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Quantifying critical conditions for seaward expansion of tidal marshes: A transplantation experiment

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ABSTRACT

The alternative stable states theory is increasingly applied to tidal marsh shorelines, where the two opposing stable states – a dense vegetated state on the one hand and a bare tidal flat on the other hand – can coexist in time but differ in space. The shift from the bare to vegetated state by the establishment of individual plants (seedlings, rhizome-grown shoots) on the bare tidal flat is known to be triggered by the occurrence of windows of opportunity. These are periods when species- and life stage-dependent thresholds, such as sediment dynamics or wave impact, are not exceeded. One controlling environmental parameter in intertidal wetlands is elevation as many important stressors for plants – such as hydroperiod, sediment dynamics and wave properties (wave period and wave height) – are typically correlated to it. Disentangling the respective impact of these correlated stressors remains challenging. In this paper, we present the results of a transplantation experiment where the establishment of three different life stages (seedlings, rhizome-grown shoots and patches) of the brackish pioneer *Scirpus maritimus* was tested over an elevation gradient at two locations of contrasting wave exposure. This gradient reached from the bare tidal flat into the marsh and covered an elevation range at which continuous *S. maritimus*-dominated pioneer marsh is known to occur. We found that erosion stress influences seedling survival on tidal flats while drought stress seems to limit long-term establishment of individual shoots and seedlings in the marsh. Furthermore, survival of transplants was more successful on the tidal flat of the sheltered site compared to the tidal flat of the exposed site whereas survival time within the marsh did not differ between sites. This highlights the attenuation of waves and currents in exposed marshes. However, no long-term establishment occurred on the tidal flat, emphasizing the importance of clonal integration for tidal flat colonization.

1. Introduction

Tidal marshes are habitats providing various ecosystem services to coastal and estuarine societies such as enhancing coastal protection through wave attenuation, carbon sequestration and nursery areas for fish (e.g. Barbier et al., 2011; Möller et al., 2014; Temmerman et al., 2013). This is why it is important to preserve and restore them. In this regard, lateral shoreline dynamics (i.e. the processes controlling expansion and contraction of the marshes) are highly relevant. In the past, many studies have been conducted on the risk of vertical drowning of marshes by sea-level rise, but recent studies highlight that many marshes are more vulnerable to lateral erosion (Fagherazzi et al., 2013; Mariotti and Fagherazzi, 2010; Van de Koppel et al., 2005). Nevertheless, field studies on the threshold conditions for lateral landward erosion or seaward expansion remain relatively scarce.

In the past decade, the concept of alternative stable states, originally developed to explain drastic shifts in the states of entire ecosystems (Scheffer et al., 2001), has been increasingly applied to tidal marshes (Marani et al., 2010; Van Wesenbeeck et al., 2008; Wang and Temmerman, 2013). In these bio-geomorphic environments, two alternative stable states – i.e. continuous marshes or

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vegetation patches on the one hand, and bare tidal flats on the other hand – may coexist simultaneously. This means that the alternative states are not only distinguished in time, but also in space, with sharp transition zones from high vegetation densities to bare tidal flat (Van Wesenbeeck et al., 2008). The temporal shift from one state to the other may either be induced through gradual change of environmental conditions or by episodic events, in both cases causing a threshold in environmental conditions to be exceeded (Scheffer et al., 2001; Balke et al., 2014). Those shifts will, over a relatively short time span (months, years), convert bare tidal flat into densely vegetated marsh or vice versa.

The stability of both alternative stable states is the result of positive feedbacks. For example, vegetation that established on a bare tidal flat and passes a critical density or biomass enhances sedimentation and decreases erosion due to its flow-attenuating effect. This will in turn lead to increased elevation, which facilitates further plant establishment and growth and thus sediment trapping (Temmerman et al., 2007; Bouma et al., 2009). Such positive feedbacks will lead to the further development of established vegetation and enhance the long-term stability, as the disturbance threshold required to convert the expanding vegetation back into a low bare tidal flat increases with the amount of sediment trapped. After some time, the disturbance threshold might only be exceeded during extreme events such as during a storm, or through other mechanisms such as cliff erosion. Unvegetated tidal flats, in contrast, are more prone to alternating phases of disturbance and stabilization of the sediment, e.g. through hydrodynamics and bioturbating benthos (Van Wesenbeeck et al., 2007), which then hampers vegetation establishment.

Given that the positive feedback loop between vegetation and sediment accretion in marsh formation only works once a critical biomass has been obtained (Bouma et al., 2009), the most important process in colonizing a bare tidal flat is the initial survival success of pioneer plants that are still too small to benefit from such feedback. For most marsh species, colonization can typically occur either through seedlings or through propagules, i.e. parts of rhizomes of various extents that have detached from an existing mature plant or marsh, and from which new shoots can grow. There are many different kinds of regular environmental stressors (e.g. cyclic tidal inundation stress, currents and waves, sediment dynamics) and episodic disturbances (events such as storm surges), which may counteract plant establishment or expansion. Given this, plant establishment can only succeed in periods during which no critical, generally species- and life stage-dependent thresholds of these stressors are exceeded. This concept of requiring short periods with favourable conditions has been introduced as "windows of opportunity" (Balke et al., 2014, 2011; Mateos-Naranjo et al., 2008).

In highly dynamic environments such as the intertidal areas of marshes or mangroves (Dijkema et al., 1990), windows of opportunity result from regular and stochastic variations in hydrodynamic conditions (Balke et al., 2014; Hu et al., 2015). An example of this might be an unusually long windless phase (reducing wave forcing) or the absence of a winter storm in one particular year (absence of an extreme event that could uproot and wash away freshly established vegetation). Typically a succession of events, such as dispersal followed by a disturbance-free period sufficient in length for germination and establishment (Balke et al., 2014, 2011), is required. An additional constraint is that this succession of events needs to occur in the time of the year during which seeds are available (Zhu et al., 2014).

Different types of thresholds for successful establishment or expansion of marshes have been suggested in previous experimental and modelling studies. Firstly, the plants themselves have specific thresholds, such as (i) a threshold in aboveground biomass of individual plants in order to survive (e.g. Angelini and Silliman, 2012; Van Wesenbeeck et al., 2008), but which can differ either due to different life stages (seedlings, shoots) or different sizes of clonal rhizomes (number of shoots) and (ii) the belowground root length of individual plants (Balke et al., 2011). Secondly, the environment can represent abiotic thresholds such as (i) elevation within the tidal frame which determines inundation time (Fagherazzi et al., 2012; Kirwan et al., 2010; Marani et al., 2010; Wang and Temmerman, 2013); (ii) sediment erosion and accretion rates that will highly affect the survival chances of seedlings (Balke et al., 2011); (iii) currents and waves (Callaghan et al., 2010; Hu et al., 2015; Mariotti and Fagherazzi, 2010) as they induce sediment dynamics and mechanical stress that can lead to uprooting or limit growth and, more specifically, (iv) wave period (Silinski et al., 2015). For most perennial marsh plants, colonization of the bare tidal flat by individual seedlings or shoots is complementary to colonization by clonal expansion from the marsh edge. Contrary to the colonization by individuals that need to survive on their own, clonal shoots growing from the marsh edge benefit from clonal integration (Amsberry et al., 2000; Bertness and Hacker, 1994; Burdick and Konisky, 2003). This means that shoots that are clonally connected to each other can alleviate local physical and biochemical stress by accessing distant resources that are redistributed through the clone (Burdick and Konisky, 2003; Charpentier and Stuefer, 1999).

As elevation relative to mean sea level typically lumps the effect of a series of environmental variables (such as increasing hydroperiod and duration of wave exposure with decreasing elevation) the effects of distinct variables are typically tested separately in lab experiments or in numerical models. In nature, however, they overlap and disentangling their respective impacts on plant establishment remains challenging due to their high covariance. Despite these constraints, field experiments offer the opportunity to look at patch-size effects and actual thresholds, which would be impossible or impractical to mimic in the laboratory.

While previous similar studies used *Spartina*-species or *Phragmites australis* (e.g. Amsberry et al., 2000; Burdick and Konisky, 2003; Mateos-Naranjo et al., 2008; Van Wesenbeeck et al., 2008), we conducted a full-scale field experiment in the brackish part of the macro-tidal Scheldt Estuary (Belgium and the Netherlands, Fig. 1) with the local dominant pioneer species: *Scirpus maritimus*. Three biomass classes, i.e. life stages (seedlings, individual rhizome-grown shoots and clonal patches), were transplanted to five levels along an elevation gradient from the tidal flat into the pioneer *S. maritimus* marsh zone at two sites of contrasting wave exposure. These levels covered an elevation range at which continuous *S. maritimus*-dominated pioneer marsh existed and expanded at other locations along both marshes. Inundation time and sediment dynamics were monitored in parallel to survival of transplants. We hypothesized a life-stage (or biomass) threshold as well as an elevation threshold for successful establishment. We compared the survival of transplants of *S. maritimus* to the reported survival of *Spartina*-species. Finally, we explored the importance of clonal integration for colonization by *S. maritimus* as clonal marsh expansion had occurred within the range of elevations at which the transplantation experiment was performed.

2. Materials and methods

2.1. Site description

We selected two sites along the Scheldt Estuary (Groot Buitenschoor, Belgium (51°21.78′ N, 4°14.88 E), and Rilland, The Netherlands (51° 24.05′ N, 4° 10.65′ E), Fig. 1) where the pioneer marsh zone consists entirely of *Scirpus maritimus* L. Palla. The seaward marsh edge