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ORIGINAL RESEARCH

Control of Non-migrating Bar Morphodynamics on Survival of *Populus nigra* Seedlings during Floods

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Abstract

Populus nigra seedling survival to flood stresses during their first stage of development was analyzed in the Loire River, France. We related bar dynamics (assessed from bathymetrical, topographical, flow velocity, scour chains, and sediment grain size surveys) to seedling survival. The study highlights (i) the influence of flood succession and flood stages on seedling survival after establishment, (ii) the spatial distribution of fluvial processes at the bar scale and their relative contribution to seedling mortality, (iii) threshold values for each process. At the bar scale, 28% of mortality is explained by uprooting associated with erosion of sediments. To a lesser extent, uprooting by drag force applied on the stems and burying by sediments also contribute to seedling mortality. The majority of seedling mortality is ultimately due to a combination of erosion and burial (50.6%) during flood events. The relative contribution of each process depends on the combination and phasing of erosion and deposition processes, sediment supply (quantity and grain size), and flow velocity governed by hydrological variations. Based on the results of this study we hypothesize that the survival of seedlings during floods may be a function of local processes involved in bar dynamics.

Keywords Non-migrating bar · Uprooting · Burial · Riparian vegetation · Seedlings

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Introduction

Vegetation constitutes a fundamental component of river channel dynamics (Hickin 1984) influencing fluvial morphodynamics (e.g., Tal and Paola 2007, 2010; Gurnell 2014). Established vegetation increases flow resistance (Freeman et al. 2000) and flow deflection (Euler et al. 2014), creating specific topographical signatures (Rodrigues et al. 2007; Bertoldi et al. 2011; Wintenberger et al. 2015a). Plants act as 'ecosystem engineers' in rivers (Corenblit et al. 2009, 2011; Corenblit and Steiger 2009) leading the conversion from highly disturbed environments into more stable surfaces favorable for later successional species (Johnson 1994). The modification of the balance between erosion and deposition induced by riparian vegetation leads to the morphological evolution from the local scale (obstacle-mark) to the river planform scale (Gurnell 2014).

Initial conditions suitable for the establishment of pioneer trees depend on hydrological and morphological dynamics (Braatne et al. 1996; González et al. 2010); their importance highlighted in the "Recruitment Box" concept (Mahoney and Rood 1998) and "Window of Opportunity" (Balke et al. 2011)

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for fluvial and tidal environments, respectively. The woody pioneer vegetation colonizes fluvial landforms by sexual (seedlings) or asexual reproduction. This strategy allows a distribution of vegetation across a wide range of disturbance levels (Barsoum 2002; Moggridge and Gurnell 2009) but only sexual reproduction ensures genetic diversity (Karrenberg et al. 2002).

The germination and survival of seedlings during low-flow periods is controlled by hydrology (Stella et al. 2010) through (i) the formation of landforms that provide suitable recruitment sites during seed dispersal (Mahoney and Rood 1998) and (ii) the availability of optimum water resources for seedling viability and growth (Guilloy et al. 2011).

Seedlings that survived hydric stresses during the first growing season are likely to have to stand up to subsequent flood disturbances and associated sediment dynamics (Ewing 1996). Effects of flood disturbance on tree seedling survival have been documented through investigations often carried out at large temporal (several years) and spatial scales (reaches of kilometers), and in which vegetation survival was mainly related to discharge characteristics (Shafroth et al. 1998; Johnson 2000; Dixon 2003; Vreugdenhil et al. 2006).

To understand the control of fluvial processes on seedling establishment at the river reach scale, studies need to focus on processes at a finer scale (Bornette et al. 2008). During floods, seedlings endure three stresses: (i) drag force exerted on the stem induced by flowing water (Type I of Edmaier et al. 2011), (ii) substrate erosion combined with the drag force exerted on the stem (Type II), and (iii) burial. Several experimental studies highlighted the local disturbances exerted on plants (e.g., drag force exerted by the flow) and their ability to withstand these disturbances (Scippa et al. 2008; Edmaier et al. 2011; Schoelynck et al. 2015). Most of these mechanistic studies focused on resistance of seedlings to flood stresses after germination and were performed using flume experiments (Kui et al. 2014). Mechanistic studies integrating the complexity of sediment dynamics at the scale of the bar unit in natural rivers remain rare (Bendix and Stella 2013). Specifically, local sedimentary processes (erosion and burial) involved in seedling mortality are poorly understood.

The most suitable morphological units for recruitment in alluvial environments - for example bars (Charron et al. 2011), channel margins, secondary channels - are often those subject to disturbances leading to high seedling mortality (Auble and Scott 1998). In rivers, migrating bars and non-migrating bars (corresponding to free and forced bars of Seminara and Tubino, [Seminara and Tubino 1989; see review in Rodrigues et al. 2015]) can be distinguished.

Non-migrating bars (or forced bars) develop because of changes in channel planform, variations in channel width (Repetto et al. 2002), or are induced by the presence of a steady local perturbation (riffle, groyne, vegetation). Because of their relative stability in river channels (Crosato et al. 2011), we assume that non-migrating bars provide suitable conditions for recruitment and survival of woody pioneer trees of the softwood forest (e.g., *Populus nigra*) in relatively large and low-gradient sandy-gravel bed rivers. More precisely, contrasting sediment dynamics at the bar scale, highlighted by the presence of fixed and spreading areas (see Fig. 6 in Wintenberger et al. 2015b) could significantly influence seedling survival.

This study relates survival patterns of *Populus nigra* seedlings to bar dynamics across flood phases on a non-migrating (forced) bar of the Loire River. Specifically, we connect seedling survival with the spatial and temporal distribution of fluvial stresses related to bar dynamics. We quantify the respective contribution of each stressor (drag force on stems, erosion of the substrate, burial), their sequencing during floods, and the threshold values of each stress endured by seedlings. We also investigate whether seedlings recruited on a fixed area (stable sediments) are characterized by higher survival rates compared to those developed on a spreading area (mobile sediments).

Study Area Description

General Context of the Loire River

The Loire River (the longest river in France) drains a catchment area of 117,000 km^2 for a length of 1012 km. Floods occur during winter and spring as a result of upstream storms and Atlantic rainfall. Low flows occur during summer with a minimum water level in September. Along its middle reaches the river exhibits a range of fluvial patterns from single channel (straight or meandering) to anabranching.

To prevent flooding, the French regional environment agency currently implements a plan of fluvial management works (FMW) consisting of vegetation removal and topographical lowering. By converting islands into bars, these works result in rejuvenated landforms suitable for seedling recruitment.

Study Site: Bar and Vegetation Dynamics

This study focuses on a non-migrating mid-channel bar located in the Nature Reserve of Saint-Mesmin, 649 km downstream of the Loire's source. The average discharge measured at the Orleans gauging station 10 km upstream is 344 m^3.s^{-1} and the 2-year flood discharge is 1700 m^3.s^{-1}. The site is characterized by a contraction and expansion area combined with sinuous main channel (Fig. 1a). Channel width varies from 270 m to 430 m, sinuosity index is 1.04 and average slope is 0.01° (Latapie et al. 2014). This morphological configuration associated with natural outcrop riffles leads to an anabranching pattern composed of islands several decades old. Specifically, it provides suitable conditions for the

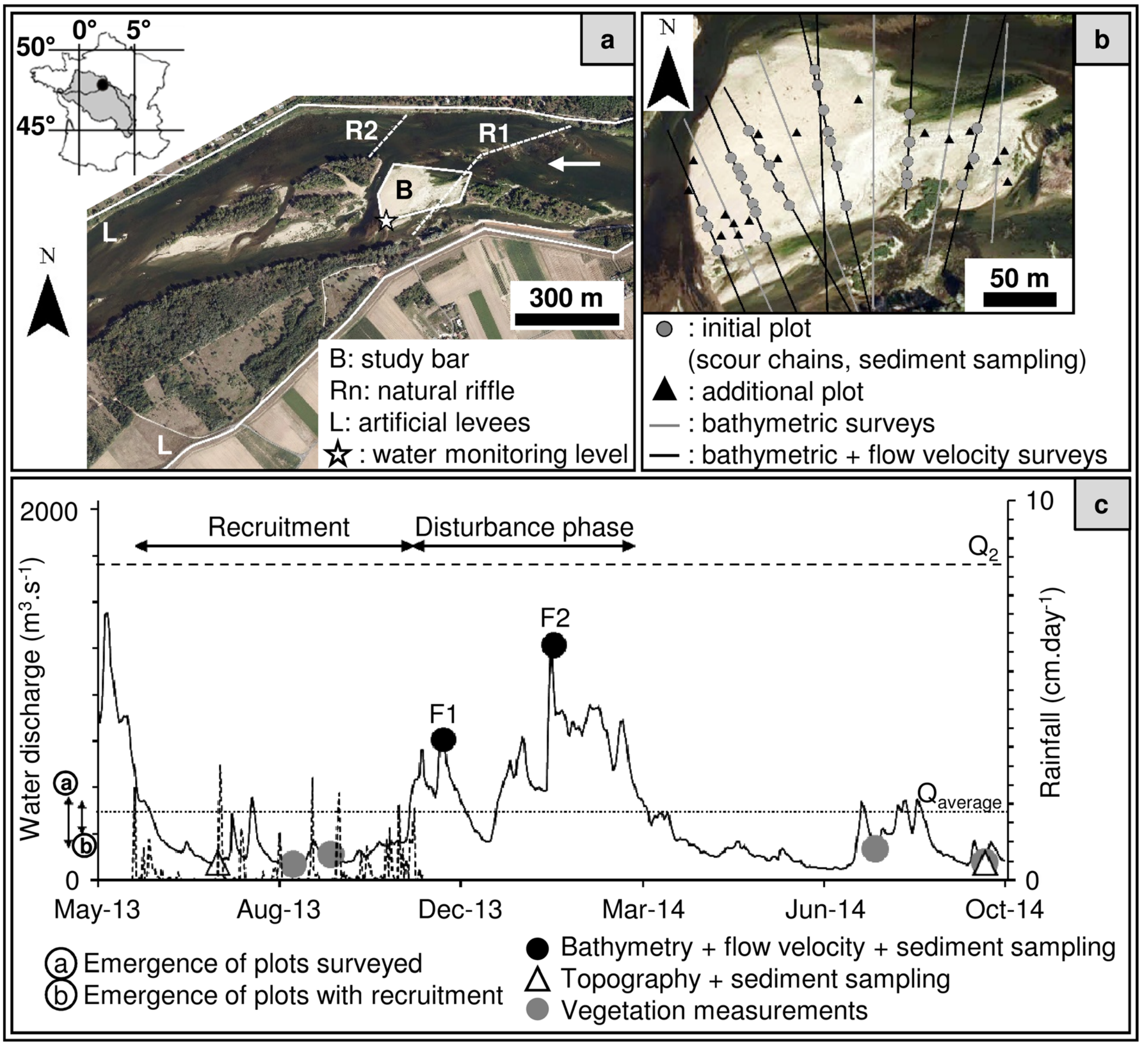


Fig. 1 **a** Morphological context of the study site. **b** Protocol of measurements. Vegetation measurements (density) were performed on initial (gray circles; I.1 to I.30) and additional (gray triangles; A.1 to A.18) plots. **c** Measurements campaigns; discharge variations between 2013 and 2014; rainfall (dashed black line) recorded at the meteorological station of Orléans-Bricy (Code: 07249, available at http://asso.infoclimat.fr/) during summer 2013. During summer 2013: the highest plot surveyed emerged from 448 $m^3.s^{-1}$ and the lowest at 159 $m^3.s^{-1}$ that respectively correspond to an elevation of 84.7 m and 83.9 m (circled a). The highest and lowest vegetated plots respectively have 84.6 m and 84.1 m of elevation (circled b)

formation of the non-migrating bar studied (Fig. 1a) composed mainly of siliceous sands, gravels, pebbles and cobbles.

This bar was colonized by *Populus nigra* in 2004 and evolved rapidly into an island until 2012 (Wintenberger et al. 2015a). In September 2012, FMW were carried out consisting of grinding the vegetation stems and branches, extracting the root systems, lowering the elevation, and homogenizing sediments up to 0.5 m of depth. No vegetation and no original morphological units remained. The new bar was characterized by a flat surface of 26,700 m^2 and homogeneous sediment grain size with elevations ranging between 83.1 m and 84.5 m above sea level (a.s.l.).

This rejuvenated bar was the focus of a study aimed at identifying the driving factors of non-migrating bar morphodynamics during floods occurring after FMW (Wintenberger et al. 2015b). This pre-recruitment study (see details in Wintenberger et al. 2015b), conducted between 2012 and 2013, and clearly showed the presence of two distinct areas on the bar during a typical 2-year flood on the Loire River (Fig. 2):

– a fixed area characterized by minor morphological changes (erosion and deposition at a scale ranging from centimeters to decimeters) located at the center of the bar;
– a spreading area where sedimentary processes were intense (eroded and/or deposited sediments with thicknesses on the order of decimeters to one meter).

This present study focused on the relation between bar dynamics and seedling survival following their recruitment on this bar in summer 2013.

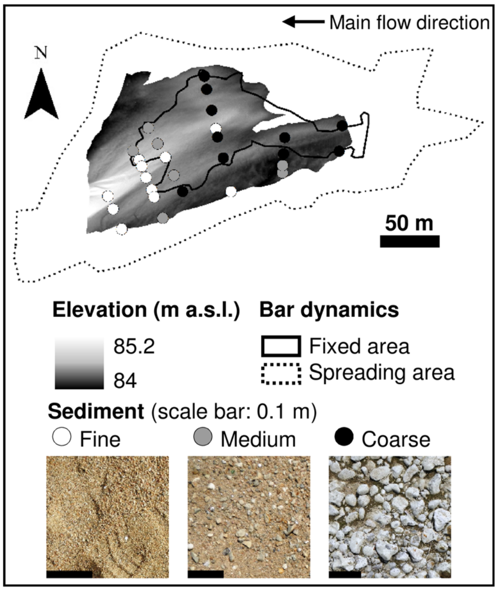


Fig. 2 Elevations and sediment texture distributions on initial plots (2013)

Material and Methods

Field Measurements: Bar Dynamics and Vegetation

Bar dynamics were investigated according to protocol detailed in Wintenberger et al. (2015b) and vegetation was surveyed in parallel (Fig. 1b and c). Three conditions were studied (Fig. 1c):

(i) initial conditions of recruitment: grain size, elevation and seedling density,
(ii) conditions during floods: changes in elevation of the bar, bed shear stress, flow velocity and associated drag force applied on seedlings,
(iii) floods consequences on bar morphology (elevation, grain size) and the fate of seedlings.

Erosion and Deposition Processes on the Bar

Stresses caused by erosion and deposition of sediments on seedlings were quantified based on bathymetric and topographic surveys and scour chains.

Bathymetric surveys were conducted during two multi-peak floods, F1 (700 $m^3.s^{-1}$) and F2 (1300 $m^3.s^{-1}$), that occurred after recruitment in November 2013 and January 2014 respectively (Fig. 1c). Twelve cross-sections (Fig. 1b) were surveyed using a mono-beam echo-sounder (Tritech PA500–500 kHz) coupled with a Differential Global Positioning System (DGPS) (Magellan Proflex 500) and controlled using the Hypack 2009 software with a vertical accuracy of 0.1 m.

Topographic surveys were conducted in 2013 (recruitment year) and 2014 (survival year), during low flow, using a Terrestrial Laser Scanner (TLS) Leica HDS 3000 (average of 800 points per square meter). Digital Elevation Models (DEMs) were created using the Triangulated Irregular Network (TIN) function of ArcGIS 10 software. All elevation data in the paper are reported in meters above sea level (Fig. 2).

Scour chains were used to detect and quantify the active sediment layer and to detail maximum erosion and deposition events during floods. As such, 30 metal-link chains (Laronne et al. 1994; Rodrigues et al. 2012) were inserted into the bar along six cross sections (Fig. 1b) with a representative range of elevations and sediment textures. The chains were relocated after floods using the DGPS and a metal detector in conjunction with digging. Erosion was determined by measuring the disturbed length of the chain, and deposition was determined by measuring the thickness of sediments that accumulated on top of the chain.

Scour chain measurements provided (i) maximum erosion depths on seedling plots during floods and (ii) final depth of burial. Seedling survival coupled with topographic and bathymetric data provided the resistance threshold of seedlings to erosion and burial stresses.

Grain Size Analyses

Surface sediments were sampled at each scour chain location prior to scour chain recovery. When an armor layer was present, two sediment samples were collected: one of the armored layer and one of the sediments under the armor layer (sublayer).

Sediment samples down to 63 μm (finer fractions in the Loire River bed are negligible [Macaire et al. 2013]) were analysed by dry sieving using a vibratory sieve shaker (Retsch 3D - AS450) and cumulative curves were constructed from these results. The D_{50} (median grain size) and D_{90} (90% of the sample is finer than this size) were obtained using Gradistat 4.0 (Blott and Pye 2001). Characterisation of the grain size and armor layer provided information about the critical bed shear stress required for erosion.

Water Levels and Flow Velocity

Water level was obtained from the pressure difference measured between an emergent probe (Baro) and a submerged probe (Diver) located in a piezometer (Fig. 1a) with an accuracy of 5 mm and a time step of 30 min. Water level was converted to meters above sea level to characterize the emersion and submersion periods on the bar (duration and level) as well as the water table decline.

Flow velocity measurements were performed during bathymetric surveys (F1 and F2). They were measured over seven cross-sections (Fig. 1b) using a Riversurveyor M9 ADP (Sontek), which has two sets of four profiling beams (at 3 MHz and at 1 MHz) connected to a DGPS.

Four successive tracks were recorded per cross-section from a boat traveling at a speed of approximately 1 $m.s^{-1}$. Mean flow velocities were calculated using the Velocity Mapping Toolbox (VMT) available from U.S. Geological Survey (Parsons et al. 2013) and the velocities near the bed were obtained using the law of the wall method proposed by Claude et al. (2014).

The drag force F_d exerted on stems was obtained using the classical approach proposed by Hoerner (1965):

$$F_d = \frac{1}{2}\rho v^2 C_D A \quad (1)$$

with F_d the drag force (N), ρ water density ($kg.m^{-3}$), v mean flow velocity ($m.s^{-1}$), C_D the dimensionless drag coefficient and A the characteristic reference area of the stem (m^2). Since *Populus nigra* seedlings present on the bar recruited during the same period we assumed C_D to be uniform (taken here as a constant as are ρ and A). Thus, F_d will mainly depend on the squared velocity of flow.

Bed shear stress was calculated using the following equation (see details in Claude et al. 2014):

$$\tau_b = \rho \left[\frac{ku}{ln\left(\frac{z}{(z_0)_{SF}}\right)} \right]^2 \quad (2)$$

where τ_b the bed shear stress ($N.m^{-2}$), u is the flow velocity ($m.s^{-1}$) at height z (m) over the bed, k is the von Karman constant equal to 0.4 for clear waters, and $(z_0)_{SF}$ is the grain roughness (m) (or the height at which u = 0), equal to 0.095 D_{90} (Wilcock 1996).

Recruitment and Survival of Seedlings

At the end of the growing season of year 2013, attested by the presence of a red-brown apical bud, the density of *Populus nigra* seedlings was measured at 48 plots georeferenced using a DGPS (Fig. 1b and c).

Thirty initial plots (0.25 m^2/plot) located on the cross-sections used to characterize morphology (topography, bathymetry) and hydrodynamics (flow velocity) and close to the scour chains and sediment sampling sites were surveyed to compare seedling survival to the bar dynamics (Fig. 1b).

These plots, randomly located with respect to recruitment, did not describe the recruitment pattern on the entire bar (because seedlings did not recruit on all of them). Consequently, for a better description of recruitment at the bar scale, a second set of 18 additional plots were surveyed. The latter were chosen in areas where seedlings recruited homogeneously. In summary, these additional plots are located all over the bar to take into account seedlings patches that were not surveyed with initial plots (Fig. 1b).

This survey provided a view of the seedlings present on the bar before the floods F1 and F2 (Fig. 1c).

During summer 2014, seedling survival (density measurements) was surveyed at the emergence of the bar (before potential dry season stresses). We specifically conducted a second field survey at the end of the growing season in 2014 to assess seedling survival on plots affected by sediment deposition (Fig. 1c). Surviving seedlings were visually distinguished from newly recruited seedlings (annual scar bend vs. cotyledon). All measurements were converted to a density of seedlings per square meter and percentages of survival were calculated from these densities.

Statistical Analyses

Plots where seedling recruitment occurred in 2013 ($n = 30$) were ordinated with regard to their abiotic characteristics using a Hill Smith analysis (Hill and Smith 1976). This multivariate technique (package ADE4, [Chessel et al. 2004)]) allows to take into account qualitative and quantitative data simultaneously.

Quantitative data for each plot included: initial elevation (2013) and final elevation (2014) of the survey as well as during the flood peaks F1 and F2, total magnitude of erosion and deposition events, drag forces at F1 and F2, bed shear stress during F1 and F2, and number of days of submergence during the growing period 2013.

Qualitative data consisted of sediment texture (medium, fine, coarse). Germination success of *Populus nigra* as well as survival on these plots was visualized by projecting seedling densities and survival and mortality rates on a factorial map. Differences of seedling survival in the Hill-Smith groups were tested using a Kruskal-Wallis test.

In parallel, statistical significance of the ordinal parameter "grain size classes" on seedling establishment, i.e. initial density, and survival were tested using analysis of variance (ANOVA) and Tukey tests for multiple comparisons of means (95% family-wise confident level). The impact of the continuous variable "plot elevation" on seedling density and survival was tested under a generalized linear model, assuming the response variable had a Poisson distribution.

All statistical tests were considered significant at $P < 0.05$ and were conducted using the program R (R Core Team 2016).

Results

Bar Dynamics and Sedimentology

A synthetic view of the dataset relative to bar dynamics is presented in Appendix 1.

Bar Elevation and Sediment Grain Size

In summer 2013, bar elevation ranged between 83.9 m and 85.2 m with an average elevation of 84.5 m (Fig. 2).

Based on the cumulative grain size curves, three sediment textures were identified:

- fine sediments ($D_{50} < 2.10^{-3}$ m), composed mainly of siliceous relatively well sorted sand supplied by the main channel during floods (Wintenberger et al. 2015b) and mainly located downstream at elevations ranging between 83.9 m and 84.7 m (Fig. 2, see also Fig. 4d);
- medium sediments ($2.10^{-3} < D_{50} < 6.10^{-3}$ m), composed mainly of siliceous sand and gravels (sometimes with some pebbles) characterized by a slope break in the cumulative curve, and located in the median and southern parts of the bar at elevations ranging between 84 m and 84.6 m (Fig. 2, see also Fig. 4d);
- coarse sediments ($D_{50} > 6.10^{-3}$ m), composed of pebbles and some gravels located upstream at elevations ranging between 84 m and 84.5 m (Fig. 2, see also Fig. 4d). These coarse sediments were not eroded and transported for the range of discharges surveyed during this study. They correspond to armor layers (Wintenberger et al. 2015b) and are characterized by a concave cumulative curve.

Ordination of Plots According to Abiotic Characteristics

A Hill Smith test was performed in order to understand the relative weight of each abiotic parameter. The ordination of sampling plots by the Hill-Smith analysis opposes on the first factorial axis plots with high drag forces and shear stresses and overall high elevations (negative values) with plots with the opposite features (positive values; Fig. 3a). The second axis represents a sediment/deposit gradient: it opposes plots with fine sediments and/or high deposits (negative values) with plots with coarse sediments and/or erosion (positive values). Four groups of plots can be distinguished (Fig. 3b) as well as one outlier plot (A1). Group 1 plots present positive values on both axes, i.e. are linked to low drag forces and shear stresses and coarse sediment. Group 2 plots occupy a central, i.e. intermediate, position on both axes. Group 3 plots are characterized by low values on axis 2, i.e. fine sediments and high deposits, and group 4 plots by low values on axis 1, i.e. high drag forces and shear stresses and rather high elevations.

Group 4 plots are mostly situated within the central area of the bar, Group 1 plots on its upstream part, Group 3 plots on its downstream part and Group 2 plots were scattered at intermediate locations around the centre. As shown on Fig. 3c, Groups 1 and 3 correspond to plots located on the spreading area while Groups 2 and 4 correspond to plots located on the fixed area.

On the bar, erosion prevailed during the rising stage, deposition during the falling stage, and sediment reworking during the emergence of the bar (Wintenberger et al. 2015b). However, as a function of discharge, the fixed and spreading areas showed contrasted morphological behaviors. For example, erosion prevailed on the spreading area and deposition on the fixed area between F1 and F2. During this study, the intensity of erosion and deposition was always higher in the spreading area compared to the fixed area (Fig. 6 and Wintenberger et al. 2015b for further details).

Seedling Establishment and Survival

Populus nigra Recruitment in 2013

On the 48 plots surveyed, 30 plots had successful *Populus nigra* recruitment at the end of the growing season of 2013 (Fig. 4a) with densities ranging between 2 and 184 seedlings per square meter (mean value for plots with recruitment = 30.7 seedlings.m^{-2}) (Fig. 4) and at elevations between 84.1 m and 84.6 m.

Those plots were located across the whole range of gradients (Fig. 2), with 14 plots (representing 1200 seedlings; 18.2 seedlings.m^{-2}[mean value that takes into account all the plots with and without vegetation]) situated in the spreading area and 16 in the fixed area (representing 1036 seedlings; 20.7 seedlings.m^{-2} [mean value that takes into account all the plots with and without vegetation]). *Populus nigra* seedling density was higher on fine sediment (vs. coarse) and at higher elevations. Based on the results of the ANOVA test (Table 1), only elevation had an influence on seedling survival (Table 1). Seedling densities reached the highest values in plots belonging to Hill-Smith Group 1 (Fig. 5).

Populus nigra Seedling Survival (2014)

The vegetation survey of 2014 allowed us to estimate the survival rate of seedlings after floods (F1, F2) and the low-flow period between April 2014 and October 2014.

During the first year, 92.3% of *Populus nigra* seedlings died (Table 2) because of stresses associated with floods (Tables 2 and 3). This high mortality rate is common for riparian young seedlings (Johnson 2000). Average densities of seedlings were 2.2 seedlings.m^{-2} and 0.9 seedlings.m^{-2} for the fixed and spreading areas, respectively.

Complete seedling survival occurred only at 4 plots (3 in the fixed area and only 1 in the spreading area), complete mortality occurred on 14 plots (9 in the spreading area, 5 in the fixed area). Seedling survival differed significantly between Hill-Smith groups (Kruskall-Wallis test, $p = 0.021$). While no survival occurred in plots from Group 1, despite its relatively high seedling density in 2013 (Fig. 5), two thirds of plots from Group 2, half of

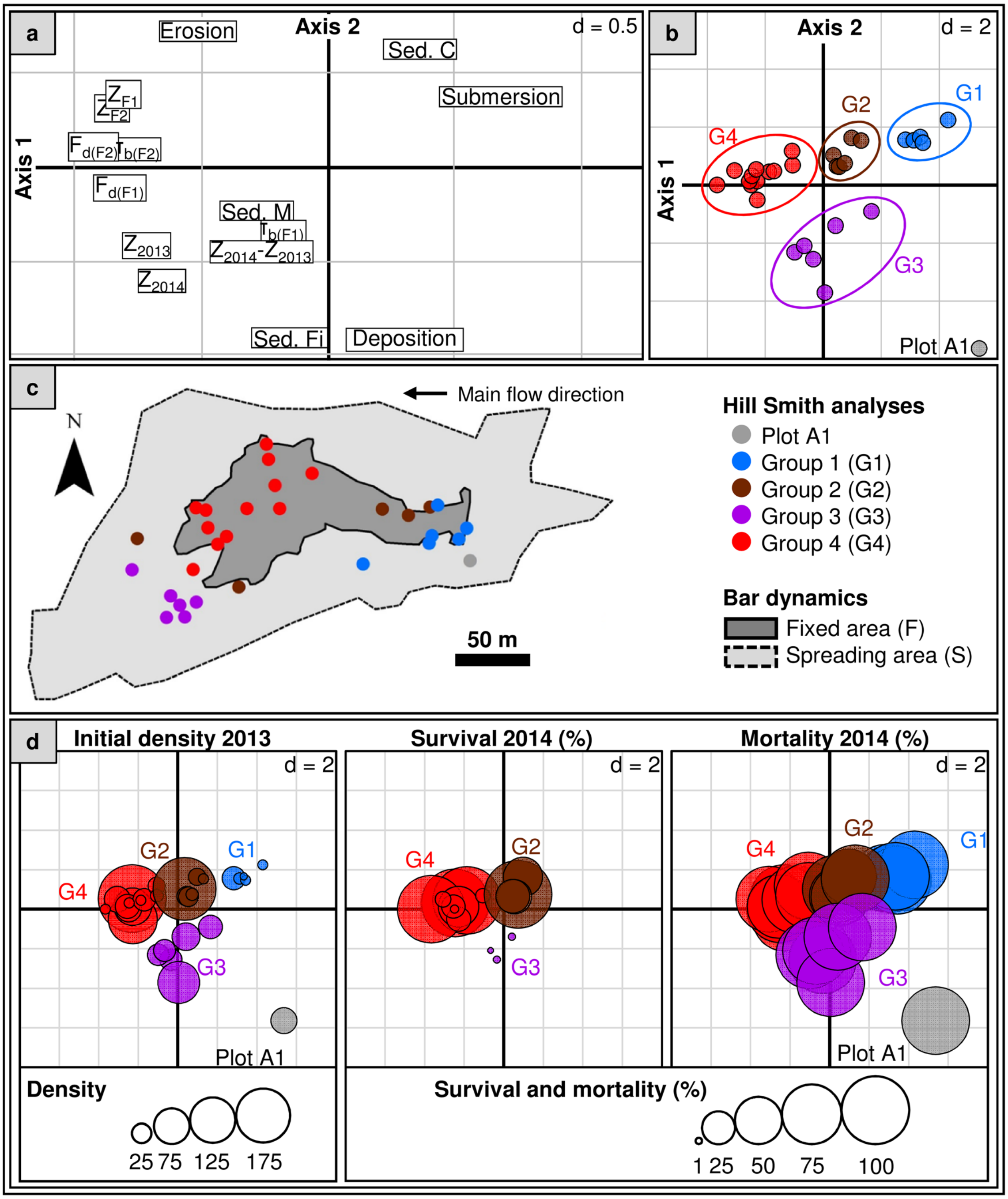


Fig. 3 Hill Smith analyses. **a**. Factorial axis representing abiotic parameters (axis 1: drag forces, bed shear stress and elevation; axis 2: grain size and deposition/erosion heights). **b**. Groups of plots determined according to the combination of abiotic parameters. **c**. Location of the plots of each group on the bar. **d**. Initial density of seedlings (2013), survival in 2014 and mortality. Parameters tested are: 1) elevations: initial (Z_{2013}), final (Z_{2014}), during F1 (Z_{F1}) and F2 (Z_{F2}), 2); sediment textures: fine (Fi), medium (M), and coarse (Sed. C), 3); erosion and deposition processes: maximum values (Erosion, Deposition) and balance between 2013 and 2014 (Z_{2014}- Z_{2013}); drag forces: during F1 ($F_{d(F1)}$) and F2 ($F_{d(F2)}$); bed shear stress: during F1 ($\tau_{b(F1)}$) and F2 ($\tau_{b(F2)}$); and number of days of submergence during the growing period 2013 (Submersion)

plots from Group 3, and three quarters of plots from Group 4 had some seedling survival. Seedling survival rates differed according to Hill-Smith groups (Kruskall-Wallis test, $p = 0.023$), with survival rates being highest in Group 2, followed by Group 4 (Fig. 3d, Fig. 5).

Figure 5a–c shows that median survival rates are lower in the spreading area (1.1% or less for Groups 1 and 3) while median rates of survival are significantly higher on the fixed area (Groups 2 and 4, 29.4 and 41.3%, respectively). Survival range is low in Groups 1 and 3 and high for groups 2 and 4

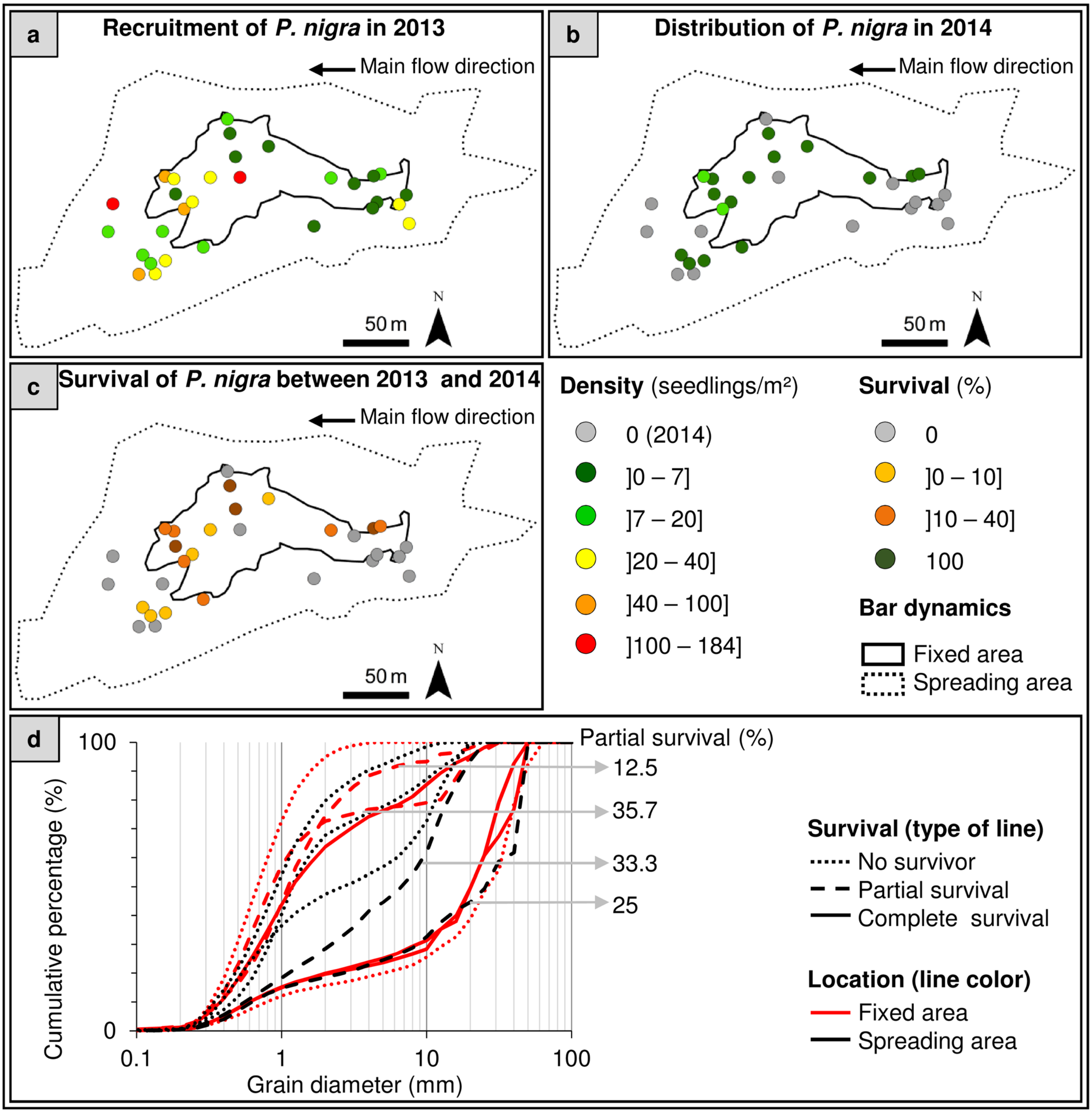


Fig. 4 Density of seedling recruitment (**a**) and survival (**b**) with associated survival rates (**c**). **d** Cumulative curves of sediment grain size on initial plots. Percentages of survival are given on the right of the graph for plots where partial survival occurred (grey arrows and percentage associated)

with survival not depending on the initial seedling density (Fig. 5d).

The initial elevation of seedlings had a significant effect on survival rates (Table 1). Seedlings located on the highest initial elevation survived on sandy sediment ($D_{50} < 2.10^{-3}$ m). Although ANOVA tests showed that survival was not statistically correlated with the presence of coarse particles (Table 1), Figs. 2 and 4d suggest that, for seedlings located at the same elevation (between 84.4 m and 84.5 m), higher rates of survival were observed on sediments with the highest median grain size ($D_{50} > 2.10^{-2}$ m) corresponding to armor layers. Moreover, complete survival was only observed on sediments with a cumulative curve showing poor sorting (Fig. 4d) associated with the armor layer mentioned above (see Fig. 2). When a portion of seedlings survived, percentages are higher on plots with poorly sorted sediments versus sandy and better sorted sediment (Fig. 4d).

Table 1 Impact of sediment texture, plot elevation and location of sedimentary processes on seedling recruitment and survival

	Initial density (2013) *p* value	Survival (2014) *p* value
Coarse vs. medium texture (a)	0.149	0.495
Coarse vs. fine texture (a)	0.035	0.231
Medium vs. fine texture (a)	0.566	0.760
Fixed vs. spreading area (a)	0.827	0.191
Initial elevation of plots (b)	$<10^{-16}$	$<10^{-16}$

(a) Results from ANOVA followed by Tukey multiple comparison of means, (b) results from Generalized Linear Models

Flood Stresses Tolerated by Seedlings

The seedlings survived up to 0.1 m of erosion in the fixed area and up to 0.2 m in the spreading area. Although not statistically significant (Table 1), Fig. 3 and a quantitative analysis suggests that seedlings tend to survive on more plots and at higher (survival) rates in the fixed area than in the spreading area (Fig. 5). Most seedlings that survived endured successive erosion and deposition processes. For example, in the spreading area, higher survival rates, ranging from 25% to 100%, were associated with erosion lower than 0.1 m and subsequent burial ranging from 0.1 m to 0.2 m (Fig. 6).

Drag Force Exerted on Seedlings

Maximum values of square velocity were 1.7 $(m.s^{-1})^2$ during F1 and 2.4 $(m.s^{-1})^2$ during F2 (Fig. 7). The highest drag force associated with total survival of seedlings on a plot was 2.3 $(m.s^{-1})^2$ (Fig. 7).

This suggests that uprooting of seedlings does not only depend on the drag force exerted on the stem. Bathymetric surveys reveal that 2 plots were buried at the peak discharge of F1 and 4 plots between F1 and F2 peak discharges (Fig. 6), probably reducing the maximum value of drag force applied on seedlings (Figs. 7 and 8d).

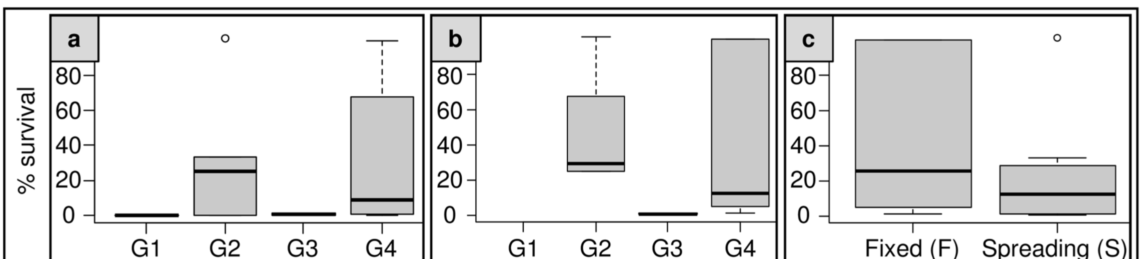
Discussion

Contribution of Fluvial Processes to Seedling Mortality at the Bar Scale

This study allowed quantification of seedling survival and mortality of *Populus nigra* according to sediment grain size characteristics, elevation, and different potential stresses associated with flooding and sediment dynamics.

While good seedling survival was associated with specific combinations of plot characteristics as revealed by the Hill-Smith analysis, a striking result was the overall high seedling mortality even on plots that seemed similar to high survival plots on the basis of the measured parameters. A more detailed analysis and the integration of supplementary features is needed to explain this pattern.

At the bar scale, three processes may affect seedlings, (i) uprooting by the drag force (Type I, Edmaier et al. 2011), (ii) erosion of the recruitment substrate associated with the drag force exerted on a stem (Type II, Edmaier



d	G1	G2	G3	G4
Number of plots	5	6	6	12
Seedling density 2013	49.3 ± 61.4	28.1 ± 21.9	10.2 ± 9.3	34.6 ± 54.6
Median density 2013	23.1	21.9	6.4	12.0
Survival range on plots (%)	[0 0]	[0 101.3]	[0 1.2]	[0 100]
Number of plots with survival	0	4	3	9
% survival on plots	/	46.3 ± 36.9	1.0 ± 0.24	41.3 ± 45.1
Median % survival on plots	/	29.4	1.1	12.5

Fig. 5 Boxplot of poplar survival on plots belonging to the four Hill-Smith groups. **a**. Plots with no survival were taken into account as "0 survival". **b**. Plots with no survival were not taken into account. **c**. Boxplot of poplar survival on plots belonging to the fixed and spreading zone. Plots with no survival were not taken into account. **d**. Table of initial seedling density and seedling survival on plots belonging to the different Hill-Smith groups. Indicated are means ± standard deviation. Density values are seedlings.m^{-2}

Table 2 Relative importance of each process leading to seedling mortality on the bar

Processes	Fixed area	Spreading area	Entire bar
Uprooting (Type I)	0.1% (2)	0.0% (0)	0.1% (2)
Erosion (Type II)	12.7% (2)	15.3% (3)	28.0% (5)
Burial (Type III)	13.6% (5)	0.0% (0)	13.6% (5)
Erosion – Burial (Combination)	15.9% (5)	34.7% (13)	50.6% (18)
Total	42.3% (14)	50% (16)	92.3% (30)

Values correspond to the percentage of seedling loss that occurred from each cause associated with flood stresses and from each area (fixed vs. spreading). In brackets, number of plots

et al. 2011), including lateral erosion, and (iii) burial (Type III, this study).

As mentioned above, Type I processes are responsible for only a small proportion of total seedling mortality. Two assumptions are proposed here to explain this based on the location of the seedling recruitment on the bar (fixed or spreading areas). In the fixed area, i.e. in Group 2 and Group 4 (Hill-Smith groups), seedling survival was often highest on plots characterized by the presence of armor layers that possibly (i) prevented substrate erosion and (ii) increased flow resistance close to the bed (which induced dissipation of energy by friction on the coarse particles that in turn decreased the drag force applied on seedlings and prevented them from uprooting).

This is in line with flow velocity measurements showing that the highest flow velocity values were recorded on this area during floods (while complete survival of seedlings was observed on some plots). In the spreading area (Groups 1 and 3, Hill-Smith groups), it is difficult to distinguish the relative contribution of processes I & II because sediments in this area are fine and easily eroded during floods and deposits are locally high.

About 28% of seedlings disappeared (Table 2) after the erosion of substrate (Type II). In this case, it is clear that the drag exerted on the stem also contributes to seedling mortality. This process is significant regarding seedling mortality and suggests once again that bed shear stress and sediment grain size (and also their balance) are key parameters governing seedling survival. On our study site, Type I dominates on plots with coarse sediment grain size while Type II dominates on plots with finer sediment grain size.

Although the strong ability of riparian species to survive burial stresses has been shown in the literature (Gurnell 2014), about 13.6% of seedlings died after burial in the present study (Table 2).

Finally, the combination of erosion-burial processes, due to the hydrological regime (flood stages and succession of floods; Fig. 6), led to 50.6% of the mortality observed (Table 2). This combination was the dominant parameter influencing seedling mortality at the bar scale but at different levels according to the area considered (15.9% on the fixed area vs. 34.7% on the spreading area). As presented in the results section, the density dropped from 20.7 to 2.2 seedlings.m^{-2} and 18.2 to 0.9 seedlings.m^{-2} for the fixed and spreading areas, respectively.

To resume, at the bar scale and over the course of 1 year (with two flood events), the mortality of seedlings was significant and could not be explained by the measured parameters in a completely satisfying manner.

The spatial distribution of seedlings that survived was however significantly influenced by a combination of parameters linked to the morphodynamics of the bar such as sediment grain size and the succession of processes (combination of Types II and III) due to the hydrological regime (Wintenberger 2015).

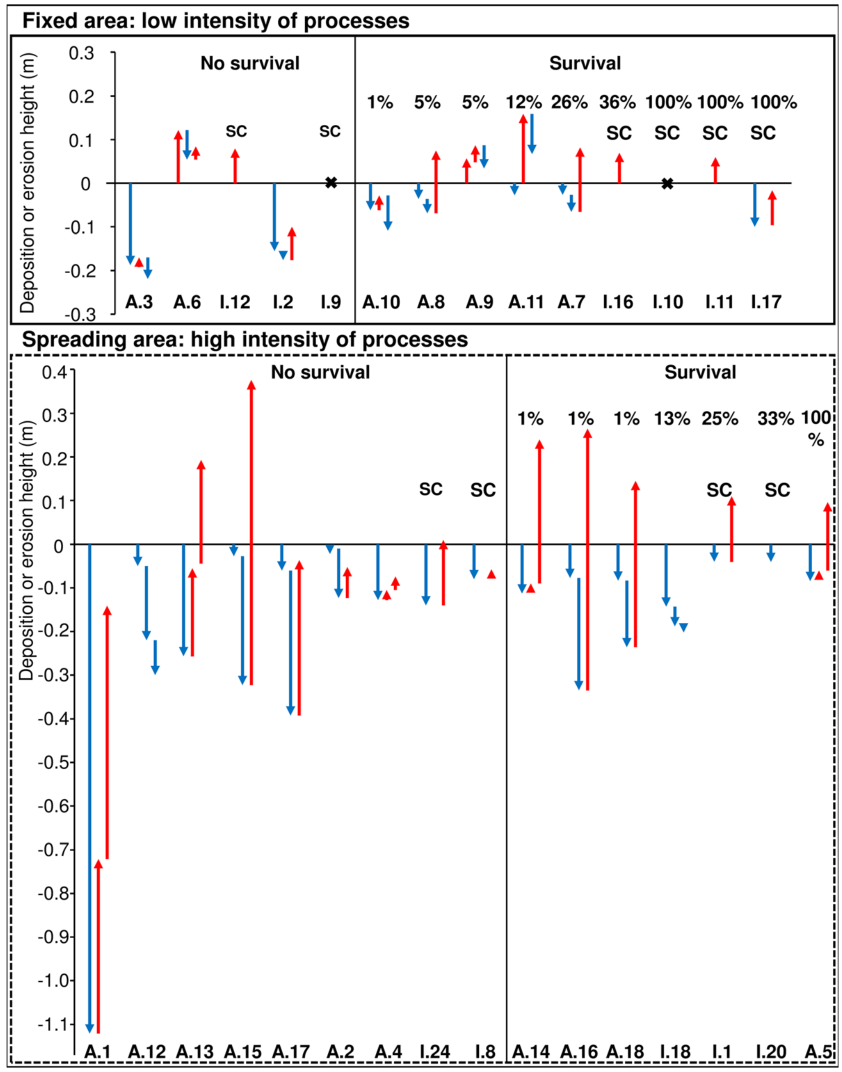
According to Figs. 3 and 5, it appears that the location on the bar (spreading vs. fixed area) can potentially influence the survival rate of seedlings from 1 year to another. As mentioned previously, in the fixed area (Hill Smith groups 2 and 4) the number of plots with seedling survival are higher as well as the survival rates (29.4 and 43.1% for the fixed area vs. 1% for the spreading area). These results are not in line with the ANOVA results (no significant differences in seedling densities nor in seedling survival between the fixed and spreading area). Nevertheless, these latter should be interpreted with care in the present study. We assume that the robustness of the dataset is weak for such statistical tests (92.3% of seedlings died between 2013 and 2014).

Table 3 Highest values of each process for which a portion or all seedlings survived

Processes	Units	Fixed area	Spreading area
Uprooting (Type I)	$m^2.s^{-2}$	2.30	no plot
Erosion (Type II)	m	−0.10	−0.20
Burial (Type III)	m	0.07*	no plot
Erosion – Burial (Combination)	m	−0.10*	−0.35
	m	0.15	0.60

The asterisks refer to scour chains measurements with 0.01 m accuracy. For combination in the fixed area, the maximal stresses tolerated by seedlings do not refer to the same plot

Fig. 6 Phasing of erosion (blue arrows) and deposition (red arrows) processes between 2013-F1, F1-F2 and F2–2014 on vegetated plots (x-axis). The three successive arrows refer respectively to elevation variation documented using bathymetric and topographic surveys. "SC" corresponds to scours chains results. The black crosses indicate the absence of sediment movement. Plots named I.number and A.number respectively refer to initial and additional plots



Influence of Seedling Variability

Abiotic processes led to overall 92.3% of the mortality on the bar but several plots showed different survival rates although physical conditions were similar. At the plot scale, sensitivity of seedlings to prevailing abiotic conditions can be modulated by individual biological factors especially anchoring characteristics such as root depth, strength, and shoot/root ratio and characteristics (Manners et al. 2015; Wintenberger 2015).

First, the flexibility of the shoot of the young seedling could decrease the drag force applied on it (Crouzy et al. 2013). Secondly, the strength and depth of root anchorage of seedlings could be an important factor influencing the spatial pattern of survival.

In short, the balance between the drag force applied on the shoots and the strength of the root system (with combined effects of architecture, biomass, and root structure) is a key factor determining survival ability of the seedlings (Wintenberger 2015). Although Karrenberg et al. (2003) studied the anchorage of saplings and cuttings of *Populus nigra* an accurate understanding of seedling resistance against uprooting is required. The root growth of riparian seedlings, including *Populus nigra*, has been experimentally studied to quantify the growth rates required to survive multiple water table declines (Segelquist et al. 1993; Van Splunder et al. 1996; Guilloy et al. 2011) but results are difficult to transpose to a field study due to discharge fluctuation.

Suggestions for Future Research and Application

The present study highlights the complexity of seedling survival in a highly disturbed environment influenced by physical fluvial stresses, specifically in terms of (i) relative contribution and phasing of those stresses during flood events and

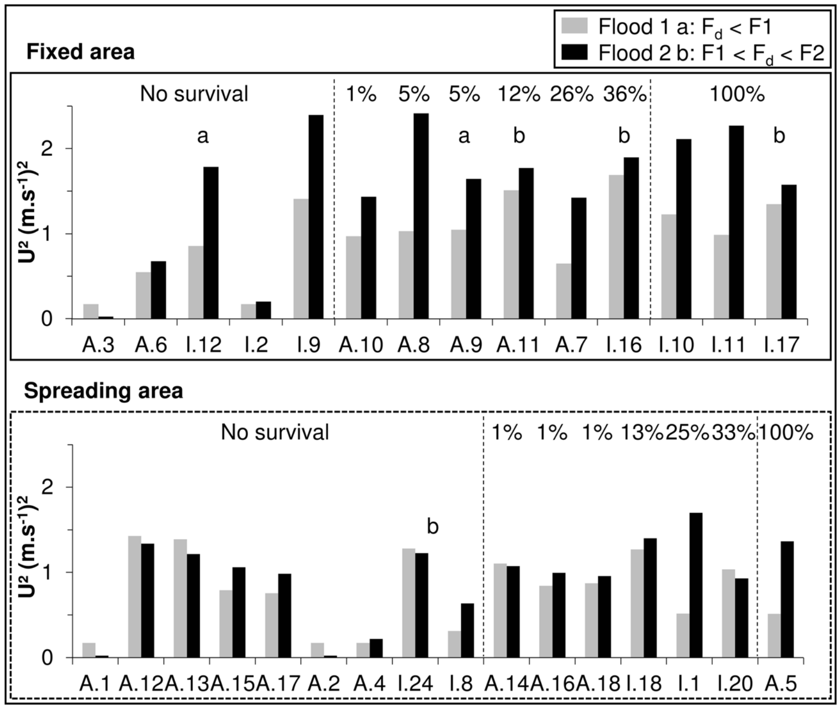


Fig. 7 Seedling survival as a function of square velocity (assumed to be representative of the drag force)

(ii) in terms of individual biological adaptation of seedlings. Some of these points remain a challenge for future studies (Corenblit et al. 2013; Wintenberger 2015).

The first point to be tested is relative to the role of the root system. Investigation of the *Populus nigra* root system (growth, architecture) for several environmental conditions, grain size and nutrient availability for example, are needed for a better understanding of the establishment of seedlings during the first year. Wintenberger (2015) showed that the length of the root system of *Populus nigra* seedlings coming from seeds from two distinct mother trees varies from 0.15 to 0.4 m (Fig. 8c) for the same environmental conditions without hydric-stress. Knowledge about the growth of the root system could feed numerical models and improve their accuracy to simulate interactions between vegetation and fluvial morphological trajectory (Bertoldi et al. 2014).

The second point is related to the threshold conditions of plant resistance to burial stresses. These conditions depend on the species, the age of the plant (Maun 1998; Levine and Stromberg 2001), timing of burial in the vegetative cycle (Johnson 1994) and burial characteristics (depth, frequency). However, the ability of seedlings to sprout after burial is not fully understood (Fig. 8a and b) even though this could be an important driver of seedling survival along channel margins and on bars.

The third point pertains to the effect of coarse sediments on flow resistance, turbulence near the bed, and possible protection of seedlings. The protective role of armor layers on sublayer sediments has been known for a long time (Church et al. 1987; Parker and Sutherland 1990; Vericat et al. 2006) but studies investigating the role of these armors on overlying flow conditions are rare (Packman et al. 2006; Cooper et al. 2018) and do not integrate their effect on seedling survival. Correlated to this point, testing the role of local morphodynamics (fixed and spreading areas) on seedling survival should be carried out in a wider study that integrates several alluvial bars to validate this hypothesis.

The last point to be investigated should be to differentiate the role of migrating (free) bars and non-migrating (forced bars) on pioneer vegetation survival and on ecological succession. The hypothesis here is that, for classical hydrological conditions, free bars should permit the recruitment of seedlings but rarely their survival (in comparison with non-migrating bars).

Research suggestions proposed above could contribute to a better management of large and low-gradient sandy-gravel bed rivers affected by pioneer woody vegetation development. The determination of stress thresholds endured by seedlings is of interest for process-based restoration projects using artificial floods to manage vegetation in river beds (Jourdain et al. 2017).

On the other hand, *Populus* riparian species should be studied as it constitutes the dominant vegetation of the active floodplain in north temperate zone rivers (Malanson 1993), and is considered to be one of the most threatened tree species in Europe as a result of habitat degradation, demographic pressure and lack of genetic diversity.

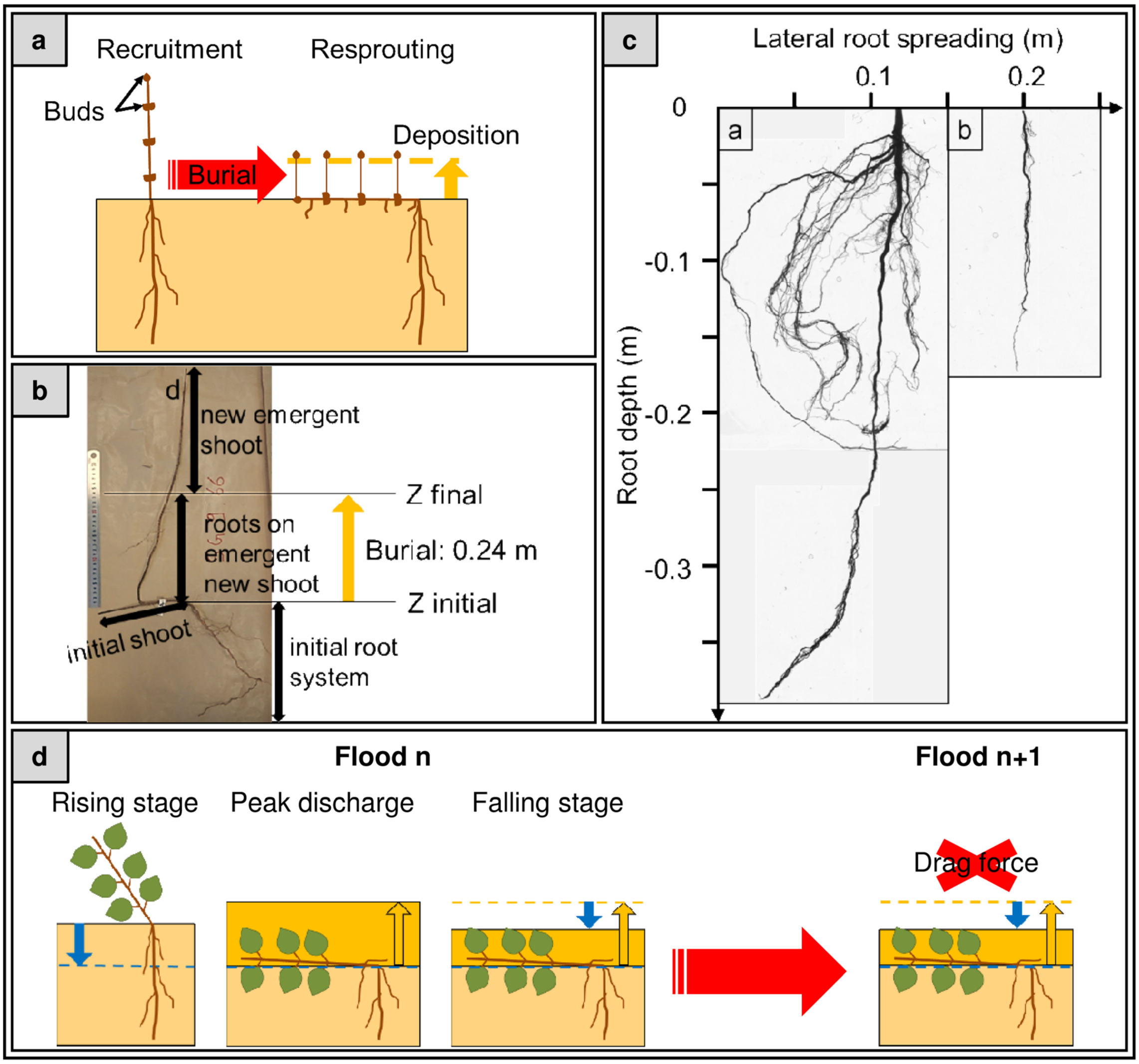


Fig. 8 **a** Potential response of a *Populus nigra* seedling on burial stresses. **b** Observed response of a 1 year burying under 0.25 m of sand, occurring after the first growth period, of a *Populus nigra* seedling: one shoot emerged, the buried part of this new shoot has roots and the emergent part has buds. **c** Illustration of the diversity of root growth. Two root systems of *Populus nigra* seedlings (aged of 260 days) grown from seeds coming from the same female tree, in the same controlled conditions in a sand substrate. The associated aerial growth are 40.3 cm (**a**) and 10.9 cm (**b**). **d** Influence of the temporal succession of processes

Conclusion

This field based study linked bar morphodynamics during floods and survival of *Populus nigra* seedlings for the first time in a quantitative manner. It was also able to provide quantitative data of resistance of seedlings to prevailing abiotic conditions. The working hypothesis for this study was that non-migrating bars present in relatively large and low-gradient sandy-gravel bed rivers constitute a preferential area for the survival of riparian seedlings such as *Populus nigra* subjected to flood stresses occurring during the first year after recruitment. Detailed field surveys lead us to the following conclusions:

– sediment texture and initial plot elevation both influence initial seedling densities, with higher densities on finer textured sediments (relative to coarse) and at higher plot elevations;
– stresses applied on seedlings depend on non-migrating bar dynamics namely phasing of erosion and deposition processes, grain size, sediment supply, and flow velocity;
– the relative contribution of three types of processes leading to mortality of seedlings during floods was identified and quantified, (i) uprooting by drag force, (ii) uprooting by erosion of sediments and drag force, and (iii) burial. All these processes can be combined during flood events; this combination explains more than 90% of the mortality on the bar studied;
– the combination of individual stresses (drag force, erosion and burial) complicates the determination of seedling

survival thresholds which depend on the combination and succession of the individual flow stresses during floods.

We did find large differences between the fixed and spreading areas with mean survival values 29 to 41 times higher on the fixed area but because of a large global (fixed and spreading areas) mortality these differences were not statistically significant.

Future investigations should be carried out to validate the hypothesis that spreading or fixed areas can influence seedling survival at the bar scale (Figs. 3 and 5). Additionally, the effect of coarse grain size on survival rates of seedlings during floods was not statistically shown in this study. However, evidences presented highlight that testing the role of coarse particles on substrate stability and on possibly increased flow resistance near the bed (leading to reduction of the drag force applied on seedlings) would be of interest.

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