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Seed retention by pioneer trees enhances plant diversity resilience on gravel bars: Observations from the river Allier, France

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ABSTRACT

Pioneer riparian trees which establish in river active tracts on gravel bars enhance fine sediment retention during high flows within their stands and in their lee side, forming obstacle marks. Fine sediment retention can be accompanied by deposition of seeds transported by water dispersal, i.e. by hydrochory. We tested the hypothesis that pioneer riparian trees significantly control seed deposition on gravel bars by forming sediment obstacle marks. We described the seed bank structure and compared samples collected from obstacle marks and bare coarse-grained bar surfaces. At the surface (at 2 cm depth), seed abundance (N) and richness (S) (expressed as mean ± sd) were significantly higher in areas directly affected by riparian trees, i.e. obstacle marks, (N: 693 ± 391; S: 17 ± 3) than in bare surfaces (N: 334 ± 371; S: 13 ± 5). Surface and sub-surface (at 20 cm depth) samples were also significantly different, with the sub-surface samples almost devoid of seeds (respectively N: 514 ± 413; S: 15 ± 5 and N: 3 ± 6; S: 1 ± 2). These results suggest a biogeomorphic feedback between sediment and associated seed retention mediated by hydrochory, vegetation growth and local seed dispersal mediated by barochory. Such feedback may improve plant diversity resilience on gravel alluvial bars of high-energy rivers.

1. Introduction

Woody pioneer riparian species that belong to the Salicaceae family (e.g. *Populus* and *Salix* spp.) colonize bare alluvial surfaces and secondary channels within fluvial corridors and are well adapted to hydrogeomorphic constraints [16,19,26,35,60]. Pioneer trees and shrubs can establish on alluvial bars over a wide range of degrees of exposure to water flow and particle sizes. They are able to colonize exposed gravel surfaces dominated by pebbles and gravels and in such contexts they have important effects on the riparian habitat by enhancing sediment and organic matter trapping with their above-ground structures and substrate cohesion with their roots [17,18,38,41,44,53,55–57,61].

Frontal scouring and downstream depositional patterns related to the presence of vegetation are very common in dynamic environments at the Earth surface, such as coastal margins and rivers [12,13]. Within rivers, isolated pioneer trees impact water flow (e.g. by causing eddies in their surroundings) during flood pulses [46,47]. These impacts enhance frontal scour and downstream, in their lee side, the formation of a sediment tail (i.e. an obstacle mark) [41,45,54]. Sediment tails are generally made of fine-grained sediment dominated by sand, depending, however, on hydraulics and sediment availability. Furthermore, dense tree patches of the same or of different species are able to trap large amounts of sand within their stand [14,20,21,28,37,67]. Within high-energy river reaches micro- to meso-scale landforms consisting of fine sediment would not persist on a homogeneous exposed gravel bar without trees that form firmly anchored structures, thus enhancing positive feedbacks of vegetation growth and mineral and carbon accretion [3,28]. Within a few years or decades, such biogeomorphic dynamics lead to the formation and stabilization of vegetated islands and floodplain levees within high-energy rivers [15,26,31].

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Studies have indicated that fine sediment accretion occurring downstream in the lee side of isolated trees or within vegetated patches can be accompanied by the deposition of diaspores (i.e. seeds, spores, fruits and other vegetative fragments) [17,21,24]. Fluvial seed banks are a fundamental component of river corridors that enhance plant diversity resilience [23,27,62]. However, their functioning is not yet well understood because of its inherent complexity associated with the combined effects of several modalities of seed input, i.e. barochory, anemochory, zoochory and hydrochory [39,42,49].

Natural fluvial corridors show a strong hydrogeomorphic and biological connectivity between upstream and downstream reaches [29,66]. Water flow and the related disturbance regime (i.e. frequency, magnitude and timing of floods) control vegetation dynamics through their impact on habitat conditions [22], aboveground vegetation structure and biomass [5] and seed dispersal [23,27,30,48,62]. Seed input is recognized to be a key driver of plant abundance and richness within any ecosystem. In undisturbed terrestrial ecosystems seed input is mainly related to barochory, anemochory and zoochory [42,52]. Andersson et al. [2] and Tabacchi et al. [62] showed that seed input in disturbed fluvial corridors results from a combination of these three processes but that they are overridden by water flow transportation (i.e. hydrochory), which during flow pulses and floods acts as the main source of seed input on exposed alluvial bars (see also [23]). In such circumstances, sediment accretion in the lee side of an isolated tree and within a dense vegetation patch is likely to function as an *island of fertility* [21]. The feedback loop leading to the formation of an island of fertility can be schematized with four theoretical steps: (i) an isolated pioneer tree or a vegetated patch initially forms a resistant structure on an exposed gravel bar; (ii) the resistant structure enhances sediment and seed deposition downstream in the lee side; (iii) seeds deposited by hydrochory germinate, form herbaceous or woody mats which stabilize the sediment tail and further enhance fine sediment and seed retention during flow pulses [16]; (iv) established plants on the sediment tail or within the vegetated patch disperse new seeds within the corridor by means of hydrochory and on site by means of barochory, thus supplying additional seeds to the on-site seed bank.

The aim of this article is to provide a prospective analysis of the effect of pioneer riparian vegetation on potential plant diversity resilience on gravel bars by specifically considering the seed bank structure within the deposited sediments. We hypothesize that within a highly exposed gravel surface the presence of a tree or a vegetated patch is required for seed deposition in association with the deposition of fine sediment because it forms a rough stable structure [45]. Here, in accordance with the *stress gradient hypothesis* proposed by Bertness and Callaway [6] and the *facilitation hypothesis* of Bruno et al. [9], pioneer vegetation is expected to play a key facilitation role in plant biodiversity resilience in a disturbed environment due to its control of fine sediment and seed input by hydrochory. We analyzed seed bank structures both in the lee side of individual trees and within vegetated patches composed of several coalescent individuals and compared both patterns of seed abundance and richness with the one observed on bare coarse-grained bar surfaces (control). The main objective was to test if pioneer engineer plants significantly impact seed bank structure in their immediate surroundings using a comparison with the exposed unmodified local environment.

2. Material and methods

2.1. Study reach

The study reach is located in the lower river Allier, a tributary of the river Loire, in the Natural Reserve of the *Val d'Allier* near the town of *Châtel-de-Neuvre*, France (Fig. 1). At *Châtel-de-Neuvre*, the river Allier drains a catchment of 12,430 km² with a mean annual discharge of 118 $m^3 s^{-1}$ (1986–2012) (source: '*Banque Hydro*', http://www.hydro.eaufrance.fr). The hydrological regime has a strong seasonal and interannual variability (Fig. 2). Therefore, seed input during high flows and flood pulses related to hydrochory and sediment deposition on alluvial bars of the river Allier is likely to occur frequently and during different periods of the year.

The study reach was selected because lateral channel erosion is still very active on the outer bends of the floodplain, whilst large gravel point bars continually form and migrate within the inner bends (Fig. 1). When hydrological conditions are favorable, those gravel bars are colonized by pioneer trees, mainly *Populus nigra* L, forming linear strips and dense vegetation patches in the more exposed areas, but dispersed individuals of *Salix eleagnos* L. also colonize these more exposed areas, whereas *Salix alba* L. colonizes more protected ones, e.g. on the downstream end of gravel bars and within abandoned channels [34].

2.2. Field sampling and seed bank structure analyses

Two representative exposed gravel point bars were selected in the study reach (point bar 1: 46°24′48″N, 3°19′22″E, 219 m a.s.l., 700 m long and 200 m wide; point bar 2: 46°25′0.1″N, 3°19′52″E, 215 m a.s.l., 600 m long and 230 m wide; Fig. 1). These two gravel point bars were chosen for their representativeness within the *Natural Reserve of the Val d'Allier*: (i) they are highly exposed to water and sediment flows; (ii) their sediment texture is dominated by a mixture of sand, gravel and pebbles; (iii) they are regularly colonized by pioneer isolated trees and dense woody vegetation patches. Two different methods of analysis of the seed bank structure (i.e. seed abundance and species richness) were employed in this study: (i) manual sorting of seeds on sediment samples (collected on point bar 1) using a stereomicroscope at the laboratory; and (ii) a seedling emergence test on sediment samples (collected on point bar 2) undertaken within a greenhouse. The manual sorting led to an exhaustive description of seed input (i.e. viable and dead seeds) on point bar 1, and thus the whole potential of floristic resilience. The seedling emergence test provided indication about the viable seeds contained in the seed bank on point bar 2, and thus the effective resilience at the surface.

On point bar 1, eight sediment tails ranging from 3–5 m long and 1–2 m wide developing downstream in the lee side of isolated trees were systematically selected in areas that were not submerged during the field sampling in November 2013. Observations from aerial photographs (2005, 2006 and 2009) indicated that the sampled sediment tails had formed on the river Allier between 2003 and 2013. At each of the eight sediment tails, two samples of 10 l of sediment each were collected; one on the surface (at 2 cm depth) and another one at the sub-surface (at 20 cm depth) (Fig. 3a,b). Two other samples of 10 l each were collected in the near vicinity of the sediment tails at the surface and sub-surface of the bare coarse-grained gravel bar in order to obtain a control (Fig. 3a,b). A total of 32 samples corresponding to 320 l of sediment was collected on point bar 1. In addition, 21 extra sediment samples were randomly collected from the sediment tails and 24 from the bare gravel surface (control) to perform sediment texture analyses in the laboratory. These 45 extra sediment samples were sieved according to the standard method to assess particle size distributions.

The thirty-two sediment samples collected for seed bank analysis were sieved individually using water and laboratory sieves of 10 mm, 2 mm, 0.5 mm and 300 µm mesh sizes. Diaspores were sorted manually and examined using a stereomicroscope (Leica) with a magnification of X10-63. Diaspores were counted and most of them identified to the species level by V. Vidal, M. Cabanis