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Limits to seaward expansion of mangroves: Translating physical disturbance mechanisms into seedling survival gradients

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ABSTRACT

Mangroves are valuable coastal habitats that are globally under pressure due to climate change and coastal development. Small-scale physical disturbance by tidal inundation and wave-induced sediment dynamics has been described as the main bottlenecks to mangrove seedling establishment on exposed tidal flats. However, such biophysical bottlenecks remain poorly studied.

Mangrove progradation at our study site at the Firth of Thames (New Zealand) has been described as rapid but disturbance limited. For this site, we apply a mechanistic model according to the 'Window of Opportunity' (WoO) concept, which analyses real time series of external forcing for disturbance free periods. The model was parameterized with manipulative experiments on seedling stability and monitoring data. The modelled inundation free periods for initial anchoring were validated by a caging experiment with loose and tethered propagules. Although the time series of external forcing derived from monitoring data are simplified, our model confirms the absence of mangrove progradation due to failed recruitment events on the tidal flat since 1997. The model also shows, that a temporary reduction in external forcing would lead to a sudden progradation of the mangrove forest.

WoO dynamics, where vegetation establishment requires temporarily benign conditions, may be of general importance to other ecosystems with stochastic external forcing. Understanding the biophysical interactions between vegetation and geomorphic processes is key to better manage and protect disturbance-driven ecosystems in times of changing wind pattern and accelerated sea-level rise.

1. Introduction

Mangrove forests are valuable ecosystems occupying the intertidal zone along tropical and subtropical coasts. Despite their numerous ecosystem services (Donato et al., 2011; Gillanders et al., 2003; Hutchings et al., 2005; Koch et al., 2009), large-scale loss of mangrove habitat has occurred associated with, for example, aquaculture and coastal development (Alongi, 2002; FAO, 2007; Giri et al., 2011). Increasing appreciation of the societal and ecological consequences of mangrove deforestation for e.g., carbon storage, coastal protection and coastal fisheries has created a need to better understand the biophysical drivers of mangrove–forest ecosystems, including the establishment of seedlings on unvegetated tidal flats.

Apart from climatic constraints, mangroves are typically described to be limited to 'sheltered' or 'low energy' coasts (Bird, 1986; Thom, 1967) and to intertidal areas above mean sea level (MSL) (Clarke and Myerscough, 1993; Semeniuk, 1980; van Loon et al., 2007). Accordingly, it is usually advised for mangrove restoration to be only attempted in areas above the local MSL (Lewis, 2005). The importance of dispersal and establishment processes in structuring the mangrove forest (i.e., supply side ecology) has been widely recognized (Sousa et al., 2007). However studies about the effects of flooding on seedling establishment have been focused on the floatation time of propagules in stagnant water (Clarke and Myerscough, 1993; Clarke et al., 2001), possible tidal sorting mechanisms inside the mangrove forest mainly under microtidal conditions (Rabinowitz, 1978; Sousa et al., 2007) or on soil anoxia and inundation stress for already established seedlings (McKee, 1993; Skelton and Allaway, 1996; Youssef and Saenger, 1996). Studies from dynamic muddy coasts such as the Guyana coastal system (Fromard et al., 2004; Winterwerp et al., 2007), Thailand (Thampanya et al., 2002) or the Firth of Thames in New Zealand (Lovelock et al., 2010) do however show, that tidal flooding induced currents, waves and sediment deposition/erosion play a major role in determining seedling establishment success. Few studies have observed or tried to quantify the effects of hydrodynamic forcing by currents and waves (Balke

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et al., 2011; Thampanya et al., 2002) or short term sediment erosion (Balke et al., 2013a, 2013b; Swales et al., 2007) on seedling establishment success. The high number of failed restoration (planting) projects on bare tidal flats due to wave exposure supports the need to understand such biophysical bottlenecks to establishment (Friess et al., 2012; Primavera and Esteban, 2008).

Balke et al. (2011) have experimentally shown for the common mangrove pioneer species *Avicennia alba* that successful stranding and early anchorage of propagules are restricted to stochastic windows of opportunity with absent or reduced physical disturbance by hydrodynamic energy. The propagules anchor rapidly upon stranding and the root length at the time of the following disturbance (flooding) determines how well the seedling is able to resist dislodgement by drag forces due to buoyancy, wave action and tidal currents. As mangrove propagule dispersal is hydrochorous (water dispersal), stranding of propagules on the tidal flat can only occur after previous inundation. This process makes inundation followed by an inundation free period a necessity for establishment of mangroves on bare tidal flats. After initial rooting a few cm of sediment erosion (e.g., due to wave action) can still lead to toppling failure and excavation of the rooted seedling (Balke et al., 2013a, 2013b). The disturbance frequency and magnitude are highly stochastic in a tidal environment. Apart from the regular tidal cycle there are stochastic events of no disturbance (e.g., inundation free periods during abnormally low water levels, calm weather) and periods of extreme disturbance (e.g., storm events). Tidal-flat elevation and water levels are the two most important factors determining if and when an establishing mangrove seedling will experience disturbance (Balke et al., 2014). This is followed by the magnitude of external forcing (e.g., wave height) which determines how strong the disturbance is when the tidal flat is inundated.

The present study aims to integrate the effects of stochastic physical disturbance processes on unvegetated tidal flats with the mangrove seedling stability at different life stages in a mechanistic model. For this purpose the length of the required inundation free period for stranding and initial rooting, a first Window of Opportunity (WoO1) was experimentally determined. This WoO1 is followed by a second experimentally quantified WoO2, the required period below a critical sediment disturbance magnitude causing toppling of seedlings. Due to the stochastic nature of the physical drivers we use a mechanistic model of propagule stranding and establishment along an elevation gradient. Disturbance time series are generated from a 17 year record of sea level and wind speed/direction for a field site in the Firth of Thames, New Zealand (Fig. 1). We validate the WoO1 prediction in a short term manipulative field experiment and compare the final model output with the present spatial extent of the mangrove forest. Finally, we apply the model to investigate the effects of changes in external forcing (e.g., due to climate change).

2. Methods and model formulation

2.1. Firth of Thames field site and available data

The Firth of Thames is a mesotidal embayment located on the Northeast coast of New Zealand's North Island. The Firth receives freshwater runoff from the Piako and Waihou Rivers (Fig. 1). The mangrove forest at the study site along the southern shore of the Firth has evolved from a sandy intertidal flat to a 1 km wide mangrove forest with accreting mud flats since the 1950s. Seaward expansion is occurring periodically, with the last major progradation event between 1991 and 1995, likely linked to changes in prevailing wind direction creating calm conditions for mangrove recruitment (Lovelock et al., 2010; Swales et al., 2007). The Firth of Thames mangrove forest is located close to the southern latitudinal limit of mangrove distribution in New Zealand and consists of a monospecific stand of *Avicennia marina* var *australasica*. A sediment disturbance depth (i.e., short term alternation of sedimentation and erosion) of up to 7 cm on the mudflat fronting the forest edge has been estimated in 2006 and net deposition of fine sediments was shown to be 2 cm y^{-1} on average (Swales et al., 2007). This field site has been chosen for this study as wave induced erosion is reportedly the main cause of failure for recently established *A. marina* seedlings on the tidal flat (Swales et al., 2007).

The Firth of Thames field site is located in the vicinity of long-term monitoring stations and measuring equipment has been installed inside the mangrove forest. Wind records (1995–2012) are available from the Paeroa climate station (B75362). Daily maximum windspeeds from the seaward direction at Paeroa (248 to 68°) show good correlation with the data from a climate station deployed at the field site with data from November 2010–December 2012 (Pearson, $r = 0.61$, $P < 0.001$). Long-term measured sea levels are available from the Tararu tide gauge approximately 12 km NE of the field site (Fig. 1) from 1992 onward. Time-series of sea level at the field site was provided by a Greenspan PS1000 vented pressure sensor deployed at an instrument station in the fringe forest ~40 m from the mud flat. Daily maximum water levels from June 2012 to March 2013 correlated well with the Tararu tide gauge data (Pearson, $r = 0.97$, $P < 0.001$), low water levels could not be compared as the sensor was not inundated. A continuous record (May 2102 to February 2013) of suspended sediment concentration (SSC) was provided by a Seapoint optical backscatter sensor (OBS) deployed at the instrument station, with SSC burst-sampled at ten-minute intervals (4 Hz, 480 samples/burst) while the sensor was submerged. The OBS was calibrated in a laboratory tank with concentrations of up to 2400 mg/l using mud collected from the field site. Data from the field site were recorded by a Campbell CX-1000 logger and retrieved via a cellular-modem telemetry system.

2.2. Modeling structure and parameterization

The modelling approach is based on the Window of Opportunity (WoO) concept by Balke et al. (2014). Real time series of external forcing are analyzed for disturbance free periods (WoO) which are sufficiently long to allow vegetation establishment under otherwise disturbance limited conditions. The present model separates a WoO into two parts, depending on the life stage of the mangrove seedling. The first, WoO1, represents a critical time period without inundation after flooding that allows propagules to disperse, strand and anchor against flooding. For the parameterization of WoO1 root-growth and the critical root-length to withstand dislodgement by waves were determined experimentally. Tidal water levels are used as the disturbance time series for the WoO1. The second, WoO2 represents a time period without wave-driven sediment re-suspension causing erosion at the tidal flat surface to allow seedlings to gain stability against toppling and excavation (see Fig. 2). For the parameterization of the WoO2 a critical erosion threshold was determined experimentally by excavating seedlings. Monitoring data of wind speed, water level and suspended sediment concentration are combined to form the disturbance time series for WoO2. Individual seedlings must pass through WoO1 and WoO2 to develop into an established seedling that is likely to survive to become an established sapling. The model was implemented using the statistical computing software R.

2.3. Model formulation

The survivorship of mangrove seedlings on the tidal flat is modelled as:

$$N(x,a,t+1) = [N(x,a-1,t) + R(MWL(t), seas(t))] * \{1-[D_1 + (1-D_1) * D_2]\} \quad (1)$$

where N(x,a,t) denotes the number of individuals at height x (i.e., intertidal elevation), of age a and at time t, both counted in days and referring to real dates.