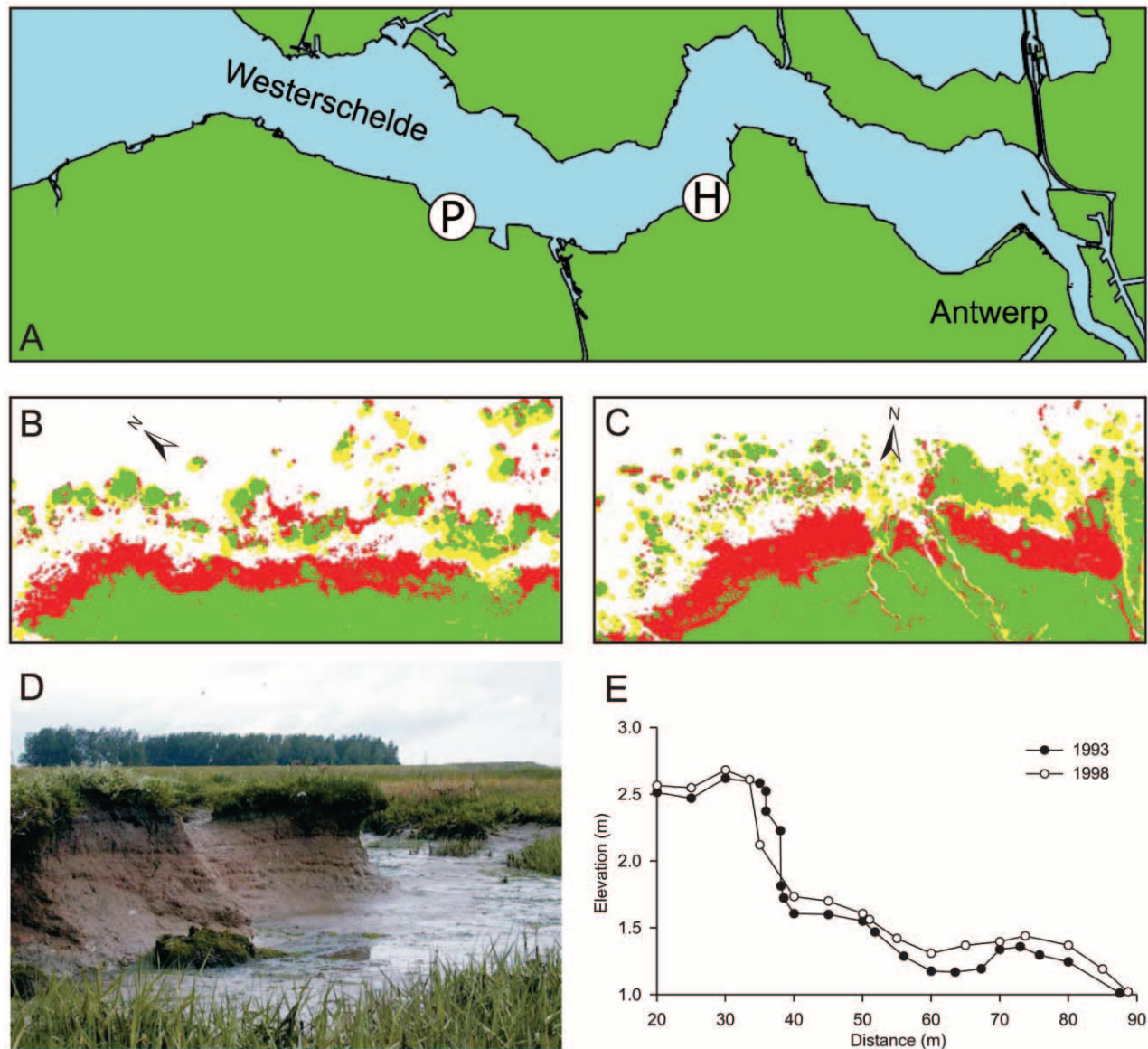


Figure 6: GIS analysis of vegetation changes between 1982 and 1998 in two sections of the salt marsh of Paulinapolder (P) and Hellegatpolder (H) in the Westerschelde, the Netherlands. A, Position of both salt marshes in the Westerschelde. B, C, Vegetation changes at the marsh edge of the Paulinapolder and Hellegatpolder, respectively. Green depicts vegetation that remained stable between 1982 and 1998; red depicts vegetation that disappeared; yellow depicts new vegetation appearing between 1982 and 1998. Note that cliff erosion (horizontal red band in B and C) occurs simultaneously with regrowth. D, Photograph of the cliff at the right part of B, taken in 2002. E, Elevational changes measured along a government-monitored transect at Paulinapolder near B (included solely for illustration). Note that cliff erosion occurs at 40 m from the start of the transect, while sedimentation occurs in front of the cliff.

the model prediction that cliff erosion can be an autonomous process intrinsic to salt marsh ecosystems.

Discussion

The model analysis presented in this article suggests that the general developmental pattern of mineralogenic salt

marshes can be explained by a simple positive feedback between plant growth and sedimentation. This feedback invokes self-organization in which the variation in physical stress that underlies the marine-terrestrial boundary is buffered by the formation of a salt marsh plateau with lush vegetation. However, self-organization also leads to

focusing of wave energy and hence to increased physical stress on the edge of the salt marsh. The model suggests that salt marshes may develop toward a critical state due to accumulation of sediment at the seaward edge. Near this critical state, disturbances may invoke a cascade of vegetation collapse, followed by strong erosion and the formation of a cliff, in turn leading to more vegetation collapse. Hence, continuing retreat of salt marsh cliffs, commonly observed in mature salt marshes, may result from autonomous processes within the salt marsh. Our model predictions are in agreement with empirical observations of salt marshes on the island of Schiermonnikoog and in the Westerschelde estuary.

Previous studies on salt marsh erosion relate the occurrence of retreating cliffs to sea level rise, changes in the positions of nearby channels, and increased shipping activity (Gray 1972; Pringle 1995; Adam 2002). Others view cliff erosion as an intrinsic characteristic of salt marshes, an inevitable consequence of differential rates of sedimentation on the marsh and the adjacent intertidal flat (Yapp et al. 1917; Dijkema 1997; Allen 2000). Our model analysis shows that both views may hold merit because a disturbance at the lower marsh (e.g., a storm or sea level rise) is required in our model to initiate the formation of eroding cliffs. Once erosion at the edge occurs, our model predicts a runaway reaction of ongoing vegetation collapse and the formation of a cliff, which may retreat inland even without further disturbance or hydrodynamic stress. This is evident in our Westerschelde study, where regrowth is occurring in front of actively eroding cliffs. Moreover, it concurs with several case studies described in the literature (Yapp et al. 1917; Allen 1989, 2000). If erosion was the sole consequence of changed hydrodynamic forcing, no regrowth of vegetation would be expected in front of actively eroding cliffs. Our observations point at an intrinsic origin of erosion, which causes ongoing degradation of the marsh even in places where disturbances have little effect.

The model analysis only touches upon the true morphological complexity of salt marsh ecosystems (Allen 2000). Despite its lack of detail, our model captures the broad pattern of salt marsh development. Hence, our results emphasize that complex dynamics in ecosystems may emerge from simple nonlinear feedback interactions (Levin 1998), which stresses the importance of emergence

in the development of ecosystems, even those that are relatively simple in ecological terms. The sensitivity analysis furthermore predicts that autogenous cliff erosion is most prevalent in systems with high sediment availability, which concurs with the absence of cliff erosion as a dominant force in organic salt marshes with very low sedimentation rates.

The question of whether self-organization induces stability in ecosystems or pushes ecosystems toward the edge of collapse has been a dominant topic in the study of ecological complexity (May 1973; Ulanowicz 1979; Levin 1992, 1998; Sole et al. 2002). A number of studies of self-organized complexity, in terms of species interaction patterns (De Ruiter et al. 1995; Neutel et al. 2002) or in terms of spatial complexity (Klausmeier 1999; Von Hardenberg et al. 2001; Rietkerk et al. 2002; Van de Koppel and Rietkerk 2004), indicate that ecosystem stability and functioning is improved by self-organization. This study shows the opposite: salt marsh ecosystems, as a consequence of local interaction of plants and sediment, develop to a critical state, becoming more vulnerable to disturbances as more clay accumulates. Salt marshes share this property with disturbance-dominated systems such as, for instance, mussel beds (Bak 1996; Jensen 1998; Sole et al. 1999; Guichard et al. 2003). The dynamics of disturbance-dominated systems are governed by avalanche-like collapses in species abundances, species numbers, or ecosystem organization. Salt marshes provide a clear mechanistic example of an important underlying assumption of this theory, that self-organization in ecosystems may lead to ecosystem collapse and induce avalanche-like dynamics that may in part determine the spatial organization of natural systems.

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APPENDIX

Table A1: Description of the variables and parameters used in the model

| | Values | Units | Descriptions | References |
|-------------|--------|--------------------|-------------------------------------------------------------------------------------------------------------------|---------------------------------------------|
| Variables: | | | | |
| S_x | | m | Depth of the sediment layer (sediment elevation) | |
| P_x | | g/m ² | Plant standing crop | |
| Parameters: | | | | |
| I_{\max} | .01 | m/year | Maximal sediment accumulation rate | van Wijnen and Bakker 2001 |
| K_s | 1 | m | Maximal depth of the sediment layer | Allen 2000 |
| e_{\max} | .05 | year ⁻¹ | Maximal rate of erosion on horizontal surface | |
| a | 50 | g/m ² | Level of P at which flow erosion is reduced by 50% | Widdows and Brinsley 2002 |
| $\tau(x)$ | 0–1 | | Standardized bottom shear stress, as a function of distance, ranging from 1 (estuarine edge) to 0 (landward edge) | |
| d_s | 2 | year ⁻¹ | Wave erosion constant for sediment | |
| b | 20 | g/m ² | Level of P at which wave erosion is reduced by 50% | Widdows and Brinsley 2002 |
| r | 4 | year ⁻¹ | Intrinsic growth rate of vegetation | Groenendijk 1984 |
| K | 1,000 | g/m ² | Maximum standing crop of vegetation | Groenendijk 1984; Van de Koppel et al. 1996 |
| d | .6 | year ⁻¹ | Loss rate of plants due to senescence | Groenendijk 1984 |
| c | 1 | m | Parameter determining the effect of sediment elevation on plant growth | |
| d_p | 30 | year ⁻¹ | Wave erosion constant for plants | |

Note: Some of the parameters have values that were given realistic parameter values based (in a loose manner) on the references shown. As no information was found in literature on the remaining parameters, their values were estimated based on general ecological insight. Note that the model is used in the article as a conceptual formulation of a hypothesis rather than an accurate description of salt marsh development. The model omits many important processes, and the parameter values may therefore deviate from realistic figures.

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