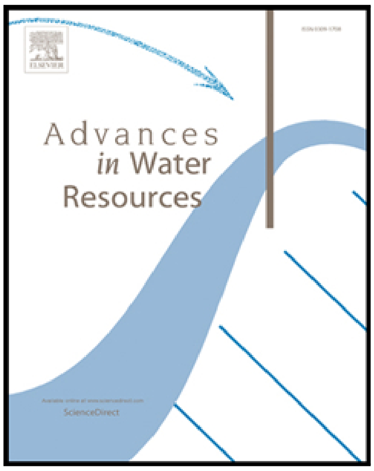
# Biogeomorphic feedback between plant growth and flooding causes alternative stable states in an experimental floodplain

**Reference:**
Wang Chen, Wang Qiao, Meire Dieter, Temmerman Stijn, et al..- Biogeomorphic feedback between plant growth and flooding causes alternative stable states in an experimental floodplain
Advances in water resources - ISSN 0309-1708 - 93:B(2016), p. 223-235
Full text (Publishers DOI): http://dx.doi.org/doi:10.1016/j.advwatres.2015.07.003




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

Chen Wang , Qiao Wang , Dieter Meire , Wandong Ma , Chuanqing Wu , Zhen Meng , Johan Van de Koppel , Peter Troch , Ronny Verhoeven , Tom De Mulder , Stijn Temmerman

PII: S0309-1708(15)00150-5
DOI: 10.1016/j.advwatres.2015.07.003
Reference: ADWR 2415

To appear in: *Advances in Water Resources*

Received date: 1 February 2015
Revised date: 25 May 2015
Accepted date: 7 July 2015

Please cite this article as: Chen Wang , Qiao Wang , Dieter Meire , Wandong Ma , Chuanqing Wu , Zhen Meng , Johan Van de Koppel , Peter Troch , Ronny Verhoeven , Tom De Mulder , Stijn Temmerman , Biogeomorphic feedback between plant growth and flooding causes alternative stable states in an experimental floodplain, *Advances in Water Resources* (2015), doi: 10.1016/j.advwatres.2015.07.003

**Highlights**

- We test biogeomorphic alternative stable states by flume experiments with alfalfa.
- Thresholds in plant growth and flooding magnitude determine seedling survival.
- A bimodal distribution of vegetation biomass indicates two alternative states.
- The spatial pattern formation facilitates the establishment of the vegetated state.
- We provide empirical indicators for biogeomorphic alternative stable states.

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

Chen Wang[a,b], Qiao Wang[a], Dieter Meire[c], Wandong Ma[a], Chuanqing Wu[a,*], Zhen Meng[d,*], Johan Van de Koppel[e], Peter Troch[c], Ronny Verhoeven[c], Tom De Mulder[c], Stijn Temmerman[b]

[a] Satellite Environment Center, Ministry of Environmental Protection of People's Republic of China, Fengde East Road 4, 100094 Beijing, P.R. China

[b] Ecosystem Management Research Group, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

[c] Department of Civil Engineering, Hydraulics Laboratory, Ghent University, Sint-Pietersnieuwsstraat 41, 9000 Ghent, Belgium

[d] Institute of Microelectronics of Chinese Academy of Science, Beitucheng West Road 3, 100029, Beijing, P.R. China

[e] Center for Estuarine and Marine Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Korringaweg 7, 4401NT Yerseke, The Netherlands

* Corresponding authors at: Satellite Environment Center, Ministry of Environmental Protection of People's Republic of China, Fengde East Road 4, 100094 Beijing, P.R. China; Institute of Microelectronics of Chinese Academy of Science, Beitucheng West Road 3, 100029, Beijing, P.R. China

E-mail adresses: wangchen_ch@163.com (C. Wang), wangqiao@sepa.gov.cn (Q. Wang), dieter.meire@ugent.be (D. Meire), mawdcn@163.com (W.-D. Ma), wu.chuanqing@sepa.gov.cn (C.-Q. Wu), mengzhen@ime.ac.cn (Z. Meng), johan.van.de.koppel@nioz.nl (J. Van de Koppel), peter.troch@ugent.be (P. Troch), ronny.verhoeven@ugent.be (R. Verhoeven), tomfo.demulder@ugent.be (T. De Mulder), stijn.temmerman@uantwerpen.be (S. Temmerman)

**Abstract (100-150 words)**

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 state in a disturbance-driven ecosystem associated with biogeomorphic feedbacks, which could contribute to the protection and restoration of vegetation in such ecosystems.

**Keywords (max 6 keywords):**

Biogeomorphic feedback, alternative stable state, flooding, plant, floodplain, flume experiment

## 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 state 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 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 (Figure 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 (Figure 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 was adapted so that the inflow and outflow was 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 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 24h per day by fluorescent lamps. Temperature varied slightly around 21 °C and humidity between

65 % and 75 % in the lab.

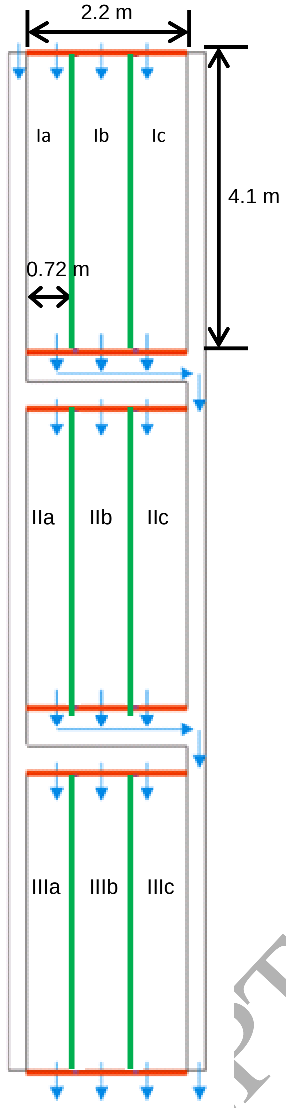



Figure 1. Schematic sketch representing the division of the 15 m flume into three sections (I, II and III) and further into nine narrow strips (Ia, Ib, …, IIIc) used for the experiments. Black lines are the permanent outlines of the flume. Blue arrows indicate the flow direction. Red lines indicate the inflows and outflows across the entire width of the flume sections for the long-term evolution experiments. Green lines indicate the temporary cross boards added for the single flood experiments.

### 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 discharges (0.17, 0.43, 0.77, 1.11 and 1.44 l/s) were chosen to be combined (the reason why these conditions were chosen is explained in the paragraph below). Alfalfa was uniformly seeded with a density of about 20000 seeds per $m^2$ (44 $g/m^2$ of seed material) on a flat sand bed in the middle 3 m of each narrow strip of 4.1 m length. At the head and the end of each strip, respectively 0.3 m and 0.8 m were kept bare to avoid boundary effects. Next, the alfalfa seeds were allowed to germinate and grow for a certain number of days (2, 4, 6 or 8 days). During the growing phase alfalfa was gently sprayed with equal amounts of water once a day. Subsequently, the resulting alfalfa vegetation was flooded once for 1 hour with a certain discharge (0.17, 0.43, 0.77, 1.11 and 1.44 l/s). In order to avoid preferential flow and channel formation along the smooth wooden sidewalls, artificial grass mats of about 4 cm thickness were fixed to the sidewalls of the strips in order to increase the roughness of the sidewalls. For each of the four growth stages, one single flood experiment per discharge was performed, but only the experiment with the intermediate discharge of 0.77 l/s was replicated three times, and one more experiment was replicated for the lowest discharge of 0.17 l/s (Table 1). More replications were not performed due to the time limitation. In total, 29 experiments were performed and used in this study.

Table 1. Replications of experiments at different discharges and different growth stage.

| Replications | 2 days | 4 days | 6 days | 8 days |
|---|---|---|---|---|

| | | | | |
|---|---|---|---|---|
| 0.17 l/s | 2 | 1 | 1 | 1 |
| 0.43 l/s | 1 | 1 | 1 | 1 |
| 0.77 l/s | 3 | 3 | 3 | 3 |
| 1.11 l/s | 1 | 1 | 1 | 1 |
| 1.44 l/s | 1 | 1 | 1 | 1 |

The choice of the experimental conditions (number of growing days and discharges) were selected based on data in the literature and based on primary tests. Alfalfa is reported to start germination after 24 hours and to reach maximum sprout size (shoot length) after 8 days [62]. Therefore, we chose the number of growing days (2, 4, 6 and 8) so that the full range from minimal to maximal sprout sizes would be covered. The seeding density was twice the value used by Tal and Paola [62] in their long-term reseeded experiments, because no reseeding process was carried out in our single flood experiments. Furthermore, the doubled seeding density made the vegetation establishment in the short period of 2–8 days more detectable in the photograph analyses. In addition, seeding density was found to play a less important role in vegetation establishment compared to the growing days [65]. The intermediate discharge of 0.77 l/s over the strips of about 0.72 m width was comparable with the discharge used by Tal and Paola [62]. The second lowest discharge of 0.43 l/s was the lowest discharge required to move the sediment, which was determined after several testing experiments. The second highest discharge of 1.11 l/s was chosen as it has the same difference (± 0.34 l/s) with the intermediate discharge (0.77 l/s) as the second lowest discharge (0.43 l/s). The lowest and highest discharges were chosen as the technically possible minimum and maximum discharges in that flume with the experimental set-up.

The eroded plants and the plants remaining in the flume were collected after the flood. For each experiment the root length and shoot length were measured for 30 randomly sampled eroded plants and 30 remaining plants. In total, 420 plants from seven experiments were sampled for each growth stage (i.e., all experiments listed in Table 1 except the one replicate at discharge 1/two days). The weight (biomass) of eroded plants and remaining plants, including both above-ground and below-ground parts, were measured after drying at 105 ˚C for 48 hours, and will further be referred to as eroded biomass and remaining biomass. The initial biomass before flooding was calculated by adding up the eroded biomass and remaining biomass after flooding. Survival rate was calculated as the remaining biomass divided by the initial biomass.

In order to quantify the spatial patterns of the remaining biomass, aerial photographs with a resolution of about 0.2 mm/pixel were taken before and after the floods from a height of about 1 m above the sand surface using a NIKON D300s camera. The camera was fixed on a mounting system on a bridge that could be moved over the flume via rails. Each time before and after the floods, photographs were taken for each experimental strip (4.1 m × 0.72 m) with a minimum overlap of 60 %. We selected one photo before the flood and one photo after the flood for the same section (about 0.64 m × 0.57 m) located in the middle of the strip. A vegetation index – further referred to as the “Greenness” - was calculated for the selected photographs and used as a proxy of vegetation biomass:

$$\text{Greenness} = \text{Green} / (\text{Red} + \text{Blue}), \qquad [1]$$

where Green, Red and Blue were the pixel values of the green, red and blue bands of the photograph. The Greenness index was selected after comparing several vegetation indices [66], which have been empirically used to estimate above-ground biomass [67]. High values of Greenness indicate high vegetation cover and vice versa. The resulting Greenness images were resampled into rougher resolutions of 2×2 cm, 4×4 cm, 6×6 cm and 8×8 cm by calculating the mean value of the original pixel values in windows of 2×2 cm, 4×4 cm, 6×6 cm and 8×8 cm, so as to smooth out the impact of reflection differences by leaves, stems and roots, as well as to take into account the possible scale effects (i.e., the alternative stable states are more obvious in the patch scale). The frequency distribution of Greenness values was calculated for the resampled Greenness images, in order to test for the bimodality in the frequency distributions as an indication for the emergence of two stable states, either a bare sand bed or densely vegetated sand bed. The hypothesis was tested that before the flooding a unimodel distribution of Greenness values occurred (corresponding to a spatially homogeneous vegetation cover), while after the flooding a bimodal distribution occurred with one peak of low Greenness values (corresponding to patches of bare sand) and another peak of high Greenness values (corresponding to patches of dense vegetation), while intermediate Greenness values (corresponding to intermediate vegetation density) did not occur frequently. The analyses were done using MATLAB.

### 2.3. Long-term evolution experiments

In order to test the hypothesis that geomorphological pattern formation of channels and bars promote the development of patches of alternative bare and densely vegetated stable states, three long-term evolution experiments were processed. The experiments started from flat sand beds with alfalfa uniformly seeded over the entire surface of all the three sections (4.1 m × 2.2 m) with a density of 10000 seeds per m$^2$ (22 g/m$^2$), which was the same seeding density as in the long-term evolution experiments of Tal and Paola [62]. Water was sprayed every day gently and uniformly on the flume surface to let the seeds germinate. Two days after seeding, the three sections were flooded for 1 hour with a discharge of 3.3 l/s, 2.3 l/s and 1.3 l/s, respectively (these three discharges correspond to the discharges of 1.11, 0.77 and 0.43 l/s in the smaller strips used in the single flood experiments). After every flood, alfalfa was seeded again with the same density, and two days later the next flood was simulated, etc. In between two floods, water was sprayed every day to keep the sand surface moist and suitable for sprouts to grow. This procedure of seeding and flooding every two days was repeated. The experiments were run for at least 37 days for the three discharges, but only the first 33 days were considered in the analyses, because the vegetation got infected by funghi at the end of the experiments.

Top view photographs with a resolution of about 0.4 - 0.8 mm/pixel were taken before and after the floods from a height of 1 - 1.8 m above the sand surface using a RICO GX200 camera fixed on a mounting system on the movable bridge or fixed on a metal pole held by the photographer. Each time before and after the floods, photographs were taken for the experimental section (4.1 m × 2.2 m) with a minimum overlap of 60 %. The series of overlapping photographs were used to create 3D elevation models of the experimental section with a spatial accuracy up to 5 mm, and further to extract the orthophoto and Digital Elevation Model (DEM) with a resolution of 1 cm, based on the structure from motion (SFM) algorithms and the multi-view 3D reconstruction technology using the AgiSoft Photoscan software [68, 69]. In order to exclude edge effects, borders of 5 cm were cut off at the edges of the orthophoto and DEMs. Vegetation coverage was determined by extracting the number of green pixels using Photoshop CS5, and calculated as the absolute number of green pixels relative to the total number of all pixels. The temporal evolution of biomass development was presented by the change in vegetation coverage. Frequency distribution of Greenness was calculated for sample photos located in the middle of the experimental section and with more healthy vegetation patches after the 15th flood (i.e., Day 31), using the same method as for single flood experiments.

## 3. Results

### 3.1. Indicators for alternative stable states based on single flood experiments

#### *3.1.1. Growth curve of alfalfa sprouts*

A sigmoid growth curve was observed in both the root length and the shoot length (Figure 2). Seedlings geminated after one day. Plants grew fast in the first four days and then the growth slowed down. Since there is considerable variation in the root and shoot length after a same number of growing days (Figure 2), the mean root length was used in the following analyses as the variable representing the growth stage before flooding instead of the number of growth days. Root length was used rather than shoot length, because the interaction between roots and sands stabilized the plants from being eroded by the floods.

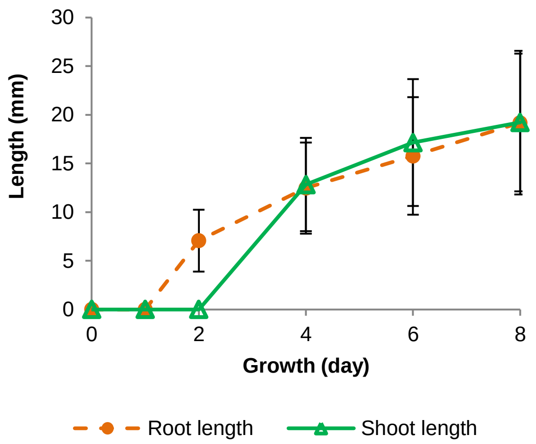


Figure 2. Growth curve of root length and shoot length of alfalfa sprouts with mean length and standard deviation of 420 sprouts sampled for each growth stage.

### *3.1.2. Thresholds in vegetation survival*

The survival rate of the plants to the single flood experiments increased with the mean root length (growth stage) of the plants, and decreased with increasing discharge (Figure 3). A low survival rate indicated that many plants were flushed away. For the shortest root length (between 6 and 7 mm), a low survival rate (below 30 %) was observed for even the lowest discharge (Figure 3A), and almost no sprouts survived the higher discharges (Figures 3B–3E). On the contrary, up to 70 % of the sprouts with a slightly longer root length of 9 mm survived the lowest discharge (Figure 3A). For the same root length, the survival rate declined to below 40 %, 10 %, and further to almost 0 % for the subsequent higher discharges, respectively (Figures 3B–3E). For experiments with the highest discharge, the survival rate was never more than 30 %, even for the longest root length (Figure 3E).

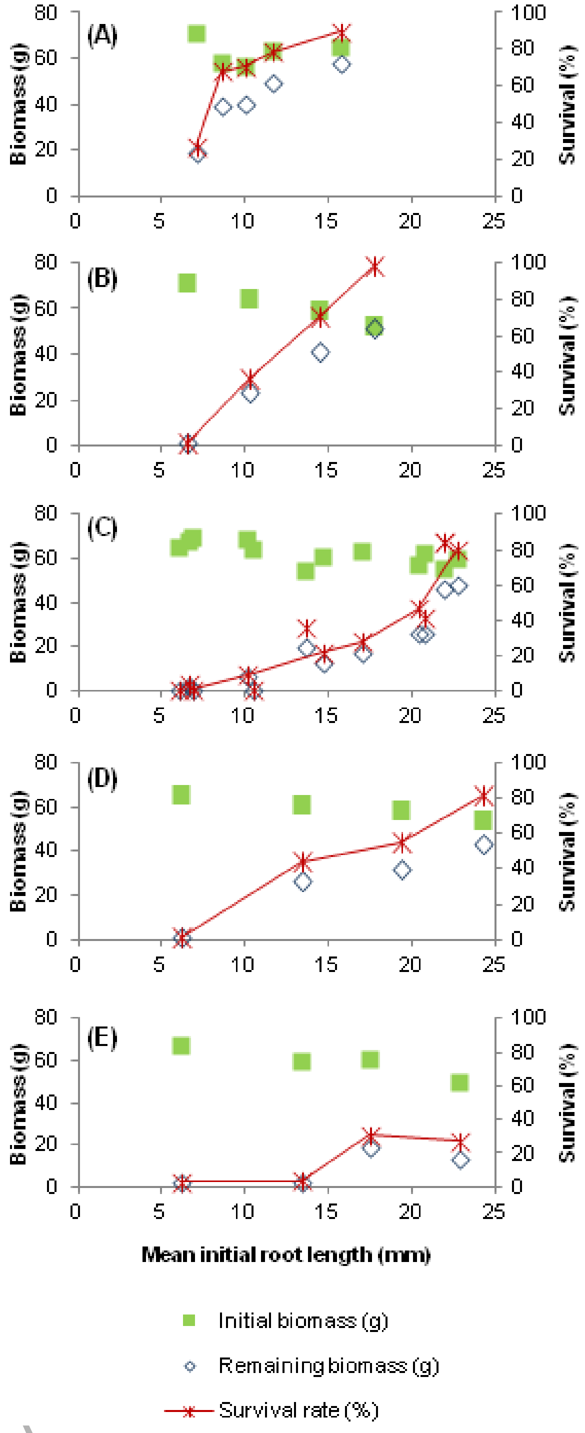



Figure 3. Initial biomass before flooding, remaining biomass after flooding, and survival rate as a function of mean root length after flooding with discharges of 0.17 l/s (A), 0.43 l/s (B), 0.77

l/s (C), 1.1 l/s (D) and 1.44 l/s (E). Both above-ground and below-ground parts were included in the biomass measurement. The survival rate was calculated as the percentage of remaining biomass relative to the initial biomass.

These experimental results indicate the existence of a threshold root length above which plants can survive a certain discharge and a threshold discharge below which plants with a certain root length can survive, which results in a threshold line in the discharge – root length relationship (Figure 4). In conditions below the threshold line, almost no plants could survive the flood (with a survival rate < 5 %). In contrast, some of the plants could survive the flood in conditions above the threshold line (with survival rate > 20 %). A higher threshold in root length was observed with increasing discharge. Correspondingly, a higher threshold in discharge was observed for plants with longer root length.

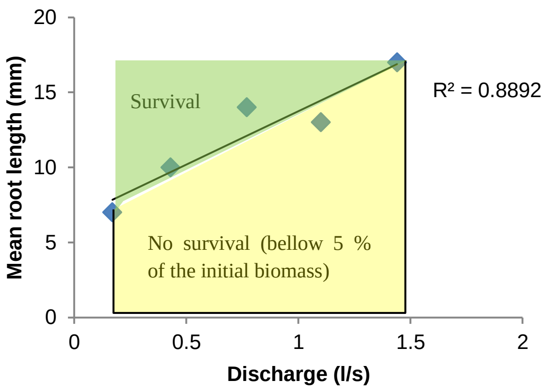



Figure 4. The relationship between the shortest mean root length and the highest discharge for which the plants could survive the flood.

### *3.1.3. Bimodal spatial distribution in vegetation biomass after the flooding disturbance*

The analyses of Greenness values calculated from the digital pictures (see Eq. 1) gave an indication of the spatial patterns in vegetation biomass, as shown in the example (Figure 5). A unimodal distribution of the Greenness values was observed in all photos before flooding and at all spatial scales (i.e., when mean Greenness values were calculated for larger pixel sizes). A bimodal distribution of the Greenness values was often observed in photos after flooding when the mean root length was long enough so that plants could survive. The original image resolution of 0.2 mm was not used because this resolution is too fine: at this scale of 0.2 mm you can see individual plants, leaves and very small bare spots in between plants and leaves even within pictures with a continuous vegetation cover (e.g. figure 5A). Hence the frequency distribution of the greenness values of original images with 0.2 mm resolution would be bimodal even for pictures completely covered by a continuous vegetation cover (e.g. figure 5A). Therefore the original picture resolution needs to be upscaled in order to identify large-scale vegetated and bare zones within pictures.

Similar results were found for all experiments with different discharges (Figure 6 and Appendix). For a certain discharge, the Greenness values after flooding were observed to have a bimodal distribution when the mean root length exceeded the threshold value for plant survival as shown in Figure 4 (marked in red rectangles in Figures 6 and Appendix). The right peak in the distributions (i.e., the peak corresponding to a dense vegetation biomass), became higher, wider and more obvious with increasing mean root length (i.e. longer number of growing days). For a certain growth stage (i.e. root length), the bimodal distribution occurred when the discharge was below the threshold value for plant survival as shown in Figure 4. The vegetation peak became higher and wider with decreasing discharge. In addition, the bimodality was scale dependent. It was sometimes more obvious in high resolution pictures and sometimes in low resolution pictures, depending on the size of vegetation patches.

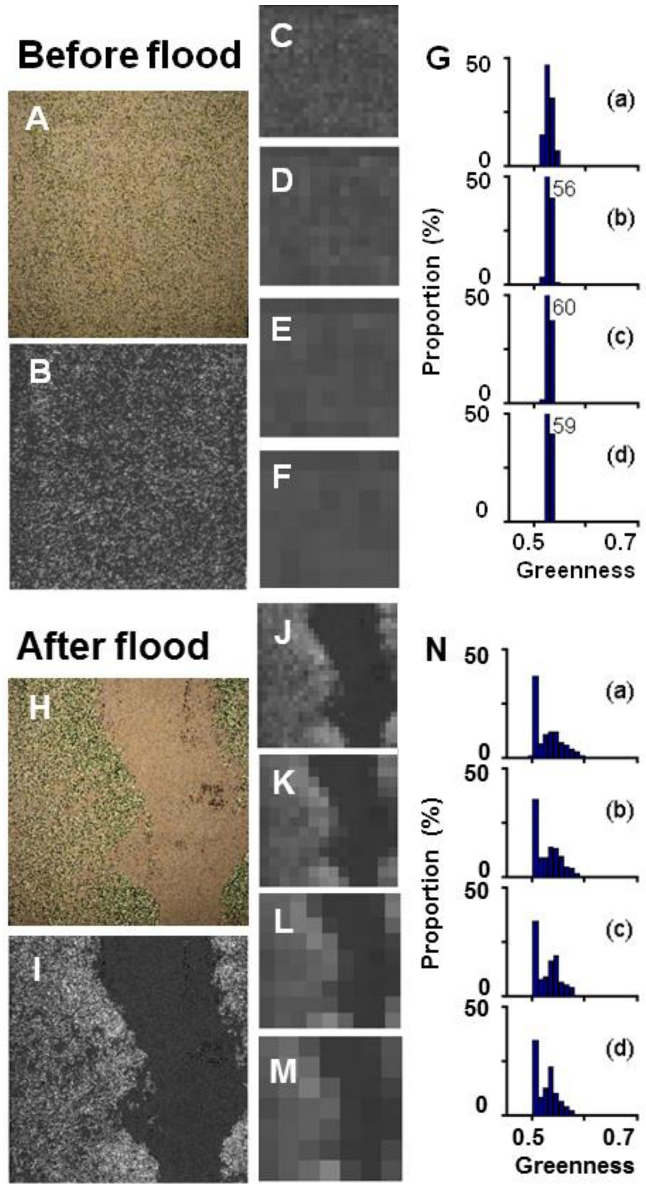



Figure 5. Example of analyses of Greenness values on photos for the experiment with mean root length of 12 mm before (A-G) and after flooding (H-N) with discharge of 0.17 l/s. Original photograph with resolution of 0.2 mm (A, H); Greenness image with same original resolution (see Eq. 1) (B, I); Rescaled Greenness image with resolution of 2 cm (C, J), 4 cm (D, K), 6 cm (E, L) and 8 cm (F, M); and Frequency distribution of Greenness values (G, N) for the rescaled Greenness images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical

axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its numerical value is noted by text.

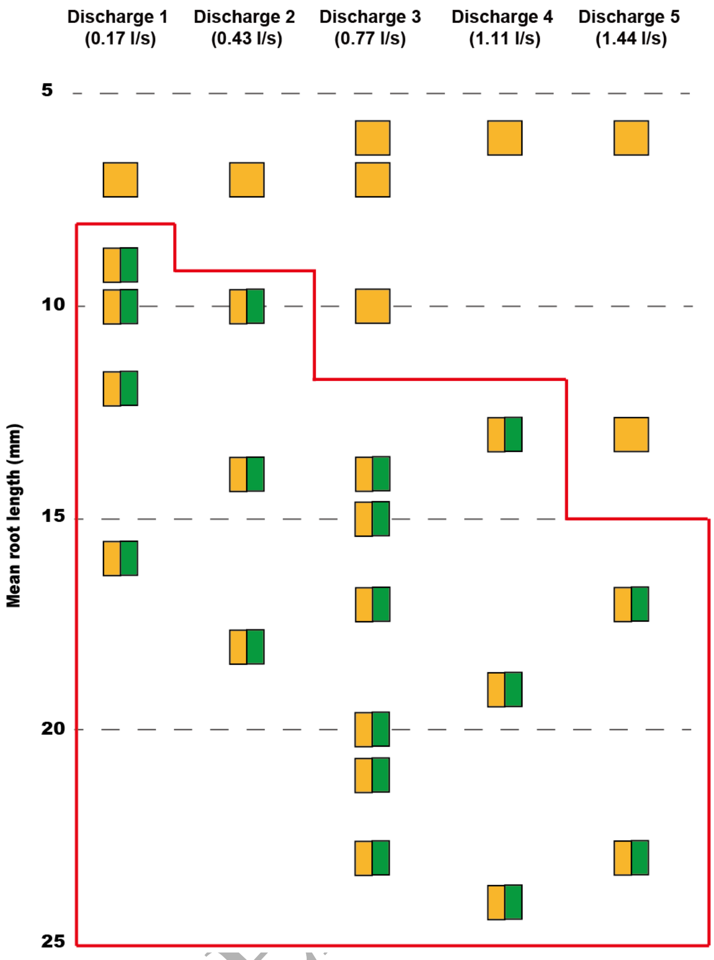



Figure 6. Summary of results of frequency distributions of greenness values for all single flood experiments. For discharge 3, the box at root length 7 mm represent the results for three replicate experiments, and the box at root length 10 mm represent the results for two replicate experiments. Before flooding, all distributions were unimodal for all experiments (i.e. uniformly vegetated state in the flume). Yellow boxes indicate unimodal frequency distribution of greenness after the flood event (i.e. all vegetation eroded and only one bare state remains in the

flume). Mixed yellow and green boxes indicate bimodal frequency distribution of greenness after the flood event (i.e. patches of bare and vegetated state remain in the flume). Red line indicates conditions for which the root length exceeded critical value for vegetation survival. Graphs with all frequency distributions for all experiments are attached in Appendix.

### 3.2. Pattern formation facilitates the establishment of vegetated state

#### *3.2.1. Temporal evolution of biomass development*

In the long-term evolution experiments, for which seeding and a 1 hour flooding with three different flood discharges was repeated every two days, vegetation coverage kept increasing in the first 33 days with 16 floods (Figure 7). Vegetation establishment started first in the low flood discharge regime and 2 floods later in the intermediate and high flood discharge regimes (Figure 7). The vegetation coverage dramatically increased first in the experiment with the highest discharge, and became twice the value of the other two experiments before the acceleration of vegetation establishment in the other two experiments. The vegetation coverage in the experiment with the lowest discharge increased sharply after the 10$^{th}$ flood, exceeded that of the other two discharge regimes after three floods, and at the end reached the highest vegetation coverage in all the three discharge regimes. The increase in vegetation coverage slowed down when decay started to be observed in the vegetated patches that formed the earliest. After that, larger and larger areas of old vegetated patches decayed due to fungal infestation (by *Fusarium sp*.), but new vegetated patches were still establishing on bare sand surface at the same time, which kept the total vegetation coverage increasing. These interpretations of alfalfa growth over time are based on only one time series, in each case. The apparent differences between curves in Figure 7 may be actually within the bounds of uncertainty/natural variation.

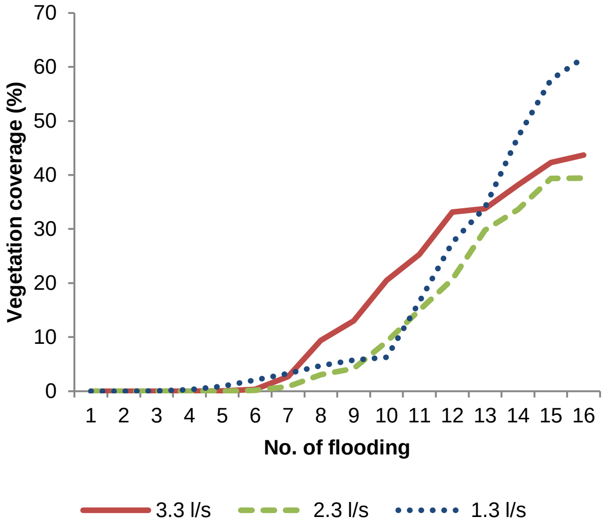



Figure 7. Temporal evolution of vegetation coverage developing under a flooding regime (with 1 hour flooding every two days) with three different flooding discharges.

In the experiments with high discharge (Q = 3.3 l/s and Q = 2.3 l/s), the high discharge caused the geomorphological development of channels and sand bars (Figure 8A and 8B). The vegetation could colonize the sand bars, while the vegetation could not establish in the channels. In the experiment with low discharge (Q = 1.3 l/s) the discharge was not high enough to develop obvious channels and sand bars, but only some small shallow water courses developed and the vegetation was able to colonize most of the flume area (Figure 8C).

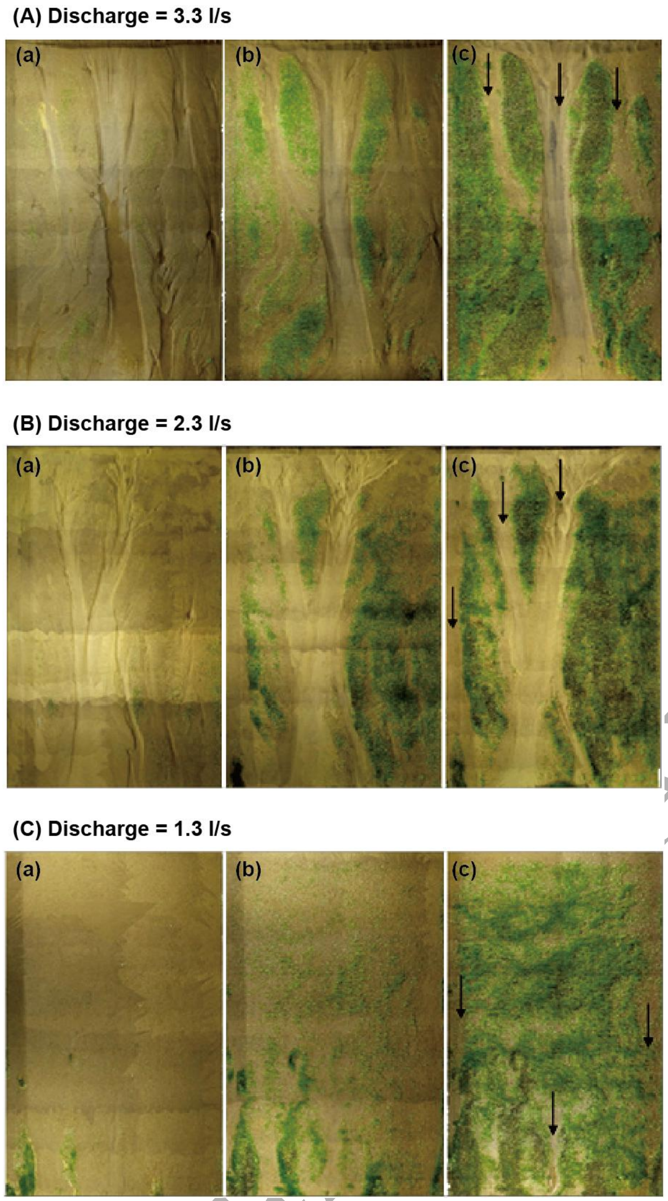



Figure 8. Development of vegetation, channels and sandbars in the experiment with 1 hour flooding every two days with a discharge of 3.3 l/s (A), 2.3 l/s (B), and 1.3 l/s (C) after the 6th flood (a) , 11th flood (b) and 16th flood (c) . Channel formation was indicated by black arrows.

### *3.2.2. Bimodal distribution of biomass at the end of the experiments*

The frequency distribution of Greenness values (Figure 9) was calculated for sample photographs after the 15th flood when the plants were not so much influenced yet by the fungi. Bimodal distribution was observed for the two highest discharges (Figures 9A and 9B), indicating that two stable states have developed, either densely vegetated platforms or bare channels. The right peak for vegetation was more clear for the resampled Greenness image with a rougher resolution (Panel (d) in Figures 9A and 9B) because the difference in Greenness of leaves, stems and roots were smoothed out. The left peak for bare state in the experiment with the highest discharge was compared to the intermediate discharge (Figures 9A and 9B), because the higher discharge promoted the development of channel and sandbar formation. This encouraged the development of alternative stable states and thus a more obvious bimodality in the Greenness values. For the lowest discharges, a unimodel distribution of the Greenness values developed, which is indicative for the development of only one stable state (Figure 9C), i.e. a vegetated platform without channels.

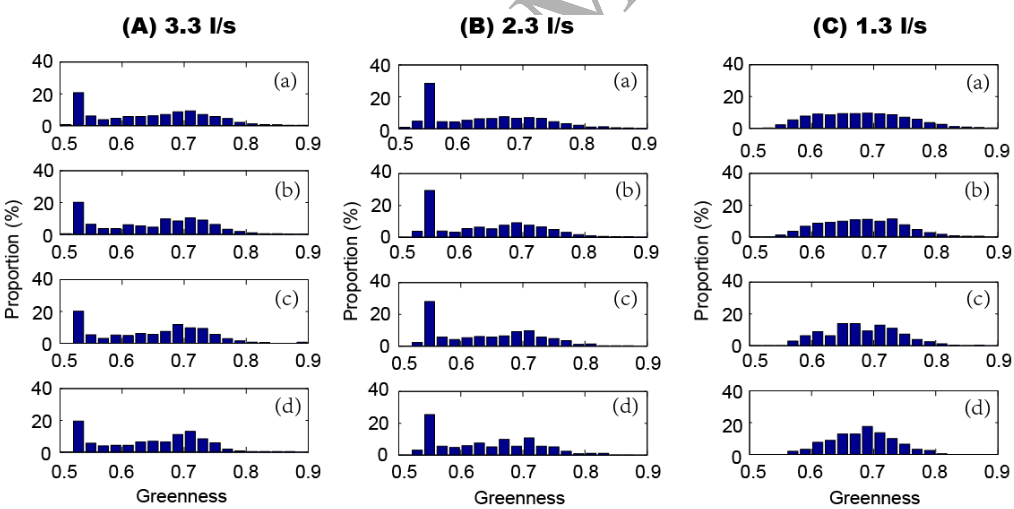



Figure 9. Frequency distribution of Greenness values for sample photographs after the 15$^{th}$ flood with discharge 3.3 l/s (A), 2.3 l/s (B), and 1.3 l/s (C). The spatial resolutions are 2 cm (a), 4 cm (b), 6 cm (c) and 8 cm (d), respectively.

### *3.2.3. Temporal evolution of landscape geomorphology*

In the experiments with the two high discharges, a braided system was already created after the first floods (Figures 10Aa and 10Ba). Channels changed dynamically by disconnection and reconnection after each flood. Bigger and deeper channels were observed in the experiment with the highest discharge (Figure 10Aa) as compared to the experiment with the intermediate discharge (Figure 10Ba). After vegetation started to establish, the channel system started to stabilize (Figures 10Ab and 10Bb). Small channels were gradually colonized by vegetation and became less important flow paths. The flow started to concentrate in a few bigger channels, which were deepening faster due to the increased flow velocity. In the experiment with the highest discharge regime, the biggest channel in the middle of the flume had developed a depth of 5 cm at the end of the experiment (Figure 10Ac). The intermediate discharge regime resulted in a shallower but wider channel system (Figure 10Bc), which also coincided with the lower vegetation coverage (Figure 7). On the vegetated bars, less sediments were eroded. The apparent increase in elevation on the bars mainly reflects the thickness of the vegetation canopy above the sand surface. On the contrary, the lowest discharge was strong enough to transport sands and seeds, but not enough to create big channels, so that the landscape kept nearly flat until the end of the experiment (Figure 10C), and vegetation was able to establish almost homogeneously (Figure 8C).

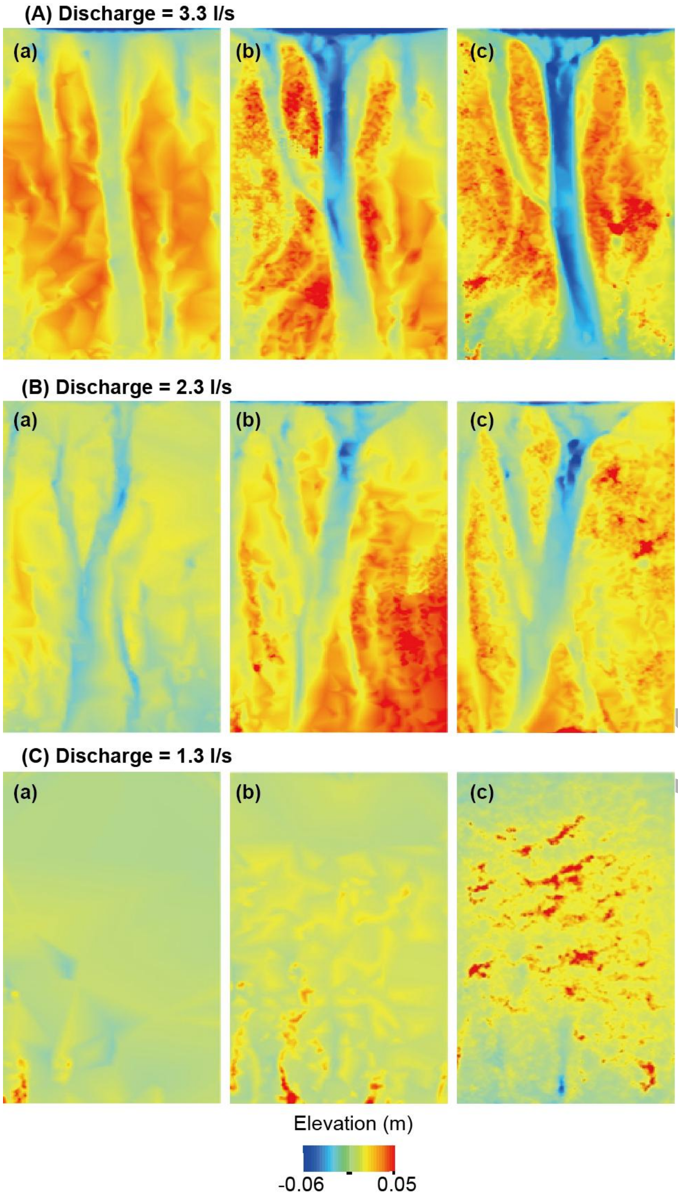



Figure 10. Evolution of geomorphology in the experiment with discharge of 3.3 l/s (A), 2.3 l/s (B) and 1.3 l/s (C) after the 6th flood (a), 11th flood (b) and 16th flood (c).

## 4. Discussion

Recent studies have provided increasing evidence that vegetated and bare states in disturbance-driven biogeomorphic ecosystems behave as alternative stable states (e.g., [1, 5-7, 9-11]).

However, little is known about the mechanism of vegetation establishment on bare substrate and the role of pattern formation in the formation of alternative stable states in biogeomorphic ecosystems. In this study, we tested the hypothesis that biogeomorphic feedbacks between plant growth and flooding lead to alternative stable state behavior in a disturbance-driven experimental floodplain. We found that: (1) A combination of biological threshold in plant growth (minimum root length) and disturbance threshold in flooding strength (maximum discharge) limit the survival of seedlings to flooding disturbances; in addition, these two kinds of thresholds are positively related with each other (Figures 3 and 4). (2) A bimodal distribution in biomass, corresponding to either a vegetated state or a bare state, develops after the flooding disturbance from the initially unimodally distributed biomass (Figures 5, 6 and Appendix). (3) In the long term, spatial pattern formation of channels and sand bars promotes the development of bare and vegetated states co-existing next to each other (Figures 7–10).

Plants have to grow above certain thresholds in size (Figures 3 and 4), biomass, and density to survive the disturbance before the positive biogeomorphic feedback between soil surface stabilization and plant growth starts to work; and the stronger the disturbance, the higher these thresholds [6, 7, 51]. Three thresholds in root growth have been suggested for mangrove seedlings in order to resist three sources of disturbance with increasing magnitude during seedling establishment, which are first floating up of seedlings by flooding, then hydrodynamic forces by waves and currents, and finally sediment bed dynamics such as mixing and erosion [6]. The threshold root length of mangrove seedlings to resist dislodgment increased with the experimentally applied bed shear stress, vertical erosion, and drag force [6].

Flow thresholds to remove seedlings after the dispersal of plant seeds have been suggested as a key question for better understanding the relationship between plant establishment and flow variation in riparian ecosystems [70]. The thresholds in bed shear stress, vertical erosion, and drag force were observed to increase with the root length of mangrove seedlings [6]. First-year seedling establishment of riparian pioneer shrubs and trees was reported by field observations and model simulation to be negatively correlated with monthly flow magnitude during the growing season, and the strongest negative correlation was found within 1–3 months after the dispersal depending on species [70-75]. The drastic influence of discharge on vegetation survival (Figure 3) suggests that the increase in flow discharge could cause a shift from vegetated state to bare state, which is in accordance with the field observations in desert streams [11].

Our finding that vegetation biomass changes from unimodal distribution to bimodal distribution in response to flood disturbance (Figures 5, 6, 9 and Appendix) provides an evidence for the occurrence of alternative attractors in the system [26]. This process agrees well with the field observation in desert streams, where the distribution of vegetation cover was approximately normal before the monsoon season but diverged towards an increasingly bimodal distribution after a series of floods [11]. Similar bimodality indicating vegetated state and bare state has also been found in tidal marshes based on frequency distribution of vegetation biomass [41, 76] and intertidal elevation [1, 5, 77]. In addition, the bimodal distribution in our experiments only occurs when the flow discharge is below a threshold value (Figure 4), which is in accordance with the observation in the desert streams that the bimodal divergence did not appear in years with large flood events [11].

As shown in the long-term evolution experiments, the spatial pattern formation of channels and sand bars allows the vegetation colonization on the sand bars. The flooding of every 2 days is too frequent for seedling to survive as suggested by the single flood experiments with limited development of spatial pattern formation, but the vegetation still succeeds in colonizing large areas during the long-term evolution experiment as a result of the full-scale development of spatial pattern formation. In the experiments with high discharges (Q = 3.3 l/s and Q = 2.3 l/s), the water flow is redistributed within the landscape after the formation of channels and bars by the first few floods (Figures 8A–8B and 10A-10B). Discharge is concentrated towards channels with higher flow velocity, and reduced on sand bars, leading to locally lower flow velocity and less erosion, hence making the bars suitable for seedling establishment. Once seedlings start to establish on the bar, the local positive biogeomorphic feedback starts to work by reducing the local flow velocity and in return promoting further seedling establishment into vegetated patches. At the same time, water is forced to concentrate towards the channels, resulting in increased shear stress deepening the channel and preventing the vegetation establishment. The process can be explained by the theory of spatial self-organization [28, 56], an important mechanism causing alternative attractors in the landscape, which can coexist side-by-side as mosaics of patches of one stable state benefitting from the neighboring area in the alternative state [26]. Similar pattern formation has been observed in tidal marshes [32, 41, 57, 58] and island-river systems [78, 79]. Our long term evolution experiments suggests that systems with strong disturbance are more likely to exhibit alternative stable states as proposed by Didham, Watts [80]. However, our single flood experiments suggest the existence of an upper limit in the magnitude of disturbance causing alternative stable states, as empirically observed in desert streams [11]. External abiotic factors have been traditionally emphasized in disturbance-driven ecosystem, but internal biotic feedbacks also play an important role in creating alternative stable states [10]. In general, our results support the hypothesis that the occurrence of alternative stable states is determined by the relative strength of internal biogeomorphic feedbacks and external physical disturbances, rather than the absolute magnitude of either of them [11]. The time scales of flood events versus time scales of vegetation growth are determinant whether vegetation can establish or not, because vegetation needs a certain disturbance-free period to grow up above a critical biomass threshold (often a critical rooting depth) in order to survive the next flood [6, 7, 53].

Biogeomorphic ecosystems in general are likely to exhibit alternative stable states because of the nonlinear interactions between geomorphic thresholds and ecosystem engineers in response to external disturbance [35]. The alternative stable states described above are strictly local with meta-stable pattern formation rather than system-wide global bi-stability [56]. Our long-term experiments show clear evidence for the development of two different ecogeomorphological states, but they were not run long enough to show conclusive evidence that these states are stable in the long term. This type of laboratory experiments is a powerful way to test the existence of alternative stable states and to understand the underlying mechanisms. It provides a controlled environment in which the process of vegetation establishment on a bare substrate could be simulated and replicated. It is possible to analyze the processes over timescales which would preclude analyses of the same processes through field observations, and to change the external forcing so as to quantitatively analyze the impact of the disturbance in such disturbance-driven dynamic system. There are several limitations in our experiments, such as lack of sediment input, synthetic versus actual flooding discharges, use of non-cohesive sediments, limited replicates, etc. Considering the advantages and limitations, this type of experiments could provide valuable investigations and new insights on the crucial role of feedbacks among flow, erosion and vegetation growth promoting the development of alternative stable states in erosive systems, serving as effective verification and supplement to the results of existing theoretical and empirical work.

## 5. Conclusion

In this paper, we tested for empirical indications of the existence of local alternative stable states controlled by biogeomorphic feedbacks in a disturbance-driven ecosystem by flume experiments with feedbacks between flooding, sediment bed dynamics and establishment of alfalfa vegetation. Our results demonstrate the co-occurrence of a biological threshold in plant growth (root length) and disturbance threshold in flooding discharge, which are positively related with each other. It suggests that vegetation persistence depends on both erosive energy and vegetation size and abundance. The biogeomorphic feedbacks cause divergence of vegetation cover toward either unvegetated or densely vegetated states, which behaves as alternative attractors in the system as shown by the bimodality in the spatial vegetation distribution after flooding. The spatial pattern formation of channels and sand bars in long term facilitates the persistence of both stable states on the landscape, consistent with theoretical and empirical studies of pattern formation in other ecosystems. These insights on local alternative stable state behavior address an important gap in the current understanding of self-organization of biogeomorphic systems. It may contribute to the protection and restoration of vegetation on bare dynamic substrate in disturbance-driven biogeomorphic ecosystems, and provide basic knowledge for using riparian flood plain vegetation, tidal marsh and mangrove vegetation against river bank erosion, shoreline erosion, dune erosion and coastal flooding.

**Acknowledgements**

This work has been supported by the European Union Programme Erasmus Mundus External Cooperation Window (EMECW) - Lot 14 – China, the FWO for the Scientific Research Network

(WOG) “The functioning of river ecosystems through plant-flow-soil interactions”, the National Natural Science Funds of China (41401413 and 41376120) and National Key Science and Technology Special Project of China (2014ZX07508). We thank Stefaan Bliki, Davy Haerens, Jan Quets, Gerlinde Beyens, Joost Eens, Pieter Claeys, Pieter Corthier, and Diederik De Bruyn for help with the experiments and data analyses. We also wish to thank Andrea D'Alpaos, Kevan Moffett, Andrea Rinaldo and the anonymous reviewer for the careful reviews and constructive comments.

**Appendix**

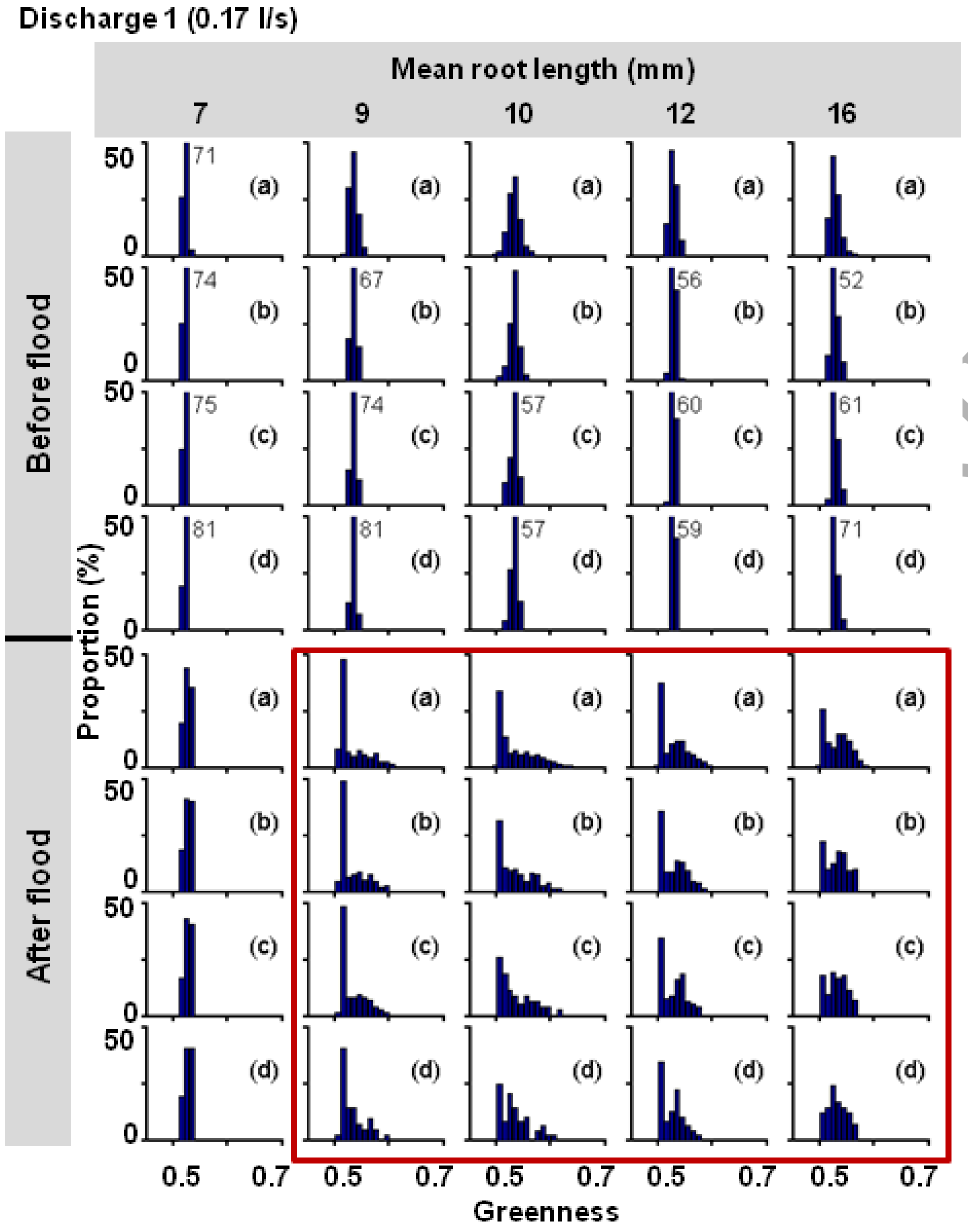



Figure A1. Frequency distribution of Greenness values as a function of mean root length before and after flooding with discharge 1 (0.17 l/s). For each experiment, results are shown for Greenness values calculated from images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its

numerical value is noted by text. The red rectangule demarcates distributions after flooding for experiments for which the root length exceeded the threshold value for plant survival (derived from Figures 3 and 4).

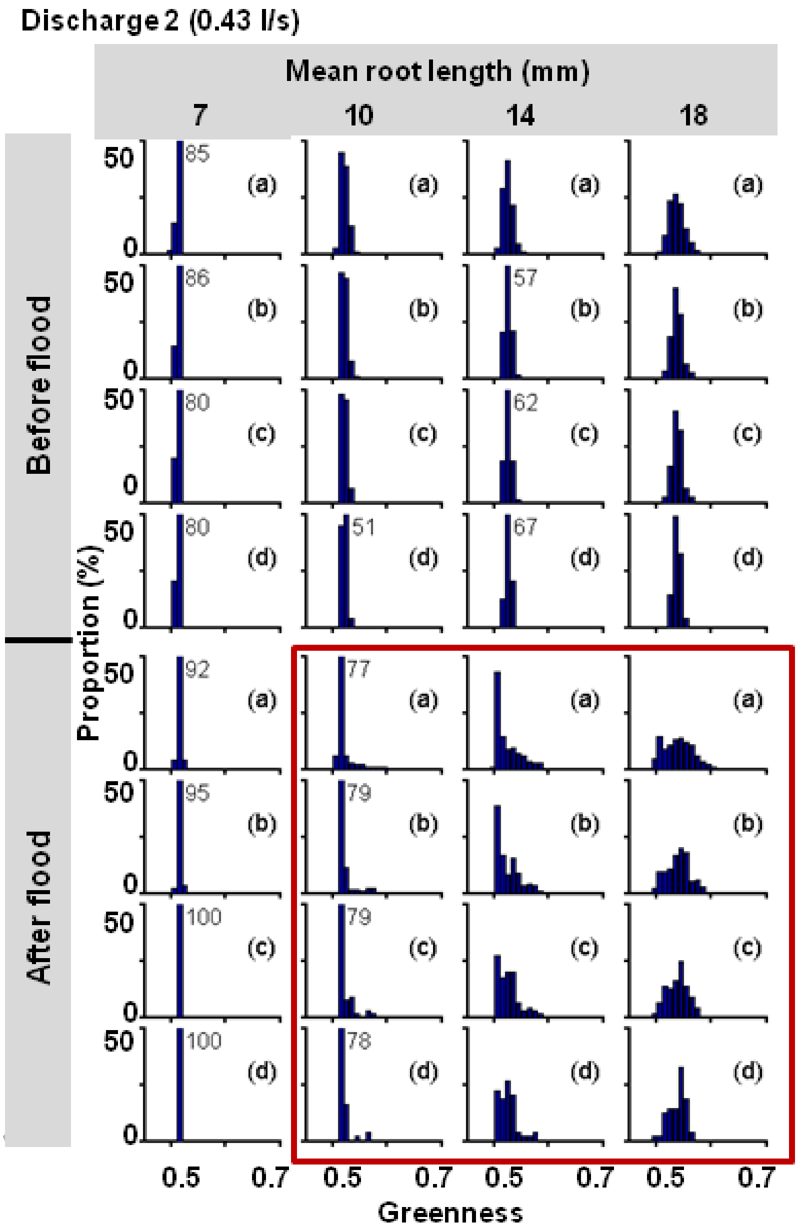
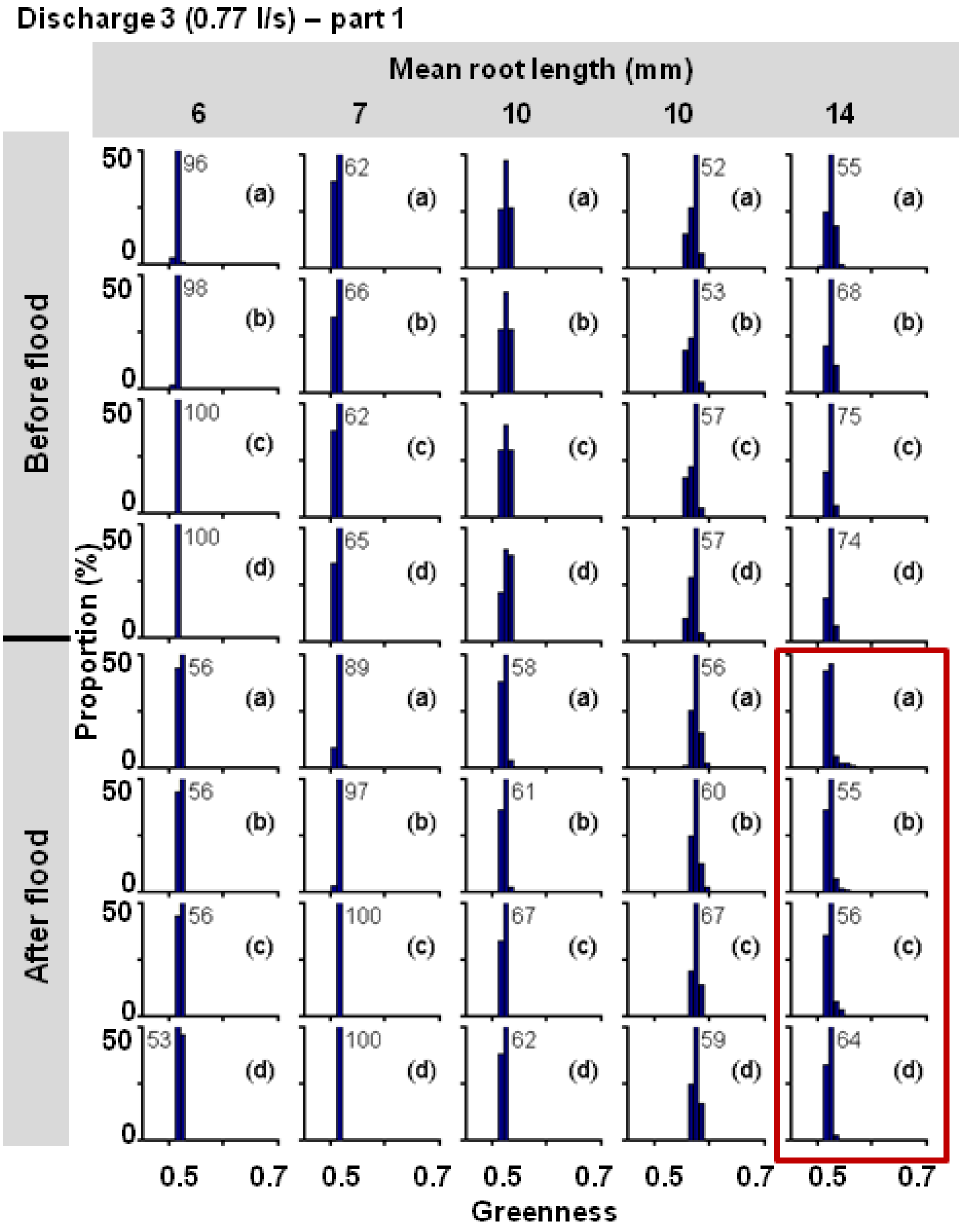



Figure A2. Frequency distribution of Greenness values as a function of mean root length before and after flooding with discharge 2 (0.43 l/s). For each experiment, results are shown for

Greenness values calculated from images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its numerical value is noted by text. The red rectangule demarcates distributions after flooding for experiments for which the root length exceeded the threshold value for plant survival (derived from Figures 3 and 4).


Discharge 3 (0.77 l/s) – part 1
Mean root length (mm)
6
7
10
10
14
Before flood
After flood
Proportion (%)
50
0
96
62
52
55
98
66
53
68
100
62
57
75
100
65
57
74
56
89
58
56
56
97
61
60
55
56
100
67
67
56
53
100
62
59
64
(a)
(b)
(c)
(d)
0.5
0.7
Greenness

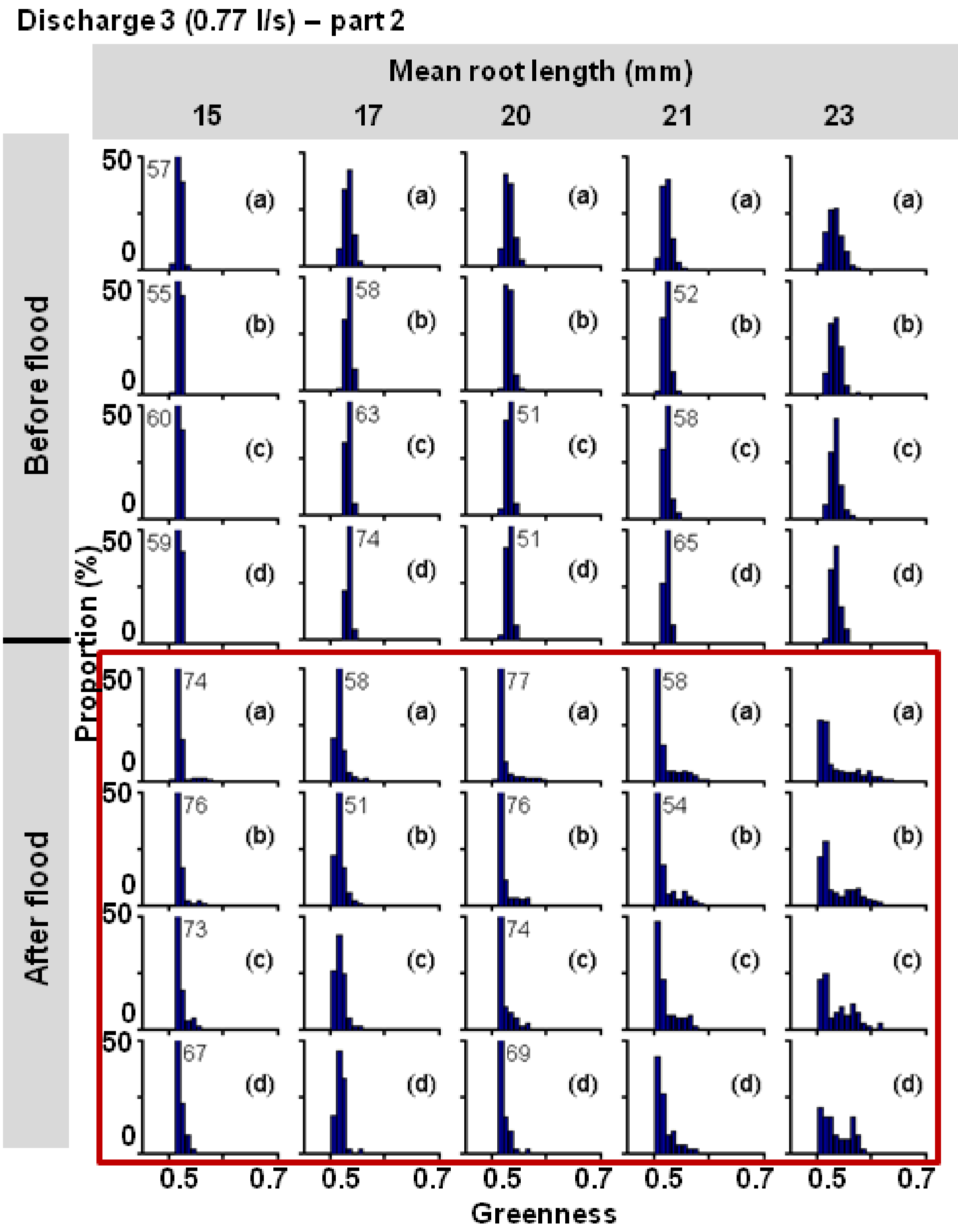



Figure A3. Frequency distribution of Greenness values as a function of mean root length before and after flooding with discharge 3 (0.77 l/s). For each experiment, results are shown for Greenness values calculated from images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its

numerical value is noted by text. There are three replicate experiments with root length of 7 mm with similar graphs, while only one example is shown here to save space. The red rectangule demarcates distributions after flooding for experiments for which the root length exceeded the threshold value for plant survival (derived from Figures 3 and 4).

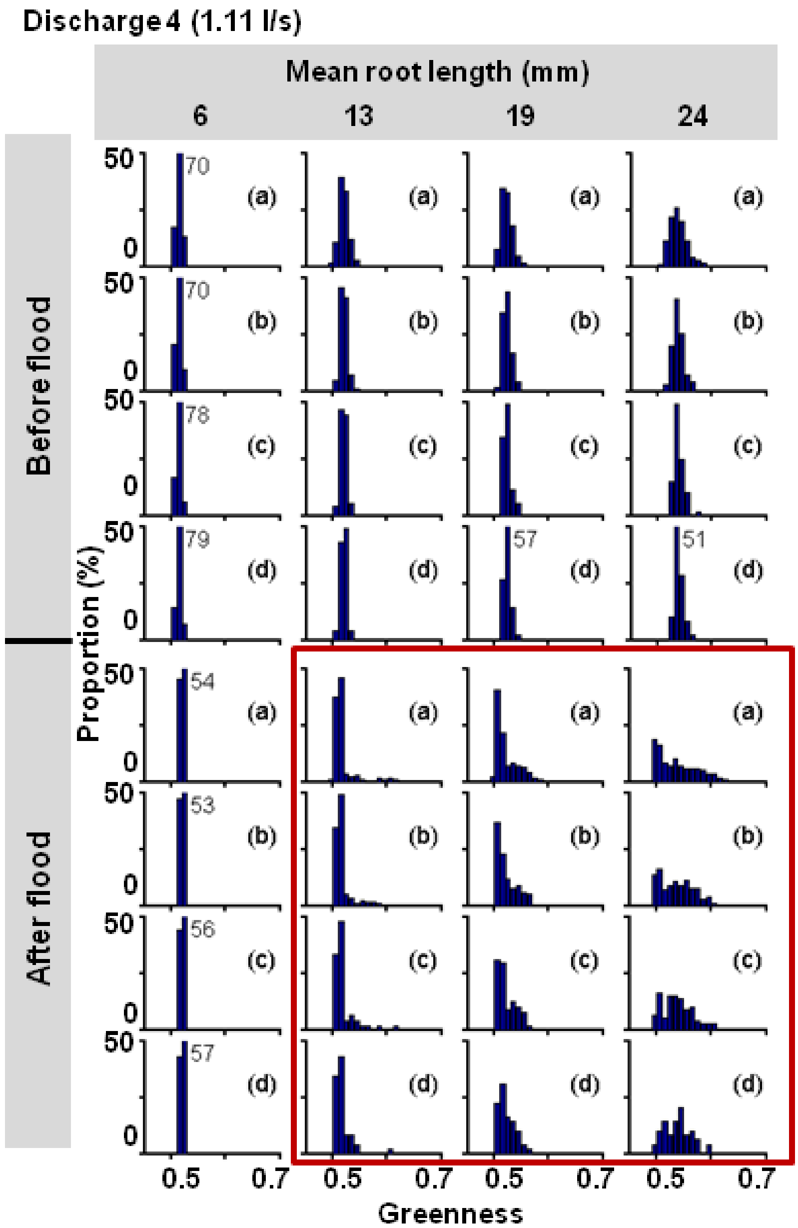


Figure A4. Frequency distribution of Greenness values as a function of mean root length before and after flooding with discharge 4 (1.11 l/s). For each experiment, results are shown for Greenness values calculated from images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its numerical value is noted by text. The red rectangule demarcates distributions after flooding for experiments for which the root length exceeded the threshold value for plant survival (derived from Figures 3 and 4).

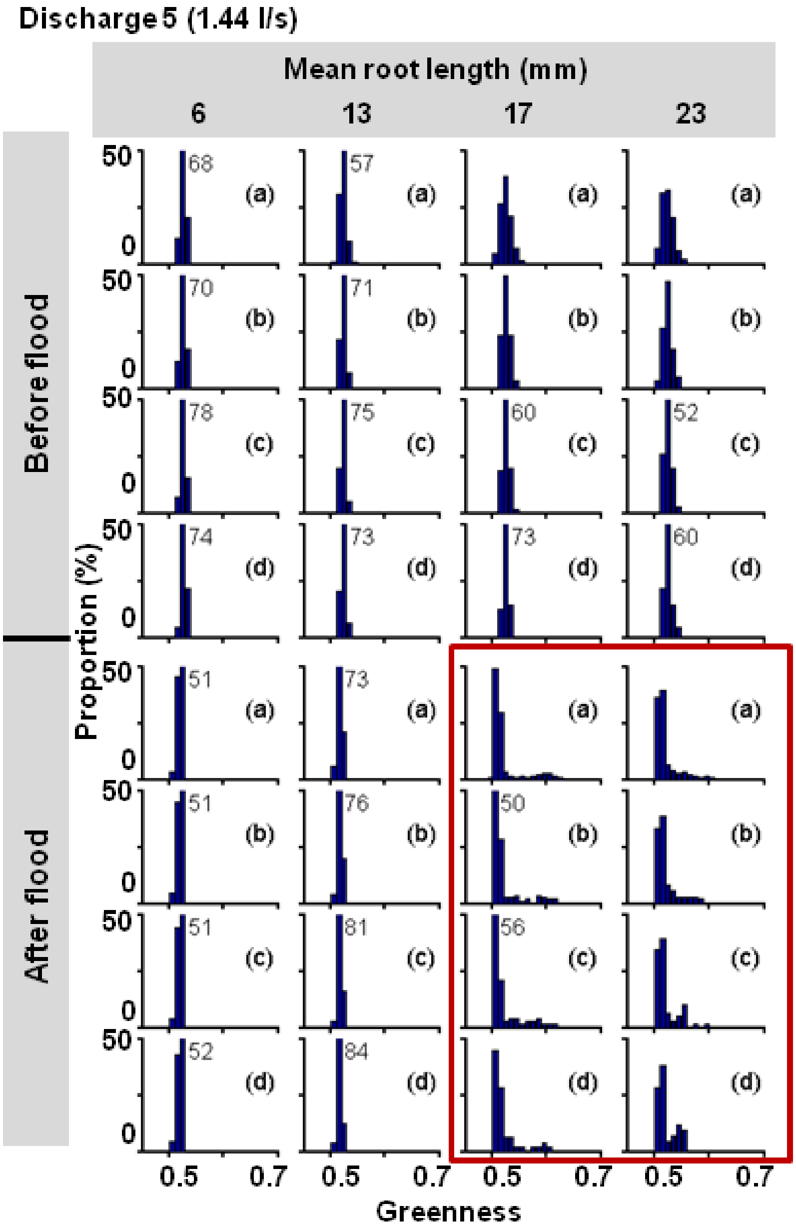



Figure A5. Frequency distribution of Greenness values as a function of mean root length before and after flooding with discharge 5 (1.44 l/s). For each experiment, results are shown for Greenness values calculated from images with a resolution of 2 cm (a), 4 cm (b), 6 cm (c), and 8 cm (d). The vertical axis is limited to 50%, so as to get a clearer presentation of the frequency distribution. If a bar is higher than 50%, then graphically it is depicted as 50% but next to it its

numerical value is noted by text. The red rectangule demarcates distributions after flooding for experiments for which the root length exceeded the threshold value for plant survival (derived from Figures 3 and 4).

**Reference**

[1] Fagherazzi S, L Carniello, L D'Alpaos, A Defina. Critical bifurcation of shallow microtidal landforms in tidal flats and salt marshes. Proc Nat Acad Sci USA. 103 (2006) 8337-41, doi: 10.1073/pnas.0508379103.

[2] Marani M, A D'Alpaos, S Lanzoni, L Carniello, A Rinaldo. Biologically-controlled multiple equilibria of tidal landforms and the fate of the Venice lagoon. Geophys Res Lett. 34 (2007) L11402, doi: 10.1029/2007gl030178.

[3] Marani M, A D'Alpaos, S Lanzoni, L Carniello, A Rinaldo. The importance of being coupled: stable states and catastropic shifts in tidal biomorphodynamics. J Geophys Res. 115 (2010) F04004, doi: 10.1029/2009JF001600.

[4] Kirwan ML, AB Murray. A coupled geomorphic and ecological model of tidal marsh evolution. Proc Nat Acad Sci USA. 104 (2007) 6118-22, doi: 10.1073/pnas.0700958104.

[5] Wang C, S Temmerman. Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. J Geophys Res Earth Surf. 118 (2013) 229-40, doi: 10.1029/2012jf002474.

[6] Balke T, TJ Bouma, EM Horstman, EL Webb, PLA Erftemeijer, PMJ Herman. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. Mar Ecol Prog Ser. 440 (2011) 1-9, doi: 10.3354/Meps09364.

[7] Balke T, PMJ Herman, TJ Bouma, C Nilsson. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J Ecol. 102 (2014) 700-8, doi: 10.1111/1365-2745.12241.

[8] Adema EB, AP Grootjans, J Petersen, J Grijpstra. Alternative stable states in a wet calcareous dune slack in The Netherlands. Journal of Vegetation Science. 13 (2002) 107-14, doi: 10.1111/j.1654-1103.2002.tb02027.x.

[9] Adema E, A Grootjans. Possible positive-feedback mechanisms: plants change abiotic soil parameters in wet calcareous dune slacks. Plant Ecol. 167 (2003) 141-9, doi: 10.1023/A:1023947411605.

[10] Dent CL, GS Cumming, SR Carpenter. Multiple states in river and lake ecosystems. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences. 357 (2002) 635-45, doi: 10.1098/rstb.2001.0991.

[11] Heffernan JB. Wetlands as an alternative stable state in desert streams. Ecology. 89 (2008) 1261-71.

[12] Heffernan JB, RA Sponseller, SG Fisher. Consequences of a biogeomorphic regime shift for the hyporheic zone of a Sonoran Desert stream. Freshwat Biol. 53 (2008) 1954-68, doi: DOI 10.1111/j.1365-2427.2008.02019.x.

[13] Siteur K, MB Eppinga, D Karssenberg, M Baudena, MFP Bierkens, M Rietkerk. How will increases in rainfall intensity affect semiarid ecosystems? Water Resour Res. 50 (2014) 5980–6001, doi: 10.1002/2013WR014955.

[14] Temmerman S, P Meire, TJ Bouma, PM Herman, T Ysebaert, HJ De Vriend. Ecosystem-based coastal defence in the face of global change. Nature. 504 (2013) 79-83, doi: 10.1038/nature12859.

[15] Temmerman S, MB De Vries, TJ Bouma. Coastal marsh die-off and reduced attenuation of coastal floods: A model analysis. Global Planet Change. 92-93 (2012) 267-74, doi: 10.1016/j.gloplacha.2012.06.001.

[16] Gedan KB, ML Kirwan, E Wolanski, EB Barbier, BR Silliman. The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. Clim Change. 106 (2011) 7-29, doi: 10.1007/s10584-010-0003-7.

[17] Barbier EB, SD Hacker, C Kennedy, EW Koch, AC Stier, BR Silliman. The value of estuarine and coastal ecosystem services. Ecol Monogr. 81 (2011) 169-93, doi: 10.1890/10-1510.1.

[18] Sweeney BW, TL Bott, JK Jackson, LA Kaplan, JD Newbold, LJ Standley, et al. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proc Nat Acad Sci USA. 101 (2004) 14132-7, doi: 10.1073/pnas.0405895101.

[19] Brauman KA, GC Daily, TK Duarte, HA Mooney. The nature and value of ecosystem services: An overview highlighting hydrologic services. Annual Review of Environment and Resources. 32 (2007) 67-98, doi: DOI 10.1146/annurev.energy.32.031306.102758.

[20] Feld CK, S Birk, DC Bradley, D Hering, J Kail, A Marzin, et al. From natural to degraded rivers and back again: a test of restoration ecology theory and practice. Adv Ecol Res. 44 (2011) 119-209.

[21] Løvås SM, A Tørum. Effect of the kelp Laminaria hyperborea upon sand dune erosion and water particle velocities. Coastal Engineering. 44 (2001) 37-63.

[22] Kobayashi N, C Gralher, K Do. Effects of woody plants on dune erosion and overwash. Journal of Waterway, Port, Coastal, and Ocean Engineering. 139 (2013) 466-72.

[23] Durán O, LJ Moore. Vegetation controls on the maximum size of coastal dunes. Proceedings of the National Academy of Sciences. 110 (2013) 17217-22, doi: 10.1073/pnas.1307580110.

[24] May RM. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature. 269 (1977) 471-7.

[25] Scheffer M, S Carpenter, JA Foley, C Folke, B Walker. Catastrophic shifts in ecosystems. Nature. 413 (2001) 591-6, doi: 10.1038/35098000.

[26] Scheffer M, SR Carpenter. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol. 18 (2003) 648-56, doi: 10.1016/j.tree.2003.09.002.

[27] Scheffer M. Alternative stable states and regime shifts in ecosystems. in: SA Levin, (Ed.). The Princeton guide to ecology. Princeton University Press, Princeton, 2009. pp. 395-406.

[28] Rietkerk M, SC Dekker, PC de Ruiter, J Van de Koppel. Self-organized patchiness and catastrophic shifts in ecosystems. Science. 305 (2004) 1926-9, doi: 10.1126/science.1101867.

[29] Hirota M, M Holmgren, EH Van Nes, M Scheffer. Global resilience of tropical forest and savanna to critical transitions. Science. 334 (2011) 232-5, doi: 10.1126/science.1210657.

[30] Staver AC, S Archibald, SA Levin. The global extent and determinants of savanna and forest as alternative biome states. Science. 334 (2011) 230-2, doi: 10.1126/science.1210465.

[31] Van De Koppel J, PMJ Herman, P Thoolen, CHR Heip. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology. 82 (2001) 3449-61, doi: 10.1890/0012-9658(2001)082[3449:DASSOI]2.0.CO;2.

[32] Bouma TJ, LA van Duren, S Temmerman, T Claverie, A Blanco-Garcia, T Ysebaert, et al. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field,

flume and modelling experiments. Cont Shelf Res. 27 (2007) 1020-45, doi: 10.1016/j.csr.2005.12.019.

[33] Mudd SM, A D'Alpaos, JT Morris. How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation. J Geophys Res Earth Surf. 115 (2010) F03029, doi: 10.1029/2009JF001566.

[34] Naylor LA, HA Viles, NEA Carter. Biogeomorphology revisited: looking towards the future. Geomorphology. 47 (2002) 3-14.

[35] Stallins JA. Geomorphology and ecology: Unifying themes for complex systems in biogeomorphology. Geomorphology. 77 (2006) 207-16, doi: DOI 10.1016/j.geomorph.2006.01.005.

[36] Bruno JF. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. Ecology. 81 (2000) 1179-92, doi: 10.1890/0012-9658(2000)081[1179:Focbpc]2.0.Co;2.

[37] Corenblit D, ACW Baas, G Bornette, J Darrozes, S Delmotte, RA Francis, et al. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. Earth-Sci Rev. 106 (2011) 307-31, doi: 10.1016/j.earscirev.2011.03.002.

[38] Murray AB, MAF Knaapen, M Tal, ML Kirwan. Biomorphodynamics: Physical-biological feedbacks that shape landscapes. Water Resour Res. 44 (2008) W11301, doi: 10.1029/2007wr006410.

[39] Reinhardt L, D Jerolmack, BJ Cardinale, V Vanacker, J Wright. Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology. Earth Surf Proc Land. 35 (2010) 78-101, doi: 10.1002/Esp.1912.

[40] Bull WB. Discontinuous ephemeral streams. Geomorphology. 19 (1997) 227-76, doi: http://dx.doi.org/10.1016/S0169-555X(97)00016-0.

[41] Van Wesenbeeck BK, J Van de Koppel, PMJ Herman, TJ Bouma. Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems? Oikos. 117 (2008) 152-9, doi: 10.1111/j.2007.0030-1299.16245.x.

[42] Schröder A, L Persson, AM De Roos. Direct experimental evidence for alternative stable states: a review. Oikos. 110 (2005) 3-19, doi: 10.1111/j.0030-1299.2005.13962.x.

[43] Drake JM, BD Griffen. Early warning signals of extinction in deteriorating environments. Nature. 467 (2010) 456-9, doi: Doi 10.1038/Nature09389.

[44] Carpenter SR, JJ Cole, ML Pace, R Batt, WA Brock, T Cline, et al. Early warnings of regime shifts: a whole-ecosystem experiment. Science. 332 (2011) 1079-82, doi: DOI 10.1126/science.1203672.

[45] Lewis R, PA Erftemeijer, A Hodgson. A novel approach to growing mangroves on the coastal mud flats of Eritrea with the potential for relieving regional poverty and hunger: comment. Wetlands. 26 (2006) 637-8, doi: 10.1672/0277-5212(2006)26[637:CANATG]2.0.CO;2.

[46] Primavera JH, JMA Esteban. A review of mangrove rehabilitation in the Philippines: successes, failures and future prospects. Wetlands Ecol Manage. 16 (2008) 345-58, doi: 10.1007/s11273-008-9101-y.

[47] Wolters M, JP Bakker, MD Bertness, RL Jefferies, I MÖLler. Saltmarsh erosion and restoration in south-east England: squeezing the evidence requires realignment. J Appl Ecol. 42 (2005) 844-51, doi: 10.1111/j.1365-2664.2005.01080.x.

[48] Grootjans AP, HWT Geelen, AJM Jansen, EJ Lammerts. Restoration of coastal dune slacks in the Netherlands. in: PH Nienhuis, RD Gulati, (Eds.). Ecological Restoration of Aquatic and Semi-Aquatic Ecosystems in the Netherlands (NW Europe). Springer Netherlands2002. pp. 181-203.

[49] Kondolf GM, E Micheli. Evaluating stream restoration projects. Environ Manage. 19 (1995) 1-15, doi: 10.1007/BF02471999.

[50] Shafroth PB, VB Beauchamp, MK Briggs, K Lair, ML Scott, AA Sher. Planning Riparian Restoration in the Context of Tamarix Control in Western North America. Restor Ecol. 16 (2008) 97-112, doi: 10.1111/j.1526-100X.2008.00360.x.

[51] Bouma TJ, M Friedrichs, BK Van Wesenbeeck, S Temmerman, G Graf, PMJ Herman. Density-dependent linkages of scale-dependent feedbacks: a flume study on the intertidal macrophyte *Spartina anglica*. Oikos. 118 (2009) 260-8.

[52] Van Wesenbeeck BK, J van de Koppel, PM Herman, MD Bertness, D van der Wal, JP Bakker, et al. Potential for sudden shifts in transient systems: distinguishing between local and landscape-scale processes. Ecosystems. 11 (2008) 1133-41, doi: 10.1007/s10021-008-9184-6.

[53] Perona P, P Molnar, B Crouzy, E Perucca, Z Jiang, S McLelland, et al. Biomass selection by floods and related timescales: Part 1. Experimental observations. Advances in Water Resources. 39 (2012) 85-96, doi: http://dx.doi.org/10.1016/j.advwatres.2011.09.016.

[54] Di Nitto D, F Dahdouh-Guebas, JG Kairo, H Decleir, N Koedam. Digital terrain modelling to investigate the effects of sea level rise on mangrove propagule establishment. Mar Ecol Prog Ser. 356 (2008) 175-88.

[55] Mahoney, JM Rood, S.B. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands. 18 (1998) 634–45.

[56] Rietkerk M, J van de Koppel. Regular pattern formation in real ecosystems. Trends Ecol Evol. 23 (2008) 169-75, doi: 10.1016/j.tree.2007.10.013.

[57] Temmerman S, TJ Bouma, J Van de Koppel, DD Van der Wal, MB De Vries, PMJ Herman. Vegetation causes channel erosion in a tidal landscape. Geology. 35 (2007) 631-4, doi: 10.1130/G23502a.1.

[58] Vandenbruwaene W, S Temmerman, TJ Bouma, PC Klaassen, MB De Vries, DP Callaghan, et al. Flow interaction with dynamic vegetation patches: implications for bio-geomorphic evolution of a tidal landscape. J Geophys Res. 116 (2011) F01008, doi: 10.1029/2010JF001788.

[59] Meire DW, JM Kondziolka, HM Nepf. Interaction between neighboring vegetation patches: Impact on flow and deposition. Water Resour Res. 50 (2014) 3809-25.

[60] Tal M, C Paola. Dynamic single-thread channels maintained by the interaction of flow and vegetation. Geology. 35 (2007) 347-50.

[61] Gran K, C Paola. Riparian vegetation controls on braided stream dynamics. Water Resour Res. 37 (2001) 3275-83.

[62] Tal M, C Paola. Effects of vegetation on channel morphodynamics: results and insights from laboratory experiments. Earth Surf Proc Land. 35 (2010) 1014-28.

[63] Comino E, P Marengo, V Rolli. Root reinforcement effect of different grass species: A comparison between experimental and models results. Soil and Tillage Research. 110 (2010) 60-8.

[64] Pollen-Bankhead, Na Simon, A. Hydrologic and hydraulic effects of riparian root networks on streambank stability: Is mechanical root-reinforcement the whole story? Geomorphology. 116 (2009) 353-62.

[65] Van de Lageweg WI, WM Van Dijk, R Hoendervoogt, MG Kleinhans. Effects of riparian vegetation on experimental channel dynamics. Proc River Flow2010.

[66] Gitelson AA, YJ Kaufman, R Stark, D Rundquist. Novel algorithms for remote estimation of vegetation fraction. Remote Sens Environ. 80 (2002) 76-87, doi: http://dx.doi.org/10.1016/S0034-4257(01)00289-9.

[67] Lu D. The potential and challenge of remote sensing - based biomass estimation. Int J Remote Sens. 27 (2006) 1297-328.

[68] AgiSoft. Agisoft PhotoScan User Manual: Professional Edition, Version 0.9.0. Moscow, 2012.

[69] Verhoeven G. Taking computer vision aloft – archaeological three-dimensional reconstructions from aerial photographs with photoscan. Archaeological Prospection. 18 (2011) 67-73, doi: 10.1002/arp.399.

[70] Dixon MD, MG Turner. Simulated recruitment of riparian trees and shrubs under natural and regulated flow regimes on the Wisconsin River, USA. River Res Appl. 22 (2006) 1057-83, doi: Doi 10.1002/Rra.948.

[71] Dixon MD, MG Turner, CF Jin. Riparian tree seedling distribution on Wisconsin River sandbars: Controls at different spatial scales. Ecol Monogr. 72 (2002) 465-85, doi: Doi 10.2307/3100052.

[72] Dixon M. Effects of flow pattern on riparian seedling recruitment on sandbars in the Wisconsin River, Wisconsin, USA. Wetlands. 23 (2003) 125-39, doi: 10.1672/0277-5212(2003)023[0125:EOFPOR]2.0.CO;2.

[73] Johnson WC. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrological Processes. 14 (2000) 3051-74.



ACCEPTED MANUSCRIPT

[74] Johnson WC. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecol Monogr. 64 (1994) 45–84.

[75] Johnson WC. Equilibrium response of riparian vegetation to flowregulation in the Platte River, Nebraska. Regulated Rivers: Research and Management. 13 (1997) 403–15.

[76] Wang C, S Smolders, D Callaghan, Jv Belzen, T Bouma, S Temmerman. Can we predict pending shifts between alternative ecosystem states?: the case of marsh formation on intertidal flats (In preparation).

[77] Carniello L, A Defina, L D'Alpaos. Morphological evolution of the Venice lagoon: Evidence from the past and trend for the future. J Geophys Res. 114 (2009) F04002, doi: 10.1029/2008jf001157.

[78] Francis R, D Corenblit, P Edwards. Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. Aquat Sci. 71 (2009) 290-304, doi: 10.1007/s00027-009-9182-6.

[79] Carter Johnson W. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrological Processes. 14 (2000) 3051-74, doi: 10.1002/1099-1085(200011/12)14:16/17<3051::AID-HYP134>3.0.CO;2-1.

[80] Didham RK, CH Watts, DA Norton. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos. 110 (2005) 409-16.

ACCEPTED MANUSCRIPT