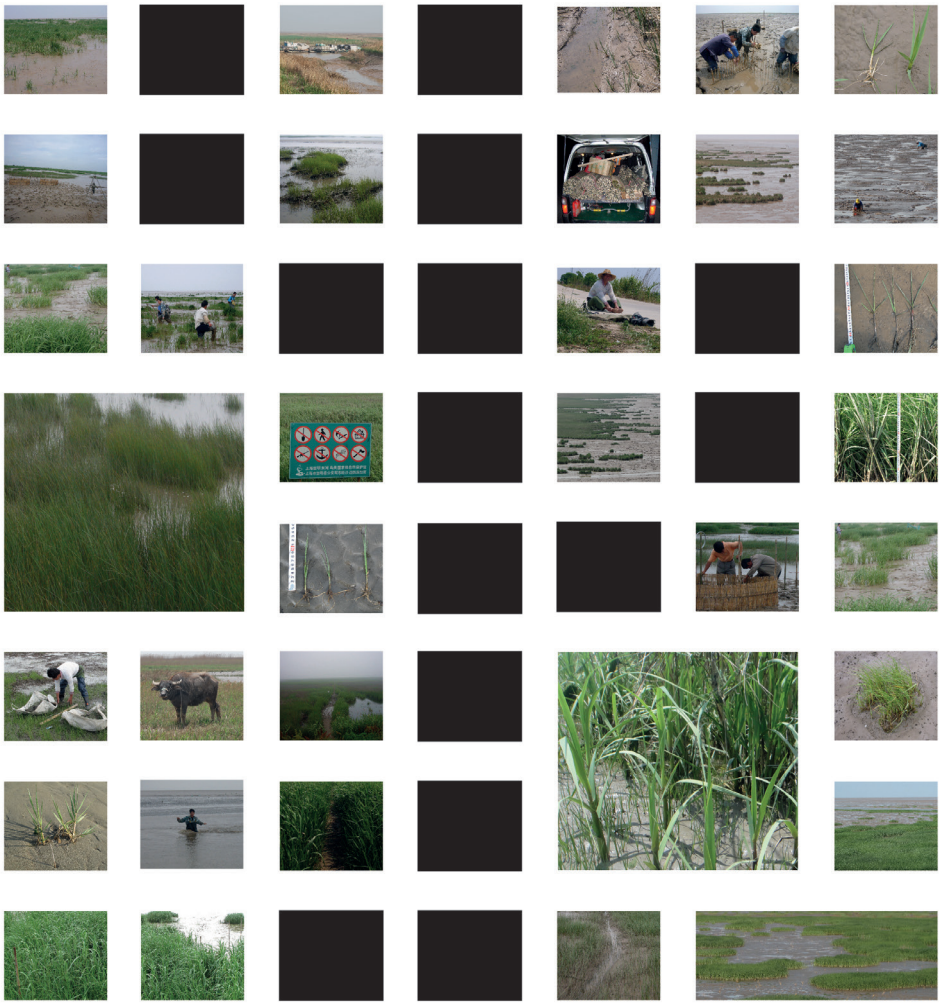

IMPLICATIONS OF BIOGEOMORPHIC FEEDBACKS ON TIDAL LANDSCAPE DEVELOPMENT

Christian Schwarz

Implications of biogeomorphic feedbacks on tidal landscape development

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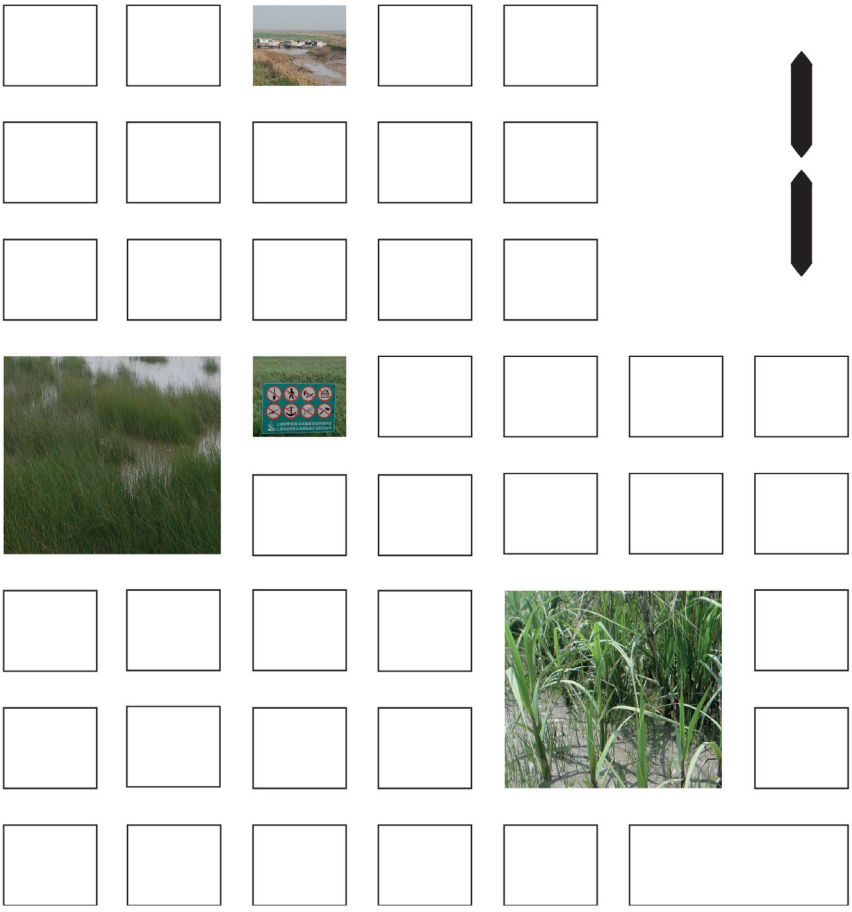


Introduction

Geomorphology and Biogeomorphology

The land surface is sculptured through interactions between driving and resisting forces. Driving forces, such as the force of gravity acting on water, wind and ice, solar radiation and the earth's internal heat are contending against resisting forces, such as geologic structure, lithology and sediment properties sculpting landform characteristics [Leopold and Leopold, 1995]. Geomorphology investigates and describes the produced landform characteristics and analyses the processes forming and modifying them. In an estuarine setting, which is the focus of this thesis, the main driving forces are related to hydrodynamics (e.g. flow velocities and wave motion), whereas the main resisting forces are represented by bed stability (erodibility) [Winterwerp and Van Kesteren, 2004].

Biogeomorphology studies the impact of organisms (i.e. animals or plants) on interactions between the above-mentioned driving and resisting forces [Hupp et al., 1995]. A relatively young concept emerging within the field of biogeomorphology is "ecosystem engineering" [Jones et al., 1994]. Ecosystem engineering describes how species can influence their abiotic environment and how this resulting change in the abiotic environment again feeds back on the species themselves (i.e. the biotic environment) [Hastings et al., 2007]. Within ecosystem engineering, literature distinguishes between allogenic and autogenic ecosystem engineers. Allogenic ecosystem engineers are organisms actively influencing their environment (e.g. dam building beavers). Autogenic ecosystem engineers are organisms changing their environment through their presence. The interaction between the physical structures of the autogenic engineer and the abiotic environment precipitate the creation of a variety of coastal and inland habitats (e.g. salt marsh and river ecosystems) [Jones et al., 1994].

Ecosystem engineering was shown to be an important mechanism for the establishment of biogeomorphic feedback loops. Tidal marshes are an example of biogeomorphic systems. Marsh vegetation reduces hydrodynamic stress, hence preventing erosion and promoting accretion of sediments (influencing geomorphology). This at the same time facilitates plant growth resulting in a positive feedback between plant growth and abiotic stress reduction [Mudd et al., 2010; van

Wesenbeeck et al., 2008a; C Wang and Temmerman, 2013].

The ability of autogenic ecosystem engineers to modify their immediate surroundings depends on both their physical properties and the prevailing abiotic conditions, also referred to as context dependency [Jones et al., 2010]. Physical organism properties influencing the ecosystem engineering ability are for instance stiffness and height for salt marsh plants or burial depth and size for bivalves [Bouma et al., 2009a; Sousa et al., 2009]. Abiotic conditions influencing the ecosystem-engineering outcome are for instance hydrodynamics and sediment properties. Recent studies tried to elucidate the role of physical organism properties interacting with hydrodynamic forces in modifying the habitat on a local scale [Balke et al., 2012; Bouma et al., 2005b; Peralta et al., 2008]. Although these studies incorporate interactions between hydrodynamics, sediment properties and organism properties, they still seem to miss the relative importance of the different factors within these properties and their implications on interpreting the context dependent outcome of ecosystem engineering. A well-founded evaluation of the context dependent outcome of ecosystem engineering needs to identify all influential factors and subsequently incorporate these factors and their interactions. For instance, interactions between sediment properties (such as erodibility), organism properties and hydrodynamics have not been investigated so far, although they were assumed to be of major importance determining the ability of ecosystem engineers to modify their habitat [Hastings et al., 2007; Perillo et al., 2009]. The interaction between abiotics and physical organism properties determines the ability of organisms to structure their habitat, nevertheless the ability of organisms to deal with (withstand) abiotic stressors determines whether the organisms can establish in the first place and ergo execute their ecosystem engineering ability. This ability to cope with abiotic stressors is dependent on physiological organism traits such as stress tolerance or adapted growth velocities. Physiological organism traits are not only important in determining species establishment thresholds. They are also prone to influence ecosystem-engineering outcome and the effect species exert on landscape development, such as mussels which are able to faster aggregate into patterns avoiding detachment [De Jager et al., 2011] or fast growing salt marsh plants preventing lateral erosion leading to faster meadow formation [Zhu et al., 2011].

Habitat modification through ecosystem engineering can also influence biotic ecosystem properties such as community structure [Crooks, 2002]. From an ecological point of view, plant communities are structured by the co-occurrence of local processes such as facilitation and competition [Bruno, 2000; R M Callaway and Walker, 1997]. Facilitative effects or positive interactions among species (often mediated by the alleviation of environmental stress), are the most known interspecific effects of ecosystem engineering [Bruno et al., 2003]. Facilitation has been shown to be more characteristic in structuring communities under harsh environmental conditions, where neighbours can buffer one another from physical stress [Bertness and Shumway, 1993; Bruno et al., 2003]. In contrast, predation and inter- /intraspecific competition were shown to be more important under benign conditions [Menge and Sutherland, 1976; van Wesenbeeck et al., 2007b].

Previous literature studying these biogeomorphic feedback loops in stressed environments showed that their influence on organisms is scale dependent, and that this scale dependency exerts a major influence on spatial habitat structure [Bouma et al., 2009b; van de Koppel et al., 2012]. An observed reoccurring feature across different species (e.g. salt marsh halophytes or mussels) was a local positive effect (e.g. increased survival through promoted sedimentation within salt marsh tussocks or increased survival through clumping together of mussels), being in opposition to larger scale negative effects (e.g. increased scouring at tussocks edges limiting lateral expansion of salt marsh plants or increased competition for food in mussel patches) [van de Koppel et al., 2012; van Wesenbeeck et al., 2008a]. It was further shown that these interlaced scale dependent feedbacks potentially lead to self-organized landscapes, exerting a major impact on the landscape configuration [van de Koppel et al., 2012]. The ability of biotic-abiotic interactions to form self-organized landscapes is the core of their active role in shaping geomorphologic features [Rodriguez-Iturbe and Rinaldo, 2001; Temmerman et al., 2007].

In order to evaluate the impact of ecosystem engineering (i.e. biogeomorphic feedbacks loops) on organisms and the landscape (i.e. the biotic and abiotic environment), different scales have to be considered and set in context with the influencing surrounding conditions.

Salt marshes and their relevance

Coastal wetlands include salt marshes, mangroves, tidal flats and sea grasses and can be found on all continents and latitudes. They are habitats exposed to different inundation lengths and frequencies and are populated by stress tolerant (salinity and anoxia) vegetation. Generally they can be defined as "ecosystems that are found within an elevation gradient that ranges between subtidal depths to which light penetrates to support photosynthesis of benthic plants and the landward edge where the sea passes its hydrologic influence to groundwater and atmospheric processes" [Perillo et al., 2009]. Their occurrence within estuaries, which is the focus of this study, depends on two conditions; firstly, sediment accretion levels have to exceed the rate of land subsidence and secondly, adequate protection against storms and waves allowing establishment should be present [Wolanski, 2007]. Within coastal wetlands we specifically focus on salt marsh ecosystems, which essentially provide two vital roles. Hydraulically, they protect the coastal zone by dampening waves, storing storm surges and trapping sediments. Ecologically, they form rich habitats for invertebrates and wild herbivores, resting and feeding habitats for migratory birds and nursery habitats for fish [Allen, 2000; Goodwin et al., 2001; Möller et al., 1999]. The economic importance of estuaries and their included salt marsh ecosystems is pointed out by the fact that at present about 60% of the world's population is located next to estuaries [Lindeboom, 2002], which further globally supply 90% of the fisheries in coastal waters [Wolanski, 2007].

We can generally classify the state (active/expanding, stable, eroding/retreating) salt marshes reside in by looking at their margins. Active salt marshes display a threefold continuum at their outer-edge [Allen, 1995]. Starting from the salt marsh, the edge gradational passes down through a patchy zone of pioneer plants into a mudflat of similar to slightly lower slope [Allen, 2000]. This edge configuration is typical for marshes growing seaward and upward (e.g. salt marshes in the Yangtze estuary, Shanghai, China) [Xiao et al., 2009]. An intermediate near-stable case is indicated by rammed margins, that is a marsh bordered by an outer zone with moderate slope marked at right angles by wave induced scour, parallel ridges and grooves with little or no vegetation [Perillo et al., 2009]. The eroding/retreating

case is characterized by eroding, decimetre up to meter high, cliffs [Ke and Collins, 2002]. At these edges, blocks of toppled over marsh silt at the feet of the cliff, often signify marsh retreat (e.g. marshes in the South West Delta of the Netherlands and England) [Bakker et al., 1993; Wolters et al., 2005a]. The marsh state is generally defined by the availability of sediments able to settle on the marsh surface in combination with prevailing conditions (e.g. waves, flow field, bathymetry). Sediment settling is mainly determined by the suspended sediment concentration and the hydroperiod. Previous model studies on salt marsh development showed that differential marsh growth between the sediment trapping marsh surface and the adjoined relatively exposed mudflat can increase wave impacts along the progressively steepening boundary promoting cliff formation [Ollerhead et al., 2005]. This trajectory was described as an intrinsic effect bound to happen once the marsh has built up sufficiently, nevertheless it is strongly dependent on external factors (e.g. geomorphology and hydrodynamic climate), which makes it difficult to predict [Allen, 2000].

Salt marshes are increasingly becoming targets of direct and indirect human influences. Direct influences are exerted on the salt marsh itself, mainly because of their economic importance, e.g. land reclamation for crops and settlements [Chung, 2006], recreation and fisheries and harbours/industry [Allen, 2000; El Banna and Frihy, 2009]. This for instance leads to a closer squeezing of salt marshes next to fixed (armoured) coastlines, preventing them to migrate landwards in the face of changed morphology (shipping channels) or sea level rise (i.e. coastal squeeze) [Winn et al., 2003]. Indirect influences are exerted through perturbations upstream, such as deforestation, overgrazing, road mining [Wolanski, 2007] and dam constructions [Dai et al., 2008]. Both result in altered sediment budgets [S L Yang, 1999b], changed hydrodynamic conditions and therefore altered bio-geomorphologic feedbacks [Fan et al., 2006]. This further translates in changes of their ecosystem services [Costanza et al., 1997]

Salt marshes and Geomorphology

In order to answer the question of how salt marshes are able to shape the resulting landscape configuration, literature provides two contrasting theories.

Traditional literature on salt marsh development assigns a stabilizing role to salt marsh vegetation. Vegetation stabilizes and pronounces (through increased sediment trapping) features already present on tidal flats such as existing tidal channels [Allen, 2000; D'Alpaos et al., 2005]. In recent literature the potential of vegetation inducing scale dependent feedbacks to actively shape geomorphologic features and therefore influence landscape configuration was identified by [Temmerman et al., 2007; van de Koppel et al., 2012]. Through increased sedimentation within patches and increased erosion through flow routing around patches, vegetation is potentially able to initiate tidal channel erosion and therefore holds an active role shaping salt marsh geomorphology. Nevertheless, it is hypothesized that this ability is strongly linked to species properties, hydrodynamics and sediment characteristics.

Aim of the thesis

This thesis aims to enhance the mechanistic understanding of how organisms (plants) are able to shape their environment using salt marshes as model ecosystems. Specifically, I investigated how and under which circumstances interactions between plant species traits and abiotic parameters (such as hydrodynamics and sediment properties) (i.e. biogeomorphic feedbacks) possess the potential to influence the resulting landscape configuration. This examination aims to fill the existing gap in our understanding of how and when biota are able to actively influence landscape development. In order to address this question, I am utilizing a multiple scale approach, combining field manipulative experiments, flume experiments, remote sensing data and modelling approaches. First, I examine how plant traits interacting with the abiotic environment can influence the ability of species to establish and modify their habitat on a small and intermediate scale. Subsequently, I examine the ramifications of these local scale interactions on the spatial development at the landscape scale also considering the abiotic context. This not only increases our understanding of biogeomorphic feedbacks and its influence on landscape development, but also enables us to evaluate the effect of altered biotic and abiotic parameters on ecosystems functions and the landscape configuration (i.e. species invasion, sea level rise, altered sediment budgets).

Salt marsh species and study area

Salt marsh development starts on intertidal flats, which are invaded by vascular halophytic plants forming the so-called pioneer zone. We investigated two predominant pioneer species, *Spartina alterniflora* and *Scirpus mariqueter*, in the Yangtze estuary, China (Fig. 1.1). Both species are autogenic ecosystem engineers, which induce salt marsh formation by trapping sediment and consequently increasing soil elevation. The species differ in their physical and physiological properties (Tab. 1.1). *Spartina* is a fast and high growing plant with stiff above ground biomass. In comparison, *Scirpus* is a slower and lower growing plant with flexible aboveground material [Craft et al., 1999; Sun et al., 2001; Xiao et al., 2010]. Pioneer zones are often characterized by round patchy vegetation fragments, so-called tussocks, scattered over the mudflat, subsequently merging into salt marsh meadows incised by ramified channel systems [Allen, 2000; Temmerman et al., 2007] (Fig. 1.2). Following the pioneer zone state, salt marshes grow vertically and become high marshes dominated by more effective but less stress tolerant species such as *Phragmites australis*.

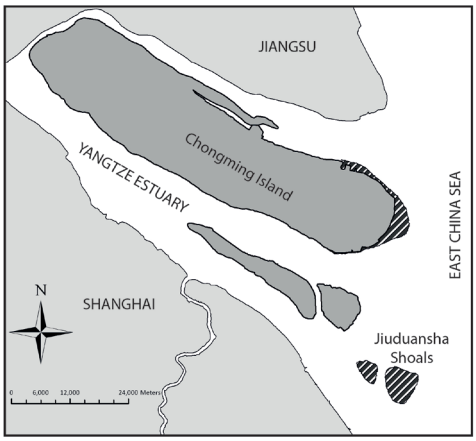


Fig. 1.1 Overview of our research area in the Yangtze estuary, Shanghai, China. Black area with white stripes denotes salt marshes on eastern Chongming Island and the Jiuduansha Shoals.

Study Area

It is noteworthy that our research area (i.e. salt marshes in the Yangtze estuary, Shanghai, China), is receiving enormous concentrations of suspended sediments (accretion 1 mm d^{-1} at marsh sites) [S L Yang and Chen, 1994], provided by the Yangtze River (Fig. 1.1). This enables the salt marshes to grow vertically and laterally, exhibiting lateral marsh expansion rates up to 36 m y^{-1} and therefore

characterizing them as active/expanding salt marshes [Zhu et al., 2011]. Thanks to these conditions, are the Chinese salt marshes exceptionally well-suited locations to study the implications of biogeomorphic feedbacks loops on geomorphology. Geomorphic time scales are significantly sped up. Effects occurring within centuries at salt marshes in the Netherlands (e.g. the Westerschelde estuary with much lower concentrations of suspended sediment) can be observed at a timescale of decades at Chinese salt marshes [De Vriend et al., 2011; B Huang et al., 2008a; C Wang and Temmerman, 2013].

S. alterniflora				***S. mariqueter***			
Parameter	Unit	Value	Ref	Parameter	Unit	Value	Ref
Plant height	m	2.5	1	Plant height	m	0.65	1
Stem density	Stems m^{-2}	800	2	Stem density	Stems m^{-2}	1600	2
Stem consistency		Stiff	1	Stem consistency		Flexible	1
Stem diameter	mm	5.2	4	Max diameter	mm	2.2	4
Vertical growth rate	m y-1	2.5	2	Vertical growth rate	m y-1	0.4	1
Lateral expansion rate	m2 y-1	0.8	1	Lateral expansion rate	m2 y-1	3.1	1
Critical inundation height	m	1.8	2	Critical inundation height	m	2.3	2

Tab. 1.1 Comparison of species traits between *Spartina alterniflora* and *Scirpus mariqueter*, grey background signifies physical plant properties, white background signifies physiological plant properties.

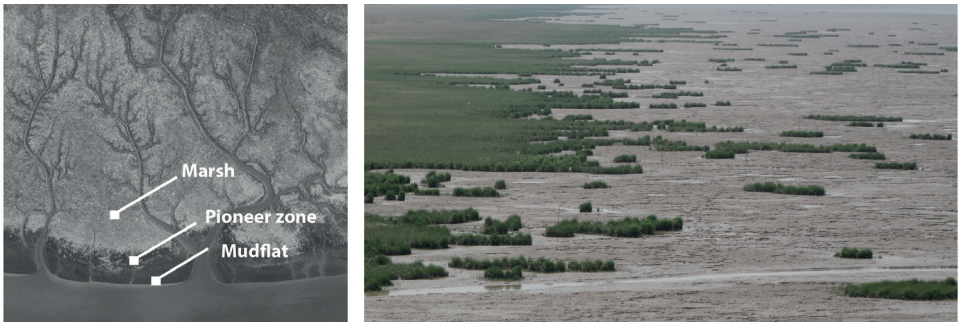


Fig. 1.2 (left) Aerial image of a salt marsh located in the Yangtze estuary, (right) Close up view on the salt marsh pioneer zone in Chongming Island, Yangtze estuary.

Outline of the Thesis

This thesis aims to increase our understanding in how organisms, interacting with the abiotic environment, are able to shape their environment on different spatial scales (Fig. 1.3). First, I investigated whether hydrodynamics and sediment properties are able to influence the survival rates of two contrasting pioneer species (*Spartina alterniflora, Scirpus mariqueter*) (Chapter 2). This established a link between

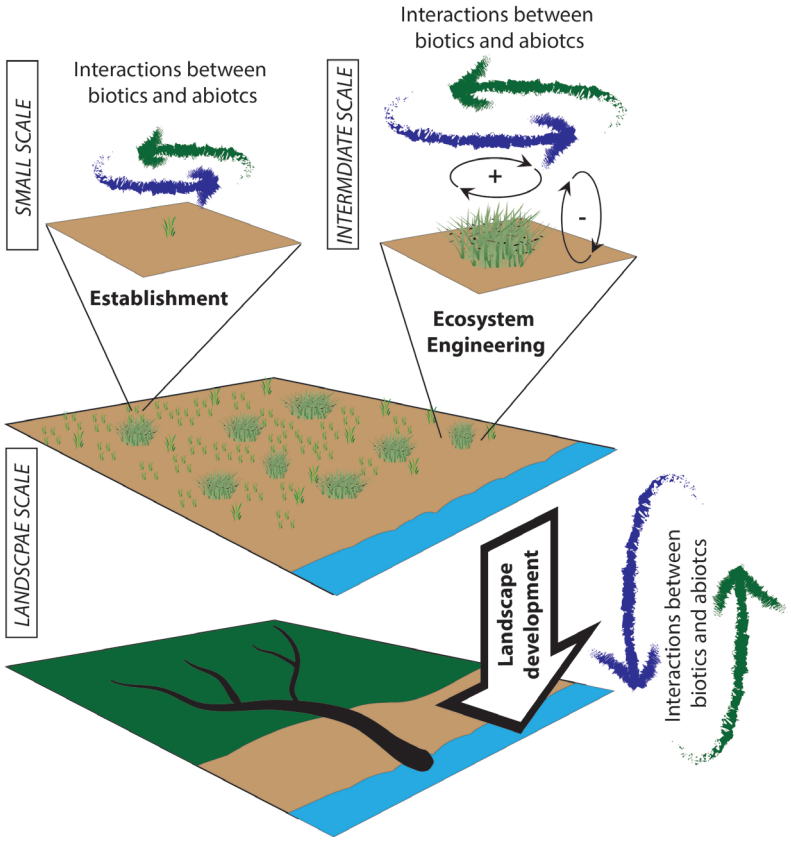
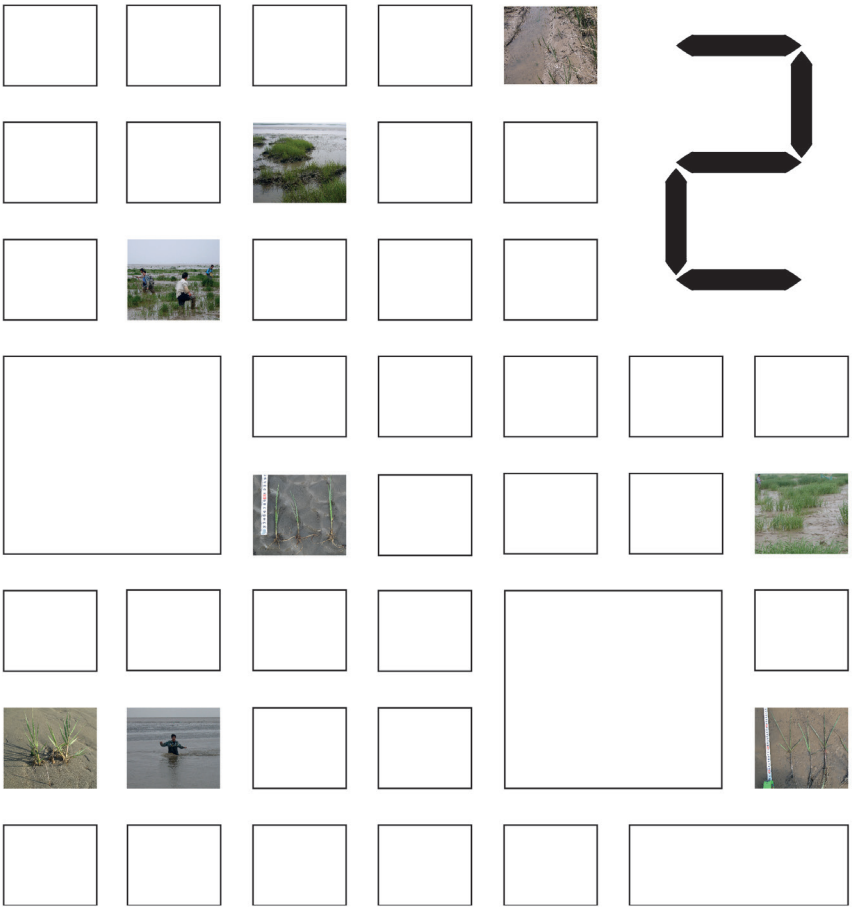


Fig. 1.3 A schematized view of estuarine, intertidal landscape development influenced by biogeomorphic feedbacks across different scales; plants colonize mudflat ecosystems (upper graph), creating saltmarsh pioneer zones colonized by seedlings and tussocks (midddle graph), which finally turn into low and high marshes ramified by intertidal channels (lower graph). All these processes are influenced by interactions between biotic and abiotic properties; Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

physical and physiological species properties and the abiotic conditions and their ability to influence species survival in the field. Second, via laboratory experiments I examined whether sediment properties evoke a physiological growth response within our two investigated species, and whether this growth response influences their resilience against erosion under hydrodynamic stress. Simultaneously we examined how physical plant properties are linked to their ecosystem engineering ability (Chapter 3) (Fig. 1.3). Subsequently, the impact of physical and physiological plant characteristics on the geomorphologic development during a mudflat-salt marsh transition is investigated utilizing a model simulation. I investigated the influence of mudflat bathymetry (i.e. existence of mudflat channels) on vegetation influenced landscape development utilizing a model system with constant abiotic conditions (hydrodynamics forcing and sediments) (Chapter 4). Finally, I explored whether change in plant species predominance (through species invasion) is able to influence geomorphologic features in already established salt marshes. I specifically investigated whether the invasive species *Spartina alterniflora*, because of its different physical and physiological properties compared to the native *Scirpus mariqueter*, is able, via changing biogeomorphic feedback loops, to change already established landscape features (Chapter 5). This underlines the impact of biogeomorphic feedback loops across different landscape scales and development stages.



Abiotic factors governing the establishment and expansion of two salt marsh plants in the Yangtze estuary, China

C. Schwarz, T. Ysebaert, ZC. Zhu, LQ. Zhang, T. Bouma, P. M. J. Herman

Published

Abstract

The survival and establishment of salt marsh plant species is mainly driven by abiotic parameters. These factors can also significantly affect the outcome of competitive interactions between plant species. In this study we identify the effect of abiotic factors such as waves, currents, and sediment properties on plant establishment and development in the pioneer zone at Chongming Island, Yangtze estuary. Different propagules (seedlings, rhizome fragments, complete tussocks) of the species *Spartina alterniflora* and *Scirpus mariqueter* were planted at sites differing in current velocity, wave height, and sediment composition. Survival was strongly size-dependent, with very few of the smallest stage (seedlings) surviving. Survival of the native species *S. mariqueter* was higher than that of the invasive species *S. alterniflora*. Survival and lateral expansion rate of the experimental plants was highest at the site with lowest tidal currents, and lowest at a strongly wave-dominated site. We suggest that competitive interactions between the species are governed by plant-abiotic interactions influenced by both plant morphology and growth rate. Further we discuss the implications of these findings on the large-scale patterns of vegetation at this salt marsh.

Introduction

Increasing human mobility has caused species introductions in previously unconnected areas [Vitousek et al., 1997]. Over the last decade, there has been a growing concern that invasive species can have a major impact on biodiversity and ecosystem functioning. Understanding the spread of invasive species becomes more and more important for wetland conservation and management [Ruiz and Carlton, 2003]. One of the most examined invasive species in intertidal coastal wetlands is *Spartina alterniflora* (Poaceae). *Spartina alterniflora* is a perennial rhizomatous cord grass native to the coasts of North America [Simenstad and Thom, 1995; Teal, 1985]. It is a strong ecosystem engineer [Crooks, 2002], which similar to other *Spartina* species reduces erosion and enhances sediment accretion [Bouma et al., 2009a; van Hulzen et al., 2007]. This ability to accrete sediment is the main reason this species was introduced worldwide and has resulted in rapid expansion and invasion in many wetland ecosystems [Balletto et al., 2005; J Callaway and Josselyn, 1992; B Li et al., 2009]. The ability of *Spartina* species to modify its habitat by accumulating sediment is mainly due to its morphology [Bouma et al., 2005b; van Hulzen et al., 2007]. The aboveground parts of *S. alterniflora* can reach heights of 1–3 m, consisting of stiff stems with hard leaves of 30-90 cm lengths. Belowground, *S. alterniflora* forms extensive rhizome networks in the upper 10–30 cm of the soil. Rhizomes are also used as clonal reproduction organs. At the end of the growing season (April to November, China) most of the ramets die off, but leave behind large amounts of standing dead litter with a low decomposition rate [Liao et al., 2008; Q Wang et al., 2006]. The mechanism by which *S. alterniflora* spreads and outcompetes native vegetation is however not always clear.

Spartina alterniflora was originally introduced in eastern China in 1979 [An et al., 2007; B Li et al., 2009], and first found in salt marshes of the Yangtze estuary in the 1990s [H M Huang and Zhang, 2007]. In 1995, it was first observed on the salt marshes of eastern Chongming Island, one of the main islands in the mouth of the Yangtze estuary. It was suspected to have arrived through natural dispersal from populations in Jiangsu province [Chen et al., 2004; B Li et al., 2009]. In 2001 *S. alterniflora* was also intentionally introduced to eastern Chongming Island, and

within only one decade it became the dominant plant species in the salt marsh pioneer zone across the whole estuary [Chen et al., 2004; H M Huang et al., 2008b; B Li et al., 2009]. This was achieved mainly through outcompeting the indigenous species Phragmites australis in the more brackish part of the estuary and especially *Scirpus mariqueter* (*Cyperaceae*) in the areas with higher salinity. *Scirpus mariqueter* is a long-lived rhizomatous corm forming plant that inhabits the pioneer zone of salt marshes in the Yangtze estuary [Sun et al., 2001; M Yang et al., 2009]. Reproduction of *S. mariqueter* occurs sexually through seeds and asexually through corms. The aboveground shoots are usually 10 to 80 cm high and composed of two leaves. The growing season lasts from May to October, ending with the dying-off of all aboveground parts, while the belowground parts overwinter [C H Wang et al., 2009]. *Spartina alterniflora* locally excluded *S. mariqueter*, forming dense monocultures, but in some areas *Spartina – Scirpus* mixtures do occur. Where both species co-occur, their different growth forms become obvious, with *S. alterniflora* being much taller and more stiff compared to *S. mariqueter*.

Previous studies in the Yangtze estuary showed that the observed expansion patterns of *S. alterniflora* on Chongming island cannot be explained by sexual reproduction (seed dynamics) [Deng et al., 2009; Xiao et al., 2009], range expansion behavior [Xiao et al., 2010], or competitive exclusion of its native competitor (*Scirpus mariqueter*) [B Li et al., 2009] alone. In the pioneer zone, none of these characteristics points to *S. alterniflora* as the superior species bound to win the competition. Other studies indicate that survival and establishment of salt marsh plants in the pioneer zone also depends on the interaction between hydrodynamic energy from currents and waves with the characteristics of the plants (size of the propagule, stiffness of the growth form) and with other abiotic characteristics, such as sediment composition [Bouma et al., 2005b; van Hulzen et al., 2007; van Wesenbeeck et al., 2008a]. The importance of such feedbacks in the displacement of *S. mariqueter* by *S. alterniflora* have not yet been investigated. Compared to most estuaries around the world, the present study site is unique in that it is has a very high sediment load delivered from the Yangtze-river, leading to exceptionally high accretion rates at the marsh (4–14 cm $year^{-1}$) [S L Yang, 1999c]. Hence, vegetation-geomorphology feedbacks may be expected to have strong impacts on short time spans, making this a potentially important factor in understanding the displacement of *S. mariqueter* by *S. alterniflora*.

In this study, we investigate the interaction between hydrodynamics and plant characteristics as a mechanism to explain the rapid expansion of *S. alterniflora* at the expense of *S. mariqueter*. We study these interactions by quantifying the survival of *S. alterniflora* and *S. mariqueter* transplants of three different size classes at hydrodynamic contrasting pioneer zones of eastern Chongming Island. We varied the size of propagules in transplanting experiments, from single small seedlings to clonal fragments and tussocks of up to 10 cm diameter. Furthermore, we chose experimental field sites differing in current and wave stress. Its spatial orientation, with tidal and salt-water dominance in the north and river and wave dominance in the south leads to gradients in sediment properties, hydrodynamics, and salinity [Chen et al., 2004] over relatively short distances. This experimental design enables us to test the influence of various abiotic factors on the establishment, survival, and expansion of these salt marsh species.

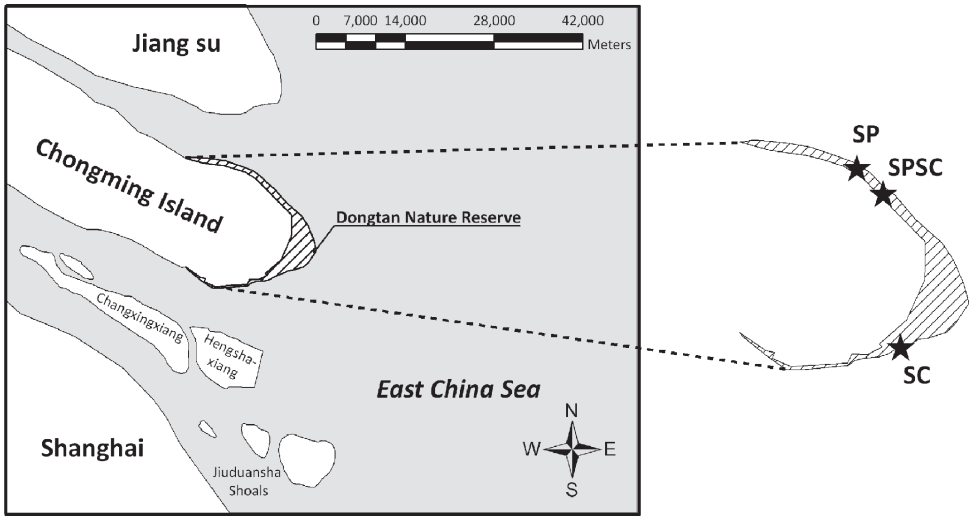


Fig. 2.1 Overview of the research area including experimental sites in the Chongming Dongtan Nature Reserve; *Spartina* front (SP), mixed *Spartina* and *Scirpus* front (SPSC) and *Scirpus* front (SC)

Methods

Field site

The Yangtze River, originating on the Tibetan plateau and flowing out into the East China Sea, is the longest river in China and one of the largest rivers in the world. Located at its mouth is the Yangtze estuary, a meso-tidal estuary with semidiurnal tides, covering large areas of Shanghai and Jiangsu province. The estuary's upper boundary is located at Datong, 624 km upstream. Its mouth is located at the shallow mouth bars in the East China Sea. The adjacent submerged delta is the major area of sedimentation, fed by silt transported by the Yangtze River [Z Gao and Zhang, 2006; Liu et al., 2010; Mikhailov et al., 2001]. There are several alluvial islands existing in the Yangtze estuary, Chongming Island being the oldest and largest Island [B Li et al., 2009] (Fig. 2.1).

It has a northern sub-tropical monsoon climate, with an average humidity of 82%. The average summer temperature is 26 °C. The average winter temperature is 15.3 °C. Annual precipitation is 1022 mm on average, 60% of which falls in the months May to September [Xiao et al., 2009]. A speciality of the climate in the Yangtze estuary is the so-called Mei-yu period, the main annual rainy period. It lasts for approximately three weeks and contains most of the heavy rain events of the year, accounting for on average 20% (217 mm) of the yearly precipitation. The beginning and end of the Mei-yu period is subject to fluctuations from year to year. Its onset can vary from late May to mid July and its end can vary from mid June to early August [Qin and Duan, 1992].

Establishment and Lateral expansion:

To investigate the influence of various abiotic parameters (sediment properties, wave stress, and current stress) on plant establishment, planting experiments with the two species at three different locations were conducted. The sites were chosen according to differences in hydrodynamic properties (wave and current magnitudes), sediment composition (median grain size (d50), sediment cohesiveness) and present plant community. Field site observations showed that within the large-scale plant

community patterns (*Spartina* dominating the northern part, *Scirpus* the southern part) [C H Wang et al., 2010a] the pioneer zones showed even more variation. Three types of growing fronts within the pioneer zone could be identified: (1) *Spartina* front (SP), (2) mixed *Spartina* and *Scirpus* front (SPSC), and (3) *Scirpus* front (SC). These different fronts also show different seed bank characteristics and growth velocity towards the seaward boundary [Xiao et al., 2010]. Transplants of three different biomass classes of the two plant species were planted in May 2010 on the mudflat adjacent to the pioneer zone at three different locations, each representing one type of observed vegetation front. The biomass classes included seedlings, small clonal fragments (further referred to as rhizomes), and large clonal fragments (further referred to as tussocks). The three biomass sizes are a good representation of natural ways of recruitment for these two species [Ranwell, 1964; Sun et al., 2001; van Wesenbeeck et al., 2008a]. Seedlings represent natural sexual reproduction. Rhizomes or tillers can break off and get dispersed [Ranwell, 1964] and then act as a dispersal unit. Finally, bigger units can also act as dispersal agents, spreading during times of high hydrodynamic energy, (e.g., during storms with high waves) justifying our third class of dispersal unit. The distance from the marsh was chosen according to a previously available elevation survey, guaranteeing that the dispersal units would receive the same amount of inundation stress. Note, however, that in practice some differences in elevation existed between the three locations, presumably as a consequence of deposition between the time of elevation measurements in 2010 and the establishment of the experimental units.

Seedlings, rhizomes and tussocks were taken from one single area in the case of *Scirpus mariqueter*. In case of *Spartina alterniflora*, due to logistic constraints, dispersal units were taken from two areas comparable in terms of relative distance to the marsh edge, coverage, and inundation stress. The seedlings selected had a maximum height of 10 cm, an already developed primary root system but no identifiable rhizome parts. Rhizome fragments had a plant height of 10–15 cm with already developed roots holding a rhizome of approx. 10–15 cm length with one to three green stems. Tussocks were defined as larger clonal fragments of 20x20 cm dimension, extracted from existing vegetation in the pioneer zone. At sites SP and SPSC, both species were planted. This was not possible, however, at site SC, where the experiment would risk introducing *Spartina* in an area where it does not yet occur. At the sites

SP and SPSC, the three dispersal classes were planted in a randomized block design (7x7 grid) with three replicate blocks parallel to the coastline (see Fig. 2.2). The minimum inter-distance between the dispersal units was chosen to be 3 m. These inter-distances were chosen according to existing literature on lateral expansion velocity, to keep the mutual disturbance to a minimum (2.0–2.70 m.yr^{-1} lateral expansion of *S. alterniflora* within one growth season [Xiao et al., 2010]). Each block (containing 49 dispersal units) consisted of 9 seedlings, 10 rhizomes, and 6 tussocks for *Spartina alterniflora* and 9 seedlings, 9 rhizomes, and 6 tussocks for *Scirpus mariqueter*. For practical reasons, only 6 tussock fragments per block were planted, while the other stages had higher representation. At the SC site, 14 seedlings, 12 rhizomes, and 10 tussocks of *S. mariqueter* were planted on a random 6x6 grid with two replicate blocks at three distances to the marsh edge. Because of the low survival rates and similar survival curves (statistically not different) the two replicates at three marsh distances were pooled and further regarded as one observational site.

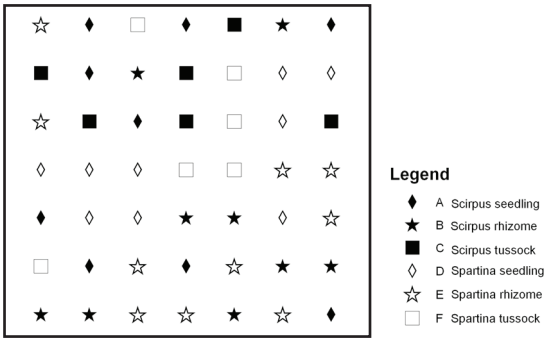


Fig. 2.2 Experimental setup at the SP and SPSC site, block design

After planting, presence/absence of the different planted units was measured on a monthly bases and lateral expansion was measured at the beginning and the end of the observation period (5 months). Survival data was analysed in Matlab® performing log-rank tests using Kaplan-Meier estimates of the survival functions [Gardillo, 2008].

Abiotic parameters:

We measured sediment characteristics and hydrodynamic forcing (i.e., tidal currents, wave action) to describe the environmental factors driving species survival and expansion. Sediment samples (5 replicates) were taken of the top 3 cm layer at

each site and analysed for its grain size distribution, using a Beckman-Coulter® LS 13320 particle size analyser. The resulting data was analysed in Matlab® using Ternary plots [Waite, 2006].

Currents and waves were measured over a spring-neap cycle in the Mei-yu period (9th of July – 20th of July) parallel to the three different locations. Current parameters were assessed using an Aquadopp® HR 2Mhz current profiler (downward looking 60 cm above the bottom surface, minimum cell size= 3 cm) at the SP-site, an Aquadopp® HR 1Mhz current profiler (downward looking 60cm above the bottom surface, minimum cell size= 3 cm) at the SPSC-site and a Sontek® XR current profiler (upward looking, minimum cell size= 20 cm) at the SC-site. Over the same period, wave parameters were measured using three Seabird® SBE 26plus wave sensors deployed directly on the marsh surface. All measurements were filtered according to signal quality thresholds suggested by the manufacturer and by previous literature in Matlab® [Cheng et al., 1999; Horstman et al., 2010]. Wave energy was computed using the manufacturer's software of the SBE26plus, calculated via the spectral wave density function. For statistical analysis, the non-parametric Kruskal-Wallis test was used because the data was non-normally distributed (significance level; 0.05).

Results

Survival:

Bigger dispersal units (especially tussocks) showed higher survival rates at all sites, as demonstrated by the survival curves (Fig. 2.3). Log-rank comparisons show that tussocks have significantly higher survival than all other dispersal units. The highest survival rates can be observed at the SPSC site, where all dispersal units of *Scirpus* and also the tussock dispersal units of *Spartina* exhibit the highest survival rates. Survival rates of all *Scirpus mariqueter* dispersal units were significantly higher than the corresponding units of *Spartina alterniflora* at the field sites SP and SPSC (Fig. 2.3), except for seeds at site SP (seedlings of both species had disappeared during the first month) and tussocks at site SPSC where survival of both species was very high. No *Spartina* seedlings survived the first observational time step. *Scirpus*, which is the only species we were able to plant at all three locations, performed best at the SPSC site and worst at the SC site.

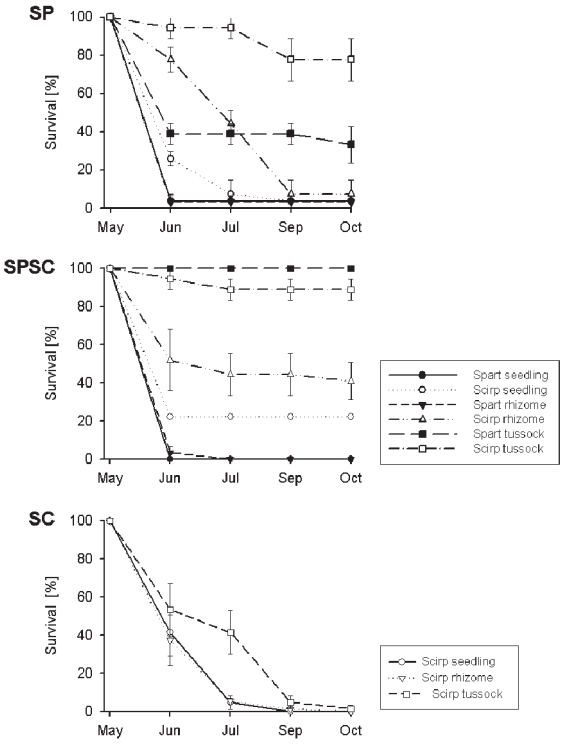


Fig. 2.3 Survival curves of *Spartina* and *Scirpus* dispersal units at sites SP, SPSC and SC (the latter only having *Scirpus* stages). Mean and standard error of the pooled replicates are shown.

Lateral expansion:

The lateral expansion rates showed a clear difference between species and sites, with a much larger lateral expansion of both species at the SPSC site compared to the SP site and with *Scirpus* expanding at a faster rate than *Spartina* (Fig. 2.4). Lateral expansion at the SC site was estimated as zero, since the low survival rate did not allow to measure any lateral expansion. Fig. 2.5 illustrates the large differences in lateral expansion between the sites.

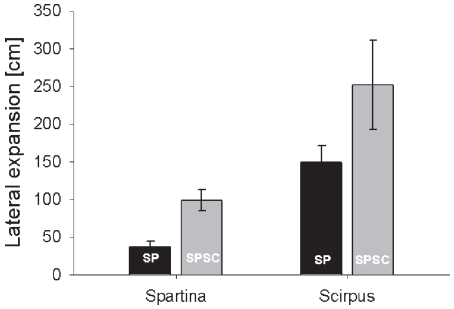


Fig. 2.4 Lateral expansion of tussock diameters 5 months after planting, SC site not shown since the low survival did not allow to measure lateral expansion rates, mean and standard error of the measure replicates polled per site are shown

Fig. 2.5 Comparison between lateral expansion: (a) *Spartina* at the SP site (8.Oct.2010), (b) *Scirpus* at the SP site (8.Oct.2010), (c) *Spartina* at the SPSC site(9.Oct.2010), (d) *Scirpus* at the SPSC site (9.Oct.2010);

Sediment properties:

Analysis of the sediment samples taken at the three sites, showed a large difference in grain size distribution between the more muddy northern part (SP, SPSC; d50=6.46 ± 0.24 and 8.83 ± 0.66 µm, respectively) and the more sandy southern part of the eastern Chongming salt marsh (SC; d50=63.8 ± 2.81 µm) (Fig. 2.6). Clay content was very low at the SC site; the sediment was clearly non-cohesive. At SPSC and SP sites, clay content was higher and it exceeded the threshold level of 7.5%, which delineates cohesive from non-cohesive sediments according to [van Ledden et al., 2004].

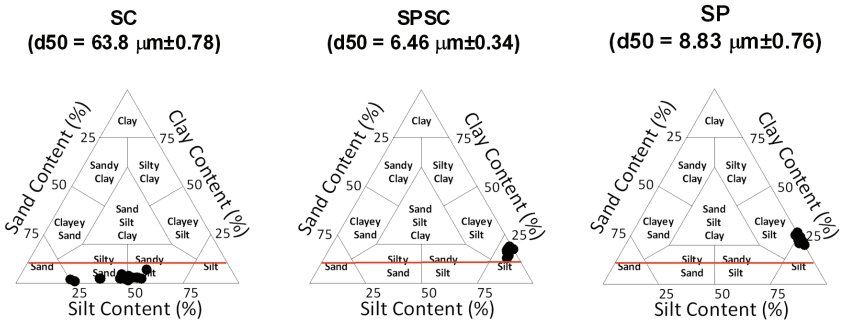


Fig. 2.6 Shepard-Ternary-Plot showing sand-silt-clay ratios at the experimental sites. Red line delineates cohesive and non-cohesive sediments according to a critical clay content of 7.5 %.

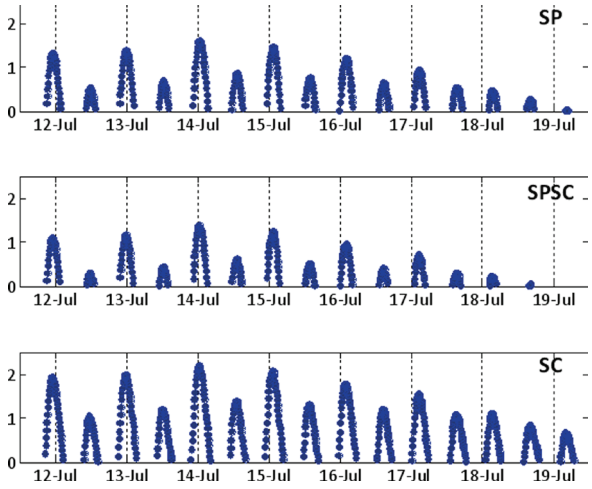


Fig. 2.7 Water level measurements at experimental sites

Hydrodynamic properties

Water levels showed tidal ranges typical for a meso-tidal estuarine system (Fig. 2.7). The two northern sites showed similar maximum inundation heights (SP, 1.69 m and SPSC, 1.53 m), whereas the southern site showed a clearly higher inundation height (SC, maximum 2.2 m).

Currents

Comparison of current velocities showed that during spring tide, maximum current velocities during ebb and flood flow at the SP site (0.72 ms^{-1}) were higher than at the SPSC (0.52 ms^{-1}) and SC site (0.62 ms^{-1}) (Fig. 2.8–2.9). The box plots in Fig. 2.9 show a similar distribution between the flood current velocities of site SP and SC, whereas the SPSC exhibits a clearly lower maximum velocity. They further show that tidal currents tend to be flood-dominated at site SP, and ebb-dominated at the other two sites, in accordance with the pattern shown in Fig. 2.8.

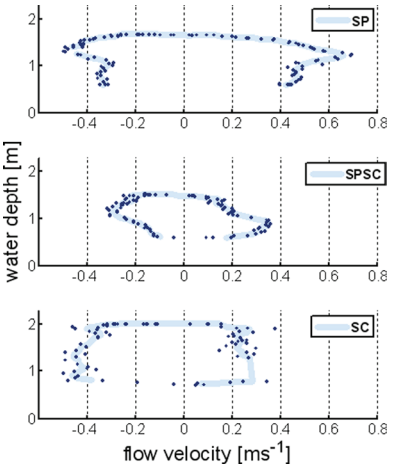


Fig. 2.8 Current velocity measurements at highest high tide; negative values represent the incoming tide, positive values the outgoing tide; dark blue points represent measured velocity time-points; thick light blue line represents the moving average

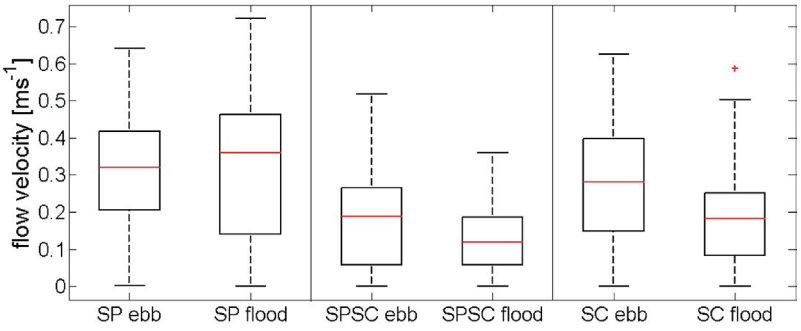


Fig. 2.9 Current velocity distribution over measured spring-neap cycle, separated in ebb and flood velocities per site, The central red mark represents the median; the edges of the boxes are the 25th and 75th percentiles; whiskers are the most extreme data points not considered as outliers, and outliers are plotted individually

Waves

A comparison between the wave characteristics observed at the three sites showed significant differences in wave heights (not shown) and wave energy from the northern to the southern parts of the salt marsh (Fig. 2.10). Mean significant wave heights at 0.3, 0.5, and 0.7 m water levels ranged from 0.11, 0.22, and 0.24 m at SP site, to 0.16, 0.31, and 0.35 m at SPSC site, to 0.21, 0.36, and 0.38 m at SC site. Wave energy (Fig. 2.10) and wave height showed an increasing trend from north to south. This trend was consistent when comparing wave characteristics at different water levels (0.3, 0.5, 0.7 m). The observed succession in wave stress can be explained through the predominant southeast wind direction within our observational period and the spatial arrangement of our planting sites.

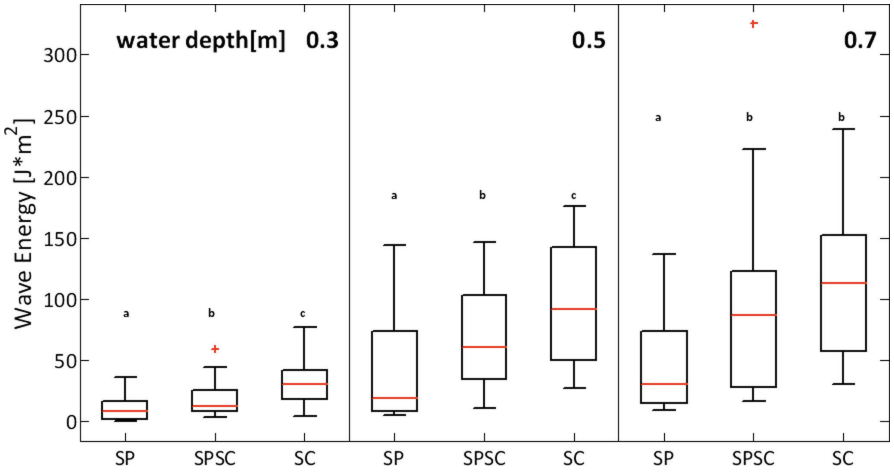


Fig. 2.10 Comparison of wave energy at three different water levels (0.3, 0.5, 0.7m) between the three different experimental sites, the central red mark represents the median; the edges of the box are the 25th and 75th percentiles; whiskers are the most extreme data points not considered outliers, and outliers are plotted individually. Different lowercase letters denote significant differences between species

Discussion

Gradients in abiotics and plant survival:

The three experimental locations along a north-south gradient of the eastern Chongming Island showed clear differences in hydrodynamic conditions and grain size distributions. Compared to the SP site, the SPSC site had lower currents but higher waves. Both sites have fine cohesive sediments, but the SP site has the highest clay content and overall the finest sediment composition. The SC site in the south was characterized by the highest waves. Currents at this site were intermediate in strength between the SP and SPSC sites. It seems that the coarseness of the sediment correlates much better with wave height than current velocity. Sediments are coarser in the sequence SP, SPSC, SC; wave height also increases in this sequence. The increase in grain size in southerly direction on eastern Chongming Island was also previously suggested by [S L Yang et al., 2008].

The survival of plant dispersal units followed a different sequence. Survival of all *Scirpus* stages was lowest at SC, where even tussocks did not survive the experimental period. However, the overall survival seemed to be higher at SPSC than at SP. The difference was significant over the entire period for *Spartina* tussocks, but not for the other stages. However, at SPSC there seems to be a difference between the first month of observation when mortality was high and later, when minimal mortality was observed over the different species and stages (Fig. 2.3). This contrasts with station SP, where mortality of smaller stages (seedlings and rhizomes) continued over summer. It is possible that the higher waves measured during the Mei-yu period at SPSC were not present during the whole summer, whereas the difference in tidal currents presumably is much more constant. However, wind statistics for the Shanghai area show very little seasonal variation in wind speed. Wind direction switches from predominantly NW during winter, to predominantly SE during summer. The transition is in March and October (www.windfinder.com). Over the growing season, winds are relatively predictable and similar to the winds measured during our study period. Also judging from lateral expansion rates, growth conditions at SPSC seem to be better than elsewhere. Presumably the lower tidal currents at

this station than at the other stations have more effect on growth conditions than waves, even if waves seem to correlate better with the sediment structure.

Size thresholds to plant survival:

Our results indicate the existence of a size threshold influencing the survival functions of the dispersal units. This is evident through the higher survival rates of the bigger dispersal units (especially tussocks) at all experimental sites (Fig. 2.3) Seedlings of both *Spartina alterniflora* and *Scirpus mariqueter* showed almost no survival in our experiment. Possibly in this system seeds are not the main dispersal unit, as is also suggested by the discrepancy between seed production and soil seed bank [Xiao et al., 2009]. This is probably caused by hydrodynamic disturbances influencing the upper sediment layers and therefore circumventing seed settlement and burial. Likely candidates for main dispersal units are detached rhizome fragments, which have a greater chance to develop a sufficient root network before the aboveground parts start emerging. However, an alternative explanation for the low survival of seedlings is the relatively late planting of the dispersal units in May, which is already at the beginning of the Mei-yu period. The time may have been too short for the root network to develop sufficient anchorage to the soil, keeping in mind *S. mariqueter's* comparatively late germination start at the beginning of May [C H Wang et al., 2009]. This explanation would imply that only early germinating seedlings would have a chance of survival. This hypothesis is strengthened by the known early germination start of *S. alterniflora* at the beginning of April [C H Wang et al., 2009; Xiao et al., 2010] and the measured higher survivorship of *Spartina* seedlings (60% to 75.3%) at SP and SPSC sites [Zhu et al., 2011].

The existence of a size threshold influencing plant survival in salt marsh pioneer zones is in agreement with previous studies on salt marsh dynamics [van Wesenbeeck et al., 2008a]. It implies that young stages have a window of extreme vulnerability where physical disturbance may easily inhibit survival. All other factors kept equal, rapid growers have an advantage under such conditions, since they will be the first to escape this window of vulnerability. However, apart from growth rate, the inherent vulnerability of the seedling may also be important. In our experiment, the only seedlings surviving are 20% of *Scirpus* seedlings at the SPSC site. But at the SP site

the *Scirpus* seedlings also exhibit a (non-significant) tendency of a higher survival than the *Spartina* seedlings. It is possible that the growth form of *Scirpus*, with more flexible plants, makes the seedlings less vulnerable to erosion [Bouma et al., 2009a].

Unravelling the displacement of *S. mariqueter* by *S. alterniflora*:

With the experimental results showing better survival of *Scirpus*, even at the site where *Spartina* dominates the pioneer zone, it is not easy to explain the occurrence of both species in nature. One explanation could be that *Spartina*, which germinates earlier than *Scirpus*, has larger seedlings by the time of the worsening of weather conditions in the Mei-yu period and therefore profits from size-dependent survival [C H Wang et al., 2009]. The combination of *Spartina's* earlier start of its growing season, together with its faster growth rate [Q Wang et al., 2006], the higher tolerance to inundation and salinity stress [C H Wang et al., 2010a] and the higher sediment trapping efficiency [H Li and Yang, 2009], might explain the observed dominance of *S. alterniflora* throughout the Yangtze estuary and other parts along the Chinese coast.

The fact that *Scirpus* exhibited higher survival in the pioneer zone than *Spartina* at all sites, but is still not able to outcompete this strong ecosystem engineer at some sites, might also be explained through a facilitation effect of *Scirpus*. Although better able to cope with abiotic stress at initial settlement, the species does not form as dense a grass mat as *Spartina* does (Fig. 2.4). Presumably, its tussocks are relatively easily invaded by the taller, faster growing *Spartina*. Facilitation by a pioneer species that makes way for the dominant competitor, which itself is restricted by physical conditions, is a well-known pattern in salt marshes [Castellanos et al., 1994].

The higher dominance of *Scirpus* at the more southern stations could be related to the higher wave stress at these locations. The stiff plant parts of *Spartina* are exposed to substantial drag in strong waves [Mullarney and Henderson, 2010], which is a disadvantage compared to the lower drag experienced by more flexible species like *Scirpus* [Bouma et al., 2005b]. The absence of *S. alterniflora* in the southern part of Chongming Island might in addition also be a consequence of the salinity gradient (north 5 g/kg soil; south 0.5 g/kg soil) [Y Li et al., 2010b] and extensive buffalo grazing in this area [B Huang et al., 2008a].

Conclusion

Our findings suggest that waves and currents may differently influence plants and sediments. Moreover, competitive interactions either through a facilitation strategy or via size-dependent survival and differential germination patterns, are more complicated than simple differences in survival of abiotic stress, setting previous studies on abiotic interactions into new perspectives [C H Wang et al., 2010a]. Further, our results question the possibility of *Spartina's* establishment in the southern part of Chongming Island, where *Spartina* in spite of its stronger ecosystem engineering capability, still did not succeed in outcompeting *Scirpus* [R Z Wang et al., 2010b]. We suggest that plant traits (competitive strength, ecosystem engineering capability) and abiotic interaction patterns always have to be thoroughly considered before being able to determine their degree of influence on plant zonation patterns and competitive outcomes. This underlines the importance of an integrated approach utilizing a combination of correlative and experimental studies to unravel complex biotic-abiotic interactions.

Plant traits and sediment characteristics influencing species establishment

C. Schwarz, LQ. Zhang, T. Bouma, T. Ysebaert, P. M. J. Herman

Abstract

The salt marsh plants *Spartina alterniflora* and *Scirpus mariqueter* are dominant pioneer species found on salt marshes in the Yangtze estuary, China. They differ in physical (e.g. stiffness) and physiological (e.g. stress tolerance) plant properties, potentially influencing their ability to establish in different habitats and to engineer their environment through biogeomorphic feedbacks. In this study we use laboratory experiments to test seedling resilience of these two species against erosion under current stress in different sediment types representing the range in their natural habitat. We further investigate in flume experiments how their physical plant properties (i.e. stiffness) influence their engineering ability under different hydrodynamic conditions (i.e. water level). The experiments were utilized to investigate how interactions between abiotic and biotic parameters influence establishment thresholds and the ability of the two species to engineer their environment. Our results indicate that not only physical plant properties such as stiffness but also physiological plant properties such as adapted root morphology due to sediment properties in combination with abiotic factors (sediment and hydrodynamics) exert a major control on species establishment thresholds. We further establish a link between ecosystem engineering ability and physical plant properties (i.e. stiffness) and show its influence on species establishment. Finally we use our insights about interactions between plants, sediment and hydrodynamics to explain species expansion trajectories in their natural habitat. The upscaling of our results proposes impacts of biogeomorphic feedbacks (i.e. ecosystem engineering) on landscape development adding important information for marsh restoration and management.

Introduction

The field of biogeomorphology investigates the interaction between ecology and geomorphology and its impact on landscape development [Hupp et al., 1995; Phillips, 1995; Stallins, 2006]. Within the framework of biogeomorphology, ecosystem engineering is a key concept describing the impacts of organisms on their immediate surroundings. Organisms (e.g. plants) can, through altering their immediate surroundings, invoke positive feedbacks improving living conditions for themselves and potentially associated species [Jones et al., 1994; Mullan Crain and Bertness, 2006]. Biogeomorphic feedbacks loops (i.e. the interaction between biotic and abiotic ecosystem processes) shape a variety of coastal and inland habitats, such as river ecosystems or salt marshes incised by ramified tidal channel networks [Tal and Paola, 2007; Temmerman et al., 2007]. Ecosystem engineering introduces spatial heterogeneity and affects ecosystem services, such as nursery habitats for fish and birds, recreation areas, sediment and nutrient sinks and coastal protection [Borsje et al., 2011; Costanza et al., 1997; Gedan et al., 2011; Ma et al., 2007].

Coastal ecosystems, for instance salt marshes, are highly stressed environments. Currents, waves, salinity, soil moisture and sediment accretion/erosion create stress gradients along which stress dependent plant species zonation develops [Marani et al., 2013; Moffett et al., 2010]. These zones, often consisting of a single plant species [C H Wang et al., 2010a], can be used as simplified systems to study biogeomorphic feedback loops and to identify specific factors influencing them.

Seedling establishment is a crucial step in dynamic coastal ecosystems (e.g. salt marshes, mangroves) to enable vegetation succession. Previous studies focused on the impact of hydrodynamics (i.e. hydroperiod, currents and waves), salinity, temperature and soil moisture on seedling establishment [Corenblit et al., 2007; Patterson et al., 1997]. Subsequently literature has shown that initial seedling settlement and therefore plant species establishment is strongly dependent on interactions between sediment dynamics and hydrodynamic conditions (i.e. currents, waves). It was specifically shown that settlement of seedlings on mudflats can only take place during periods of low hydrodynamic stress, called windows of opportunity [Balke et al., 2011]. After this bottleneck was passed temporarily established seedlings were shown to be still

vulnerable to sediment dynamics (accretion/erosion) and hydrodynamics (waves). The magnitude of this vulnerability was shown to be strongly dependent on species specific plant traits (physiological plant properties such as growth velocity) [Balke et al., 2013]. These results suggest that also sediment properties might influence this relationship, because both plant growth rate and plant-hydrodynamics interactions may depend on sediment type.

Once established, salt marsh plants tend to form round patchy vegetation units, so called tussocks, scattered over the mudflat [Allen, 2000; Castellanos et al., 1994]. At this development stage (intermediate scale) the interaction between plants traits and abiotic factors (such as currents and sediment properties) continues to exert a major control on the plant's ability to permanently establish and to ecosystem engineer its environment [Schwarz et al., 2011; van Wesenbeeck et al., 2008a]. Literature describes the outcome of ecosystem engineering to be dependent on the abiotic setting (i.e. currents and sediments), species traits and the considered scale, further referred to as context dependency [Jones et al., 2010]. The context dependent outcome of ecosystem engineering at different scales was shown through scale dependent feedbacks observed at established plant tussocks. Tussocks exhibited a small-scale positive feedback (improving living conditions) via promoted accretion (through reduced hydrodynamics) within their patches. This was in contrast to a large-scale negative feedback (deteriorating living conditions) via induced erosion (i.e. scouring, through flow routing) at their edges [van Wesenbeeck et al., 2008b]. Recent studies on context dependency showed that physical plant traits (such as stem stiffness) have a strong influence on an organism's ability to ecosystem engineer its surroundings. Stem stiffness is an important parameter for the interaction between plants and currents. Stiffer plants exhibit a higher ecosystem engineering ability than flexible ones [Bouma et al., 2010; Bouma et al., 2009b], due to a stronger dampening of hydrodynamic energy. This higher ecosystem engineering ability comes at a cost. High ecosystem engineering ability entails higher drag forces exerted on the plant and its root network and therefore increases its probability of being uprooted [Bouma et al., 2005b]. These studies focused on two aspects of interactions between plant traits and hydrodynamics; their direct effect on plant structures (increased drag and consequently uprooting probability), and their influence on the small-scale positive feedbacks i.e. increased sedimentation between stems due to reduced hydrodynamic

stress (promoted accretion) [Bouma et al., 2005b; Bouma et al., 2009b; Nepf, 1999]. It can be expected that this relation is also context dependent, but this has not been investigated so far.

In this study we first investigate how the combination of different plant traits and different sediment properties (Mud, most cohesive; MuddySand; SandyMud; Sand, most non-cohesive) under hydrodynamic stress is able to influence plant survival. We measured the influence of bottom sediment properties on the ability of plants to withstand erosion under current stress. We subsequently linked this ability to withstand erosion to plant traits such as stem stiffness and plant growth response to different sediment types. We used two contrasting salt marsh species in our experiments. The stiff *Spartina alterniflora* (further referred to as *Spartina*) and the flexible *Scirpus mariqueter* (further referred to as *Scirpus*) are grown on different sediment types, representing the sediment range encountered in their natural habitat (i.e. salt marshes in the Yangtze estuary, China). The two species differ in physical properties of the aboveground material (stiffness, maximum plant height, maximum stem diameter), the belowground material (root network organization) and in physiological properties such as growth velocity and stress tolerance (e.g. salinity) [He et al., 2012; Sun et al., 2001].

After investigating the impact of biotic-abiotic interactions on seedling establishment, we explore the influence of biotic-abiotic interactions (i.e. biogeomorphic feedbacks) on the ecosystem engineering ability of established seedlings (i.e. tussocks, intermediate scale). We are specifically investigating the influence of plant traits (stiffness) on large-scale negative feedbacks exerted by established tussocks, namely induced scour at their edges, under different abiotic conditions of water level and current flow. For this purpose we conducted a flume experiment with our two contrasting plant species (*Scirpus* and *Spartina*), inducing sediment movement (local scour) through current stress adjacent to plant patches at two different inundation stages (emerged, submerged vegetation) utilizing the most non-cohesive sediment type of the seedling experiment (Sand).

Finally we use the insights of our laboratory experiments on seedlings and tussocks in combination with hydrodynamic field measurements to elucidate species establishment and expansion patterns in their natural habitat.

Methods

Field characterization

Spartina and *Scirpus* are the most abundant halophytes present on salt marshes in the Yangtze estuary, China. They differ in physical aboveground and belowground properties (e.g. *Spartina*: stiff, max shoot height: 3m, *Scirpus*: flexible, max shoot height: 0.8m), growth season (*Spartina*: May to October, *Scirpus*: April to November), stress tolerance and competitive strength [He et al., 2012; B Li et al., 2009; Schwarz et al., 2011; Sun et al., 2001]. *Scirpus* is endemic to the Yangtze estuary and used to be the most abundant species observed in pioneer zones and low marshes. *Spartina* was first found in the Yangtze estuary in 1990 and thereafter started to outcompete the endemic species [H M Huang and Zhang, 2007]. On Chongming Island, the biggest Island in the Yangtze Estuary China (31.6619°N, 121.4780°E), *Spartina* was planted in 2001 in the northern part of Eastern Chongming. Thereafter, it began to spread across existing *Scirpus* marshes accounting for 50% coverage of vegetated intertidal area in 2005 [Q Wang et al., 2006]. The predominant spreading direction of *Spartina* on Chongming Island was northwards (characterized by muddy, cohesive sediment) whereas only limited spreading from the planted sites towards the south (characterized by sandy, non-cohesive sediment) could be detected [B Li et al., 2009; R Z Wang et al., 2010b].

Critical vertical erosion threshold experiment

Seedling Growth Conditions

Seeds from *Spartina* and *Scirpus* were collected from salt marshes on Chongming Island, Yangtze estuary, China and brought to the Netherlands. They were germinated and cultivated in a climate room, which was held at 25°C and provided with an average of 12h d^{-1} of 550µmol $m^{-2}s^{-1}$ photosynthetic active radiation (PAR). Seedlings were planted at 1cm depth below sediment surface in four different sediment types in individual PVC pipes (160mm height and 120mm diameter), with open bottoms and placed in large polyethylene bags. The composition of the four different sediment types was chosen following sediments types present on the

pioneer zones (i.e. mud flat – salt marsh transition) in the Yangtze estuary. Artificial Silt, Sand and Clay (Sibelco benelux®) with a determined grain size were combined with a nutrient mix (osmocote®) to mimic 3 types of natural sediments (Mud, MuddySand, SandyMud). The properties of these mixed sediment types were; Mud (Sand: Silt: Clay - 0:60:40) with a d50 of 3.5 microns, MuddySand (Sand: Silt: Clay - 37:52:11) with a d50 of 35.6 microns and SandyMud (Sand:Silt:Clay - 49:43.5:7.5) with a d50 of 60.3 microns. The fourth sediment type (Sand) was taken from a mudflat in the Oosterschelde estuary (The Netherlands) with the properties Sand (Sand: Silt: Clay - 96:3:1) with a d50 of 184.9 microns, also subsequently mixed with osmocote® to ensure a surplus of nutrients. Fig. 3.1 shows the positions of the chosen sediment mixtures in comparison to sediment samples taken in the pioneer zones in the Yangtze estuary. The sediments were all mixed with the same volume of water and kept waterlogged throughout the experiment. The duration of the growth phase was chosen to be 33 days, representing the average time available for seedlings before the onset of the disturbed period in the Yangtze estuary [Schwarz et al., 2011]. During their growth phase all treatments experienced a semidiurnal 1.5h flooding, simulating tidal inundation on a tidal flat.

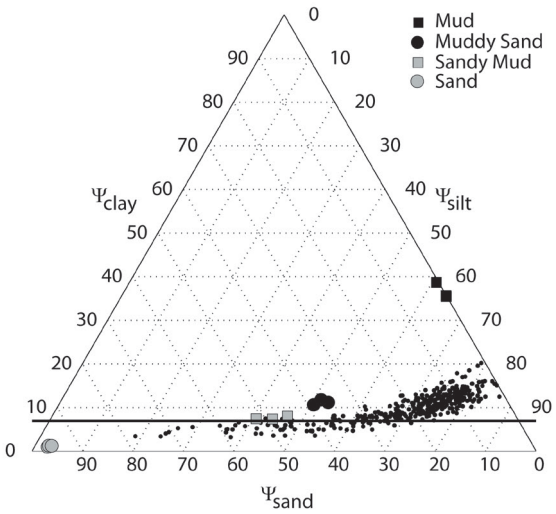


Fig. 3.1: Composition (Sand:Silt:Clay) of our chosen sediment mixtures(big Symbols) to sediment samples from salt marsh pioneers zones at various locations in the Yangtze estuary(little Symbols), the black horizontal line indicates the empirical cohesive/non-cohesive boundary [van Ledden et al., 2004]

Flume experiment and seedling erosion

The NIOZ flume consists of a 17.5 m long and 0.6 m wide oval racetrack that can produce currents and waves [Balke et al., 2011; Bouma et al., 2009a]. At the double bottom test section, the cut PVC pipes filled with sediment were inserted plane with the flume bed, leaving only the seedling exposed [Balke et al., 2011; Balke et al., 2013]. No significant scouring was observed. Flume water depth was maintained at 32cm. A constant current of 0.35 m s^{-1}, representing the averaged field situation [Schwarz et al., 2011], was applied with a conveyor belt. Bed shear stress due to current flow was calculated by the apparent roughness height for the flume bottom in combination with velocity profile measurements (Nortek Vectrino) [van Rijn, 1993]. Equations are stated in the appendix.

The pots were slowly placed into the test section of the flume and current stress was applied (0.35 m s^{-1} equivalent to a bottom shear stress of 0.38 N m^{-2}). For seedlings resisting this bottom shear stress the critical vertical erosion threshold was determined, by defining the amount of sediment that needed to be removed from around the seedling to topple it over. The amount of critical erosion for seedling toppling over was determined by raising the sediment incrementally through placing PVC discs of 1 to 3 mm thickness underneath the pipe. After each incremental step, sediment at the top of the PVC pipe was gently removed using a water jet to keep the sediment level with the flume bottom. Subsequently, seedlings were put back into the flume and exposed to the same current stress (0.38 N m^{-2}, see above). This cycle was repeated until toppling over occurred. In a field situation toppling over would be followed by burial and therefore death of the seedling. For *Scirpus*, which also grew vegetative ramets, erosion cycles were continued until also the ramets toppled over. After toppling over, seedlings were carefully removed from the sediment and their biomass was measured. We separated above- and belowground biomass and determined the dry weight (drying until constant weight at 80°C). For belowground biomass three subcategories were chosen: 0 to 2 cm sediment depth, 2 to 4 cm sediment depth and deeper than 4 cm.

Patch Erosion measurements

We investigated sediment dynamics next to vegetation patches in a flume

experiment. In the setup, half the flume was blocked out by a patch of vegetation (Fig. 3.4, 3.5). To assess sedimentation and erosion patterns in relation to physical plant properties we cultivated *Spartina* (shoot density: 800 m^{-2}, average stem diameter: 3.62±0.75 mm) and *Scirpus* (shoot density: 1500 m^{-2}, average stem diameter: 2.37±0.48 mm) in their natural densities (as found in the Yangtze estuary, China) from seed to a height of 33cm [H Li and Yang, 2009; Sun et al., 2002]. These densities also resulted in similar frontal plant areas facing the incoming current for *Scirpus* (0.018 m^2) and *Spartina* (0.019 m^2). To be able to investigate sediment dynamics also in front of and behind the vegetation patch, a one meter long (consisting of 3 sub patches, due to logistic reasons) and 30cm wide patch of vegetation was placed adjacent to the flume wall in the middle of the 2m test section of the NIOZ flume (Fig. 3.5) [Bouma et al., 2005a; Bouma et al., 2009b]. The sediment type used was the above-mentioned Sand category, since sand erosion thresholds are lower compared to cohesive sediment types pronouncing potential occurrence of scour. As flow could move freely through and around the plants this setup allowed us to study how flow and subsequently local sediment transport are influenced by plant species traits (stiffness). A bare sediment control was carried out.

Current velocity was measured using an acoustic Doppler flow sensor (Nortek Vectrino) at different heights above the bottom. The flow velocity during the experiment was set to be 0.35 m s^{-1}. Water level was varied between low (0.22 m) and high (0.37 m), further referred to as emerged and submerged scenario (relative to plant height 0.33 m). Erosion and Deposition were measured after 30 min exposure to free flow conditions, via the distance scan mode of the acoustic Doppler sensor. The spatial grid had a resolution of 50 mm in the x- (longitudinal, parallel to the flow) and y- (transversal, cross-stream) direction, with a sub mm vertical resolution. Erosion and deposition within the vegetation patch was not measured due to logistic constraints.

The percent (%) of blocked flow by vegetation was calculated by multiplying the average stem diameter by plant density and plant height and subsequently relating this area to the cross-sectional wet flume area. For *Scirpus* the bended plant height was used, according to observations during the flume experiment.

Results

Critical vertical erosion threshold

On average *Spartina* seedlings could withstand significantly more sediment erosion before toppling over in muddy sediments compared to *Scirpus*. As we reduced the degree of cohesiveness (i.e., clay content; Mud to MuddySand to SandyMud treatment), *Spartina* and Sciprus exhibited similar Critical vertical erosion thresholds (Fig. 3.2). After further clay content reduction (Sand treatment), the situation inverted, with *Scirpus* becoming significantly more resilient against sediment erosion combined with hydrodynamic stress than *Spartina* (Fig. 3.2). The critical erosion threshold of *Scirpus* was linked to the biomass investment in certain sediment depths. For the cohesive sediment treatments (Mud, MuddySand and SandyMud) *Scirpus* showed higher biomass allocation in the highest sediment layer (0 cm to 2 cm) compared to *Spartina*. This consequently led to a lower biomass allocation in the deepest sediment layer (4 cm to the end of the root network).

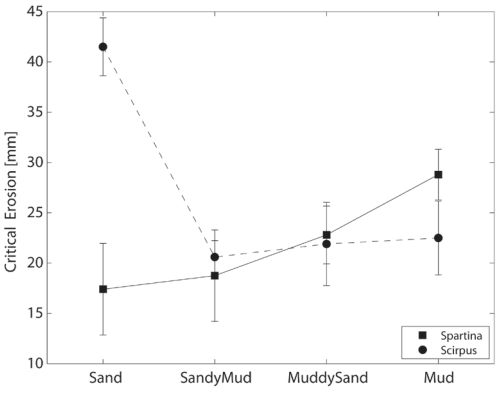


Fig. 3.2: Critical vertical erosion threshold for *Spartina alterniflora* and *Scirpus mariqueter* seedlings on different bottom sediments; filled markers represent average values, whiskers represent the standard deviation

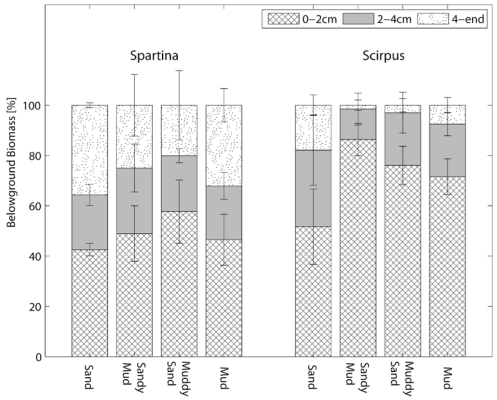


Fig. 3.3: Allocation of belowground plant biomass of *Spartina alterniflora* and *Scirpus mariqueter* to different layers across the four different sediment treatments, bar height denotes the average value of biomass allocation in percent, whiskers denote the standard deviation

In all treatments *Spartina* allocated more biomass in the deepest sediment layer than *Scirpus*. Nevertheless, the trend in critical erosion threshold with sediment type was not linked to belowground biomass allocation for *Spartina*, which does not show significant differences between treatments (Fig. 3.3). A comparison of absolute biomass values of *Spartina* and *Scirpus* between treatments showed no significant differences in either above- or belowground biomass, probably due to the high variability.

Patch Erosion measurements:

Sediment:

In all tested scenarios, bare sediment controls exhibited no significant change in sediment elevation. When vegetation was present, sediment elevation changed and sediment was eroded adjacent to the vegetation patch. In the emerged scenario (water level did not exceed vegetation height), the eroded volume adjacent to the patch was in the same range for both species ($0.0147 m^3/m^2$ for *Scirpus* and $0.0139 m^3/m^2$ for *Spartina*). In the submerged scenario (water level exceeded vegetation height) the treatment with the stiff plant (*Spartina*) eroded about 40% more sediment adjacent to the patch, than the flexible plant treatment (*Scirpus*) (Fig. 3.4). It was further visible that the start of the gap erosion zone differs between the plant species. At both water levels, the flexible vegetation exhibited a more downstream onset of the scouring hole compared to the stiff vegetation.

Elevation within the vegetation patch was due to logistic constraints measured in presence of the plants. Although the measured values (at all treatments) within the patch, suggested the occurrence of sediment accretion as reported by [Bouma et al., 2009b], we nonetheless had to exclude this area from further calculations due to high measurement errors.

Flow:

Flow velocity measurements at different longitudinal locations along the gap and at 1 cm above the bottom (Fig. 3.5 a,b,c) showed flow acceleration in the downstream direction of the vegetation patch's leading edge for all species at all water levels. In the submerged scenario the flow velocity increased about 29%±2.3

(of the initial value) for *Spartina* and 33%±1.8 (of the initial value) for *Scirpus*. In the emerged scenario increases were about 22%±4.1 for *Spartina* and 24%±4.8 for *Scirpus*. We could not observe significant differences in velocity at any position along the gap in the emerged scenario. In the submerged scenario, the gap flow velocity of the *Spartina* treatment appeared to be significantly different from the *Scirpus* treatment (Fig. 3.5 a,b,c).

We further calculated the flow area blocked out by vegetation, using the projected stem density, stem diameter, plant height (stiff) and bended plant height (flexible) (Fig. 3.5 d). In the emerged scenario approximately the same area of the water column was blocked out by the two species, whereas in the submerged scenario the *Scirpus* vegetation blocked about 40% less flow than *Spartina* (Fig. 3.5 d).

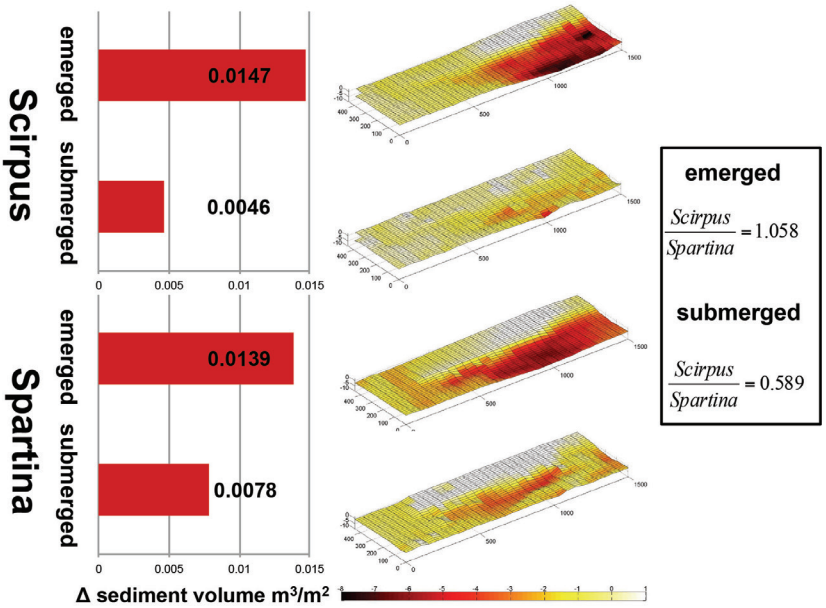


Fig. 3.4: Sedimentation/Erosion flume experiment *Spartina alterniflora*, *Scripus mariqueter*; left: eroded sediment volume [m^3/m^2], middle: erosion map (the green square identifies the place of the vegetation patch), right: ratio of the eroded sediment volumes per treatment (emerged/submerged)

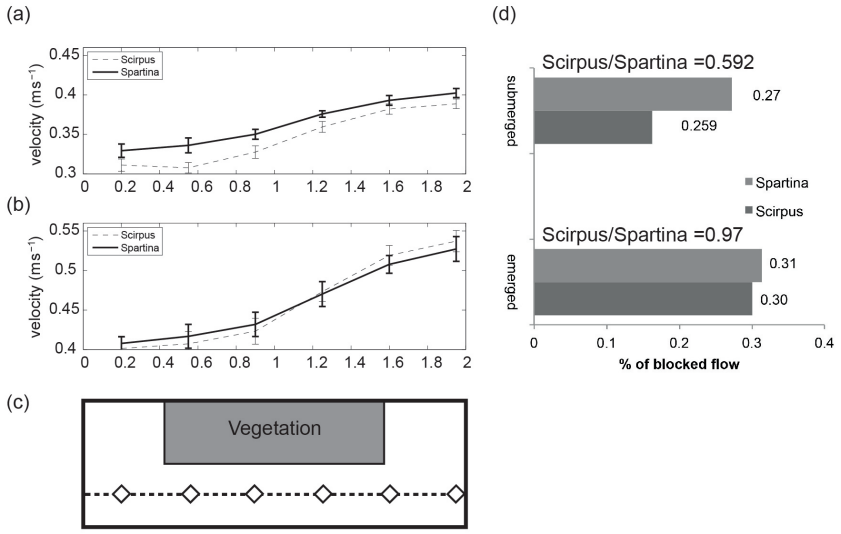


Fig. 3.5: Flow measurements: velocities at 1cm above ground in the gap adjacent to the vegetation patch at submerged (a) and emerged (b) scenario; (c) flume setup and current velocity measurement locations; error bars signify the standard deviation over the Vectrino measurement interval, (d) Flow blocked out by vegetation stems [%]

Discussion

Previous studies on seedling establishment focused on the influence of abiotic stressors on initial plant units (seedlings). The present study extended this understanding by including the influence of sediment properties. Our study further shows that species establishment is not only dependent on biotic-aboitic interactions (hydrodynamics, sediment and plant traits) on the small scale of the individual seedling, but also on the intermediate scale of established plant units due to ecosystem engineering. Hence, for the assessment of species establishment thresholds, interactions between processes on small and intermediate scales have to be considered.

Spartina shows higher resilience to erosion than *Scirpus* in muddy sediment (Fig. 3.2). It is striking that throughout our different sediment treatments it does not significantly change its relative belowground biomass allocation pattern (Fig. 3.3).

This was confirmed by visual comparison of the developed root networks (picture not shown). Hence, for *Spartina* the reduction in critical vertical erosion threshold between sediment treatments was related to sediment cohesiveness. Cohesiveness is linked to structural sediment properties. Non-cohesive beds are granular with little interaction between sediment particles. In contrast, cohesive beds form a coherent mass with electrochemical interactions between particles leading to the observed binding effect (i.e. stickiness) [Grabowski et al., 2011; Winterwerp and Van Kesteren, 2004]. *Spartina* was able to grow equally well in all investigated sediment types, showing no significant changes in above or belowground biomass between treatments. *Scirpus* follows a different growth strategy than *Spartina* (Fig. 3.6 a ,b). Rhizomes of *Spartina* mainly grow vertically down, whereas rhizomes of *Scirpus* mainly grow laterally ending in daughter ramets, which themselves grow roots. Our experiments showed that the depth to which rhizomes of *Scirpus* penetrated was strongly linked to sediment properties (Fig. 3.3), influencing its resilience against erosion. In Mud sediments the root network did not penetrate into deeper sediment layers, causing a lower critical erosion threshold compared to *Spartina* (Fig. 3.2, Fig. 3.6 c-f). In the Sand sediment type, *Scirpus* also invested biomass into deeper sediment layers (by growing ramets in diagonal direction) (Fig. 3.3, Fig. 3.6 c-f), which had a strong influence on its ability to withstand erosion (Fig. 3.2, Fig. 3.6 c-f). The observation that *Spartina* and *Scirpus* have similar erosion thresholds at MuddySand and SandyMud sediment types, although *Spartina* shows more investment in deeper sediment layers, might be due to plant stiffness of the aboveground plant material. Shoot morphology (stiff or flexible) is important for hydrodynamic drag on the plant. In order to withstand strong drag forces (induced by current or waves), plants need to invest in tissue construction and shoot anchoring to prevent an enhanced risk of breaking or being detached [Bouma et al., 2005b]. This could explain the investment into deeper sediment layers for the stiffer plant (*Spartina*) paired with the similar erosion behaviour compared to the more flexible plant (*Scirpus*) [Bouma et al., 2010].

It is not possible to deduce from our experiments whether *Scirpus* was unable to grow deeper roots in cohesive sediments due to mechanical or physiological limitation or, alternatively, showed inherited adaptive behaviour where investment in roots is restricted to sediment types likely to undergo erosion in the field. The

artificial sediments used were poor in organic matter, so that sulphide stress or oxygen limitation was unlikely. In fact, the sandy sediment was more organically enriched and thus more likely to yield physiological stress. The experimental cohesive sediments were not very consolidated, rendering mechanical limitation also unlikely. Interestingly the bottom sediment composition is mainly a result of the existing hydrodynamic conditions [Orton and Reading, 1993]. This opens the possibility that the observed response in morphology and growth strategy of *Scirpus* to sediment composition is the consequence of an evolutionary adaptation to sediment properties and their corresponding hydrodynamic climate. Thus, deeper rooting in sandy sediment may be advantageous because these sediments usually have stronger hydrodynamics. This suggests to incorporate sediment properties in the evaluation of species distributions along hydrodynamic stress gradients [van Wesenbeeck et al., 2007a]. The present study cannot evaluate this hypothesis, but it is an interesting direction for future research.

The flume experiment investigating the ecosystem engineering ability of our two plant species showed that in the emerged stage approximately equal volumes of sediment were eroded next to the vegetation patches of the two species. In the submerged stage, 40% more sediment got eroded next to the *Spartina* patch compared to the *Scirpus* patch (Fig. 3.4). Flow velocity measurements in the gap showed that this increased erosion was due to increased flow routing adjacent to the *Spartina* patch (Fig. 3.5 a,b,c). This increase in gap flow routing was explained by the differences in blocked out flow by the vegetation (Fig. 3.5 d). In the emerged scenario the amount of blocked out flow by vegetation stems was similar. During the submerged scenario *Scirpus* stems blocked out less flow due to bending permitting more overhead flow than in the *Spartina* case, leading to less gap erosion.

The insight that erosion adjacent to vegetation patches is strongly dependent on water levels (emerged, submerged) and physical plant properties led us to investigate the distribution of water levels during one spring-neap cycle at two distinct salt marsh sites on Chongming Island. Water level measurements (wave sensor, Seabird® SBE 26plus) taken in two pioneer zone locations of eastern Chongming Island during one spring neap cycle showed that *Spartina* predominantly remains (partly) emerged (North and South), whereas *Scirpus* only emerges for 30% of the time in

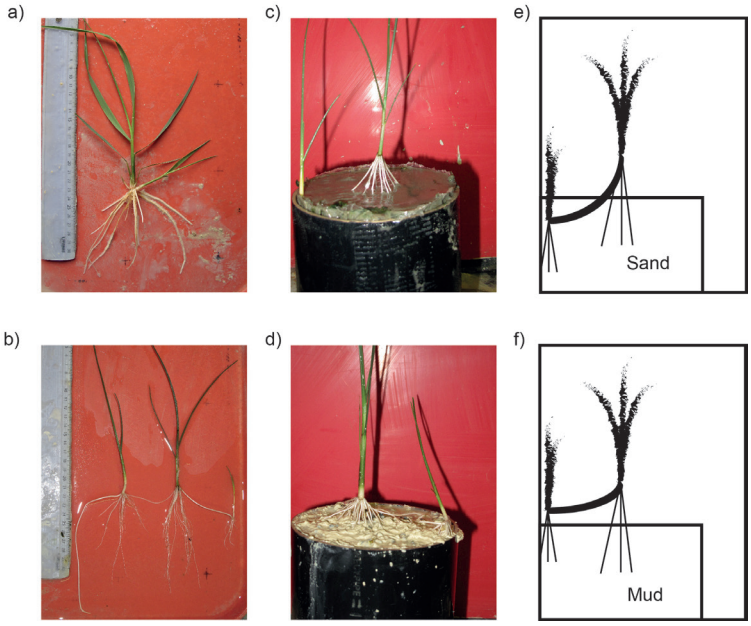


Fig. 3.6: Comparison in plant habitus between our two species and between *Scirpus mariqueter* grown on two different sediment types; a) *Spartina alterniflora*; b) *Scirpus mariqueter*; c) *Scirpus mariqueter* grown on Sand (non-cohesive) after several steps of sediment erosion, d) *Scirpus mariqueter* grown on Mud (cohesive) after several steps of sediment erosion, it is visible that in the Sand sediment type roots, tillers and rhizomes can penetrate deeper in the sediment than in the Mud sediment type, this is schematized in e) growth on Sand and f) growth on Mud

the South and 55% in the North. This will pronounce the differences between the two species in patch adjacent erosion as shown during our flume experiment. *Scirpus* is expected to experience less patch-adjacent erosion due to its flexibility, as shown in our flume experiment, and due to its lower plant height as shown with the water level measurements from the field. This could decrease the establishment probability of *Spartina* in the southern part, where it is especially vulnerable to patch adjacent erosion in the non-cohesive bed sediment subjected to strong wave influence. Since the introduction of *Spartina* in the northern part of Chongming Island, it managed to outcompete *Scirpus* in the entire north and middle of the Island where muddy sediments prevail. To the present day it was not able to establish in the southern part on sandy sediment.

The high ecosystem engineering ability of *Spartina* increases its erosion risk due to this scale dependent negative feedback (scour induced at tussock edges)

[van Wesenbeeck et al., 2008b]. Although we tested patch-adjacent erosion only at constant current velocity with 2 different water levels, whereas in the field flow velocities also vary due to water level, we nevertheless think this is a good approximation. Velocity water level relationships are connected to factors such as tidal amplitude and shore geometry but in general high velocity is found at relatively high water levels. Submersion is likely at times of high velocity, where differences in ecosystem engineering between flexible and stiff plants are expected to peak.

Synthesis and Conclusion

Our experiments showed that sediment properties with or without species growth responses are able to influence seedlings resilience to erosion and might therefore potentially form a bottleneck for plant colonization in certain habitats [Schwarz et al., 2011]. We could further hint the importance of physical plant properties (such as stiffness) in combination with hydrodynamics (inundation time and currents) on the ecosystem engineering ability and stress occurrence. This is in agreement with previous laboratory and field studies on ecosystem engineering efficiency of other plant species [Bouma et al., 2010; Bouma et al., 2009a; van Wesenbeeck et al., 2008b]. We propose sediment will also exert a major impact on the ability of plants to sculpt geomorphologic features such as tidal channels (shown in [Temmerman et al., 2007]). This study highlights the importance of incorporating sediment properties in the assessment of species establishment and their potential influence on landscape development. A deeper understanding of biogeomorphic feedback loops influencing seedling establishment and their ability to sculpt the landscape will have further consequences for wetland restoration and management.

Appendix

Bed Shear stress calculation for the Flume experiment

$$\tau_{b,c} = 0.125\, \rho\, f_c\, \bar{v}^2$$

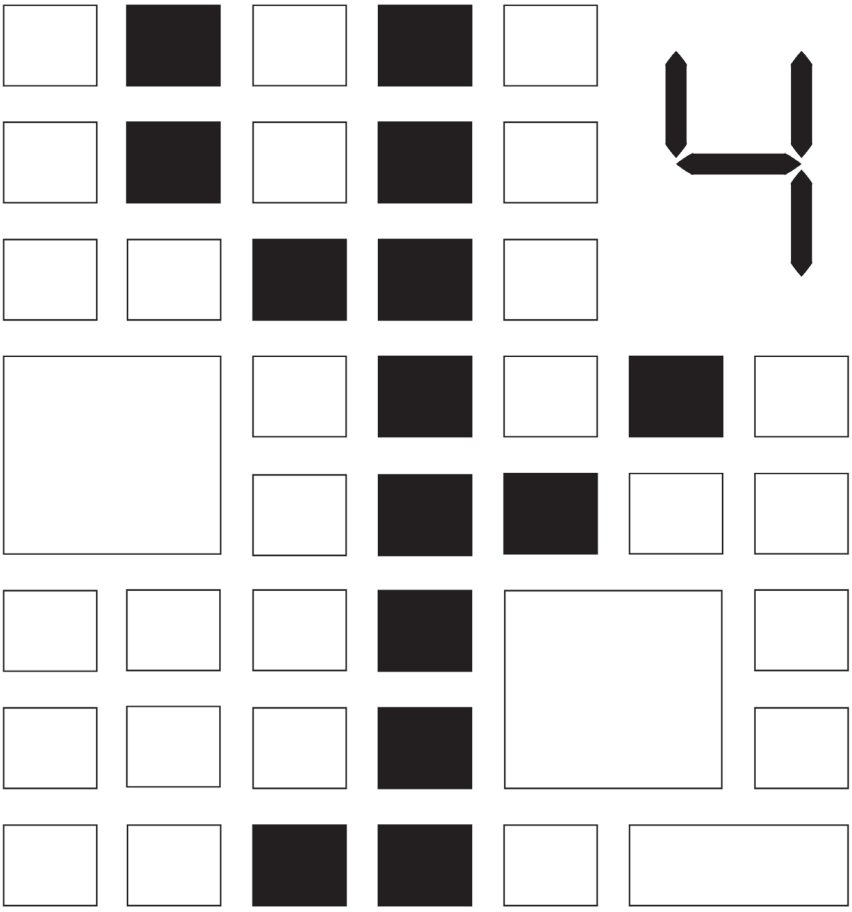
The time-averaged bed shear stress due to current flow can be calculated using the friction coefficient (f_c), the depth averaged velocity ($\bar{v}$) and water density (ρ).

$$f_c = 8\, \frac{g}{C^2}$$

The friction coefficient due to water flow (f_c) can be calculated using Chezy coefficient (C).

$$C = 18 \log \frac{12\, h}{k_s}$$

The Chezy coefficient can be calculated from the roughness height of the bed material (k_s), which is assumed to be 2×10^{-5} for smooth material (glass) covering our flume sides and bottom, (h) represents the water height.



Impacts of salt marsh plants on tidal channel initiation and inheritance

C. Schwarz, QH. Ye, D. van der Wal, LQ. Zhang, T. Bouma, T. Ysebaert, P.M.J. Herman

Accepted

Abstract

At the transition between mudflat and salt marsh, vegetation is traditionally regarded as a stabilizing factor for already incised mudflat channels, able to conserve the channel network via bank stabilization following plant colonization (i.e., vegetation-stabilized channel inheritance). This is in contrast to recent studies revealing vegetation as the main driver of tidal channel emergence (through vegetation-induced channel erosion). We present a coupled hydrodynamic morphodynamic plant growth model to simulate plant expansion and channel formation by our model species (*Spartina alterniflora*) during a mudflat-salt marsh transition with various initial bathymetries (flat, shoal dense, shoal sparse and deep initiated channels). This simulated landscape development was then compared to remote sensing images of the Yangtze estuary (China) and the Scheldt estuary (The Netherlands). Our results reveal the existence of a threshold in pre-existing mudflat channel depth for favouring either the vegetation-stabilized channel inheritance versus the vegetation-induced channel erosion processes. With increasing depth in pre-existing mudflat channels flow routing via these channels is favoured, leaving less flow and momentum remaining for the vegetation-induced channel erosion. This threshold channel-depth will be influenced by field specific parameters such as hydrodynamics (tidal range and flow), sediment characteristics and predominant plant species. Hence our study shows that the balance between vegetation-stabilized channel inheritance and vegetation-induced channel erosion depends on ecosystem properties.

Introduction

Tidal wetlands are often dissected by networks of channels shaped through tidal oscillations and their related water fluxes [S Fagherazzi and Sun, 2004]. These tidal channels are striking features in coastal environments; they constitute basic pathways for the exchange of water, sediment, organic matter, organisms, nutrients and pollutants between the wetland and the adjacent open water body [Perillo et al., 2009]. Despite the widely known relevance of tidal channels, their formation mechanisms are not very well understood.

The traditional literature on tidal-channel development separates the process into two sequential stages. During initial development the tidal network quickly cuts through intertidal mudflats and acquires its basic structure [Allen, 2000; D'Alpaos et al., 2005; Rinaldo et al., 1998]. This phase is followed by a slower elaboration phase where bank stabilization through plant colonization and meandering reinforce and elaborate the basic channel structure [Marani et al., 2002; Perillo et al., 2009; Pestrong, 1972]. The initial development phase, which is the focus of our study, starts with topography-guided overland flows concentrating their discharge into depressions. Locally the critical erosion threshold in bed shear stress is surpassed, leading to incision of small channels which further grow by headward erosion [Allen, 2000; D'Alpaos et al., 2007; S Fagherazzi and Sun, 2004; Perillo et al., 2009]. Supported by experiments and modelling studies, this conceptualization suggests that channel incision is mainly controlled by topology-induced water surface elevation gradients [D'Alpaos et al., 2007; Steel and Pye, 1997]. Vegetation is considered mostly as a passive agent stabilizing the banks of already incised mudflat channels. We refer to this concept as "vegetation-stabilized channel inheritance".

More recently, tidal channel development has been coupled to the effect of vegetation. Intertidal vegetation acts as ecosystem engineers that reduces flow and enhances sedimentation within vegetation patches. This flow reduction is tightly coupled with flow acceleration around the vegetation patches, where soil erosion is initiated. This stress divergence and local concentration was identified as a main factor generating spatial heterogeneity in salt marsh pioneer zones. [Bouma et al., 2009b; Bouma et al., 2007; Prosser and Slade, 1994; van Wesenbeeck et al., 2008a].

[Temmerman et al., 2007] modeled the consequences of these positive and negative feedbacks on intertidal landscape development. They demonstrated the ability of intertidal vegetation to actively influence channel incision by channelling the tidal flow into narrow passages between patches. We refer to this alternative hypothesis for channel generation as "vegetation-induced channel erosion" during a mud flat – salt marsh transition.

In this paper, we argue that vegetation-stabilized channel inheritance and vegetation-induced channel erosion are both occurring in the field and that the relative importance of each mechanism depends on the physical setting of the system. We subsequently identify the specific conditions favouring either channel inheritance or channel erosion. Both aspects are studied using the modeling suite Delft3D to simulate the channel development on a mudflat in the presence of our model salt marsh pioneer species *Spartina alterniflora*. The model we used is a fully coupled hydrodynamic, morphodynamic and vegetation model. We used this model to simulate simultaneous channel and vegetation development with and without the presence pre-formed mudflat channels. Finally, we validate our model results with data from salt marsh ecosystems in both the Yangtze estuary (China) and the Scheldt estuary (the Netherlands).

The Model

Model description:

We used Delf3D, developed by WL/Delft Hydraulics [Roelvink and van Banning, 1995; Z B Wang et al., 1995]. Delft3D is a finite difference numerical modeling system composed of modules describing waves, currents, sediment transport and bottom changes, linked by a steering module (Delft3D FLOW) [Lesser et al., 2004]. The depth-averaged mode of the Delft3D FLOW module computes tidal flow by solving the unsteady depth-averaged shallow water equations in two dimensions [Lesser et al., 2004; Marciano et al., 2005]. The implemented morphodynamic model is based on the advection-diffusion equation for suspended sediment transport; computing sediment transport based on time dependent flow

fields. The source-sink terms of the advection-diffusion equation are described by semi-empirical formulae. Erosion and deposition boundary conditions are flow-dependent, and the morphodynamic model updates the bathymetry, which is fed back to the hydrodynamic module.

In this study we combined the 2D depth averaged Delft3D-FLOW module with an ecological module. The ecological module was developed within Delft3D-WAQ using an Open Process Library (OPL). The ecological module takes care of two types of processes. First, it accounts for the influence of vegetation on flow and turbulence. This is modeled by an adapted k-ε formulation explicitly accounting for the influence of rigid cylindrical plant structures on drag and turbulence [Baptist et al., 2007; Uittenbogaard, 2003]. Vegetation stems and leaves exert an additional drag force on the flow and generate turbulence. Details of the model formulation are given by [Temmerman et al., 2007] and [Baptist, 2005]. The net result of vegetation on the flow is that flow is decelerated in vegetation patches and accelerated in the immediate surroundings. This has effect (through the morphodynamic model formulations) on the entrainment and transport of sediment, as well as on the local deposition processes. Secondly, the vegetation module simulates spatio-temporal changes in stem density and stem height of *Spartina alterniflora* [Temmerman et al., 2007]. Initial plant establishment on bare grid cells is modeled stochastically with a user defined initial plant cover and tussock diameter. Lateral expansion of plants to neighbouring cells is modelled through a diffusion equation. Stem density grows up to a carrying capacity according to a logistic growth equation. Stem height growth is also modeled as logistic growth to a maximum. Stem diameter grows linearly in time, depending on stem height. Plant mortality is determined by tidal flow stress, modelled proportional to bed shear stress exerted by flow, and by inundation stress, modeled proportional to inundation height at high tide [Temmerman et al., 2007]. A detailed description of the Delft3D model including the ecological module can be found in [Ye, 2012].

Hydrodynamic processes such as tidal flow and morphodynamic processes such as suspended sediment transport and bed load transport (with bed slope effects) are used from the Delft3D-FLOW module. All processes (hydrodynamic, morphodynamic and ecological) are considered to have mutual interactions at user

defined time steps. The used plant flow interactions have been extensively described and validated against flume experiments [Baptist, 2005; Bouma et al., 2007; Uittenbogaard, 2003], salt marsh field measurements [Temmerman et al., 2005b] and previous modeling studies [Temmerman et al., 2007; Ye, 2012] (Fig. 4.1).

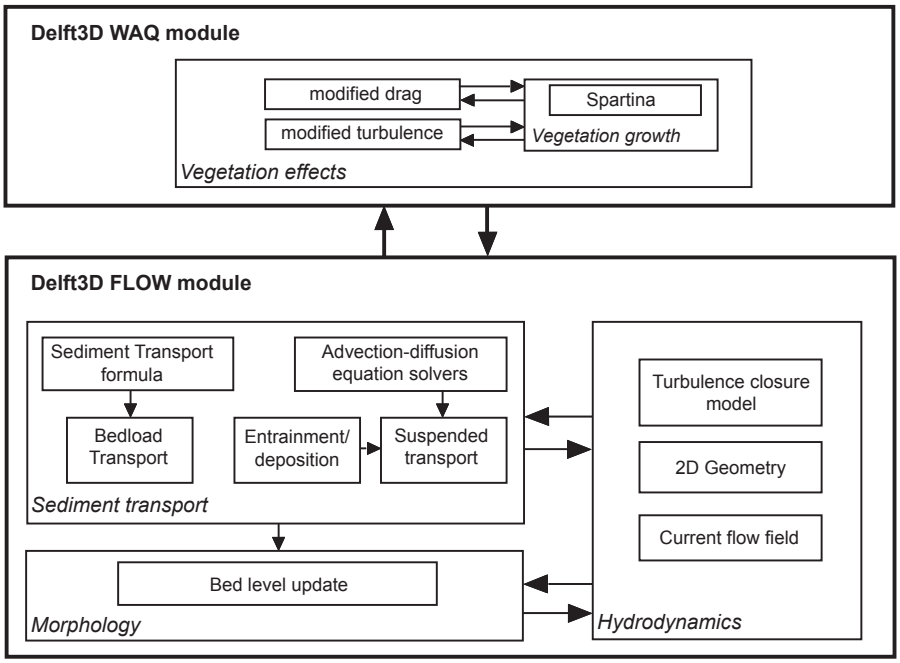


Fig. 4.1: Model Flow-Diagram describing interactions between sediment transport, morphology, hydrodynamics and vegetation

Model Setup:

The model uses a schematic representation of a tidal basin with a meso-tidal range. It focuses on tidal currents; waves are not accounted for. A rectangular grid is used in the numerical computation, in order to combine a manageable computation time with sufficient resolution of the basin morphology. The model covers an area of 1800 m* 600 m, with a grid size of 6m and a slope of 0.1%. It is confined by three closed boundaries and one open water-level boundary at the seaward edge. It has a uniform bottom sediment composed of fine sand (d50=80μm). This hypothetic

mudflat corresponds to mudflats and pioneer zone wetlands found in the Yangtze estuary, China [S L Yang et al., 2011; Zhu et al., 2011].

We simulated four different cases of initial bathymetries on which vegetation was added: "plain", "shallow dense channels, "shallow sparse mudflat channels" and "deep mudflat channels". The first simulation ("plain") started with a uniform bathymetry (Fig. 4.3c-plain). This simulation was run to dynamic equilibrium to determine the form of a natural channel network (Fig. 4.3d-plain). Subsequently, artificial channel networks based on this blueprint were imposed onto the model domain before introduction of the vegetation (Fig. 4.3c Shoal ChD, Shoal-ChS, Deep Ch). This was done in different ways. In the "shallow dense channels" case (Shoal ChD) the full network topology of channels was used, but the depth was reduced by 50 % compared to the dynamic equilibrium network. (max. depth=0.35m, number of induced channels =5). In the "shallow sparse mudflat channels" case (Shoal ChS) the number of main channel branches was reduced from 5 to 3, but the total initial channel volume was the same as in the "shallow dense channel' case. Consequently, the channels are deeper than in that case (i.e., max. depth=0.6m, number of induced channels = 3). Finally, in the "deep mudflat channels" case (Deep Ch) the dynamic equilibrium channel network is used at full extent in the initial conditions (i.e., max. depth=0.7m, number of induced channels =5).

S. alterniflora			
Parameter	**Unit**	**Value**	**Ref**
Max density	Stems m^{-2}	800	1
Max height	m	1.7	2
Max diameter	mm	10	1
Vertical growth rate	m y^{-1}	2.5	3
Lateral expansion rate	m^2 y^{-1}	2	2
Salinity	ppt	35	2
Critical shear stress	N m^2	0.26	4
Critical inundation height for plant mortality	m	1.8	2
Stem density initial established tussock	m^{-2}	0.1 * Max density	2
Stem height initial established tussock	m	0.1 * Max height	2

Tab. 4.1: Model parameters Vegetation: *Spartina alterniflora* References; 1: Field assay Chongming Island in 2010 ; 2: [Schwarz et al., 2011]; 3: [Zhu et al., 2011];4: [van Hulzen et al., 2007]

Tidal action was simulated by applying a sinusoidal water-level fluctuation at the open boundary (Amplitude = 1.2m), where also an equilibrium sediment concentration was assumed. Tidal range and sediment concentration correspond to actual field situations. Hydrodynamic and morphodynamic processes were solved with a time step of 2s. The ecological module interacts with the hydrodynamic module at a 30 minutes interval updating ecological parameters, such as; stem height, stem diameter and stem density which are further incorporated in the hydrodynamic and morphodynamic computations. The model simulates an average month (27d), which is then up scaled using a morphologic factor to an overall time of 3 years (8 months vegetation period per year; 24 months = 3 years).

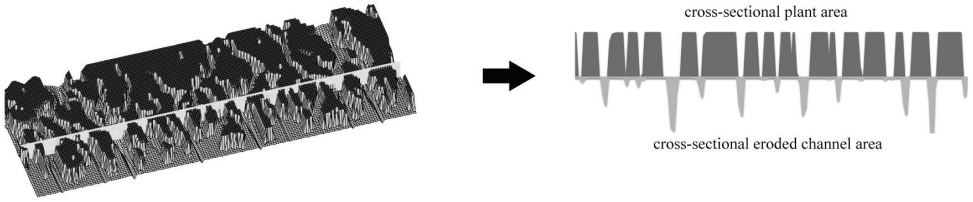


Fig. 4.2: Schematic representation of the model analysis, (left) model domain containing vegetation and eroded channels, the light grey long-shore plane represents the wet cross-sectional area at the location of maximum channel erosion; its height indicates the water level of maximum sediment transport, (right) shows the cross-sectional plant area and the cross-sectional eroded channel area at the location of the long-shore plane

Statistical properties of the initial plant cover were derived from multiple remote sensing images of the pioneer zone of the *Spartina alterniflora* marsh at the beginning of the growing season. In these images, the average plant cover was 25% with an average tussock diameter of 18.3m. Based on these observations, the initial plant cover in our modelling domain was realized as a random pattern of tussocks with a diameter of 18m and overall area coverage of 25%. Initial plant density within tussocks (80 stems m^{-2}) and initial plant height (0.17 m) at the starting point of our simulations were set at 10% of the maximum density (800 stems m^{-2}) and height (1.7m height) respectively (Tab. 4.1).

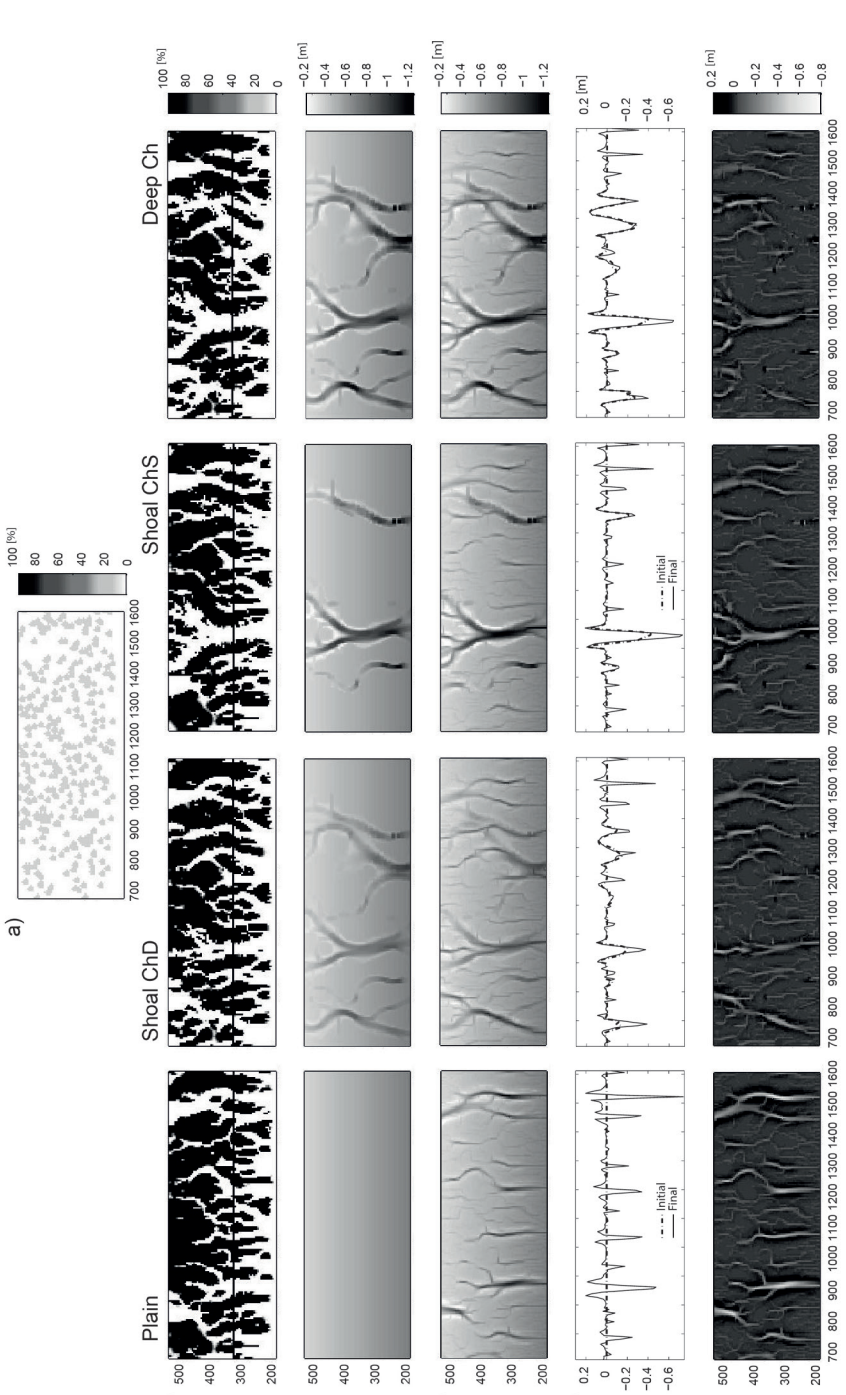


Fig. 4.3: Modeling results for initial flat bathymetry (Plain), shallow imposed channels with high density (Shoal ChD), shallow imposed channels with low density (Shoal ChS) and deep imposed channels (Deep Ch), : (a) Initial plant cover[stem density %]; (b) Plant cover after 3 years [stem density %]; (c) Initial bed level [m]; (d) Bed level after 3 years; (e) Eroded channels at a long-shore transect shown in b(initial and final bed configuration); (f) Cumulative sedimentation/erosion after 3 years [m]

Simulations showed that the chosen time frame was sufficient for plant growth, hydrodynamics and sediment transport to reach a dynamic equilibrium (data not shown).

Model analysis:

A region in the centre of the modelling domain was identified and further regarded as the closed boundary independent results of our modelling computation (i.e., impact by domain boundaries were negligible) (Fig. 4.3). In this area a long-shore profile was drawn at the location of maximum channel erosion (see Fig. 4.2 grey long-shore plane, see also black horizontal line in Fig. 4.3.b). At the location of this long-shore profile we calculated the cross-sectional plant area and the cross-sectional eroded channel area (Fig. 4.2, Fig. 4.3.b).

We calculated the cross-sectional plant area [m^2] at the long-shore profile by multiplying the plant height (model output) until the water height of maximum sediment transport (i.e., 0.4m above bed) by the length of our long-shore profile. The cross-sectional plant area was calculated at two time points; (1) at the start (after the initial pattern established a temporal equilibrium with sediment transport, initial pattern see also Fig. 4.3.a) and (2) at the end of our model simulation (final pattern see also Fig. 4.3.b). The cross-sectional eroded channel area [m^2] depicts the cross-

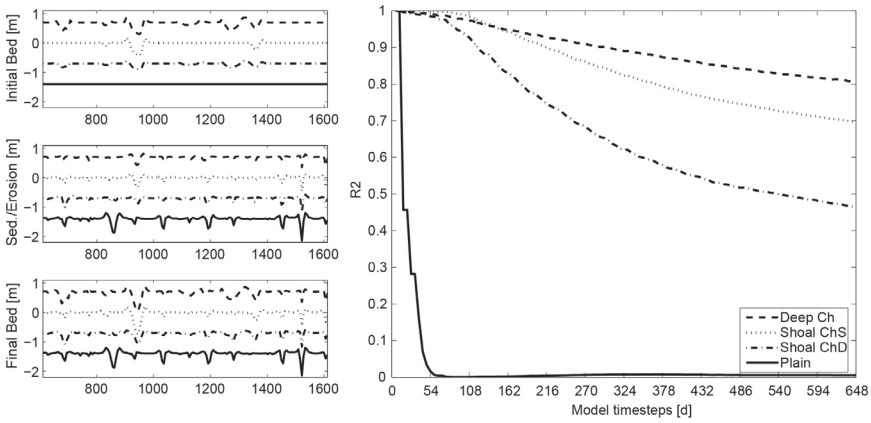


Fig. 4.4: (left) Comparison of eroded channels along the long-shore transect; (top) initial bed level; (middle) cumulative sedimentation/erosion; (below) final bed level (scaled for 1:1 comparison), (right) Correlation coefficients between the initial long-shore bathymetry and long-shore bathymetry after n-simulations, plotted over simulation time [d]

sectional eroded channel area along our long-shore profile at the two time points. The cross-sectional channel area was calculated at two time points; (1) at the start (after the initial pattern established a temporal equilibrium with sediment transport, initial pattern see also Fig. 4.3.a) and (2) at the end of our model simulation (final pattern see also Fig. 4.3.a).

We further used the Pearson product-moment correlation coefficient(R2) as a proxy for the self-organization of our system. We calculated, how well the bathymetry along the long-shore transect remained correlated with the initial bathymetry over the course of our simulation. A drop in Pearson product-moment correlation to zero i.e. the current bathymetry becoming independent from the initial one was interpreted as an indication for self-organization. The ability to alter the habitat independent of its initial state is a characteristic of a self-organized system. In this context self-organization denotes the ability of organisms (through local feedbacks) to physically alter their environment producing spatial heterogeneity (Fig. 4.4, right panel) [Rietkerk et al., 2002; van de Koppel et al., 2005].

Validation:

Our model results were qualitatively validated through a time series of digitized aerial photographs (2003) and Quickbird satellite images (2005) of an expanding *Spartina alterniflora* salt marsh located on Chongming Island (Yangtze estuary, China). We specifically identified the emergence of salt marsh channels at a mud flat – salt marsh transition, at locations with and without pre-existing mudflat channels. This was compared with the emergence of tidal channels with and without pre-existing mudflat channels of our model simulation.

In addition, we compared our model output to an expanding salt marsh located in the Southwest delta of the Netherlands (Walsoorden tidal flat in the Westerschelde estuary, 51.4° N, 4.1° E). On this tidal flat, a salt marsh started developing in the late 1990's as isolated clumps of plants, mostly *Salicornia procumbens* and *Aster tripolium*. [van der Wal and Herman, 2012; van der Wal et al., 2008] give the results of detailed field studies of this development. We made use of aerial photographs, digital elevation models and water level measurements in 2004 and 2008 as a basis of our calculations. Water level data were interpolated from two adjacent tide

gauge stations Hansweert and Bath. The data showed high conformance with field measurements at our research sites. DEM data were obtained from airborne laser altimetry. Cross-referenced in situ dGPS assays at our investigated site confirmed the DEM's accuracy. Plant height data of the mixed community (Salicornia procumbens and Aster tripolium) were based on field assays and literature [van der Wal and Herman, 2012; van der Wal et al., 2008]. We fixed a long-shore profile in the developing marsh at the location in the cross-shore direction where channel incision was maximally developed. We determined the water height at the tidal phase when current velocity and hence sediment erosion was maximal (0.5 m above NAP, the Dutch Ordnance Level). The distribution of plants along our long-shore transect was assessed by calculating the NDVI of our aerial images. Based on these measurements in 2004 and 2008, we calculated how much the cross-sectional area of plant stands, as well as the cross-sectional are of eroded channels had changed in this 4-year period.

Results

The simulations start from a homogeneous flow field. After imposing the starting configuration, flow is obstructed by the vegetation patches, and is deflected to the immediate vicinity of the patches, where velocity and bed shear stress increase. Due to plant growth and thus increase of the density, height and lateral extension of the patches, this effect increases through time. When the bed shear stress in between patches surpasses the critical threshold for sediment movement, tidal channels are initiated. In turn, the high flow and bed shear stress in the channels inhibit further lateral development of the vegetation and fix the channel. During this phase of self-organization of the landscape, not all gaps between vegetation patches develop into channels. In many places the currents do not surpass the critical threshold and the patches merge to form the vegetated marsh platform. Channels are formed at more or less regular intervals in space (Fig. 4.3 b-f, Plain).

The cases with pre-formed channels present before the start of the simulation show a different pattern (Fig. 4.3 Shoal ChD, Shoal ChS, Deep Ch). The influence of vegetation on the resulting channel pattern is dependent on how well-formed

the channels are before development starts. When the mudflat channels are shallow, there is enough momentum left for channel erosion through plant-flow interactions, even though erosion within the channels is promoted. This results in a new equilibrium for emerging channel networks and vegetation patch arrangement (Fig. 4.3 Shoal ChD, b-f). In the case where the number of channels is reduced but the total channel volume is kept exactly equal, erosion was even more concentrated in the channels and less pronounced in the adjacent areas. The channels in this

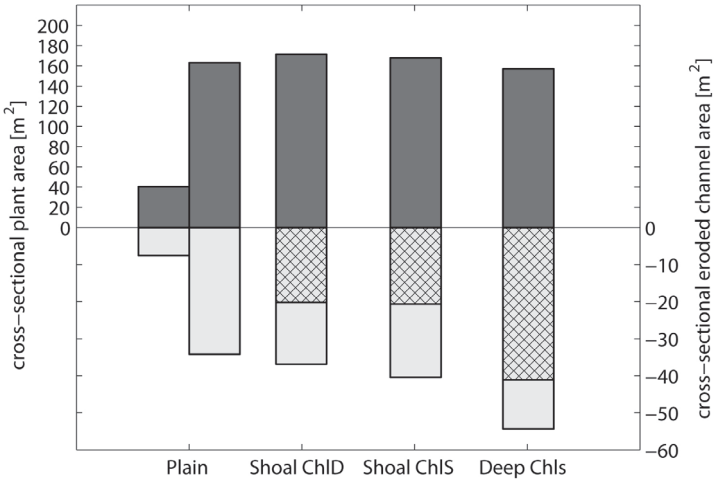


Fig. 4.5: Comparison between the cross-sectional plant area (dark gray), with the cross-sectional eroded channel area (light gray) in combination with the cross-sectional imposed channel area (hatched) at the start (left bar, plain) and the end of our model simulation (right bar)

case were deeper than in the Shoal ChD case, and this apparently attracts flow and erosion to further concentrate in these places (Fig. 4.3.Shoal ChS, b-f, middle). When the imposed mudflat channels were even deeper and the network was fully extended (Deep Ch), the above described impacts (i.e., deepening of pre-existing incised channels, reduction of new channels formed by plant-flow interactions) got more pronounced (Fig. 4.3 Deep Ch, b-f; Fig. 4.4 left panel).

We then calculate how well the bathymetry along the long-shore transect remained correlated with the initial bathymetry. This revealed that in the plain scenario all correlation with the initial bathymetry was quickly lost (Fig. 4.4 right

panel), which can be interpreted as a sign that the landscape was self-organizing without memory of its previous state. In the cases where channels were pre-imposed onto the landscape, the correlation decreased over time due to (more restricted) self-organization, but there always remained a considerable correlation with the initial bathymetry. The deeper the imposed channels were, the more the bathymetry remained correlated with the initial state over time, showing that self-organization was limited and the imprinted morphology was largely retained.

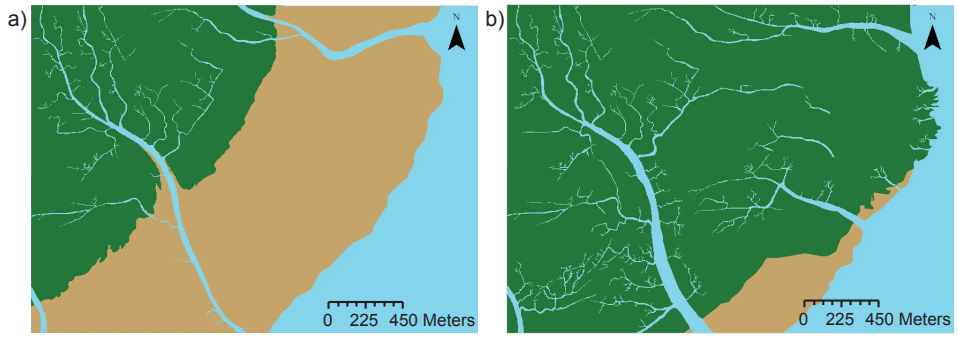


Fig. 4.6: Digitized aerial photographs; salt marsh expansion and channel development on Chongming Island, Yangtze estuary, China; 2003 (a), 2005 (b)

A comparison between the cross-sectional plant area, cross-sectional eroded channel area and the cross-sectional imposed channel area along the long-shore transect (Fig. 4.5), reveals that with homogeneous initial bathymetry (i.e., without pre-imposed channels) the change between cross-sectional eroded channel area is clearly related to the change in cross-sectional plant area (increase cross-sectional plant area: increase channel area is 4.1-fold: 4.4-fold) (Fig. 4.5, Plain). The fact that the cross-sectional area of eroded channels matches the increase of cross-sectional plant area, implies that these channels are generated solely by plant-flow interactions. As soon as mudflat channels are imposed (i.e., pre-imposed cross-sectional imposed channel area increases), the cross-sectional eroded channel area decreases significantly, decoupling the relationship between the increase cross-sectional plant area and newly eroded cross-sectional eroded channel area.

The deeper the pre-imposed channels get, the lesser explanatory power the cross-sectional plant area seems to have over the resulting bed configuration (Fig. 4.5, Shoal ChlD, Shoal ChlS, Deep Chls). This is also visible in the comparison of the increase in cross-sectional plant area: increase channel area, for Shoal ChlD, Shoal ChlS and Deep Chls, which gives, 4.2-fold: 2.7-fold, 4.2-fold: 2.7-fold and 3.9-fold: 1,7-fold respectively. The slight increase in cross-sectional plant area from plain to shallow channels dense (Shoal ChD) in Fig. 4.5 is a function of the higher drainage density of the incised channels in the plain case..

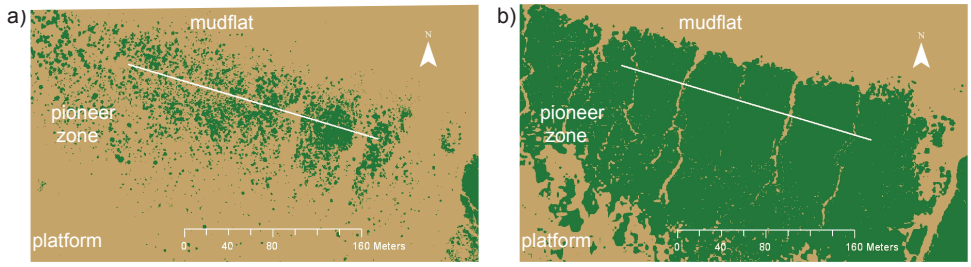


Fig. 4.7: Salt marsh expansion and channel development Walsoorden, Scheldt estuary the Netherlands; 2004 (a), 2008 (b)

Validation (China):

Comparing a digitized aerial photograph from January 2003 (Fig. 4.6 left figure) with a Quickbird image from November 2005 (Fig. 4.6; right figure) shows the rapid expansion of the *Spartina alterniflora* pioneer vegetation on Chongming Island (Yangtze estuary, China). The pictures were taken outside of the season when the pioneer zone expands, thus showing the closed marsh vegetation versus the bare mudflat areas. The dense *Spartina* vegetation is clearly intersected by tidal channel systems, which discharge into mudflat channels. Compared to 2003, the salt marsh has expanded over a distance of about 700 m in 2005. In this process, the former mudflat/pioneer zone was transformed into a dense colonized meadow dissected by channels. The comparison of these two photographs shows on the one hand the

inheritance of pre-existing mudflat channels into the salt marsh channel network, while on the other hand it shows the incision of new mudflat/salt marsh channels potentially caused by vegetation-induced channel erosion (channels located between the former mudflat channels). This corresponds qualitatively with the predictions from our model. It strongly suggests that some salt marsh channels originate from plant-flow interactions whereas others from stabilizing characteristics of vegetation inheriting existing mudflat channels.

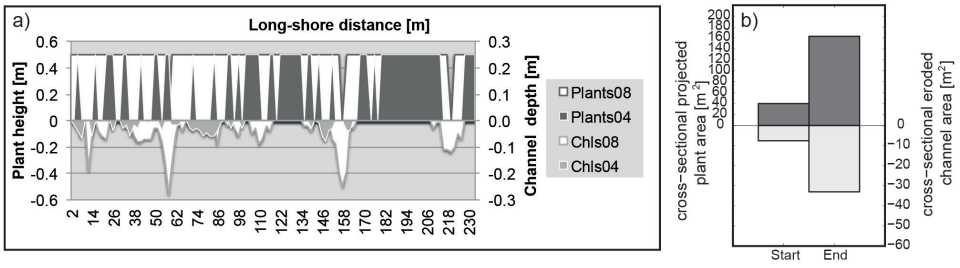


Fig. 4.8: a) Long shore profile Walsoorden 2004 and 2008 at its maximum erosion zone, see also white line Fig.7; b) comparison between the cross-sectional plant area (dark gray) and the cross-sectional eroded channel area (light gray) along the long shore profile at this two time points (2004 to 2008)

Validation (The Netherlands):

In 2004, on a mudflat with recently established vegetation patches (characterized by Salicornia procumbens and Aster tripolium [van der Wal and Herman, 2012]) (Fig. 4.7; left panel), channel initiation was not yet visible from the aerial photograph, as was also confirmed by little variation in initial bathymetry. In fact, at this time the variation in bathymetry was within the uncertainty range of laser altimetry. By 2008 the vegetation patches had expanded laterally, forming a dense meadow intersected by tidal channels (Fig. 4.7; right panel). Our model reproduces this observed pattern of plant expansion and channel initiation very well. Channels were well developed. Comparing the cross-sectional plant area with the cross-sectional eroded channel area along a long-shore transect through the zone of maximal channel incision (white line in Fig. 4.7) at the two time points, reveals a close correspondence in the relationship between the measured (Fig. 4.8; right panel) and modeled (Fig. 4.5; plain) increase in cross-sectional areas (increase cross-sectional plant area: increase

channel area, validation: 1.9-fold:2.1-fold, plain: 4.1-fold:4.4-fold). In both cases it is visible that the increase in eroded channel area is due to an increase in cross-sectional plant area. The increase of eroded channel area will depend on vegetation cover, hydrodynamic conditions and sediment properties.

Discussion and Conclusions:

Previous studies already highlighted the influence of vegetation on flow [Hickin, 1984; Nepf, 1999; 2012], local sediment transport [Bouma et al., 2009b; van Wesenbeeck et al., 2008a] and channel incision [Temmerman et al., 2007]. The present study extends the previous knowledge by linking initial bathymetry to plant-flow interactions. Our model results confirm the influence that plants may exert on the formation of channels, as was already shown by [Temmerman et al., 2007]. However, we also showed that the degree to which these interactions determine the final landscape depends strongly on the configuration of the landscape at the stage when colonization by plants takes place. The absence or presence of already existing mudflat channels will determine whether enough momentum is present in the water outside the pre-formed channels to incise new ones. Our model results also indicate that in cases where channels attract most of the flow, additional erosion is likely to occur within the preformed channels rather than as extension of the channel network. These results are in agreement with [Temmerman et al., 2007], who expressed the expectation that plant-flow interactions are most important in landscapes with rather homogeneous gradients in topography and soil conditions (further referred to as 'excess momentum' concept). They are also applicable to vegetation-stabilization observed in alluvial systems [Gran and Paola, 2001].

Our study does not address the origin of mudflat channels, namely the interaction of flow with heterogeneous mudflat topography as mentioned in the introduction [D'Alpaos et al., 2005]. We more focus our attention on the result of these flow-topography interactions (mudflat channels) and discuss its repercussions on intertidal vegetation and geomorphology.

From the comparison of our modeling results with field observations, it appears that the balance between erosional and stabilizing vegetation properties is strongly

linked to the presence or absence of halophyte vegetation during the short time span in which tidal channel incision takes place. In the absence of vegetation during this incision phase, vegetation is more likely to fulfil a stabilizing function on already incised mudflat channels [D'Alpaos et al., 2005]. With vegetation present during the channel incision phase a mixture between erosional and stabilizing properties of vegetation (linked to mudflat topography) can be expected, as shown on our research area in China and in the Netherlands. In this case the predominance of erosional or stabilizing properties will depend on hydrodynamics, sediment- and plant properties [J Gao et al., 2011; Temmerman et al., 2007; van der Wal and Herman, 2012; Xu and Zhuo, 1985].

The conducted simulations suggest that channel inheritance is the dominant mechanism on mudflats with a pre-existing deeply incised channel system. This suggests a threshold in mudflat channel depth favouring either channel inheritance or new channel incision. In this context, what is "deep" and "shallow" is a relative measure. In our study we refer it to the maximum depth in a channel system entirely produced by vegetation-induced self-organization, but in field studies this depth is unknown. It will be determined by field-specific parameters such as hydrodynamics (tidal range, waves, and flow), sediments and predominant plant species. The predominance of either inheritance or erosion depends on the significance of plant-flow routing compared to flow routing by mudflat topography. For instance on a topographically heterogeneous mudflat colonized by flexible, sparse, slow growing vegetation, the magnitude of plant flow interactions might still be insufficient to cause channel erosion, only allowing vegetation to colonize areas between incised mudflat channels and hence stabilize them. If the same mudflat were colonized by stiff, dense, fast growing vegetation, the magnitude of plant-flow interactions will become predominant over topography-guided erosion

Our process-based model shows channel initiation through erosive processes caused by flow routing causing local bottom shear stress to exceed the threshold for initiating sediment motion. In fact, most studies on channel formation stress the importance of erosion processes, although some previous studies also found depositional processes guiding tidal channel emergence. Deposition guided channel emergence was shown to originate from the coalescence of marsh islands during

delta progradation, where vegetation colonization splintered the incoming river into randomly merging tributaries [Hood, 2006]. The basic processes needed for these depositional channel modifications are incorporated into our model: enhanced sedimentation inside vegetation patches, and coalescence of laterally expanding patches without channel formation in between. Thus, our model implicitly also represents this mechanism. Application to river systems could provide a test whether the mechanism at this large scale can also be reproduced.

Our model does not explicitly account for soil and bank stabilization by plant roots. Nevertheless, it indirectly accounts for this stabilizing plant property by the interactions of the above ground structures on local drag and turbulence and the resulting hampered sediment erodibility adjacent to vegetation stems. One constraint of our simulation consists in the prohibition of erosion at wet-dry cell interfaces (e.g. bank erosion during channel filling) since the model only accounts for erosion of wet cells. This probably leads to an overrepresentation of channel bed erosion and bank stabilization, and an underrepresentation of bank erosion. However, since our simulation is intended to mainly simulate the initial channel development phase these processes are of less importance, compared to the subsequent elaboration phase (characterized by processes such as channel meandering).

We did not include seedling establishment in our simulation since starting from an established plant pattern (based upon our field situation), an additive number of random seeding by seedlings would not affect the resulting patterns significantly. This is due to the fact the seedlings possess a lower stress tolerance than existing tussocks and are therefore unable to occupy bare spots which can be occupied by lateral tussock growth.

We are aware that our model depicts an oversimplification and is therefore not able to completely explain the above shown validation scenarios (Fig. 4.6 and Fig. 4.7). A major difference is caused by sediment composition. Sediment characteristics (e.g. cohesive vs. non-cohesive) are the determining factors for critical bottom shear stress thresholds of sediment erosion and therefore channel initiation[van Ledden et al., 2004]. This impacts the probability of mudflat channel existence on the one hand and also the amount of force necessary to initiate channels via plant-flow interactions on the other hand. Further, our simulation did not include wave effects

which can also have a big impact on intertidal sediment transport [Callaghan et al., 2010; Defina et al., 2007]. Nevertheless, our simple hypothetical mudflat model was able to grasp the main aspects of tidal channel initiation and inheritance in the validation cases, giving new insights on ramifications of local vegetation properties on landscape evolution.

The above-described concept of 'excess momentum' could be practically used in landscape restoration such as reforestation or wetland rehabilitation. Plant-flow interactions could be optimized in relation to initial topography, hydrodynamics and sediment properties resulting in increased channel drainage density promoting spatial heterogeneity. Furthermore, this concept can be applied to the observed vegetation assisted establishment of dynamic single-thread channels in stream ecosystems. In stream ecosystems it was observed that vegetation has the ability to reorganize flow patterns through bank stabilization and subsequently convert the planform morphology from braided to single-thread [Tal and Paola, 2007].

Our model was able to qualitatively represent channel development in Chinese salt marshes, as well as in the widely different marshes in the Dutch validation case. This suggests the wide applicability of our results. It is interesting to investigate also the validity of the predictions beyond salt marsh ecosystems. Channel development in mangrove and sea grass ecosystems might also be liable to initial bathymetry.

Since we did not aim to create a complete landscape model but rather wanted to utilize this simple set up to investigate interactions between abiotic and biotic processes, our approach provides the opportunity to the implement a range of scenarios and test their ramifications on landscape development. Further biotic- (such as: different plant species, species competition and the presences of different benthic organisms) and abiotic parameters (such as; different suspended sediment concentrations, different mixtures of suspended and bottom sediment and the occurrence of waves) can be implemented to identify the drivers of landscape development within variety scenarios. This provides a unique opportunity to investigate the impact of biota on landscape development and to identify circumstances pronouncing or concealing biotic impact on the resulting geomorphology. Such dynamic view on the development of vegetated landscapes may provide the insights needed to identify the signatures of life on the landscape [Dietrich and Perron, 2006].

Impacts of a species invasion on geomorphologic processes in mature salt marshes

C. Schwarz, T. Ysebaert, P. M. J Herman

Abstract

Species invasions in general and specifically in salt marsh ecosystems are known to change biotic ecosystem characteristics such as community structure and cycling of materials. Their ability to alter interactions between biotic and abiotic ecosystem parameters (i.e. biogeomorphic feedback loops) was also pointed out, but possible impacts on landscape configuration in tidal wetland ecosystems were not yet demonstrated. We studied the impact of altered biogeomorphic feedbacks on geomorphologic features (i.e. tidal channels), by comparing proxies for channel network geometry (unchanneled flow lengths, fractal dimension) over time between non-invaded and invaded salt marsh habitats. The non-invaded habitats (salt marshes in the Scheldt estuary, the Netherlands, and in the south of eastern Chongming Island, Yangtze estuary, China) show little change in network geometry over time with a tendency for an increased drainage density. The invaded site (salt marshes in the north of eastern Chongming Island) showed a clear decrease in channel drainage density throughout and after the species invasion. This shows that species invasions not only affect biotic ecosystem characteristics, but also their ability to change biogeomorphic feedback loops, potentially leading to changes in existing geomorphologic features and therefore landscape configuration. We could further show that the species invasion also altered sediment composition. Based on observations we propose a mechanism explaining the change in channel drainage density by an alteration in plant properties. The physical and physiological characteristics of the invading species *Spartina alterniflora* clearly differ from the native species *Scirpus mariqueter*, inducing different biogeomorphic feedback loops leading to the observed change in salt marsh channel configuration. We discuss the ramifications of our insights for the evaluation and management of species invasions with respect to different ecosystem functions.

Introduction

The Smooth Cordgrass *Spartina alterniflora* is one of the most examined species in intertidal coastal wetlands. It is a perennial rhizomatous cord grass native to the coasts of North America [Simenstad and Thom, 1995; Teal, 1985]. *Spartina alterniflora* has strong ecosystem engineer capabilities [Crooks, 2002], similar to other *Spartina* species [Bouma et al., 2009b; van Hulzen et al., 2007]. The ability of *Spartina* to modify its habitat is mainly due to its morphology, reducing erosion and increasing accretion within its patches [Bouma et al., 2005b]. Introductions of these species worldwide have resulted from a variety of causes, ranging from accidental introductions via agriculture and ship ballasts, to deliberate introduction for erosion control and accelerated rates of accretion for land reclamation [J Callaway and Josselyn, 1992; B Li et al., 2009]. *Spartina* species are among the few salt marsh species that have been introduced outside their native range; such as plantings of *Spartina* anglica in New Zealand [Hubbard and Partridge, 1981], China [Chung, 2006] and Europe [Ranwell, 1964]. *Spartina alterniflora* has mostly been introduced along the Pacific coast of North America [Frenkel and Boss, 1988], in New Zeeland [Partridge, 1987] and the East Coast of China [An et al., 2007]. *S. alterniflora* was mainly introduced because of its high stress tolerance and reproduction rate, entailing its wide distribution across the intertidal zone. It has the ability to rapidly colonize open areas and stabilize eroding shorelines [J Callaway and Josselyn, 1992].

Many studies already discussed the general impact of species invasions on ecosystem processes, such as shifts in species composition, accumulation of materials and interactions with abiotic factors [B Li et al., 2009; Strayer et al., 2006; Theoharides and Dukes, 2007]. Specifically with respect to *Spartina alterniflora* introductions, literature reports many positive and negative effects. This includes effects on the invaded biota such as competition with the native flora [Frenkel and Boss, 1988; H M Huang and Zhang, 2007], altered habitat for the native fauna including benthos [Chen et al., 2004; B Li et al., 2009; R Z Wang et al., 2010b] and loss of shorebird and wading bird foraging grounds [Goss-Custard and Moser, 1988; Ma et al., 2007]. For the abiotic environment, *Spartina* invasions were reported to influence estuarine sediment dynamics (e.g. promoted accretion) [S L Yang, 1999a].

This not only altered sediment quantity and quality in existing marsh ecosystems [S L Yang et al., 2008], but also led to accelerated marsh expansion rates altering pioneer zone composition as observed on salt marshes in the Yangtze estuary and North America [H M Huang and Zhang, 2007; B Li et al., 2009; Rosso et al., 2006].

Although the influence of *S. alterniflora* invasion on the morphology in the vertical plane (e.g. accretion rate) was already investigated, its impact on the organization of the horizontal plane remains unclear. The spatial organization of the horizontal plane can be regarded as the integrated outcome of various processes (abiotic and biotic), modified by the invader and influencing hydrodynamic and sedimentation patterns (i.e. biogeomorphology). Knowledge about changes in the organization of the horizontal plane is essential to judge impacts of species invasions on ecosystem services provided by tidal wetlands, such as storm surge protection, sustainability with rising sea level and nursery function for fish and crustaceans.

The development of drainage networks organizing the tidal marsh's horizontal plane are the result of physical, chemical and biological interactions which further control hydrodynamics and sediment exchange between salt marsh, tidal flat and the adjacent open water body [Marani et al., 2002]. Previous research already showed that changes in vegetation cover (i.e. vegetation removal) have the potential to change spatial marsh flow, sedimentation patterns and consequently are also able to alter tidal channel morphology [Temmerman et al., 2012]. We hypothesize that also species replacement, through the process of species invasion, has the potential to change spatial sedimentation patterns and hence existing tidal channel network geomorphology and landscape configuration.

This idea is an extension of the previously highlighted role of biota on initial landscape development. It was previously described that vegetation is able to sculpt landscape patterns via scale dependent feedbacks. Scale dependent feedbacks describe the phenomenon of increased sediment accretion within vegetation patches due to reduction of flow (small scale positive feedback) and enhanced erosion around vegetation patches due to flow routing (larger scale negative feedback) [van de Koppel et al., 2012; van Wesenbeeck et al., 2008b]. The results of these ideas on the spatial organization of the horizontal plane were shown to be an increase

in channel drainage density from mudflat to salt marsh systems, explained by flow routing around emergent vegetation patches, potentially leading to channel incision [D'Alpaos et al., 2006; Temmerman et al., 2005a; Vandenbruwaene et al., 2012].

In this study we investigate the impact of species replacement (via invasion) on existing geomorphologic features (tidal channel networks). Because the replacing species, *Spartina alternilfora*, has different physical (e.g. plant height, stiffness) and physiologic (e.g. stress tolerance) properties compared to its native predecessor, we hypothesize it will establish different feedback loops and therefore reshape existing channel networks. First, we investigate the development of tidal channel networks over time (using the unchanneled flow lengths and fractal dimension as a proxy) in the absence of invading species, further referred to as the reference cases. Subsequently, we compare these reference cases to the spatiotemporal tidal channel network development of an invaded salt marsh system.

We utilize two reference cases for the non-invaded scenario, one in the Scheldt estuary, The Netherlands and the other in the Yangtze estuary, China. The channel network in the Scheldt estuary is regarded as a stable drainage system, experiencing only little growth in the horizontal and vertical direction. This is due to the fact that its incoming sediment concentration and elevation are close to the system' s equilibrium concentration at the beginning of our observation period and at equilibrium at its end [Meire et al., 2005; Vandenbruwaene et al., 2012; Wilderom and de Bruin, 1973]. The channel networks in the Yangtze estuary are regarded as expanding drainage systems. Because the amount of incoming suspended sediments lies above the system's equilibrium concentration, salt marshes and therefore the channel systems are expanding seawards and also grow in the vertical direction [S L Yang, 1999b]. We compare these network developments with a recent species invasion on salt marshes in the Yangtze estuary, China [H M Huang et al., 2008b; J Li et al., 2010a]. In addition to a comparison of network characteristics we assess changes in sediment composition between multiple Chinese invaded and non-invaded sites, potentially caused by species invasion. Finally, based on literature and field evidence, we propose a mechanism enabling the invasive species (*Spartina alterniflora*) to change established channel network features.

Methods

The Study areas

In order to evaluate the development of tidal channel network drainage densities pre and post species invasion, we first studied channel evolution in two systems without recent invasions and used these insights as reference cases. These reference cases are located in different estuarine systems to underline the generality of the observed signature.

The first reference case, the Scheldt estuary, is located in the Northwest of Belgium and the Southwest of the Netherlands and is about 5 km wide at its mouth [De Vriend et al., 2011]. The estuary is characterized by a semi-diurnal mesotidal regime, with an average tidal range of about 3.75m near the mouth (Vlissingen) [Vandenbruwaene et al., 2012] (detailed description see also [Meire et al., 2005]). The Saeftinghe study area (51.3536 ˚N, 4.1650 ˚E) is a 3000ha intertidal area located in the brackish zone of the estuary with a local mean tidal range of 4.88m. The extensive salt marsh area originates from a *Spartina anglica* introduction in 1925 [Waterstaat, 2005]. After initial establishment has taken place until the early 1930s the area can be regarded as an unaltered and natural developing system. Nowadays the Saeftinghe marsh consists of large parts of high-elevated tidal marshes (elevation around mid-sea level) dissected by extensive intertidal channel networks. The present high marsh vegetation is dominated by *Elymus athericus*, a grass species with dense cover. Low marshes are characterized by *Aster tripolium* and *Scirpus maritimus* vegetation, with *Spartina anglica* and *Scirpus maritimus* forming the pioneer zone. Highest elevations are characterized by *Phragmites australis*, which forms the climax vegetation [Vandenbruwaene et al., 2012].

The second reference case, the Yangtze estuary, is located at the east coast of Mainland China and covers large areas of the provinces Shanghai and Jiangsu, and is about 90km at its mouth. This meso-tidal estuary is characterized by semidiurnal tidal regime with a mean tidal range of 2.95m (Wusong datum). Due to the large sediment input from upstream the Yangtze estuary has been expanding in the south-eastern direction, creating a systems of islands of which Chongming Island

is the largest [De Vriend et al., 2011; B Li et al., 2009]. The intertidal areas on eastern Chongming Island (31.6619 °N, 121.4780 °E) nowadays comprise an area of 24155ha (www.dongtan.cn). Due to the large sediment inputs (sedimentation rates comprise up to 1 mm d^{-1}, at marsh sites, [S L Yang and Chen, 1994]) and species introductions, marsh expansion is significantly sped up (recent lateral expansion rates reach up to: 25m y^{-1} [Xiao et al., 2010]). Salt marshes on Chongming Island are characterized by *Spartina alterniflora* and *Scirpus mariqueter* pioneer vegetation, moving on to predominant *Spartina* meadows at mid elevations and finally ending with *Phragmites australis* vegetation at the highest elevations. *Spartina alterniflora* and *Scirpus mariqueter*, the dominating species in low and mid elevations, show major differences in physical (e.g. plant height, density, stiffness) and physiological (e.g. stress tolerance) plant properties potentially influencing the proliferation. [Chen et al., 2004; B Li et al., 2009; Schwarz et al., 2011]

At the northern part of eastern Chongming Island, *Spartina alterniflora* was planted in 2001. From there it expanded along the northern and mid-parts of the Island [B Li et al., 2009]. Three channel networks in this area were selected and will be further referred to as the invaded sites. In the southern part of eastern Chongming Island three channel systems were selected as a reference case, since this area remained mainly unaltered since the last land reclamation in 2001 and is still inhabited by the native salt marsh species (Fig. 5.1).

Channel networks in false colour aerial photographs (Saeftinghe 2004 and all Yangtze images) were digitized utilizing a pixel threshold value of the image's red band (vegetation high red band value, channels low red band value). The threshold was empirically found by comparison with the extracted channel network. Misclassified isolated pixels were reclassified using a neighbouring filter, however for clusters of misclassified pixels, situations were more complex, and errors had to be corrected manually. Extracted channels were then subsequently converted to line features, with the lines representing the boundaries of vegetated-unvegetated areas (red band classification) equal to channel edges of the networks. For the black and white aerial photographs (Saeftinghe 1935), no (semi-) automatic classification could be applied and channel networks were delineated manually. A detailed description of the tidal channel network extraction method for the Saeftinghe site can be found in [Mason

et al., 2006; Vandenbruwaene et al., 2012].

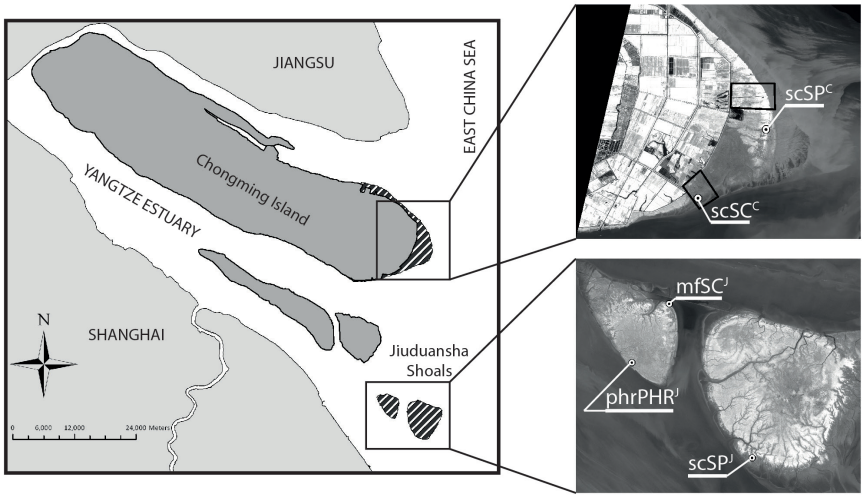


Fig. 5.1: (left) Overview map Yangtze estuary, China; (right, top) Research Area on eastern Chongming Island, Black squares denote areas of which channel networks were investigated (the northern (invaded) and southern (non-invaded) part); (right, bottom) Jiuduansha shoals, which also experienced a species invasion by Spartinas alterinlfora, Circles with centre points denote locations of sediment cores;

Time-steps and locations

For the reference case in the Scheldt estuary (Saeftinghe) we selected data for two time-steps from the north-eastern part of the salt marsh, covering two stages of mature salt marsh evolution from a lower elevated tidal marsh (1935) to a higher elevated tidal marsh (2004) (change in elevation between time steps 0.5-1m). The selection depended also on the availability of aerial photos and channel network delineation [Vandenbruwaene et al., 2012]. For these time-steps aerial photographs were digitized (0.5 m pixel resolution) and geo-referenced (1935, 2004). The selected areas within the site were chosen after delineation of watershed areas and channel network.

For the second reference case on eastern Chongming Island, we selected three channel networks in the southern part, which remained unaltered since the last event of land reclamation in 2001. To investigate the species invasion we selected three channel networks in the northern part of Chongming Island, not far from

the location of the original species introduction. The selection of time steps was dependent on the availability of aerial photographs (2m pixel resolution) (2003, 2005 and 2011) and the spatial spreading of the invasive species (*S. alterniflora*). The assignment of drainage areas and channel networks were done according to the description below.

Since the terrestrial approach of delineating watersheds according to topographic divides proves more difficult in intertidal systems, we utilized the approach described in [Vandenbruwaene et al., 2012] to determine the watershed areas of our study sites. The results of water line delineation can be seen in (Fig. 5.2), left side, indicated by the white lines and in (Fig. 5.3 g,h,i) and (Fig. 5.4 g,h,i) indicated by the grey areas.

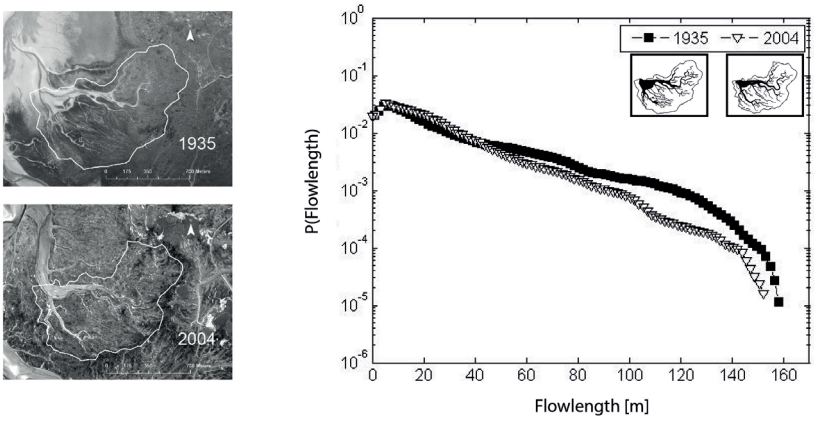


Fig. 5.2: (left) Grayscale aerial images showing salt marsh expansion over time in the Saeftinghe marsh (Westerschelde estuary, The Netherlands), with white lines indicating watershed boundaries; (right) Development of unchanneled flow lengths at the two selected time points (1935 and 2004).

Unchanneled flow lengths:

To evaluate the drainage densities of tidal channel networks, previous studies utilized the frequency distribution of unchanneled flow lengths on the marsh platform [D'Alpaos et al., 2007; Marani et al., 2003a; Marani et al., 2003b]. Unchanneled flow lengths describe the distance a water drop has to travel until it reaches the closest channel. They were calculated, per drainage area, as the shortest distance

from any platform point to the nearest channel edge. The slope of the frequency distribution of unchanneled flow lengths is then a measure for drainage density. The shorter and steeper the unchanneled flow lengths curve is, the higher is the drainage density and the shorter the maximum unchanneled flow length [Vandenbruwaene et al., 2012]. The slopes of the probability density function of unchanneled flow lengths, shown in (Fig. 5.3 a-c) and (Fig. 5.4 a-c), were calculated by fitting a linear function to the linear part of the curve using the least squares method. The linear part of the slope was defined until a flow length probability (P(Flowlength)) of 0.0003(10-3.5), since the fitted function visibly levelled off beyond this threshold. We used the change in slope of the probability density function of unchanneled flow lengths over time to identify a trend in network development. Literature reports channel drainage density to generally increase over time [Allen, 2000; D'Alpaos et al., 2005]. We therefore specifically aimed at distinguishing two trends; increase or decrease in drainage density over time. It should be noted, however, that this proxy is indicative without representing a rigorous statistical test.

Fractal dimension:

Generally, the fractal dimension describes how the detail of a pattern changes across scales in the first, second or third dimension. It hence gives a statistical index of a pattern's space-filling capacity [Falconer, 2007]. Literature already reported the fractal dimension to be linked with terrestrial channel network drainage properties [Baas, 2002; Rodriguez-Iturbe and Rinaldo, 2001]. In our study we utilized it to track channel network changes over time. The main difference to the above described unchanneled flow lengths consists in its independence to the delineated drainage area. Since it is a measure of how well a feature covers the two-dimensional plane it can also be used to compare relative changes in drainage density. The fractal dimension which was calculated using a box counting algorithm is in our case a measure of how well a channel network penetrates the two dimensional plane. The values can vary from 1, signifying the poorest plane cover (by a simple line), to a maximum of 2 denoting that the feature covers the plane completely.

Tracking species invasion

The species invasion in the northern part of our research area on Chongming Island was only tracked qualitatively by comparing the false colour areal images with the available results of previous studies discriminating plant species through differences in light reflectance in the same research area [Ge et al., 2013; H M Huang and Zhang, 2007]. According to this comparison we could identify *Spartina alternifora* as the species with high reflectance (white colour in Fig. 5.4 a,b,c) invading the northern investigated research site. It should be noted that colour intensity does not give a direct relationship to plant coverage since reflectance also varies due to growth stage. Nevertheless the spreading of the light-coloured pixels in our aerial photographs follows the exact same trajectory as previous studies suggested [Ge et al., 2013; B Li et al., 2009].

Sediment coring:

Sediment cores were taken at 5 Chinese salt marsh locations (2 locations on eastern Chongming Island, 3 locations on the Jiuduansha shoals) with varying vegetation succession states (e.g. mudflat, *Scirpus mariqueter*, *Spartina alterniflora*, *Phragmites australis*), including invaded and non-invaded sites. The locations were selected according to the species succession shown in [H M Huang and Zhang, 2007]. The resulting 5 different sample sites were characterized by: scSPC, succession from *Scirpus mariqueter* to *Spartina alterniflora* vegetation (Chongming, invaded); scSCC, constant *Scirpus mariqueter* vegetation (Chongming); mfSCJ succession from mudflat to *Scirpus mariqueter* vegetation (Jiuduansha Shoals); phrPHRJ constant *Phragmites australis* vegetation (Jiuduansha Shoals), scSPJ sucession from *Scirpus mariqueter* to *Spartina alterniflora* vegetation (Jiuduansha Shoals, invaded). Due to logistic reasons sediment cores at the Chongming stations (scSPC, scSCC) were taken to a depth of 80cm and sediment cores at the Jiuduansha stations were taken to a depth of 180cm (mfSCJ, phrPHRJ, scSPJ) (Fig. 5.1). Sediment cores were subsequently analysed (in a 2 cm depth interval) for their grain size distribution using a Beckman-Coulter® LS 13320 particle size analyser. Sediment cores have not been dated, but the change over time was compared between invaded and non-invaded sites in time scales where the invasion took place.

Results

The vegetation development in Saeftinghe between 1935 and 2004 is characterized by a succession from a relatively low-lying high marsh state (elevation: 1.97±0.33 mNAP, MHWL: 2.45 mNAP) to a high marsh state in equilibrium with mid sea level (elevation: 3±0.18 mNAP, MHWL: 2.73 mNAP) [Vandenbruwaene et al., 2012]. The investigated area did not experience species invasions or man made changes in species composition during the investigated period [Wilderom and de Bruin, 1973]. In (Fig. 5.2, right panel) we show that the probability density function of unchanneled flow lengths is not subject to major changes during the investigated period. The left panel of Fig. 5.2 shows black and white false colour

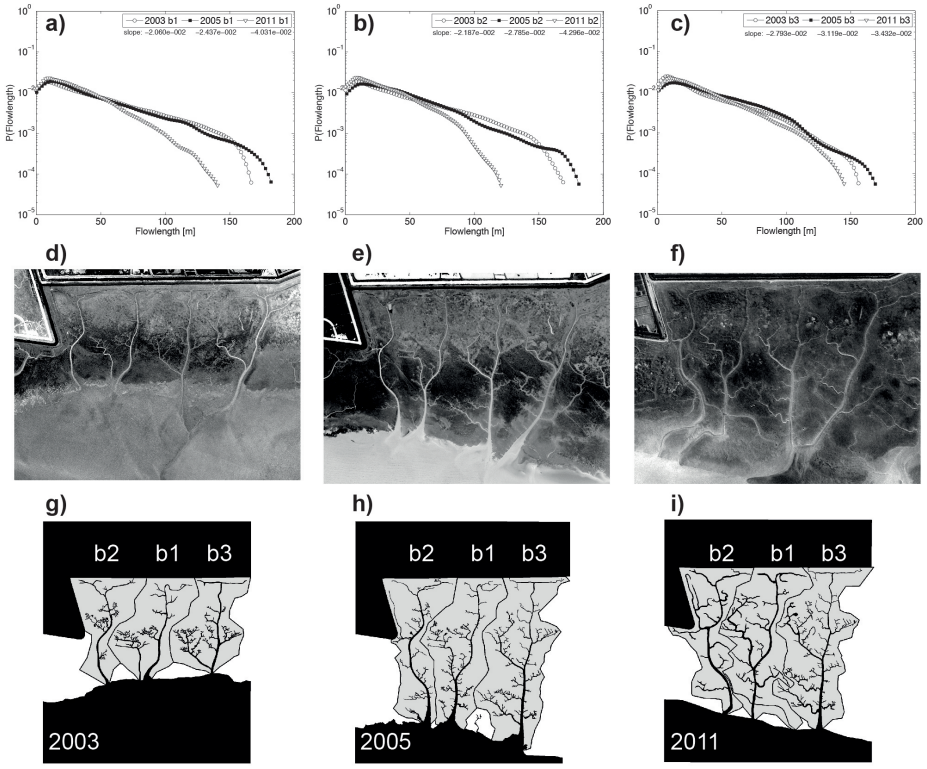


Fig. 5.3: (a-c) Unchanneled flow length of three channel networks (b1, b2, b3) in the non-invaded southern part of Chongming Island (Yangtze estuary, China) at the selected time-steps, slopes are stated below legends, (d-f) grayscale aerial images showing expanding salt marsh development over time (2003, 2005 and 2011), (g-i) digitized channel networks and drainage basins (grey area) (2003, 2005 and 2011).

aerial photographs of the research area at the selected time steps including a white line indicating the watershed. At the expanding salt marsh on southern Chongming Island (non-invaded) unchanneled flow lengths were calculated and compared for three drainage networks (Fig. 5.3, a, b, c). All of them show a similar trend as observed for the Saeftinghe area with little change between 2003 to 2005 (latest land reclamation in 2001) [Chen et al., 2004]. In 2011 the unchanneled flow lengths in all basins show a visible decrease, implying an increase in drainage density, which can be seen through the increase in slope in the probability density function of the unchanneled flow lengths (Fig. 5.3, a,b,c). It is important to note that in all our reference cases (expanding or stable), drainage density either shows an increasing trend or stays constant.

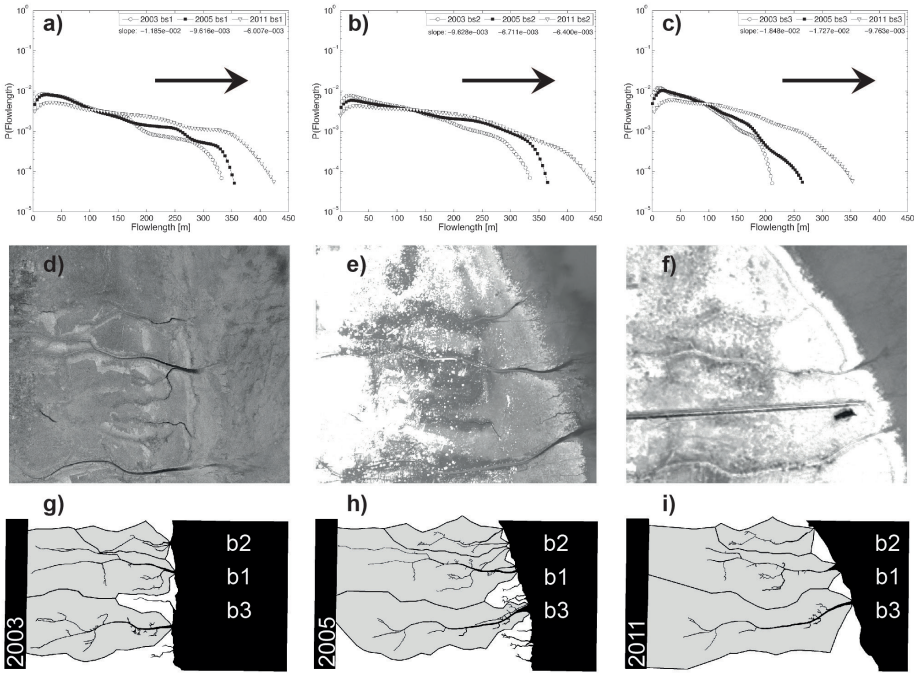


Fig. 5.4: (a-c) Unchanneled flow length of three channel networks (b1, b2, b3) in the Spartina alterniflora invaded northern part of Chongming Island (Yangtze estuary) at the selected time-steps, slopes are stated below legend, (d-f) grayscale aerial images showing salt marsh development over time (2003, 2005 and 2011), Spartina alterniflora invasion is indicated by white pixels entering the research area in 2005 (middle picture, e) and covering large parts of the research area in 2011 (right picture, f), (g-i) digitized channel networks and drainage basins (grey area) (2003, 2005 and 2011).

In the northern part of Chongming Island (Fig. 5.4 d,e,f) the species invasion is visible through the white coloured pixels (high reflectance of *Spartina alterniflora*), invading the research area and occupying the entire area by the end of 2011. In (Fig. 5.4 a,b,c) it is visible that from 2003 to 2005 unchanneled flow lengths of all three basins exhibit little change with an increasing trend. In 2011 the unchanneled flow lengths of all the northern basins show a visible decrease in slope and an increase in maximum unchanneled flow length, signifying a decrease in drainage density. This is in agreement with field observations where channels from previous years disappeared in the field.

The difference in development in drainage density is also visible in Fig. 5.5, which shows the

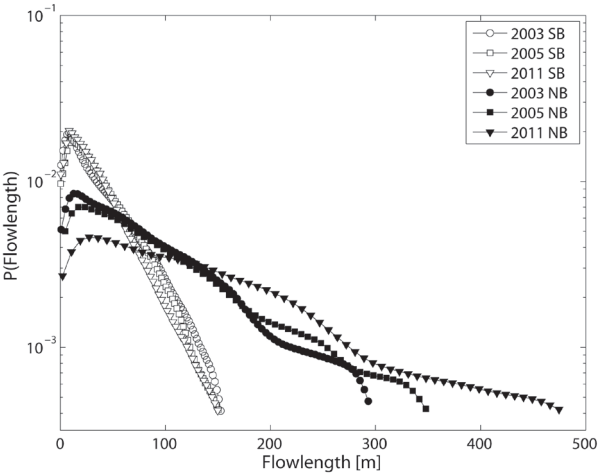


Fig. 5.5: Development of unchanneled flow lengths of the merged drainage basins over time in northern (black, NB, invaded) and southern (white, SB, non-invaded) parts of Eastern Chongming Island.

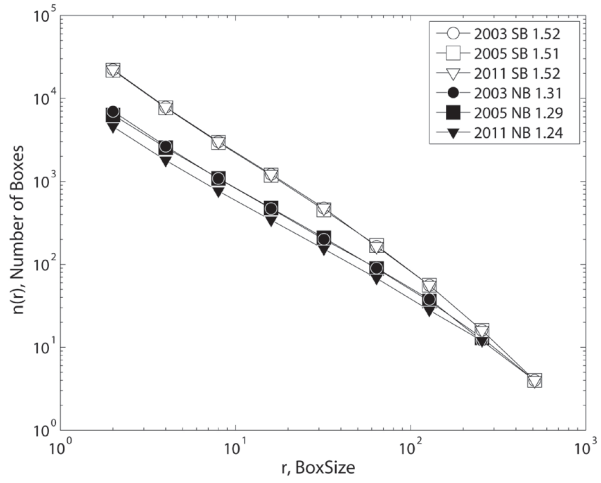


Fig. 5.6: Box counting results of the merged drainage basins over time in northern (black, NB) and southern (white, SB) parts of Eastern Chongming Island; Fractal dimensions are stated in legend.

change in the development of unchanneled flow lengths for the merged drainage area of all three basins in the north and in the south respectively. Whereas the southern reference networks show little development in channel drainage density with an increasing trend (steepening), the northern networks experience an apparent loss in channel drainage density over the investigated period (flattening). Fig. 5.6 shows a similar, although less pronounced relationship utilizing fractal dimensions as a proxy. In this comparison the fractal dimension of the merged northern networks was compared to the fractal dimension of the merged southern networks. The southern networks seem to exhibit almost no change in fractal dimension over time, whereas the northern networks show an apparent decrease in 2011. This means that a geometrical comparison of the channel networks (i.e. how well they cover the horizontal plane) shows no change in the southern part, whereas in the northern part the network coverage over the horizontal plane decreases over time.

In Fig. 5.7 we show the Sand:Silt:Clay composition and the d50 along the depth of sediment cores taken at the 5 sampling locations (Fig. 5.1). It is visible that at the two non-invaded salt marsh sites only little change in Sand:Silt:Clay composition and d50 can be observed over depth (scSCC, phrPHRJ), with at scSCC a d50 of 31.57 microns at the top layer and at phrPHRJ a d50 of 20.46 microns at the top layer. In the other non-invaded site, that developed from a mudflat into a *Scirpus mariqueter* marsh (mfSCJ), we observed a decrease in d50, starting from 100 microns and evolving towards 33.85 microns, similar to the observed value in the *Scirpus mariqueter* marsh (scSCC). This site further shows, that the reduction in d50 was accompanied by a decrease in the Sand fraction and an increase in the Silt and Clay fraction. At the two invaded sites (scSPC, scSPJ) the d50 decreased to a value of 10.51 and 9.91 microns. This observed decrease in d50 was also accompanied by a decrease in the Sand fraction and an increase in the Silt and Clay fractions (refinement).

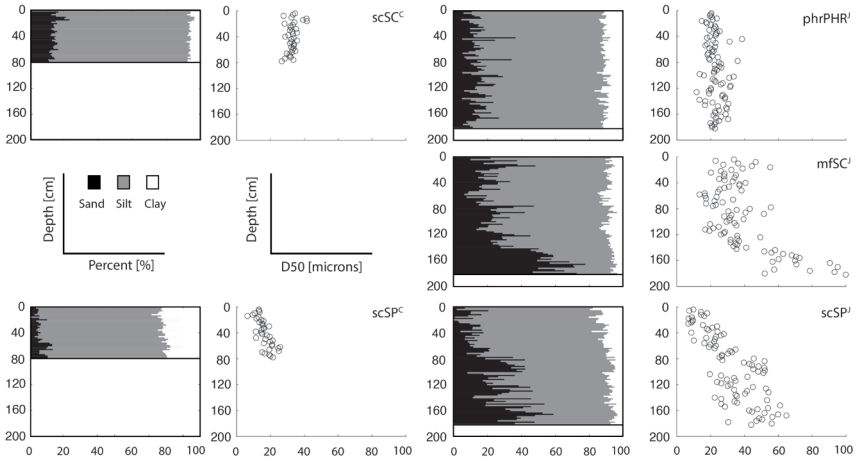


Fig. 5.7: Sand: Silt: Clay composition and d50 over depth of 80 cm sediment cores taken on Chongming Island (left), scSCC, constant Scirpus mariqueter vegetation (Chongming), scSPC, succession from Scirpus mariqueter to Spartina alterniflora vegetation (Chongming, invaded); Sand: Silt: Clay composition and d50 over depth of 180 cm sediment cores taken on the Jiuduansha shoals (right), mfSCJ succession from mudflat to Scirpus mariqueter vegetation (Jiuduansha Shoals); phrPHRJ constant Phragmites australis vegetation (Jiuduansha Shoals), scSPJ succession from Scirpus mariqueter to Spartina alterniflora vegetation (Jiuduansha Shoals, invaded).

Discussion and Conclusions

The observed channel network branching patterns (Fig. 5.1-3) in the studied salt marshes are the result of biogeomorphic feedbacks influenced by present hydrodynamic conditions (e.g. current, waves, tidal prism…), geomorphologic properties (slope, coastal alignment, sediment properties…) and vegetation characteristics (cover, density, stress tolerance, stiffness…) [Marani et al., 2003a; Marani et al., 2004]. These factors are governing the balance between erosion and deposition and vary across the studied channel network systems. This is the reason for choosing an approach investigating the relative change in network development over time utilizing proxies such as the probability density function of the unchanneled flow lengths and the fractal dimension. We use the change in these proxies over time to indicate trends in channel network development. Specifically, two trends are

distinguished, increase or decrease in channel drainage density.

Previous literature on terrestrial and intertidal channel networks suggested the fractal dimension and the probability density function of unchanneled flow lengths are good proxies assessing changes in drainage density and general channel network characteristics [Cleveringa and Oost, 1999; D'Alpaos et al., 2005; Marani et al., 2004; Rodriguez-Iturbe and Rinaldo, 2001]. These proxies proved useful comparing network properties between tidal and terrestrial networks [S. Fagherazzi et al., 1999], showing differences between channel networks on salt marshes and tidal flats [S. Fagherazzi et al., 1999; Vandenbruwaene et al., 2012], and in assessing the importance of vegetation presence shaping network structure [Pestrong, 1972].

We utilized both proxies in the assessment of the effect of species invasion on channel network structure to assure that the assumptions we made to delineate our drainage basins did not influence the results of our analysis. This is confirmed by comparing Fig. 5.5 and Fig. 5.6, showing fractal dimensions and unchanneled flow lengths of the three merged basins in north and south. Only small changes were observed at the non-invaded southern site, whereas in the northern site (invaded) the channel drainage density decreased considerably after the invasion started. This is in agreement with both the trend observed in unchanneled flow lengths of the delineated networks (Fig. 5.3-4) and of the merged networks (Fig. 5.5), documenting the independence of the observed effect from drainage basin delineation. This observation extends the applicability of the statistical descriptors (unchanneled flow lengths and fractal dimensions) from the relatively static descriptions of constant basin areas where it was used previously [D'Alpaos et al., 2005] to expanding and dynamic salt marsh ecosystems. It is also shown that small differences in network properties are more difficult to observe using only fractal dimension as a proxy compared to unchanneled flow lengths.

Fig. 5.2 and Fig. 5.3 were used as a reference scenario, showing the development of drainage density over time at a non-expanding and an expanding marsh without species invasion. Here it is important to notice that drainage density at the Saeftinghe site or the two first years (2003 and 2005) at the southern Chongming site are not exhibiting a decrease over time (Fig. 5.2 and Fig. 5.3). This is in accordance with literature, which proposes a general increase in drainage density over time,

during the so-called channel elaboration phase (succeeding the channel initiation phase). It increases network penetration mainly through tidal meandering [Allen, 2000; Marani et al., 2002; Perillo et al., 2009; Steel and Pye, 1997]. In contrast, the invaded channel networks in the northern part of Chongming Island show a decreasing trend in channel drainage density over time. This is due to the loss of small, low-order channels (Fig. 5.4 a, b, c). The observed reduction in drainage density after species invasion is to our knowledge a new phenomenon that has not been investigated so far. Previously, retreat or expansion of tidal networks has been linked to decrease or increase of the tidal prism, watershed area or to the succession from mudflat to salt marsh channels, showing the linear relation between channel drainage density and the tidal prism [Stefanon et al., 2012; Vandenbruwaene et al., 2012]. Since our Chinese research areas were under the same tidal forcing, network retreat through a reduced tidal prism should have been visible in both marshes, which was not observed. A comparison between the northern and southern areas further shows a difference in salt marsh expansion velocity between 2003 to 2005 (large increase) and 2005 to 2011 (moderate increase, section wise decrease in the southern areas). We propose that these differences could originate from altered sediment budgets due to dam constructions upstream (completion of the Three Gorges Dam in 2009) as proposed in literature [S L Yang et al., 2011].

The reduction in drainage density has also morphologic consequences. We would expect the loss of small order channels to result in increased deepening of the main channel [D'Alpaos et al., 2005], further influencing filling and emptying behaviour and sediment transport [Temmerman et al., 2012]. A detailed description of the geomorphologic and hydraulic changes is, however, beyond the scope of this paper.

In Fig. 5.7 we could show that the species invasion influenced bottom sediment grain size distribution at the invaded areas. The non-invaded salt marsh areas (scSCC, phrPHRJ) show only little variation in sediment characteristics over depth, whereas both sediment cores taken in invaded areas (scSPC, scSPJ) exhibit a trend of increasing clay and silt content with decreasing sediment depth (i.e. age) (refining). The observed grain size refinement at the non-invaded mudflat-*Scirpus mariqueter* transition, is in agreement with the previously observed influence of salt

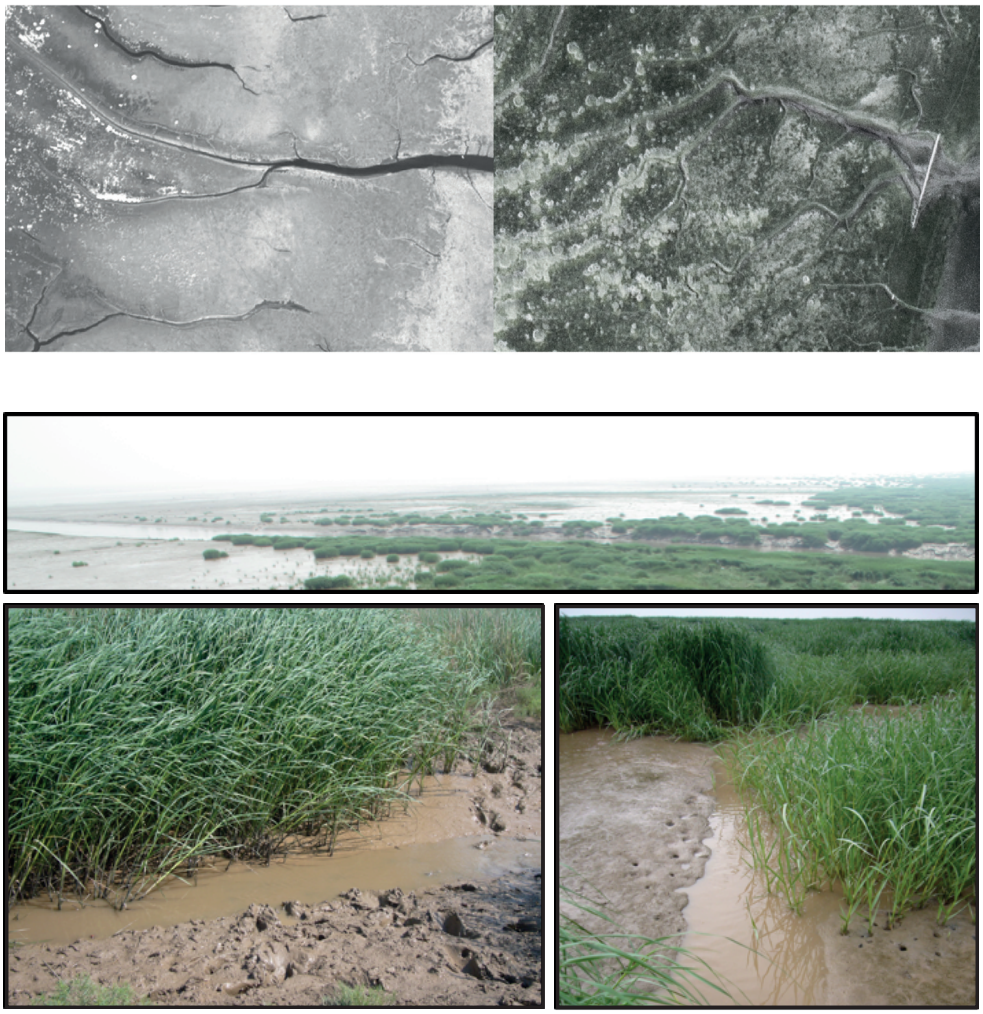


Fig. 5.8: (above) Aerial images of Spartina alterniflora (white pixels) invading existing salt marsh and mudflat channels and creek banks on Chongming Island (left) and on the Jiuduansha shoals (right) (Spartina introduction in 1997), Yangtze Estuary, China. (below) Field observations showing Spartina alterniflora growing next and into small creeks

marsh plants on grain size sorting along a mudflat-salt marsh gradient [S L Yang et al., 2008]. It also shows, in combination with the scSCC site, that grain size sorting at *Scirpus mariqueter* marshes reduced the d50 to a value of 31.57 microns, whereas sediment samples taken in the invaded areas (scSPC, scSPJ) exhibited a reduction down to 10.51 and 9.91 microns. A comparison with a further non-invaded site

(phrPHRJ) shows that in *Phragmites australis* marshes refinement did not cause such low d50 values (phrPHRJ 20.46 microns), which is in agreement with previous studies [S L Yang et al., 2008]. This gives strong evidence that the increased refinement originates from the invasion by *Spartina alterniflora*. The dike adjacent to our investigated channel network in the north of Chongming Island (see Fig. 5.4 c) was built in autumn 2010. Because channel networks and sediment samples were investigated in spring 2011 we did not consider the dike to be influential on geomorphologic processes yet.

The influence of vegetation on intertidal channel networks was already shown by [Temmerman et al., 2012]. It was shown that large-scale removal of vegetation changes intertidal flow patterns, which further translates into infilling of existing channels, hence changing network structure. In [Sanderson et al., 2001; Sanderson et al., 2000] the importance of salt marsh channels for the distribution of salt marsh plant propagules was shown, utilizing the example of the Petaluma salt marsh restoration (San Francisco Bay, California, USA). There a salt marsh was restored by breaching previously present dikes and initiating channels at these breaches, without planting vegetation [Siegel, 2002]. This resulted in species transport (i.e. plant seedlings) via channels and thereafter salt marsh colonization from channel edges [Tuxen et al., 2008]. This mechanism of marsh colonization was still visible a decade after restoration in present species richness gradients driven by channel proximity. This underlies the importance of marsh channels structuring the salt marsh ecosystem [Sanderson et al., 2000].

We propose, supported by field observations and aerial images (Fig. 5.8 a,b), that the species invasion by *Spartina alterniflora* on Chongming Island followed the same main distribution pathways as previously observed at the Petulama marsh in the San Francisco Bay, namely the tidal channel network. (Fig. 5.8 a) shows that establishment of *Spartina alterniflora* first took place at the levees of existing channels. Subsequently, because of its high stress tolerance, *S. alterniflora* was not only able to colonize and establish at channel levees and the marsh platforms but also in the channels (Fig. 5.8 b). This resulted in the observed reduction in channel drainage density by closing off small tributaries, as observed after species invasion. *S. alterniflora* has superior competitive traits such as fast growth, high productivity,

high tolerance to salt, clay and loamy sediment and a well-developed belowground system making it a specifically strong ecosystem engineer [Crooks, 2002; USDA, 2007]. The superiority of *S. alterniflora* in respect to physiological (e.g. stress tolerance) and physical characteristics (e.g. plant height) was also confirmed through a direct comparison with the native species *Scirpus mariquterer* [He et al., 2012] (see also Chapter 2 of this thesis), supporting our hypothesis.

Our field measurements and satellite image analysis show that species invasions are able to change established geomorphologic features. They indicate that an invasion by a species with different physiological and physical properties (*S.alterniflora*) can result in changing the existing spatial habitat configuration. This change in spatial arrangement of the intertidal landscape affects the distribution of water with all its particulate, solute, organic or inorganic compounds, thus creating different local sedimentation rates and an altered ecological niche structure. The results of our study give important insights for habitat management and assessment of species invasions on ecosystem functions.

Unfortunately, our study could not distinguish whether changed channel network properties are mainly due to the differences in physical (e.g. plant height, stiffness, density, hydraulic resistance) or physiological plant properties (stress tolerance, growth velocity) of the invading species (*S. alterniflora*). We nevertheless could establish a link between species-specific plant properties and changes in geomorphology on the landscape scale. An important direction for future research would be to elucidate whether physical or physiological plant properties influence channel network configurations across different salt marsh ecosystems.

Synthesis

Biogeomorphology studies the circular interactions between geomorphic and ecologic landscape components. In one direction, the distribution of biota is shaped by landforms and geomorphic processes [Parker and Bendix, 1996]. In the other direction, geomorphic processes and landforms are modified by biota [Butler, 1995; Temmerman et al., 2007].

Biogeomorphic systems, such as salt marsh ecosystems, which are the focus of this thesis, can be viewed as "complex adaptive systems". In "complex adaptive systems" a macro-scale pattern can emerge from local interactions and selection processes acting at lower levels [Dominion, 1999]. One theme underlying "complex adaptive systems" is multi-causality, which in the context of biogeomorphology is given by the process-form interaction. Biogeomophic processes shape landforms and the landforms shape biogeomorphic processes. The conundrum of multi-causality and its circularity was described by [Parker and Bendix, 1996] as: "When a certain type of vegetation shows an affinity for a particular landform, it is often difficult to decipher whether the physical characteristics of the landform or the active geomorphic processes associated with it are the underlying cause."

An important question becomes how process-form interactions (i.e. multi-causality) transform over space and time, leading to self-organized systems or systems mainly determined by environmental conditions. Self-organization proposes that small-scale localized interactions between components of a system are able to generate spatial patterns at larger scales mainly independent of external landscape-scale forcing [Levin, 1998; van de Koppel et al., 2012]. Some self-organized systems can be characterized by recursiveness, i.e. the emergence of system properties that can act as a constraint upon future development [Stallins, 2006]. It was observed that heterogeneity can emerge from recursive interactions between organisms and the geomorphic setting [Phillips, 2001]. For instance, in salt marsh pioneer zones vegetation patterns reinforce soil contrast (through litter, different nutrient composition, grain size sorting, changed hydroperiod), which in turn reinforces vegetation contrast and the differentiation of substrate properties [van Wesenbeeck et al., 2008].

Another theme underlying biogeomorphic "complex adaptive systems" is ecosystem engineering [Jones et al., 1994]. Ecosystem engineers modify geomorphic

processes and forms, transforming the environment to generate feedbacks that ameliorate circumstances for themselves and other species. Ecosystem engineering is an important factor structuring salt marsh ecosystems. It affects both biotic (e.g. community composition) and abiotic (e.g. morphology) aspects of the ecosystem [Marani et al., 2013; Temmerman et al., 2007]. Ecosystem engineering works through the establishment of biogeomorphic feedbacks. In tidal marshes, these feedbacks are particularly strong. Marsh plants modify the movement of water and sediment, which simultaneously exerts a positive influence on plant growth [Mudd et al., 2010; Wang and Temmerman, 2013]. For instance, the substrate stabilizing function of *Spartina alterniflora* on cobble beaches not only promotes its own growth but also facilitates the establishment of other species [Bruno, 2000]. By stabilizing substrates, enhancing weathering processes, creation of habitats and promotion of facilitative relationships, ecosystem engineers introduce non-linear responses needed in complex systems. In this context a non-linear response simply denotes that local rules of interactions change as the system evolves. The induced non-linearity by ecosystem engineers can lead to historical path dependency, whereby future interactions are constrained by initial effects. A consequence of path dependency is the emergence of alternative stable states, which has been previously investigated at salt marsh ecosystems. Alternative stable states are stable states through ecosystem development, which result from non-linear system responses to changed external forcing. The shift between states exhibit threshold like responses, which are sometimes difficult to reverse. For instance through salt marsh development we distinguish salt marsh and mudflat stable states [Stallins, 2006; van de Koppel et al., 2012].

As discussed above, biogeomorphic systems consist of multidirectional interactions between geomorphic and ecologic components. Previous studies identified interactions between plant properties (ecologic component), hydrodynamics and sediment characteristics (geomorphic component) to be the key players influencing the establishment of biogeomorphic feedbacks and therefore the landscape configuration in biogeomorphic systems (i.e. salt marshes) [Jones et al., 2010] (Fig. 6.1). This is a multi-faceted, multi-scale interaction with complicated dynamic consequences. Nevertheless, for practical reasons research was restricted to specific processes (such as the lateral expansion or vertical growth) [Ge et al.,

2013; Sanchez et al., 2001], specific species (such as *Spartina alterniflora* or *Spartina anglica*) [Deng et al., 2009; van Wesenbeeck et al., 2008] or specific spatial scales (such as intermediate spatial scale, i.e. established plant patches, tussocks) [Balke et al., 2012; D'Alpaos, 2011]. These restrictions enhanced insight in particular aspects, but limited the overview of how interactions between geomorphic and ecologic components are able to shape the landscape at different spatial and temporal scales.

In this thesis I examined how plant properties (e.g. physical traits such as plant height and/or physiological traits such as stress tolerance) interact with sediment properties (e.g. sediment cohesiveness or bed morphology) and hydrodynamics (e.g. tidal amplitude or current velocities) across different scales. My aims were threefold. First, I tried to elucidate how this three-way interaction influences species establishment thresholds at a small scale. Next, I investigated their influence on the establishment of biogeomorphic feedback loops at an intermediate scale. And finally, I examined the influence of this three-way interaction on the ability of biogeomorphic feedback loops to sculpt landscape geomorphology.

The results of this holistic approach enabled me to investigate the influence of biotic-abiotic interactions on seedling establishment (at small and intermediate scales) and their potential to influence the landscape configuration through path dependence. They further enabled me to discuss the influence of biotic-abiotic interactions on ecosystem engineering ability in the context of recursiveness and heterogeneity (intermediate scale). And finally led me to identify how interactions between biotic and abiotc factors either favour the emergence of a self-organized system or a system mainly influenced by the prevailing abiotic conditions (landscape scale).

This multiple-scale approach was carried out on salt marsh ecosystems in the Yangtze estuary, China. The fast expanding salt marshes of the area are highly dynamic both from a biotic (species range extensions and replacements) and abiotic point of view (rate of sedimentation, intensity of hydrodynamic disturbance). That makes them most suitable to study impacts of ternary interactions on biogeomorphic feedback loops. We investigated two dominant pioneer species, *Spartina alterniflora* and *Scirpus mariqueter*. Both species are autogenic ecosystem engineers, which induce salt marsh formation by trapping sediment and consequently increasing soil

elevation. The species differ in their physical and physiological properties. *Spartina* is a fast and high growing plant with stiff above ground biomass. In comparison, *Scirpus* is a slower and lower growing plant with flexible aboveground material.

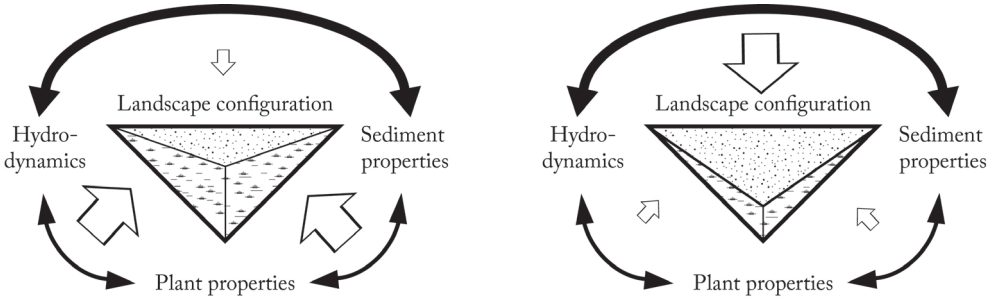


Fig. 6.1: Feedback loops between plant properties, hydrodynamics and sediment properties; areas in the triangle signify the relative contribution of different interactions on landscape development; (left) strong impact of plant properties on landscape configuration (i.e. pronounced impact of biogeomorphic feedbacks), (right) little impact of biogeomorphic feedbacks

Implications of small scale and intermediate scale interactions

My results show that plant establishment in these intertidal areas was influenced by the local prevailing abiotic conditions (hydrodynamics and sediment properties) in interaction with species traits (chapter 2), which was also confirmed by existing literature (Fig. 6.1) [Engels et al., 2011]. I could specifically show that plant establishment is determined by the interaction between currents, waves, plant traits (physical traits, such as stiffness and plant height; physiologic traits such as stress tolerance and growth velocity) and sediment characteristics (cohesive, non-cohesive). This extends previous studies on plant establishment, mainly focusing on the impact of sedimentation/erosion dynamics [Balke et al., 2013], showing that also physical properties of the aboveground plant material in combination with hydrodynamic stress and sediment characteristics (i.e. the local prevailing conditions) influence plant establishment.

Local prevailing conditions, that either favour or disfavour plant establishment,

are dictated by abiotic factors at different spatial scales. Literature reveals 2 sorts of mechanisms setting these local conditions on a big scale (i.e. the deltaic level): external components and components dynamically interrelated within the system (i.e. implied in feedback loops within the system). External components are sediment supply (riverine or oceanic), ocean circulation, direction and intensity of wind and waves, river discharge and its variability, tectonic influence. In contrast to these external forcings, components such as basin configuration, depth, subsidence pattern, erosion, transport and accumulation of sediment as well as submarine resedimentation are linked to each other by feedbacks within the system. [Harbaugh and Bonham-Carter, 1977]. At the more local scale of a specific shoreline, environmental conditions are mainly governed by the hydrodynamic disturbance regime such as nearshore wave influences. Waves sort and redistribute sediments. High nearshore wave power produces well-sorted sandy shorelines with steep concave offshore slopes, whereas low nearshore wave power is generally associated with gentle convex offshore profiles, with less well sorted sands including mud and silt [Orton and Reading, 1993]. This shows that site-specific sediment properties are mainly a consequence of big scale and near shore hydrodynamics and sediment supply.

In the context of "complex adapative systems", locally prevailing conditions, which are determined by big scale processes, are one side of the multidirectional biotic-abiotic interactions determining the ability of plants to establish. The other side is set by physical and physiological plant species traits (e.g. stiffness or stress tolerance). This further implies that also non-linear system responses resulting from initial recruitment such as path dependence and alternative stable states are influenced by interactions between plant traits and local prevailing conditions with their inherent big scale effects. The results of this thesis suggest that colonization history of salt marshes and the state the salt marsh resides in is therefore the result of the early recruitment set by biotic-abiotic interactions at different spatial scales and the change of these interactions through the system's development (chapter 2). An example for biotic-abiotic interactions influencing the salt marsh state is the suggested feedback between changes in substrate and changes in plant community [Sprugel, 1980]. It was previously shown that plant communities are able to change substrate characteristics [Yang et al., 2008]. I could show that also plant development

and their resilience to erosion is dependent on substrate characteristics (chapter 3), verifying the circular interactions proposed in the literature between geomorphic and ecologic components [Stallins, 2006].

Regarding the question of multi-causality expressed by [Parker and Bendix, 1996], this study could hint that at early recruitment of salt marsh ecosystems the affinity of specific plants was mainly determined by physical landform characteristics (sediments and hydrodynamics) rather than active geomorphic processes (e.g. accretion/erosion). However, we must restrict this insight to the investigated accreting system (salt marshes in the Yangtze estuary, China). Since landscape characteristics and geomorphic processes precipitate each other, at eroding systems early establishment might be stronger influenced by geomorphic processes such as sediment dynamics.

Previous research showed that ecosystem engineering can exert negative impacts on plant development by inducing erosion. Established salt marsh seedlings grow vegetatively in the lateral direction becoming plant patches, so-called tussocks. Through flow routing, tussock edges can experience erosion limiting their growth and potentially leading to incision of intertidal channels [Balke et al., 2012; Bouma et al., 2007; Temmerman et al., 2007]. It was suggested that the magnitude of patch adjacent erosion depends (besides hydrodynamics and sediment properties) on the patch diameter and the distance between adjacent patches [Vandenbruwaene et al., 2011]. Further studies revealed that these recursive interactions between biotic and abiotic properties (e.g. patch adjacent erosion) can promote ecosystem heterogeneity [Wright and Jones, 2006]. This thesis not only extends our knowledge of these recursive interactions by showing the impact of plant properties (stiffness) on the outcome of ecosystem engineering (patch adjacent erosion) (chapter 3) at constant abiotic conditions. It could also show that depending on the prevailing abiotic conditions these recursive interactions can even limit establishment probability. Thus, recursive interactions between plants and the abiotic environment can not only promote heterogeneity as suggested in literature [Phillips, 2001] but also prevent it by influencing establishment thresholds. The high ecosystem engineering ability of *Spartina alterniflora* might, depending on the local prevailing conditions, not only constrain its lateral tussock expansion leading to increased heterogeneity as

shown previously, but potentially lead to their detachment preventing establishment.

This insight becomes important in the face of global change, such as accelerated relative sea level rise, climate change and increased human influences. When abiotic conditions change, e.g. by increasing wave dynamics at the shoreline, species able to cope with this disturbed environment will be favoured over other, possibly stronger engineering, species [Bouma et al., 2010]. The present-day post-invasion pioneer zone community in Chinese salt marshes is characterized by two functionally different species trying to outcompete each other. This thesis suggests, that the fact that these two species possess such different physical and physiological properties not only enables them to cover a broad range of differing abiotic conditions but also potentially increases the system's adaptability and resilience [Folke et al., 2004]. This suggestion is also supported in the context of "complex adaptive systems", since our observed post-invasion pioneer zone community is the path-dependent result of the two ecosystem engineers competing against each other. Their response to changing abiotic conditions can potentially lead to shifts between alternative stable states facilitating ecosystem resilience.

Impacts of biogeomorphic feedbacks on landscape development

To answer the question whether plants and therefore biogeomorphic feedbacks are able to actively influence landscape development, literature provides two contrasting theories. Traditional literature on salt marsh development assigns a conserving role to salt marsh vegetation, stabilizing and pronouncing (through increased sediment trapping) features already present on tidal flats (vegetation mediated inheritance, 'passive' role of vegetation) [Allen, 2000; D'Alpaos et al., 2005]. Recently the potential of vegetation to induce biogeomorphic feedbacks and therefore actively shape geomorphologic features altering the landscape configuration was identified by [Temmerman et al., 2007; van de Koppel et al., 2012]. Through increased sedimentation within patches and increased erosion through flow routing around patches, vegetation is potentially able to initiate tidal channel erosion and therefore holds an active role shaping salt marsh geomorphology (vegetation induced erosion,

'active' role of vegetation).

My study in this thesis showed that the role of salt marsh plants in shaping geomorphologic features can vary depending on the abiotic context. Vegetation can primarily stabilize existing channels when these pre-exist, or play an active role in channel erosion when no network is available. My results indicate that the active or passive role of vegetation with respect to landscape development, not only depends on the physical and physiological properties of the vegetation, but also on the abiotic setting such as initial bathymetry (i.e. existence of mudflat channels), sediment type and hydrodynamics.

As mentioned above, the appearance of recursive interactions such as patch-adjacent erosion between plants and their local surroundings can indicate self-organizing systems [Levin, 1998]. My results help to define the context under which these local recursive interactions can lead to self-organized systems on a landscape level. Specifically, I could show that recursive interactions can only precipitate self-organization in a homogenous initial landscape. This validates the previously expressed hypothesis that initial landscape configuration might influence the ability of plants to form self-organized landscapes [Temmerman et al., 2007]. If mudflat channels pre-exist, recursive interactions are also present, but exert only little impact on the final landscape configuration. This extends the previous notions on the role of biota during landscape development. My results could show that the transition from biota-induced self-organized landscape patterns to patterns mainly influenced by local prevailing conditions, depends on the degree of heterogeneity of the initial landscape (i.e. pre-existing mudflat channel depth). [D'Alpaos et al., 2005; Marciano et al., 2005; Temmerman et al., 2007] (chapter 4).

This insight becomes specifically important in the context of global change. To simplify the above-described multivariate problem of vegetation influencing landscape development, I defined two extreme scenarios generated by global change. Chapter 4 investigates a change in abiotic conditions (through e.g. increased relative sea level rise or increased storm frequency) with constant plant species. Chapter 5 looks at a change in plant species (through e.g. species invasion) with constant abiotic conditions. These scenarios can act as a simplistic aid to understand the real life situation showing transitions between these two extremes.

As shown by this thesis, changes in abiotic conditions influence the role of vegetation on landscape development resulting in different channel network configurations. In the face of global change this inflicts the question whether these different pathways of channel network emergence (active or passive role of vegetation) also bring different levels of resilience against stressors such as accelerated sea level rise or storms. Self-organization can lead to increased ecosystem resilience, by buffering strong physical gradients and the establishment of alternative stable states [van de Koppel et al., 2005]. However, the progression towards increased marsh edge steepness through differential growth between marsh platform and mudflat may also cause negative effects on its ability to withstand disturbances (such as waves) in the longer run [Perillo et al., 2009]. This thesis suggests that self-organization induced alternative stable states (i.e. different channel network configurations) might be able to alleviate effects of global change induced shifts in abiotic conditions on the salt marsh ecosystem. Nevertheless the degree to which self-organization can reduce stress induced by changing abiotic conditions is limited to the point where the salt marsh form (i.e. cliff formation) enables processes such as cliff erosion, destabilizing the salt marsh as a whole.

On the response of tidal channel networks to increased sea level rise previous literature supplies contrasting views. One view expresses the unlikeliness of an increasing tidal prism (through sea level rise) to evoke a major response of the channel network configuration as long as the marsh platform stays vegetated. It further suggests that sea level rise will decrease channel flow velocities leading to silting up and changed channel diameters [Vandenbruwaene et al., 2012]. On the other hand it is suggested that change in tidal prism will influence channel drainage efficiency promoting incision of new channels, to fill the increased demand for draining the marsh area [Stefanon et al., 2012]. Nevertheless, both views are in agreement that the disappearance or change in marsh vegetation will have a major influence on channel network properties. According to my results (chapter 4 and 5) I expect global change mediated changes in both species composition and abiotic conditions to evoke a shift in channel network patterns.

This thesis showed that the change in biotic properties of the vegetation can change channel network properties, even without change in abiotic conditions. In

chapter 5 I showed the influence of the invasion by *Spartina alterniflora* on channel network structure (resulting in a reduced channel drainage density). The reduced channel drainage density could further lead to less water exchange/renewal in the salt marsh, further supporting the establishment of anoxia. Since *Spartina* is well adapted to anoxic soil conditions this in turn would create a competitive advantage for *Spartina* compared to other species. This gives an example of multidirectional and circular interaction between geomorphic and ecologic components. It further demonstrates that changes in species assemblages as a result of global change (invasions) bare the potential to influence the channel network structure and their provided ecosystem functions.

Conclusions and Recommendations for Future Research

Traditionally, coastal salt marsh conservation and restoration efforts mainly focused on ecological aspects, but recently there is an increasing consideration for the importance of biogeomorphic feedbacks to ensure success of restoration schemes. For instance, the observed variability in marsh erosion and growth patterns over time [Crooks, 2002] has led to suggest a shift in focus away from maintaining marshes in their current position to utilizing the sediment release caused by marsh erosion to stimulate growth of new marshes [Viles et al., 2008]. Literature concerning the mutual influences of vegetation patterns and salt marsh restoration is extensive and still expanding [Craft et al., 1999; Crooks, 2002; Wolters et al., 2005]. These studies identified the gain of considering the integrated approach of biogeomorphic processes in natural wetland functioning and their use in restoration [Viles et al., 2008].

The setting up of such ventures implies an in-depth understanding of current biogeomorphic feedback loops and of the response of these feedbacks to changed biotic and abiotic conditions. As a tool to attain this knowledge in different ecosystems the model approach introduced in chapter 4 could be used. Specifically, different settings of the above-described biotic and abiotic factors could be tested to investigate their impact on the landscape configuration, biogeomorphic feedbacks

and subsequent ecosystem services. Our approach could be further utilized to evaluate the impact of global change on these ecosystems (e.g. accelerated sea level rise) and to adapt management strategies accordingly. One problem in evaluating the influence of global change is the impact of shifts in community structure on landforms and geomorphic processes. This problem could be tackled by the extension of our model approach with multiple species and their interactions. This would not only investigate their influence in the context of global change, but could also solve the question of impacts of ecosystem engineering processes at multiple species assemblages as proposed by [Hastings et al., 2007].

My results further suggest a connection between plant traits (e.g. stem stiffness, root network, stress tolerance) and favoured hydrodynamics and sediment conditions. It would be worthwhile to investigate whether evolutionary selection in plant traits took place in response to different abiotic conditions (e.g. promoted root growth on sandy sediment in combination with stress avoiding flexible aboveground material). This would further solve the abovementioned question of multi-causality and circularity of biogeomorphic systems opening a variety of new research questions linking conceptual and applied ecosystem theories.

It was previously hypothesized that biogeomorphic feedbacks are able to break ecosystem symmetry, initiate pattern formation and influence landscape development. Literature further hypothesized that how these feedbacks scale up to determine ecosystem structure and functioning is determined by physical constraints on organism-environment feedbacks set by the landscape, implying that both local and landscape processes shape self-organized spatial patterns in ecosystems [van de Koppel et al., 2012]. This thesis could determine the main factors (interactions between sediment, hydrodynamics and plants properties) influencing not only plant establishment, but also biogeomorphic feedbacks and their influence on sculpting the landscape. On the one hand, this verified previous suggestions on the relevance of ecosystem engineering for landscape development. On the other hand, it could narrow the gap between theoretical considerations and the need for the practical frameworks providing factors and thresholds based on real world ecosystems. It could further show, that understanding the nature of biogeomorphic feedbacks and their role in maintaining heterogeneity of geomorphic and ecological processes and

forms is necessary in restoration and resource management.

Summary

Ecosystem engineering (i.e. organisms changing their environment through active interactions or simply their presence) is increasingly recognized to have a strong impact on biotic and abiotic ecosystem structure. Ecosystem engineers influence their habitat via biogeomorphic feedbacks, resulting in changes in the abiotic environment, ameliorating circumstances for themselves and possibly other organisms. Biogeomorphic feedbacks are interactions between abiotic (such as hydrodynamics and sediment properties) and biotic factors (such as physical and physiological species properties), influencing species survival on the one hand and potentially shaping geomorphic landscape features, such as tidal channel networks in salt marsh environments, on the other hand. Knowledge on these feedbacks is required to evaluate and predict the influence of altered environmental conditions (e.g. through global change) on ecosystem structure and provided ecosystem services.

Biogeomorphic systems, such as salt marsh ecosystems, which are the focus of this thesis, can be viewed as "complex adaptive systems". In "complex adaptive systems" a macro-scale pattern can emerge from local interactions and selections processes acting at lower levels.

In this thesis I aim to enhance the mechanistic understanding of how organisms (plants) are able to influence and shape their environment at different spatial scales using salt marshes as model ecosystems. Specifically, I investigated how and under which circumstances interactions between plant species traits and abiotic parameters (hydrodynamics and sediment properties) possess the potential to influence the resulting landscape configuration. This examination aims to fill the existing gap in our understanding of how and when biota are able to actively influence landscape development. In order to address this question, I am utilizing a multi scale approach, combining field manipulative experiments, flume experiments, remote sensing data and modelling approaches.

I show the consequences of biogeomorphic feedbacks on the biotic and abiotic organization of the landscape across different scales, using the salt marsh ecosystems in the Yangtze estuary (China) as model ecosystem. I not only determine

the circumstances under which biogeomorphic feedbacks get established, but also identify their main driving factors, being hydrodynamics, sediment properties and plant properties. The research area, the salt marshes in the Yangtze estuary, is well suited to study biogeomorphic feedbacks, because of its highly dynamic abiotic (high sediment input and strong hydrodynamic perturbations) and biotic nature (fast expanding salt marshes). In these marshes I investigated two predominant pioneer species, *Spartina alterniflora* and *Scirpus mariqueter*. Both species are autogenic ecosystem engineers, which induce salt marsh formation by trapping sediment and consequently increasing soil elevation. The species differ in their physical and physiological properties. *Spartina alterniflora*, invasive in many Chinese marshes, is a fast and high growing plant with stiff above ground biomass. In comparison, *Scirpus mariqueter*, endemic to Chinese marshes, is a slower and lower growing plant with flexible aboveground material.

Influence of the abiotic environment on plant establishment

(Chapter 2) Transplantation experiments using different propagule size classes of both *Scirpus* and *Spartina* showed that plant establishment in these intertidal areas is strongly influenced by abiotic factors such as waves, currents and sediments. The fact that *Scirpus* exhibited higher survival at the pioneer zone at all sites, but was not able to outcompete the strong ecosystem engineer *Spartina* at some sites, showed that competitive interactions like facilitation strategies or size-dependent survival and differential germination patterns prove to be more complicated than simple survival response due to abiotic stress. (Chapter 3) I could further show that plant establishment is strongly influenced by sediment characteristics (cohesive, non-cohesive) determining the ability of the two different plant species to withstand erosion. These results provided a deeper insight in the observed plant establishment behaviour in the southern part of our research area, where *Spartina* in spite of its stronger ecosystem engineering capability, still did not succeed in outcompeting its native predecessor *Scirpus*. I therefore suggest that plant traits (i.e., competitive strength, ecosystem engineering capability) and abiotic interaction patterns always have to be thoroughly considered before being able to determine their degree of influence on plant zonation patterns and competitive outcomes. This chapter emphasizes the importance of interactions between abiotic and biotic factors (i.e.

biogeomorphic feedbacks) for species survival and establishment.

Biogeomorphic feedbacks at an intermediate scale

(Chapter 3) The growth response of our two investigated species (*Spartina* and *Scirpus*) to different sediment types gave a deeper insight on how physiological plant properties, in combination with sediment properties, are able to determine plant survival under hydrodynamic stress. In a flume study I show that not only physiologic growth responses (as shown with *Scirpus* and its adapted root growth) exert a major influence on the plant's resilience to erosion under current stress, but that simple differences in sediment properties (increased cohesiveness), in absence of a growth response (as shown with *Spartina*), are also able to influence erosion resilience. This underlines the importance of plant-sediment interactions on plant establishment thresholds. I further investigated the ecosystem engineering ability of these two contrasting species by conducting a flume experiment at constant sediment and current properties. I showed that higher ecosystem engineering ability does not necessarily entail higher species survival. *Scirpus*, although being a less strong ecosystem engineer compared to *Spartina*, showed higher survival in non-cohesive sediments, due to its physiologic growth response. In this chapter I established the different implications of physiological and physical plant properties on survival and ecosystem engineering ability.

Importance of abiotic-biotic interactions for landscape development

(Chapter 4) The effect of interactions between abiotic (sediment properties and hydrodynamics) and biotic properties (plant properties) on the landscape configuration is shown utilizing a model simulation of a mudflat - salt marsh transition, based on pioneer zone settings in the Yangtze estuary. I not only, as previously proposed, demonstrate the importance of vegetation influencing landscape development. I also identified the importance of initial bathymetry, either facilitating or thwarting the impact of vegetation on landscape development (i.e. biogeomorphic feedbacks). Specifically, I could show that at mudflats with homogenous bathymetry vegetation exerts, via patch adjacent erosion, an active role in shaping intertidal channels (active role). However, if mudflat channels exist prior to vegetation establishment, vegetation

exerts a more stabilizing role on existing mudflat channels (passive role). Hence, I conclude that the role of vegetation on landscape development (active or passive) is not only depending on its physical and physiological properties, but is also strongly determined by its interactions with prevailing abiotic conditions (initial bathymetry, sediment type and hydrodynamics). This chapter stresses the importance of biotic-abiotic interactions for initial landscape development.

(Chapter 5) The salt marsh landscape configuration is based on the establishment of a dynamic equilibrium between biotic and abiotic factors. As soon as one of these factors is changed the establishment of a new equilibrium, even in already established marsh systems, becomes likely. Through the analysis of aerial images and sediment samples, I show that the invasion by *Spartina alterniflora* (taken place in the northern salt marsh region on Chongming Island, Yangtze estuary) did change the established dynamic morphologic equilibrium, abounding in reduced drainage densities of existing channel networks and changes in sediment properties. This chapter not only shows the influence of species invasions on ecological ecosystem properties, but also its potential to change established geomorphologic features, such as tidal channel networks. It further stresses the impact of abiotic-biotic interactions on already established landscape features.

Implications for management and conservation

The importance of salt marsh ecosystems can be summarized by their two major functions. Hydraulically they protect the coastal zone by dampening waves, storing storm surges and trapping sediments. Ecologically, they form rich habitats for invertebrates and wild herbivores, resting and feeding grounds for migratory birds and nursery habitats for fish. Traditionally, coastal salt marsh conservation and restoration efforts mainly focused on ecological aspects, but recently there is an increasing consideration for the importance of biogeomorphic feedbacks to ensure success of restoration schemes. The presented holistic approach of coupling biotic and abiotic processes across different spatio-temporal scales remains challenging but is nevertheless needed for an incorporation of biogeomorphic feedbacks in sustainable management and conservation of wetland habitats and generally ecosystems created under presence of abiotic stressors (e.g. coastal, estuarine, riverine ecosystems).

As a practical tool to attain this knowledge about biogeomorphic feedbacks in different ecosystems the model approach introduced in chapter 4 could be used. Specifically, different settings of the above-described biotic and abiotic factors could be tested to investigate their impact on the landscape configuration, biogeomorphic feedbacks and subsequent ecosystem services. Our approach could be further utilized to evaluate the impact of global change on these ecosystems (e.g. accelerated sea level rise) and to adapt management strategies accordingly. This would help to evaluate the potential of restoration and management schemes opening a more cost effective and sustainable way of salt marsh management.

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Samenvatting

Biobouwers, organismen die hun abiotische omgeving aanpassen door hun activiteit of hun aanwezigheid, hebben een sterke invloed op alle aspecten van het ecosysteem. Hun invloed op de habitat genereert een biogeomorfologische feedback, omdat de veranderingen in het abiotische milieu de omstandigheden verbeteren voor de biobouwende soort zelf en vaak ook voor andere organismen. Door biogeomorfologische feedbacks tussen abiotische (bv. hydrodynamiek of sedimenteigenschappen) en biotische factoren (bv. morfologische of fysiologische eigenschappen van de soort), wordt niet alleen de overleving van soorten beïnvloed maar ook de vorming en geomorfologische eigenschappen van het landschap. Het is bekend dat dergelijke feedbacks van belang zijn bij de vorming van schorren en hun netwerk van getijdengeulen. Een goed begrip van deze interacties is nodig wanneer men wil beschrijven en voorspellen hoe de mondiale veranderingen in omgevingscondities doorwerken in de structuur van het ecosysteem en in de geleverde ecosysteemdiensten.

Biogeomorfologische systemen zoals schorren, die het onderwerp vormen van dit proefschrift, kunnen worden beschouwd als 'complexe adaptieve systemen'. Kenmerkend voor dergelijke systemen is dat patronen op macroschaal kunnen ontstaan als een uitkomst van interacties op kleine schaal en selectieprocessen die zich afspelen op een lager organisatieniveau.

Ik stel mij tot doel in dit proefschrift bij te dragen tot een beter begrip van de processen waarmee planten invloed uitoefenen op de morfologie van hun omgeving, en dit op verschillende ruimtelijke schalen. Ik gebruik daarbij schorren als modelsystemen. In het bijzonder heeft mijn onderzoek zich gericht op de vraag hoe en onder welke omstandigheden de kenmerken van de plant, bv. de plantgrootte of stijfheid, van belang zijn om een correcte voorspelling te maken van de eigenschappen van het landschap dat ontstaat uit biogeomorfologische feedback. Ik beantwoord een aantal open vragen in het schoronderzoek met een benadering op meerdere schalen. Daarbij combineerde ik experimenten in het veld en in een stroomgoot in het laboratorium, met satellietobservaties en wiskundige modellering.

In de schorren van het Yangtze estuarium in China, heb ik de gevolgen van biogeomorfologische feedbacks op de biotische en abiotische kenmerken van het ecosysteem aangetoond op verschillende ruimtelijke schalen. Ik bepaalde de omstandigheden waaronder biogeomorfologische feedbacks ontstaan, en identificeerde als belangrijkste drijvende factoren de hydrodynamiek, sedimenttype en planteigenschappen. Het onderzoeksgebied is bijzonder geschikt voor dit onderzoek omdat het zo dynamisch is in zijn abiotische en biotische eigenschappen. De sedimenttoevoer is hoog, de hydrodynamische verstoringen eveneens en het schor breidt zich zeer snel uit. Ik onderzocht twee dominante pioniersoorten in dit schor, *Spartina alterniflora* en *Scirpus mariqueter*. Beide soorten zijn autogene biobouwers, die schorvorming induceren door sediment in te vangen en daardoor de bodem te doen stijgen in hoogte. De soorten verschillen in hun morfologische en fysiologische eigenschappen. *Spartina anglica*, een invasieve soort in vele Chinese schorren, is een snel- en hooggroeiende plant met stijve bovengrondse delen. De endemische Chinese soort *Scirpus mariqueter* groeit trager, blijft lager en heeft een flexibele bovengrondse structuur.

Invloed van de abiotische omgeving op de vestiging van planten

(Hoofdstuk 2) Transplantatie-experimenten met verschillende grootteklassen van propagulen van zowel *Scirpus mariqueter* als *Spartina alterniflora* toonden aan dat de vestiging van de planten in deze getijdenzones vooral wordt bepaald door abiotische factoren zoals golven, stromingen en sedimenten. *Scirpus* had een hogere overleving in alle experimenten, maar was niet in staat om de sterke biobouwer *Spartina* weg te concurreren op een deel van de experimentele plots. Dit toonde aan dat zowel interspecifieke interacties zoals concurrentie en facilitatie, als grootte-afhankelijke overleving en verschillen in kieming een rol spelen, en dat de uitkomsten geen eenvoudige functie zijn van de abiotische stress. (Hoofdstuk 3). Verder kon ik aantonen dat de vestiging van de planten sterk bepaald wordt door het sedimenttype, met het grootste verschil tussen cohesief en niet-cohesief sediment. Dit bepaalde het vermogen van de planten om te weerstaan aan erosie. De resultaten hielpen om de patronen van vestiging van beide soorten beter te begrijpen. In het zuidelijke deel van het studiegebied is *Spartina* niet in staat om zijn endemische voorganger *Scirpus* weg te concurreren, ondanks het sterke effect van *Spartina* als biobouwer. Ik

concludeer hieruit dat zowel de planteigenschappen (concurrentiekracht, biobouwer-effect) als de abiotische omstandigheden zorgvuldig moeten worden beschouwd om de zonering van planten en de uitkomst van hun concurrentie te kunnen begrijpen. Dit hoofdstuk benadrukt het belang van de interactie tussen abiotische en biotische factoren (d.i. biogeomorfologische feedback) voor de overleving en vestiging van planten.

Biogeomorfologische feedback op mesoschaal

(Hoofdstuk 3) De groei van de twee bestudeerde soorten (*Spartina* en *Scirpus*) op verschillende sedimenttypes was verschillend door een verschil in fysiologische planteigenschappen. Om de overleving van planten onder hydrodynamische stress te begrijpen, moest zowel het sedimenttype als deze fysiologische respons in rekening worden gebracht. In een stroomgoot toonde ik aan dat de fysiologische groeirespons (bv. de adaptieve wortelgroei van *Scirpus*) belangrijk is voor de weerstand van de plant tegen erosie door stroming. Maar ook eenvoudige verschillen in sedimenteigenschappen (verschil in cohesiviteit), zelfs zonder groeiverschillen zoals het geval is bij *Spartina*, kunnen volstaan om een verschillende erosieweerstand te verkrijgen. Het is dus de interactie tussen plant en sediment die de drempelwaarden voor de vestiging van planten bepaalt. Ik bestudeerde de verschillen in de mate waarin deze soorten hun omgeving veranderen in een experiment in de stroomgoot met constante stroomsnelheid en homogene sedimentkarakteristieken. Een sterkere invloed op de omgeving leidt niet automatisch tot een hogere overleving. *Scirpus* heeft minder effect als biobouwer dan *Spartina*, maar overleeft beter in niet-cohesief sediment omdat de soort een fysiologische groeirespons vertoont. Ik bespreek in dit hoofdstuk de verschillende effecten van fysiologische en morfologische planteigenschappen op overleving en effect als biobouwer.

De rol van abiotisch-biotische interacties voor landschapsontwikkeling

(Hoofdstuk 4) Aan de hand van een simulatiemodel werd het effect van abiotisch-biotische interacties op landschapsvorming op het grensvlak tussen schor en plaat bestudeerd. Het model hield rekening met sedimenteigenschappen en hydrodynamiek als abiotische factoren, en met planteigenschappen als biotische factor. Parameterwaarden werden afgeleid van veldsituaties in de pionierszone in het Yangtze estuarium. Met het model kon ik het belang van vegetatie voor de landschapsontwikkeling aantonen en kwantificeren. Ik kon ook het belang aantonen van het initiële geulenpatroon dat bestond voor de vegetatieontwikkeling. Afhankelijk van dit patroon, is het effect van vegetatie sterker of zwakker. Wanneer geen initieel geulenpatroon aanwezig is, wordt de volledige geulvorming gedreven door de vegetatie, die dan een actieve rol speelt in de landschapsontwikkeling. Als echter reeds geulen aanwezig zijn voordat de vegetatie begint te ontwikkelen, wordt de rol van de vegetatie passief. Zij helpt dan de bestaande geulen te stabiliseren. Ik besluit hieruit dat de rol van de vegetatie in de landschapsontwikkeling niet alleen afhangt van de planteigenschappen, maar ook van de samenhang met de vigerende abiotische omstandigheden, zoals initieel geulenpatroon, sedimenttype en hydrodynamiek.

(Hoofdstuk 5) De geomorfologie van het schorlandschap wordt bepaald door een dynamisch evenwicht tussen biotische en abiotische factoren. Wanneer een van deze factoren verandert, is de kans groot dat zich een nieuw evenwicht instelt, zelfs in bestaande schorsystemen. Aan de hand van luchtfoto's en sedimentmonsters kon ik aantonen dat de invasie van *Spartina alterniflora* in het noordelijke schor op Chongming Island in het Yangtze estuarium, het bestaande evenwicht heeft verstoord. De invasie heeft geleid tot een vermindering van de geuldichtheid in het bestaande krekenstelsel en tot veranderingen in de sedimentsamenstelling. Dit hoofdstuk illustreert dat een invasie niet alleen invloed uitoefent op de ecologie van het systeem, maar ook op de geomorfologische systeemeigenschappen zoals het krekenstelsel. Het illustreert eveneens, in meer algemene zin, het belang van biotisch-abiotische interacties op de geomorfologie van het landschap.

Belang voor beheer en bescherming

Schorecosystemen vervullen twee essentiële ecosysteemdiensten. Zij beschermen de kust door golfdemping, waterberging bij stormopzet en sedimentopslag. Ecologisch vormen zij rijke habitats voor ongewervelden en wilde herbivoren, rust- en foerageergebieden voor trekvogels en broedkamers voor vis. Traditioneel ging de aandacht bij beheer en bescherming van schorren vooral uit naar de ecologische aspecten, maar recent is er meer aandacht gekomen voor het belang van biogeomorfologische feedbacks in het ecologische functioneren. Succes bij restauratie hangt vaak af van het goed inschatten van deze processen. Een holistische benadering waarbij biotische en abiotische processen over meerdere ruimtelijke en temporele schalen worden gekoppeld, zoals gebruikt in deze studie, blijft een hele uitdaging. Zij kan echter essentieel zijn om de effecten van biogeomorfologische feedbacks goed in te schatten en te gebruiken bij het duurzaam beheer en de bescherming van schorren, en algemener van ecosystemen die zijn ontstaan in omgevingen met sterke fysische stress, zoals vegetaties aan de kust, in rivieren of estuaria.

De modelbenadering die werd voorgesteld in Hoofdstuk 4 kan een praktisch hulpmiddel zijn om de kennis over biogeomorfologische feedbacks toe te passen in verschillende ecosystemen. De verschillende biotische en abiotische factoren die in de experimentele hoofdstukken van dit proefschrift zijn beschreven, kunnen in de modelparameters worden voorgesteld en doorgerekend om hun effect op de landschapsvorming en de ecosysteemdiensten te bestuderen. Dit kan de basis vormen voor scenariostudies ten dienste van het beheer. De benadering kan ook worden toegepast om de effecten van mondiale veranderingen (bv. versnelde zeespiegelstijging) op de schorren in te schatten. Beheersopties en mogelijkheden voor restauratie kunnen hiermee nader worden geëvalueerd, waardoor kan worden gezocht naar meer kosteneffectieve en duurzame vormen van schorbeheer.

Chinese Summary (摘要)

‘生态系统工程师’效应(即生物通过自主性相互作用或者他们自身的存在而达到改变环境特征的效应)正日益被认为对生态系统的生物和非生物结构有极大的影响。生态系统工程师们通过生物-地貌反馈作用为其自身及同一生境中的其它生物改良栖息地环境。生物-地貌反馈作用通过物理因子(如水动力和泥沙特性)和生物因子(如物种的物理和生理特性)间的交互作用来实现。其一方面对物种的存活产生影响,另一方面也将对景观地貌特征如盐沼湿地中的潮沟网络形成的产生影响。掌握这一知识对认识和预测生态系统结构和生态系统服务功能对环境变化(如全球变化)的响应具有十分重要的作用。

生物地貌系统可以看做是‘复杂适应系统’,例如本文主要关注的盐沼生态系统。在这种‘复杂适应系统’中,宏观格局往往产生于小尺度上的局部相互作用和选择进程。本论文以盐沼作为模型系统进行研究,旨在增强对‘生物(植物)如何在不同尺度上改变和塑造环境’这一机制的理解。具体而言,本文主要关注植物性状和物理因子(水动力和泥沙特性)间的相互作用,以及在何种条件下这一相互作用将会影响所形成景观的配置。当前,对于生物体在何种情况下及如何能够对景观的形成产生积极的影响仍不清楚,本章在这些方面的探究将填补这一空白。针对这一问题,本研究将采用野外控制实验,水槽实验,遥感和模型相结合的方法,在多个尺度层面展开研究。

通过以长江口盐沼湿地作为模型系统,本论文展示了生物-地貌反馈作用对跨尺度生物和非生物景观组织形成过程产生的影响。不仅确定了产生生物-地貌反馈作用需要所需要的环境条件,也找出了驱动这一过程的主要因素:水动力,泥沙特性和植物特性。本研究所在的长江口盐沼湿地的非生物因子呈现出高度的动态变化(大量的泥沙输入以及较强的水动力干扰),生物方面也有其独特性(快速扩张的盐沼植被),因而非常适合开展生物-地貌反馈作用的研究。本文主要研究了长江口湿地中的两种盐沼先锋植物:互花米草和海三棱藨草。 他们都属于‘自源性生态系统工程师’,能够通过植被的固沙促淤作用来增加地面的高程进而促进盐沼的形成。不过这两种植物具有不同的物理和生理特性。其中,互花米草作为中国许多盐沼湿地中的入侵物种,生长迅速,地上组织质感较硬,不易弯曲。而海三棱藨草是长江

口特有物种，生长较为缓慢，地上部分柔软且易弯曲。

非生物环境对植物定居的影响

（第二章）第二章进行了先锋植物互花米草和海三棱藨草（分别使用三种大小不同的繁殖体）的移栽实验。结果表明：物理因子如波浪，水流和泥沙特性对它们在光滩上的定居有极大的影响。海三棱藨草在各个移栽实验区均表现出较高的存活率，但在一些区域却难以同具有更强‘生态系统工程师’效应的互花米草进行竞争。这说明不能简单的从对环境胁迫的响应来比较它们的相对竞争优势，还应结合其它方面的差异加以考虑，如易化策略，繁殖体大小对存活的决定作用以及萌发模式等。（第三章）第三章的结果进一步表明，泥沙的粘性特征（粘性，非粘性）决定了这两种先锋植物植物的抗冲刷能力，因而对其定居也有极大的影响。这些结果有助于解释崇明东滩南部所观察到的植被定居行为。在该区域，具有更强‘生态系统工程师’效应的外来种互花米草目前仍然未能成功取代本土种藨草。因此，只有充分的认识和理解植物性状（包括在物种竞争和‘生态系统工程师效应’方面的能力）和非生物因子间的相互作用模式，才能确定其对植被分带和竞争结果的影响程度。本章同时也强调了非生物-生物因素相互作用（即生物-地貌反馈作用）对物种存活和定居的重要性。

中尺度下的生物-地貌反馈作用

（第三章）研究互花米草和海三棱藨草的生长对泥沙类型的响应，可以更好的理解植物生理特性和泥沙特性如何共同影响植物在不同水动力胁迫条件下的存活。本章的水槽实验表明，不仅植物的生理生长响应模式影响着植物在冲刷条件下的恢复能力，泥沙特性（粘性的增加）的变化也能够影响植物在冲刷后的恢复能力。而且后者能够独立于前者发挥作用，这在互花米草的实验中得到了体现。这些结果突出了植物-泥沙相互作用在决定植物定居阈值条件中的重要性。通过恒定水流和泥沙条件下的水槽实验，我们进一步研究和比较了这两种先锋植物在‘生态系统工程师效应’方面的能力。结果表明，更强的‘生态系统工程师效应’并不一定保证更高的物种存活率。相比于互花米草而言，海三棱藨草尽管表现出较弱的‘生态工程师效应‘，但是在非粘性泥沙中却有着更高的存活率。而这主要是由它的生理生长对泥沙特性的响应模式决定的。本研究也明确了植物的生理和物理特性在影

响植物存活及生态系统工程师效应方面所具有的的不同意义。

非生物-生物相互作用在景观发育中的重要性

（第四章）在本章中，我们参照长江口盐沼湿地先锋带的环境条件，模拟了在光滩-植被过渡带这一区域环境因子（水动力和泥沙特性）-生物因子（植物特性）之间的相互作用对景观配置的影响。模型结果表明，不仅植被的影响对景观发育很重要（如前所述），而且初始水下地形条件也十分关键。它能够增强或者削弱植被对景观发育（生物-地貌反馈作用）的影响。具体来说，我们的结果表明，在水下地形条件均一的条件下（无潮沟存在），植被可以通过斑块边缘的侵蚀影响光滩上潮沟的形成（主动作用）。但是，如果潮沟先于植被存在，植被将扮演稳定既有潮沟的角色（被动作用）。因此，我们认为，植被在景观发育中的角色（主动或被动作用）不仅依赖于其物理和生理特性，也取决于他们和主要环境条件（初始水下地形条件，泥沙类型和水动力）的相互作用。本章着重强调了环境-生物因子之间的相互作用在景观发育初期阶段的重要性。

（第五章）物理因子和生物因子之间动态平衡的建立是盐沼景观成型的前提。即使在一个已经建成的盐沼系统中，只要其中改变其中一个因子，也可能导致系统转向一个新的平衡状态。本章通过对航空影像的解译分析以及泥沙样品的采集和分析，表明互花米草对在长江口崇明东滩盐沼湿地入侵打破了原有的动力地貌平衡状态，大范围地导致原有潮沟网络渠道密度的下降和泥沙特性的改变。本章不仅揭示了物种入侵对生态系统特征的影响，同时也表明入侵物种能够改变入侵地的地貌特征。本章中的潮沟网络即是一个很好的例子。这同时也强调了物理-生物因子间的相互作用在影响既有景观特征方面的重要性。

在管理和保育方面的意义

盐沼生态系统的重要性主要体现在两个方面。在水力学角度看，它们具有削减波浪，固沙促淤等保滩护岸的功能。在生态方面，它们为无脊椎动物，野生食草动物，迁徙的鸟类以及鱼类提供栖息地，觅食以及繁殖场所。传统的海岸带盐沼湿地保育和生态修复主要基于生态学过程，而近年来则更多的考虑生物-地貌反馈作用在生态修复中的重要性。本文所采用的耦合不同时空尺度上生物和物理过程这一整体性研究方法，虽然具有一定的难度，但却是实现对湿地及其它存在环境胁迫的生态系统（如河口，海岸，河流生

态系统）进行可持续保护和管理的必要一环。

第四章所介绍的模型方法可以用来将本研究得到的生物-地貌反馈作用的知识推广至不同的生态系统中。具体来讲，该模型可以用来检验不同的生物和非生物因子（如前所述）及其相互作用对景观配置，生物-地貌反馈作用及生态系统服务功能的影响。再者，该方法还可以进一步用来评估这些生态系统对全球变化（如海平面上升）的响应，从而为制定或调整管理方案和应对策略提供理论依据。这将有助于对受损生态系统的修复潜力以及管理方案的合理性进行评价，从而得出更加经济有效并且可持续的盐沼管理模式。

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天道酬勤，。。。

山外有山，人外有人，。。。

Tough times don't last, tough people (organisms) do.

(Nassim Taleb, Antrfragile 2013)

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Academic degrees

PhD. **Spatial ecology and Geomorphology** **2013**
Radboud University Nijmegen, the Netherlands (finishing date: March 2014)
Royal Netherlands Institute for Sea Research (NIOZ)
Title: "Implications of biogeomorphic feedbacks on tidal landscape development"

MSc. **Aquatic Ecology** **2008**
University of Vienna, Austria
Title: "Resource stoichiometry and the growth rate hypothesis in Verrucomicrobium spinosum"

BSc. **Environmental Biology specialization** **2007**
University of Vienna, Austria

BSc. **Chinese Studies** **2006**
University of Vienna, Austria

Training and Foreign visits

- Doctoral research **2009 - 2013**
Radboud University Nijmegen, stationed at the Royal Netherlands Institute for Sea Research (NIOZ)
- Self-directed and independently managed project and workload
- Coordinated annual work plan and field work abroad (China)
- Proficient with a variety techniques for hydrodynamic water assessments
- Carried out remote field work for sample collection and measurements
- Designed field and laboratory experiments to test research hypothesis

- Internship **2009**
Animal Production Unit of the IAEA (International Atomic Energy Agency), conducted microbiological analysis for the livestock-breeding program

- Research assistant **2008 - 2009**
Microbial Diversity and Ecosystem Functioning project in the Department of Freshwater Ecology at the University of Vienna responsibilities included nucleic acid quantification and experimental design

-Teaching assistant **2008**
Taught the undergraduate course 'Diversity and taxonomy of higher plants' at the University of Vienna

-Research assistant **2008**
Identified and quantified lipids for the project: "Resource Limitation of microbial Decomposition in Soil Organic Matter" in the Department of Chemical Ecology and Ecosystem Science at the University of Vienna.

-Language studies **2004-2005**
Study exchange year (joint study program, Beijing Language University, 北京语言大学)

Languages

German (mother tongue), English (fluent), Chinese (proficient), Dutch (proficient)

Publications

Peer-reviewed scientific articles

Schwarz, C., T. Ysebaert, Z. Zhu, L. Zhang, T. J. Bouma, and P. M. J. Herman (2011), Abiotic Factors Governing the Establishment and Expansion of Two Salt Marsh Plants in the Yangtze Estuary, China, Wetlands, 31(6), 1011-1021.

Zhu, Z., L. Zhang, N. Wang, C. Schwarz, and T. Ysebaert (2011), Interactions between the range expansion of saltmarsh vegetation and hydrodynamic regimes in the Yangtze Estuary, China, Estuarine, Coastal and Shelf Science.

Accepted articles

Schwarz, C., QH. Ye, D. van der Wal, L. Zhang, T. J. Bouma, T. Ysebaert and P. M. J. Herman (2013), Impacts of salt marsh plants on tidal channel inititation and inheritance, Journal of Geophysical Research Earth Surface.

Contributions at international scientific conferences and workshops

Schwarz et al. 2013, Impacts of salt marsh plants on tidal channel initiation and inheritance. (oral presentation at EGU, Vienna, Austria)

Schwarz et al. 2013, Impacts of small scale processes on large scale salt marsh dynamics. (oral talk at NIOZ Yerseke, The Netherlands)

Schwarz et al. 2013, Vegetation impacts on geomorphologic feedbacks: A study on tidal channel emergence. (oral presentation at NCK days, Kijkduin, The Netherlands)

Schwarz et al. 2012, Influences of vegetation and sediment type on tidal channel initiation: Consequences for estuarine landscape development. (oral presentation at ASLO, Lake Biwa, Japan)

Schwarz et al. 2012, Vegetation characteristics influencing geomorphologic feedbacks: A study on tidal channel emergence. (oral presentation at Delft3D User Meeting, Deltares, Delft, The Netherlands)

Schwarz et al. 2011, On the potential of salt marsh plants shaping tidal landscapes. (oral lunch talk at Deltares Delft, The Netherlands)

Schwarz et al. 2011, Implications of vegetation and sediment type on channel development: A First Step. (oral presentation at coastal ecology workshop, University of Antwerp, Belgium)

Additional Skills

- Delft3D
  (a process based hydrodynamic and sediment transport model developed by TU Delft)
- MATLAB
- ArcGIS
  Setup, measurement and data analysis of hydrodynamic factors
  (e.g. waves: pressure sensor; currents: ADCP, ADV)
- MS Office
- Adobe Illustrator
- SPSS
- Sigma Plot
- FISH (fluorescence in situ hybridization)
- Fluorescence microscopy
- Nucleic acid quantification
- Amino acid quantification
- Bacterial cultivation
- Drivers license