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Interactions between plant traits and sediment characteristics influencing species establishment and scale-dependent feedbacks in salt marsh ecosystems

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ABSTRACT

The importance of ecosystem engineering and biogeomorphic processes in shaping many aquatic and semi-aquatic landscapes is increasingly acknowledged. Ecosystem engineering and biogeomorphic landscape formation involves two critical processes: (1) species establishment, and (2) scale-dependent feedbacks, meaning that organisms improve their living conditions on a local scale but at the same time worsen them at larger scales. However, the influence of organism traits in combination with physical factors (e.g. hydrodynamics, sediments) on early establishment and successive development due to scale-dependent feedbacks is still unclear. As a model system, this was tested for salt marsh pioneer plants by conducting flume experiments: *i*) on the influence of species-specific traits (such as stiffness) of two contrasting dominant pioneer species (*Spartina alterniflora* and *Scirpus mariqueter*) to withstand current-induced stress during establishment; and *ii*) to study the impact of species-specific traits (stiffness) and physical forcing (water level, current stress) on the large-scale negative feedback at established tussocks (induced scour at tussock edges) of the two model species.

The results indicate that, not only do species-specific plant traits, such as stiffness, exert a major control on species establishment thresholds, but also potentially physiologically triggered plant properties, such as adapted root morphology due to sediment properties. Moreover, the results show a clear relation between species-specific plant traits, abiotics (i.e. sediment, currents) and the magnitude of the large-scale negative scale-dependent feedback. These findings suggest that the ecosystem engineering ability, resulting from physical plant properties can be disadvantageous for plant survival through promoted dislodgement (stem stiffness increases the amount of drag experienced at the root system), underlying the importance of scale-dependent feedbacks on landscape development.

1. Introduction

In recent years the importance of biogeomorphic feedbacks in shaping landscape evolution has become increasingly clear (Hupp et al., 1995; Phillips, 1995; Stallins, 2006; Murray et al., 2008). Biogeomorphic feedbacks emerge if 'ecosystem engineers' influence geomorphologic (i.e. landscape-shaping) processes. Ecosystem engineers are organisms, able to actively (allogenically) or passively (autogenically) influence their immediate abiotic surroundings (Jones et al., 1994, 2010; Bouma et al., 2013), invoking feedback loops that can improve living conditions for themselves and potentially associated species (Jones et al., 1994; Mullan Crain and Bertness, 2006). If such feedbacks affect geomorphologic processes, they become biogeomorphic feedback loops, by which ecosystem engineers can shape various coastal and inland habitats, such as tidal wetlands (D'Alpaos et al., 2007; Temmerman et al., 2007), alluvial floodplain rivers (Murray and Paola, 2003; Tal and Paola, 2007) and fluvial hillslope systems (Istanbulluoglu and Bras, 2005).

Since biogeomorphic feedbacks require the presence of ecosystem engineering organisms (i.e. plants) their occurrence is dependent primarily on the establishment probability of their initial units (e.g. plant seeds and seedlings). Further, following establishment, the occurrence of biogeomorphic feedbacks typically requires a critical biomass threshold to be surpassed (scale-dependent feedback), with no feedback present at lower densities (Bouma et al., 2009a,b; Friess et al., 2012). This raises the question (1) how biotic (i.e. plant traits) and abiotic (i.e. sediment, currents) factors influence the initial establishment in these biogeomorphic landforms, and (2) how the subsequent development from small, just established plants into larger-scale units (plant patches) depends on biotic-abiotic properties inducing biogeomorphic feedbacks.

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1.1. Initial establishment of salt marsh seedlings

Seedling establishment is a crucial step in disturbance-driven ecosystems (e.g. salt marshes, mangroves, alluvial floodplains and river macrophytes) to enable vegetation succession. Previous studies have focused on the impact of hydrodynamics (i.e. hydroperiod, currents and waves), salinity, temperature and soil moisture on seedling establishment (Scott et al., 1996; Patterson et al., 1997; Corenblit et al., 2007). Only recently, it was shown that initial seedling settlement is strongly dependent on interactions between sediment dynamics (i.e. erosion/accretion) and the magnitude of hydrodynamic stress (i.e. currents, waves). It was shown that periods of low hydrodynamic stress (i.e. windows of opportunity) can facilitate temporary establishment of seedlings on mudflats. Although temporarily established, these seedlings still stay vulnerable to changes in sediment dynamic and hydrodynamic properties (Bouma et al., 2009b; Balke et al., 2011, 2013; Infantes et al., 2011; Gurnell et al., 2012). The magnitude of this vulnerability was, for mangrove trees, shown to be strongly dependent on species specific plant traits (physiological plant properties such as growth velocity) (Balke et al., 2013), but data for non-woody pioneer species (as present in salt marshes) are still lacking. Moreover, sediment properties might influence this relationship, because both plant growth rate and plant-hydrodynamics interactions may depend on sediment type. To our knowledge, this aspect has not been tested to date.

1.2. Subsequent development from seedlings to plant patches

Once established, plants tend to form round patchy vegetation units, further referred to as tussocks, scattered over the habitat (e.g. mudflat, channel reach) (Castellanos et al., 1994; Allen, 2000; Langlois et al., 2003; Schoelynck et al., 2012). At this development stage (i.e. intermediate scale) the interaction between plant traits and abiotic factors (e.g. currents and sediment properties) continues to be important (Vandenbruwaene et al., 2011). However, their impact shifts from influencing survival probability to controlling the plant's ability to grow, expand and ecosystem engineer its environment (van Wesenbeeck et al., 2008b; Schwarz et al., 2011). Tussocks exhibit a small-scale positive feedback (improving living conditions) through reducing hydrodynamics and hence promoting sediment accretion within their patches (Bouma et al., 2009b; Balke et al., 2012). This is in opposition to a larger-scale negative feedback, where flow-routing induced erosion (i.e. scouring) deteriorates living conditions at the tussock edges (van Wesenbeeck et al., 2008a; Bouma et al., 2009a). The occurrence and magnitude of these so-called scale-dependent feedbacks often depends on abiotic conditions, hence exhibiting abiotic context-dependency (Jones et al., 2010). Abiotic context-dependency describes whether the structural change generated by the ecosystem engineer leads to abiotic change.

Previous studies have shown that the abiotic context dependency of scale-dependent feedbacks in a geomorphological context is influenced by estuarine-scale processes (e.g. tidal flow induced transport of sediment-rich estuarine water into and over the salt marsh), as well as local site-specific processes (e.g. sediment transport to and from the salt marsh depends on factors such as: local velocity of water flow; size, density of the sediment particles and bottom topography) (Allen, 2000; Wolanski et al., 2004). In this study we are focusing on scale-dependent feedbacks and their dependence on local (i.e. salt marsh) site-specific processes. As previously shown, factors as heterogeneity of bottom topography (Schwarz et al., 2014) and species properties (Langlois et al., 2003) influence local scale-dependent feedbacks. However knowledge on specific processes precipitating the dependency of local scale-dependent feedbacks on abiotic and biotic conditions, although already acknowledged in theoretical literature, is still lacking (Jones et al., 2010; Wolanski et al., 2004).The occurrence of scale-dependent feedbacks (small-scale positive and large-scale negative feedback) is an important factor influencing the transition from small established plant units into larger landscapes and therefore are important agents for landscape development (D'Alpaos et al., 2007; Temmerman et al., 2007; Vandenbruwaene et al., 2011; van de Koppel et al., 2012).

Apart from a single hydrodynamic study on scale-dependent feedback strength on real plants without measuring actual sediment dynamics/erosion (Bouma et al., 2013), and flume studies on patches made of artificial rods (Zong and Nepf, 2010; Meire et al., 2014), we are not aware of studies addressing this issue, despite its importance for understanding the development of large-scale landscapes that are sculptured through biogeomorphic feedbacks.

1.3. Study approach

In coastal tidal wetlands the biogeomorphic feedbacks between plants, water-flow and sediment, where the exerted friction of above-ground plant stems modifies the water-flow and its entrained sediment, have been determined to be the main factors driving large-scale landscape evolution (D'Alpaos et al., 2007; Temmerman et al., 2007). For this reason coastal wetlands are ideal model ecosystems to study impacts of biogeomorphic feedbacks on landscape evolution.

The questions of initial establishment and subsequent development are assessed by analysing these processes for two different (i.e. with respect to their properties) but co-occurring salt marsh pioneer species, stiff *Spartina alterniflora* (further referred to as *Spartina*) and the flexible *Scirpus mariqueter* (further referred to as *Scirpus*). The two species differ in physical properties of the above-ground material (stiffness, maximum plant height, maximum stem diameter), the below-ground material (root network organization) and in physiological properties such as growth rate and stress tolerance (e.g. salinity) (Sun et al., 2001; He et al., 2012).

We specifically investigated:

(1) how initial seedling establishment thresholds (small scale) depend on the interaction between abiotic traits (sediment properties, i.e. cohesiveness) and species-specific plant traits (stiffness, root growth) in a stressed environment (current stress), and
(2) how interactions between abiotic and species-specific traits (stiffness) influence the magnitude of the large scale negative feedback (induced scour at tussock edges, intermediate scale) in a stressed environment (current stress).

Finally, we discuss their implications on salt marsh-scale species establishment and expansion patterns.

2. Methods

2.1. Species and field characterization

S. alterniflora and *S. mariqueter* are the most abundant pioneer halophytes present on salt marshes in the Yangtze estuary, China (Fig. 1). They differ in physical properties (e.g. *Spartina*: stiff, max. Shoot height 3 m; *Scirpus*: flexible, max. Shoot height 0.8 m), growth season (*Spartina*: May to October, *Scirpus*: April to November), stress tolerance (e.g. salinity and anoxia) and competitive strength (growth form and growth rate favours *Spartina* over *Scirpus* in direct competitive interactions) (Sun et al., 2001; Li et al., 2009; Schwarz et al., 2011; He et al., 2012). *Scirpus* is endemic to the Yangtze estuary and used to be the most abundant species observed in pioneer zones and low salt marshes. *Spartina* is an invasive North American species first found in the Yangtze estuary in 1990 and thereafter started to outcompete the endemic species (Huang and Zhang, 2007). On Chongming Island, the biggest Island in the Yangtze Estuary (31.6619°N, 121.4780°E), *Spartina* was planted in the northeast in 2001. Thereafter, it began to spread across existing *Scirpus* salt marshes accounting for 50% coverage of vegetated intertidal area in 2005 (Wang et al., 2006). The predominant spreading direction