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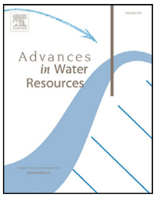

Biogeomorphic feedback between plant growth and flooding causes alternative stable states in an experimental floodplain

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ABSTRACT

It is important to understand the mechanisms of vegetation establishment on bare substrate in a disturbance-driven ecosystem because of many valuable ecosystem services. This study tested for empirical indications of local alternative stable states controlled by biogeomorphic feedbacks using flume experiments with alfalfa: (1) single flood experiments different in flood intensity and plant growth, (2) long-term evolution experiments with repeated flooding and seeding. We observed: (1) a combination of thresholds in plant growth and flooding magnitude for upgrowing seedlings to survive; (2) bimodality in vegetation biomass after floods indicating the existence of two alternative states, either densely vegetated or bare; (3) facilitation of vegetation establishment by the spatial pattern formation of channels and sand bars. In conclusion, empirical indicators were demonstrated for local alternative stable states in a disturbance-driven ecosystem associated with biogeomorphic feedbacks, which could contribute to the protection and restoration of vegetation in such ecosystems.

1. Introduction

Completely bare substrate and densely vegetated substrate have been suggested to be alternative stable states. Catastrophic shifts occur between these states in disturbance-driven biogeomorphic ecosystems, such as tidal marshes [1–5], mangroves [6,7], dunes [8,9], and riverine floodplains [10–13]. Vegetation provides plenty of important ecosystem services, such as protection against shoreline erosion and coastal floods by tidal marsh and mangrove vegetation [14–17], protection against river bank erosion by riparian floodplain vegetation [18–20], and protection against dune erosion [21–23]. Therefore, it is of significant importance to understand the mechanisms behind the conversion between bare and vegetated states for the protection and restoration of the vegetation cover and its associated landforms in biogeomorphic ecosystems.

The theory of alternative stable states has been identified as an important mechanism in ecosystems, because once the system converts to the alternative state, the recovery to the original state is difficult due to hysteresis effects [24–27]. Catastrophic shifts between alternative stable states have been broadly demonstrated in many ecosystems controlled by feedbacks between organisms and resources [26,28–30]. Only in recent years, the mechanism of alternative stable states started to be considered in biogeomorphic ecosystems controlled by feedbacks between organisms and landforms as well (e.g., [2–5,7,31]). The positive biogeomorphic feedback is generated by organisms, such as algae and vegetation, that colonize and stabilize soil surfaces that would otherwise be subject to intense wind or water erosion and deposition [32–35]. This stabilizing effect of the organisms on the soil surface in return promotes the further growth of the organisms, hence creating a positive biogeomorphic feedback loop leading to a stable state with a stable soil substrate densely covered by the organisms [35–39]. In cases where the organisms are not able to colonize the soil surface, due to too high erosion or deposition rates, an alternative bare state would develop. Alternative stable states associated with biogeomorphic feedbacks

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were explained by theoretical or numerical models for river floodplains [10,40] and tidal marshes [1–4], as well as by experiments for coastal dunes [9]. Recently, more and more empirical evidences have been found in tidal marshes [5,41], riverine ecosystems [11–13], mangroves [6,7], and coastal dunes [8]. Despite all these evidences, the hypothesis is still not strongly conclusive that bare state and vegetated state are alternative stable states in disturbance-driven biogeomorphic ecosystems. It is typically difficult to verify alternative stable states in real ecosystems as reviewed in the literature [26,27]. Controlled experiments have been suggested to be the most powerful way to diagnose the existence of alternative stable states and to uncover the underlying mechanisms [26,42–44].

As suggested by the theory of alternative stable states, it has been proved difficult to restore the vegetation cover in coastal or riparian systems once the vegetation is destroyed (e.g., [45–50]). The survival of seedlings against soil disturbances by wind and water flow has been identified as a bottleneck determining the success of the restoration projects [6,46]. Plants have to grow and exceed certain thresholds in biomass, size and density so as to securely anchor and to be able to survive the physical geomorphic disturbance before the positive feedbacks can start [6,7,51–53]. In this respect the concept of "Windows of Opportunity" (i.e. minimum required disturbance-free periods for seedling establishment following the diaspore dispersal) has been recently suggested as to control under which conditions the shift from bare state to vegetated state is able to occur in disturbance-driven biogeomorphic ecosystems such as tidal marshes, mangroves, river floodplains and dunes [6,7]. However, studies are still limited in explaining the mechanisms underlying the thresholds in seedling survival in such disturbance-driven biogeomorphic ecosystems [6,7,53–55].

Spatial pattern formation has been suggested to be a key mechanism facilitating the shifts between alternative stable ecosystem states due to the local positive feedback within patches of high organism density and long distance negative feedback in the bare zones next to these patches [28,56]. In particular in biogeomorphic ecosystems that are controlled by water flow, such as tidal marshes, mangroves, and river floodplains, the positive feedback of water flow reduction and sedimentation only occurs locally within (and behind) vegetation patches at a small scale [41,51,57–59]. In contrast, a long-distance negative feedback occurs, as water flow is forced to accelerate around and between the vegetation patches, resulting there in high flow velocity and more erosion, which may induce the erosion of channels and hamper plant establishment [32,41,57,58,60]. However, most of the studies were based on established vegetation patches [32,41,51,57,58] or mature channel networks [60], while little is known of what happens when the system is dynamically developing from the most initial stage of seedling establishment on a homogeneously flat bare landscape without channels, towards a heterogeneous landscape with development of biogeomorphic patterns.

Therefore, a better experimental understanding is needed of the role of biogeomorphic feedbacks between seedling growth and geomorphic disturbances in causing alternative stable states in biogeomorphic ecosystems, and in particular the role of spatial pattern formation in facilitating the formation of alternative stable states. In this study, we aim to test the presence of empirical indicators for alternative stable states in an experimental floodplain (in a laboratory flume) with two types of experiments, which are single flood experiments and long term evolution experiments with repeated flooding interacting with plant growth. Here, a floodplain means a sand bed that is most of the time dry and that is regularly flooded, so our experimental floodplain is not specifically mimicking a tidal floodplain but may also represent a riverine floodplain. First, we ran single flood experiments with different flood intensity (flood discharge) and different initial plant biomass (root length) to test two empirical indicators of alternative stable sates: (1) threshold behavior and (2) bimodal distribution [26]. The predictions are: (1) For a certain discharge, there is a threshold in minimal root length, above which the plants can survive the flood. Correspondingly, there is also a threshold in maximal discharge, below which the plants with a certain root length can survive. We expect that for a higher flooding discharge, a larger threshold in root length needs to be exceeded before plants can survive the flood; and that for a longer root length, plants can survive up to a larger threshold in discharge. (2) We expect a bimodal spatial distribution of vegetation biomass representing either bare patches or densely vegetated patches in response to the flooding disturbances, while zones with intermediate vegetation biomass occur less frequently. Second, we ran the long-term evolution experiments simulating the interaction between plant growth and repeated flooding, so as to test the hypothesis that in the long-term the geomorphic pattern formation of channels and bars would promote the development of local alternative stable bare and vegetated states in a floodplain.

2. Materials and methods

2.1. General description of the flume experiments

The experiments were carried out in a big flume of 15 m length and 2.2 m width with wooden side walls. This flume was divided into three working sections, each functioning as an individual smaller flume of 4.1 m length and 2.2 m width with an inlet tank and an outlet tank at the upstream and downstream ends respectively (Fig. 1). The long-term evolution experiments were carried out in this configuration. In the single flood experiments, each of the sections was further divided into three parallel narrow strips of approximately 0.72 m width (Fig. 1), which could be flooded separately, so that several experiments could be performed simultaneously. All experiments started from an initially flat sand bed of non-cohesive quartz sand ($D_{50} = 0.6$ mm) with an initial bed slope of 0.7%. The grain size was selected to avoid ripple formation.

The big flume was equipped with a tail reservoir (at the downstream end of the flume), from which water was pumped into the head reservoir (at the upstream end of the flume). From this point the water flowed via one of three calibrated V-shaped notches corresponding to the three sections respectively, and guided into the inlet tank of each section where the water was stabilized before gently flowing onto the sand bed in each of the three sections. The experimental discharge was controlled by adjusting the discharge pumped into the head reservoir, and calculated by measuring the water depth over the V-shaped notches by a gauge needle. The inlet and outlet boundary of each section were adapted so that the inflow and outflow were distributed uniformly over the entire width of the section. At the end of each section, water was guided back into the tail reservoir, where the eroded sediment and plants were filtered out by a sieve. No sediment feeding was foreseen.

Alfalfa sprouts (*Medicago sativa*) were used in the experiments to simulate natural vegetation [60–63], because the cohesion provided by alfalfa roots to non-cohesive sand has a magnitude comparable to that observed in natural river banks provided by root-reinforcement [63,64]. In this study, alfalfa seeds were seeded manually as uniformly as possible over the entire experimental sand surface. Alfalfa seeds germinated and sprouts grew up using only nutrient reserves present in the seeds. No nutrients were added in the flooding water or in the sand bed, and the photosynthetic active radiation provided by the lamps in the lab was very low. Synthetic light was present 24 h per day by fluorescent lamps. Temperature varied slightly around 21 °C and humidity between 65% and 75% in the lab.

2.2. Single flood experiments

Single flood experiments were designed to test the threshold behavior in vegetation establishment. Four growth stages (alfalfa germinated and grown for 2, 4, 6, and 8 days after seeding) and five flood