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► To cite this version:

Dov Jean-François Corenblit, Johannes Steiger, Gaspard Charrier, José Darrozes, Virginia Garófano-Gómez, et al.. Populus nigra L. establishment and fluvial landform construction: biogeomorphic dynamics within a channelized river. Earth Surface Processes and Landforms, 2016, 41, pp.1276-1292. 10.1002/esp.3954 . hal-01381848

HAL Id: hal-01381848

<https://hal.science/hal-01381848>

Submitted on 10 Jul 2024

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***Populus nigra* L. establishment and fluvial landform construction: biogeomorphic dynamics within a channelized river**

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Abstract

Populations of the riparian pioneer species *Populus nigra* L. which establish on alluvial bars within river channels modulate sediment dynamics and fluvial landforms. Dense cohorts of *P. nigra* have successfully colonised gravel bars along the channelized river Garonne, France, during the last 20 years and have enhanced the vertical, lateral and longitudinal development of the bars. During this period, the geomorphic characteristics of wooded bars on this laterally stable river are observed at two study sites to be closely linked to the spatial distribution and intensity of establishment and resistance of different cohorts of *P. nigra*. Furthermore, *P. nigra* recruitment and establishment dynamics are controlled by engineer effects of this same species. This causal relationship is suggested by a strong structural correlation between key geomorphic and biological variables measured *in situ* and characterised with a set of four aerial photographs captured between 2000 and 2010. The emergence of wooded point bars, which are discrete biogeomorphic units, over the studied period, appears to result from a specific biogeomorphic positive feedback of matter aggregation and vegetation establishment related to sediment trapping and stabilisation by pioneer engineer plants. Sediment trapping appears to improve their growth performance and resistance to hydrodynamic forces. We consider the resultant biogeomorphic units as functional from an ecological point of view because *P. nigra* enhances (i) its own inherent capacity to resist

hydrogeomorphic disturbances, and (ii) its resilience capacity as a result of successful sexual reproduction, especially downstream of mature poplar stands.

Keywords: fluvial landform, biogeomorphology, *Populus nigra* L., vegetation establishment, ecosystem engineer

Introduction

Interactions between woody plant establishment and hydrogeomorphic processes lead to the emergence of diverse types of biogeomorphic units within river channels such as wooded bars, islands and floodplains (Corenblit *et al.*, 2009; Osterkamp and Hupp, 2010; Gurnell *et al.*, 2001; Gurnell, 2014). In particular, it has been shown that in large, energetic rivers the construction of fluvial landforms can be enhanced by living woody pioneer riparian species that are well adapted to hydrogeomorphic constraints, stabilize substrate with their root systems (Pollen-Bankhead and Simon, 2010), and trap sediment with their aerial structures (Rodrigues *et al.*, 2007). Corenblit *et al.* (2014) suggested that in the case of meso-scale biogeomorphic units, such as wooded point bars (*sensu* Nanson, 1980: a point bar is a body of sediment within the channel against the convex bank of a bend) with a length of a few hundreds meters, the longitudinal and transverse variation of hydrogeomorphic parameters (e.g. hydrogeomorphic connectivity, relative altitude, texture and fine sediment thickness) and biological parameters (e.g. individual plant phenotype, population physiognomy and community assemblage) may be strongly related to the nature and intensity of feedbacks between these abiotic and biotic parameters (see also Bendix and Hupp, 2000; Tabacchi *et al.*, 2000).

Since the late 1980s, the biogeomorphic approach (*sensu* Viles, 1988, 2011) has contributed greatly to the integration of the impacts of hydrogeomorphic processes on riparian vegetation and the effects of vegetation on river geomorphology into conceptual (e.g. Bendix and Hupp, 2000; Corenblit *et al.*, 2007) and numerical (e.g. Bertoldi *et al.*, 2014; Vargas-Luna *et al.*, 2015) models. The quantification of reciprocal adjustments between riparian vegetation and fluvial geomorphology at diverse spatio-temporal scales, from individual plants to entire communities, has become a fundamental issue for understanding river dynamics and for developing sustainable river management strategies using ecological engineering (Corenblit *et al.*, 2011).

Recognition of the key ecological engineering role of pioneer woody plant species such as *Populus* and *Salix* spp. which modify fluvial landforms in the northern hemisphere needs to be accompanied by quantification of the structural relationship between the physiognomy (e.g. number, diameter and size of stems) of these species and the properties of landforms (e.g. relative elevation above the low water table, fine sediment thickness and texture, basal elevation of coarse sediments) with which they interact.

The North-European black poplar (*Populus nigra* L.) has been recognized to be an engineer species (*sensu* Jones *et al.* 1994) capable of modulating riparian ecosystem structure and function within rivers through its modification of hydrogeomorphic processes and fluvial habitat (Edwards *et al.*, 1999; Gurnell and Petts, 2006; Corenblit *et al.*, 2014). *P. nigra* is a pioneer woody riparian plant species belonging to the Salicaceae family that has evolved over millions of years within river corridors (Eckenwalder, 1996). It is a heliophilous and *r* strategist species (*sensu* Grime, 2001) colonizing bare alluvial surfaces and abandoned channels within river systems (Edwards *et al.*, 1999; Stella *et al.*, 2011; Gurnell, 2014), but poplar species only colonize river corridors in significant numbers where bare alluvial surfaces are available close to surface water and the alluvial water table (Karrenberg *et al.*, 2002). Seed release and dispersal of *P. nigra* occurs in late spring, coinciding mostly with high water flows and with the concomitant formation of alluvial bars within the river channel. Seedlings establish quickly on moist fine grained alluvial surfaces exposed during the recession of river levels in late spring and early summer. The optimal 'recruitment box' (i.e. suitable spatio-temporal domain for germination, initial growth and survival) for seedlings of *P. nigra* is defined according to four criteria (Mahoney and Rood, 1998): (1) climatic and hydrogeomorphic conditions that control the formation of alluvial bars within the river channel; (2) sediment texture that controls moisture retention; (3) topography that controls surface-subsurface hydrological connectivity and degree of exposure to mechanical stresses imposed by flowing water; and (4) the hydrological regime that controls the water level at the ground surface and in the alluvial aquifer.

In suitable climatic and hydrogeomorphic conditions, young individuals of *P. nigra* anchor firmly and grow quickly on the alluvial sediment surface. Following recruitment, young cohorts (i.e. population of individuals of the same age), often comprising thousands of saplings growing in strips next to the water channel or in compact mats across the low surfaces of alluvial bars, considerably increase substrate cohesion with their roots. Young poplars growing in dense cohorts drastically increase their resistance to shear stress during the first 2-3 years of establishment (Corenblit *et al.*, 2014). During this period, their flexible multi-stemmed morphology traps large amounts of fine sediment and organic matter and displays very strong resistance and resilience to hydrodynamic forces, erosion and sediment burial (Gurnell, 2014). Thus, dense cohorts that colonise alluvial bars promote the rapid construction of wooded alluvial bars, benches and islands, possibly representing positive niche construction (*sensu* Odling-Smee *et al.*, 2003) by the engineer species (Corenblit *et al.*, 2014).

This positive feedback of matter aggregation and vegetation establishment represents a suite of mechanisms by which the pioneer plants acting together at the patch scale improve their anchorage and growth performance, since they can develop new shoots from the adventitious roots and fragments as the plants become buried (Barsoum *et al.*, 2004; Francis and Gurnell, 2006). This increase in

aboveground and belowground biomass allows the engineer plants to continue to trap more sediment and organic matter until the stabilized and elevated topographic surface becomes disconnected from quasi-annual floods. We presume that it is during this biogeomorphic critical stage that the physiognomy of the cohorts changes from being dominated by a flexible multi-stemmed architecture to an architecture dominated by a single semi-rigid stem with a taller canopy.

It has been observed that flow regulation favours the establishment of pioneer tree species such as *Populus spp.* on gravel bars and subsequent channel narrowing (e.g. Johnson, 1994; Friedman et al., 1998, Takahashi and Nakamura, 2011). In the case of the channelized river Garonne, France, such an evolution has been observed commencing at the end of the 1990s, in which plant colonization has led to the construction and stabilisation of densely wooded bars within the river channel. We hypothesise that in the case of the river Garonne, flow regulation plays a minor role in this evolutionary trajectory compared to the artificial lateral stabilisation of the channel. Furthermore, we suggest that the geomorphologic characteristics of the wooded bars are closely linked to the location and intensity of establishment of cohorts of *P. nigra* which are currently the predominant control on fine sediment retention and the resistance of these landforms to erosion by water.

We present the results of a biogeomorphic study undertaken on two wooded point bars that are typical of the river Garonne in its piedmont zone. The objective of the study was to test at a unit (i.e. point bar) scale whether the interaction between vegetation and hydrogeomorphic processes leads, in the interval between destructive floods, to a positive feedback of fluvial landform construction and vegetation establishment. The study aimed (1) to reveal the signature of this positive feedback between vegetation and geomorphic dynamics using statistical relations between key geomorphic and biological variables and (2) to define a formal causality between (i) the ability of *P. nigra* cohorts to establish on bare point bars; (ii) the resistance of the established cohorts to floods; (iii) the effects of the established cohorts on bar geomorphology; and (iv) the physiognomic responses of the cohorts to landform construction and stabilisation.

Material and methods

Study sites

Field measurements were undertaken during the winters of 2010, 2011 and 2012 on two wooded point bars located within a 35 km long, essentially homogenous reach of the river Garonne between Toulouse (43°36'32"N; 1°24'45"E; 132 m a.s.l.) and Verdun-sur-Garonne (43°51'17"N; 1°14'35"E; 95 m a.s.l.), France (Figure 1).

The catchment area upstream from Verdun-sur-Garonne is 13 730 km². The mean channel gradient in the study reach is 0.001 m m⁻¹ and the channel width deviates little from 150 m. Sinuosity of the entire reach is low with a mean value of less than

1.3. The mean annual discharge of $193 \text{ m}^3 \text{ s}^{-1}$ has a unit stream power of 80 W m^{-2} (Steiger *et al.*, 2001), attesting of a high capacity for sediment transport and erosion. According to the 'Banque Hydro' (<http://www.hydro.eaufrance.fr>), flood return periods (T) calculated for 42 years at Verdun-sur-Garonne for daily (Qd) and flood peak maximum (Qm) discharges ($\text{m}^3 \text{ s}^{-1}$) are: T₂ Qd 1400, Qm 1800; T₅ Qd 2100, Qm 2700; T₁₀ Qd 2500, Qm 3200; T₂₀ Qd 2900, Qm 3700; T₅₀ Qd 3400; Qm 4400.

The river was strongly impacted by human activities during the second part of the 20th century. It exhibited free meandering dynamics until the 19th century (Décamps *et al.*, 1989). However, industrial gravel mining of the channel bed between the 1960s and 1980s, combined with the construction of dams upstream of Toulouse and in the Pyrenees, and extensive outer bend bank protection, particularly during the second half of the 20th century, has led to lateral stabilization of the river channel, a drastic reduction in coarse sediment supply, and channel bed incision of 1 to 3 m (Steiger *et al.*, 1998, 2000).

Following the cessation of in-channel gravel mining at the end of the 1980s, gravel bars, mainly point and lateral bars, were once more able to adjust to sediment supply from local bank erosion and longitudinal transfer within the reach downstream of Toulouse. However, as also observed by Dufour *et al.* (2007) on the river Drôme, France, river channelization led to a confinement of pioneer woody riparian vegetation with the loss of obligate phreatophyte species such as *Salix alba* L. and the dominance by *P. nigra* which is a more drought-tolerant species (James, 1996). During the 1990s, empirical investigations carried out on these gravel bars showed the successful recruitment and establishment of *P. nigra* cohorts (Langlade and Décamps, 1995; Guillois *et al.*, 2002). Today, these cohorts form dense quasi-monospecific stands.

Two representative wooded point bars were selected for this study: site 1 ($43^{\circ}47'01''\text{N}$; $1^{\circ}17'21''\text{E}$; 100 m a.s.l.) is 500 m long and 80 m wide (Figure 2a); site 2 ($43^{\circ}44'25''\text{N}$; $1^{\circ}19'12''\text{E}$; 106 m a.s.l.) is 380 m long and 60 m wide (Figure 2b). These point bars were heavily colonized by successive *P. nigra* cohorts during the 1990s. Both point bars are separated from the floodplain by chute channels and are frequently submerged during annual floods, inducing strong reciprocal interactions between vegetation establishment and hydrogeomorphic processes.

Field analysis

The objective of the field analysis was to define the relationship between *P. nigra* establishment and fluvial landform construction within this channelized reach. Correlations between parameters describing geomorphology and the physiognomy of *P. nigra* cohorts supported testing of our hypotheses of a positive biogeomorphic feedback of vegetation growth and landform construction.

For each study site, sampling was conducted along a set of 8 transects oriented perpendicular to the main channel (Figure 2) to allow analysis of biogeomorphic

correlations in both longitudinal and transverse directions across the biogeomorphic units. Patterns observed in these directions are indicative of the degree of exposure to hydrodynamic forces (i.e. from upstream to downstream and from the main channel to the floodplain) and changes in their characteristics can be investigated over time (i.e. sequence of landform construction and cohort establishment).

Measurements of the geomorphic and biological parameters were undertaken within contiguous 25 m² plots (a total of 116 plots) aligned along the transects (Figure 2).

A DGPS (DG14™ from Ashtech) with centimetre precision was used to define a georeferenced point at the beginning of each transect towards the main channel. The location and altitude (m) of each plot masked by vegetation was defined using a total station (TS02 FlexLine Power 7 from Leica; error <1cm) benchmarked to the georeferenced starting point.

Within each sample plot, a telescopic soil auger (Edelman from Zimmer) was used to collect six replicate measurements (a total of 699) of (i) the depth of fine sediment (sand and silt) deposited on top of the coarser (gravel and cobble) gravel bar sediments and (ii) sediment samples for grain size analysis. In addition, 10*20 cm² sediment samples were collected at each georeferenced point every 50 cm in the vertical (a total of 240 sediment samples) for granulometric analyses.

In the laboratory, the sediment samples were dried in an oven at 70°C for 6 hours, ground and then manually sieved to assess 9 classes of particle size (in mm): >4; [4 - 2]; [2 - 1.25]; [1.5 - 0.63]; [0.63 - 0.315]; [0.315 - 0.250]; [0.250 - 0.100]; [0.100 - 0.050]; <0.050. Gradistat 4.0 software (Blott and Pye, 2001) was used to calculate parameters of the particle size distribution. Sediment texture of the samples proved to be highly homogeneous both at the scale of the individual biogeomorphic units and between sites, with an average gravel content of 4.70% by weight and coarse sand, medium sand, fine sand, silt, and clay contents of 9.85%, 22.41%, 45.31%, 15.61%, and 2.12%, respectively. As a result of this homogeneity, particle size properties of the sediment were excluded from further analysis.

The total number of *P. nigra* stems rooted into the gravel bar and their diameter (mm) were measured at 1.20 m from the ground level in each plot using precision callipers. The age of the trees was determined by dendrochronology. At site 1 during January 2012, 18 wood sections (disks) were sawn from the stems of trees located across plots with diameters ranging from 5.5 to 15.6 cm. At site 2 during March 2012, a further 28 wood disks were sawn from trees located across the plots with diameters ranging from 1.7 to 15.9 cm. Whole tree disks (total of 46) were taken because many of the stems were too narrow to be sampled without splitting using an increment borer. The wood disks were dried, sanded (sand papers: P80 (200 µm) to P1200 (6 µm)), and two perpendicular lines were drawn on each disk following the larger and narrower diameters. Tree ring widths were measured on these 4 half diameters using a tree-ring measurement station (LINTAB5™ from Rinntech), although on two broken disks, it was only possible to obtain measurements from 2 half diameters.

Two sets of measurements were taken to correct the age of trees determined at 1.20 m to that at the root collar (ground level). First, the diameter of 85 randomly selected stems was measured at ground level within each study site (total of 170 samples). Second, the correlation between humid (i.e. field-measured) and dry (i.e. after drying in the laboratory) disc diameters was determined from a sample of 27 wood disks. Based on these two data sets, it was possible to construct an age-diameter relationship from which the age of all trees in the plots could be estimated at their root collar according to their diameter.

Following previous determinations of sediment accretion rates within river margins that have been based on tree-ring analysis (e.g. Hupp and Morris, 1990; Friedman *et al.*, 2005), we determined mean sedimentation rates of the two study sites using our dendrochronological analysis. The sedimentation rates were calculated according to 4 classes of poplar age: 0-5; 5-10; 10-15; and 15-20 years. The mean fine sediment depth (m) was divided by the mean age (year) of poplars calculated for each class to obtain the mean annual rate of sediment deposition in m yr^{-1} .

Statistical analyses

The variability in three geomorphic variables (i.e. relative elevation, fine sediment thickness, basal height of the coarse sediments) and three biological variables (i.e. stem density, diameter and height) was analysed (i) longitudinally, and (ii) transversely (i.e. from the main channel to the chute channel) for each point bar.

The significance of difference among transects and plot lines was tested using the non-parametric Kruskal-Wallis test. The dependency between biological (y) and geomorphic (x) variables was explored by estimating linear and non-linear regression models. Multivariate exploratory analyses were used to obtain a qualitative synthetic view of the biogeomorphic structure of the two study sites. These analyses included all six geomorphic and biological variables and used (i) a Hierarchical Cluster Analysis (HCA based on Ward's cluster algorithm) for defining groups; (ii) the Kruskal-Wallis test to identify the statistical significance of differences between groups formed by the HCA; and (iii) a principal component analysis (PCA) on normalized data (Z-scores) to interpret the formation of the groups according to two biogeomorphic synthetic gradients representing linear combinations of the original variables.

All statistical analyses were performed using the software PastTM v. 3.04 (Hammer *et al.*, 2001)

Spatial analysis

The objective of two- and three dimensional spatial analyses was to understand and quantify the biogeomorphic spatio-temporal pattern of *P. nigra* establishment and related landform construction. Four different aerial photographic missions (Table 1)

were used to reconstruct the evolution of the biogeomorphic units at the two study sites. Aerial photos were georeferenced and orthorectified for classical GIS analysis in 2D using ArcGIS 10.0 and MapInfo 9.0. Relative percentage (according to the length and width of the bars in 2010 which represent 100%) of wooded bar expansion was calculated upstream and downstream along the longitudinal axis and in the direction of the main channel and the chute channel along the transverse axis.

Non-orthorectified stereo-pairs of these aerial photographs were also processed using LPS (Leica Photogrammetry Suite) software for 3D photogrammetric analyses. The photogrammetric analyses permitted highly accurate reconstruction (<50 cm; see Vautier *et al.*, this issue) of vertical vegetation growth. Digital surface models (DSM) were extracted from the imagery at each date using the LPS Automatic Terrain Extraction (ATE) algorithm (Image matching algorithm). The automatized procedure of DSM extraction generated errors that were corrected using the Terrain Editor modulus of LPS. Cloud points were exported in 3Dshape format and then imported into ArcGIS 10.0. The raster Digital terrain models (DTM) and DSMs were generated through an interpolation procedure using the IDW (inverse weighted distance) algorithm. The canopy height models (CHM) were deduced from the difference between the DSM and DTM. Maps of vegetation height at the different dates were produced with an error of approximately 0.5 m. All details of the procedure are described and analysed by Vautier *et al.* (this issue).

Results

Longitudinal and transverse gradient analysis

Longitudinally (i.e. from upstream to downstream across the 8 transects; Figure 3), we observed first an increase and then a decrease in relative elevation, fine sediment depth and the basal elevation of coarse sediment. Biological variables showed a decrease and then an increase in the number of stems, and an increase and then a decrease in stem diameter and canopy height. Statistically significant differences were found among the 8 transects suggesting significant downstream variations in the analysed geomorphic and biological variables (Table 2).

Concerning transverse variations (i.e. from the main channel to the chute channel; Figure 4), we noticed a general pattern of asymptotic curves, whereby variables initially increased or decreased at increasing elevation away from the main channel and then levelled off towards a relatively stable value. Two geomorphic variables, fine sediment depth and the basal elevation of coarse sediment, showed an initial increase. Of the biological variables, the number of stems showed an initial decrease, whereas stem diameter and canopy height showed an increase. Kruskal-Wallis tests indicated a statistically significant difference between the lines of plots according to these variables at site 1 but not at site 2 (Table 2).

Correlations between geomorphic and biological variables

Regression models indicated that a significant percentage of the variability in the biological variables was explained by the geomorphic variables (Figure 5), with the models displaying a similar slope for sites 1 and site 2. There was a tendency for the number of stems to decrease and the stem diameter and canopy height to increase with an increase in relative elevation and in fine sediment thickness.

Mean annual sediment deposition rates

Dendrochronological analysis was undertaken to estimate the mean age of poplars in each plot according to the mean stem diameter (Figure 6). Stem diameter at ground level (basal diameter, y) was regressed on the diameter close to the breast height (1.20 m height, x) to yield the following strong relationship: $y = 1.0653x + 0.9734$; $R^2 = 0.99$; $p < 0.0001$. A further strong relationship was estimated when dry diameter (y) was regressed on humid diameter (x): $y = 0.9413x + 0.0494$; $R^2 = 0.99$; $p < 0.0001$. These two regression relationships were used to correct stem diameters measured in the field to the dry basal diameter. A power model was then estimated between age (in years: y) and dry diameter (in mm: x) of the dendrochronological samples (Figure 6). This model was used to obtain the (basal) age of each sampled poplar within the plots, from which the mean annual sedimentation rates on the two sites could be estimated.

Deposited sediments on the two study sites were composed mainly of fine and medium sand. Mean annual sedimentation rates related to the different poplar age classes (0-5; 5-10; 10-15; 15-20 years) were: 0-5 years = none; 5-10 years = 0.089 m yr⁻¹; 10-15 years = 0.079 m yr⁻¹; 15-20 years = 0.041 m yr⁻¹; mean = 0.077 m yr⁻¹ on site 1 and 0-5 years = 0.028 m yr⁻¹; 5-10 years = 0.034 m yr⁻¹; 10-15 years = 0.054 m yr⁻¹; 15-20 years = absent; mean = 0.042 m yr⁻¹ on site 2. Kruskal-Wallis tests indicated significant differences between sedimentation rates according to tree age class (Site 1: $H = 11.73$; $p = 0.0083$; site 2: $H = 21.10$; $p = < 0.0001$)

Exploratory analysis of the biogeomorphic units

Hierarchical Cluster Analysis (HCA) was applied to the set of six geomorphic and biological variables. Five main groups were identified from the cluster dendrogram (Figure 7). Each group displayed a different biogeomorphic structure, which broadly reflected the poplar stand age or development stage (Figure 8; Table 3). PCA undertaken on the same set of combined geomorphic and biological variables showed a clear gradient in the five groups along axis 1, again reflecting mainly biogeomorphic age or development stage. Scores along this axis discriminate (i) young groups (G1 and G2) characterised by low relative elevation, a thin layer of fine sediment, low basal elevation, numerous stems of small diameter and a relatively

low canopy height; (ii) an intermediate group (G3) with intermediate values of these properties, and (iii) mature groups (G4 and G5) with a low stem density, and larger stem diameter and a relatively tall canopy (Figures 8 and 9; Table 3).

Spatial analysis

A GIS-based analysis of the spatial extent of the vegetation cover from air photographs between 2000 and 2010 showed clear spatial extension of vegetation growth on the point bars (Figure 10; Table 4). On site 1, the vegetated area was 4 614, 6 920, 15 388, and 21 296 m² in 2000, 2002, 2006, and 2010, respectively, whereas on site 2 it was 1 831, 2 382, 5 594 and 8 292 m² in the same years. The ratio between wooded surface gain and loss showed a dominance of a net gain on the two study sites (Table 4) despite floods that were theoretically capable of achieving morphological change (i.e. with a return period of 2 years or more, Figure 11). Furthermore, the GIS analysis shows that the construction of the wooded point bars is accompanied by the development of spatially distinct, homogenous, *P. nigra* cohorts corresponding to different generations of recruitment and establishment, and that there is a clear tendency for sediment accretion and vegetation establishment on the bars to progress downstream and, to a lesser extent, in the direction of the main channel (Figure 12).

Discussion

Our results suggest a positive feedback between *Populus nigra* establishment and fluvial landform construction within the laterally stabilized channel of the river Garonne. The general pattern of co-adjustment between the geomorphic and biological variables appears to be similar between the two study sites which are representative of the general situation within the river reach. This apparently generalizable pattern corresponds to a characteristic spatio-temporal sequence of matter and energy organisation, suggesting that biogeomorphic units emerging from the interaction between *P. nigra* and geomorphic dynamics are a functional unit in an ecological sense.

Fluvial landform and P. nigra physiognomy show a predictable pattern of co-adjustment

During the last 20 years, following the cessation of gravel mining from the channel bed, there has been a progressive growth in the two studied point bars, suggesting that most floods have driven a net delivery of sandy sediment which has been retained mainly within the wooded areas. Steiger and Gurnell (2002) quantified sedimentation rates on a single point bar of the same river reach during individual flood events at the beginning of the 1990s and showed high accumulation rates of

sand and silt of up to 160.1 kg m^{-2} with typical values of 20 to 40 kg m^{-2} inside areas of riparian shrubs and trees. Based on their estimate of mean bulk density of 1 g cm^{-3} , these values translate into 0.02 to 0.04 m depth of fine sediment deposited in individual flood events. Such values are consistent with the present observations, since we estimate that the current rate of vertical fine sediment accretion is 0.077 m yr^{-1} on site 1 and 0.042 m yr^{-1} on site 2. These rates imply that sand and finer sediment trapping by dense woody vegetation can lead to an increase in ground surface elevation of from 1 to 1.5 m in 20 years. Placing this into the context of the evolution of the study sites, the GIS analysis has revealed strong resistance and resilience of woody vegetation since the 1990s at the biogeomorphic unit scale (i.e. the entire wooded point bar; Figure 10; Table 4), that has interacted with a predominantly constructing rather than remobilising hydrogeomorphic disturbance regime. In addition to the finer sediments, coarse sediment (gravel and cobble) is occasionally deposited on point bar heads during the largest floods, such as the 20 year event of June 2000 when the peak discharge was close to $3000 \text{ m}^3 \text{ s}^{-1}$.

Significant differences in sedimentation rates measured within tree cohorts of different age (i.e. 0-5; 5-10; 10-15 and 15-20 years) suggest that, in addition to the initial variation of sedimentation rates on point bars that is represented by topographic heterogeneity reflecting changes in plan morphology, discharge and sediment supply (Steiger and Gurnell, 2003; Piégay *et al.*, 2008; Rice *et al.*, 2009), sedimentation rates vary simultaneously under the control of the engineer poplars which modulate topography, changes of physiognomy and related changes in biomechanics through time.

Young cohorts (<10 years) located on low-lying point bar tails and bar sides facing the main channel are dominated by a high density of flexible stems (8 to 30 stems per 25 m^2) with a mean diameter close to 5 cm and of a mean canopy height of 6-15 m. *P. nigra* individuals subjected to mechanical stress, as is particularly the case for these low-lying individuals, develop a root architecture that improves resistance to uprooting (Scippa *et al.*, 2008), which also contributes to sediment reinforcement. Furthermore, a significant proportion of *P. nigra* stems of this age class in the study reach are clones forming units of 2-4 trees with the same genotype and growing in close proximity (Barsoum *et al.*, 2004; see also Rood *et al.*, 1994). Such new shoots developing from the numerous adventitious roots growing laterally (suckers) also increase surface roughness and so enhance a positive feedback of sediment and organic matter trapping, landform stabilization and vegetative growth (Corenblit *et al.*, 2014). Rood *et al.* (2011) noted such a positive biogeomorphic feedback associated with another riparian Salicaceae species, *Salix exigua* Nutt., which traps sandy sediments on alluvial bars in the rivers of the SW USA.

Our observations also indicate a threshold of bar elevation of up to at least 1 m above low flow stage, where the physiognomy of the cohorts changes from a bushy, multi-stem form towards trees with a single rigid trunk of mean diameter >15 cm, as the canopy height increases from 15 m to over 20 m. Within riparian systems, this

change in tree physiognomy may be a consequence of decreased exposure to annual and quasi-annual floods and a related increased intraspecific competition for light. At this threshold stage, stem density drastically decreases to less than 1 per 25 m² as most of the pre-existing stems become senescent, rigid and dry, so that they break easily and are removed during floods. Consequently, surface roughness and sediment trapping decrease as a cohort attains the mature growth stage. This represents a strategy shift of poplar at the cohort (i.e. population) scale from high resistance (both tolerance and avoidance to hydrodynamic forces *sensu* Puijalón *et al.*, 2011) to competitive behaviour (Corenblit *et al.*, 2014).

Shelter effect of upstream cohorts for younger downstream cohorts

Our results also suggest that the positive biogeomorphic feedback of vegetation growth and landform construction is favoured and reinforced through a shelter effect provided (i) by the first generations of cohorts growing to form a resistant dissipative structure at the upstream end of the point bar (Figure 10) and at the same time (ii) new generations of young poplars establishing regularly within the gaps created during large floods. Surian *et al.* (2014) noted that 2.5 year and larger recurrence floods induce recurrent and important erosion of pioneer wooded islands within the active tract of the braided Tagliamento River, Italy (see also van der Nat *et al.*, 2002; Zanoni *et al.*, 2008). Such erosion observed within the active tract of rivers such as the Tagliamento and the Allier, France, occur during flow pulses (*sensu* Tockner *et al.*, 2000) when river stage is sufficiently high for flows to erode the non-cohesive sand and gravel banks of islands or floodplain (see also Edwards *et al.*, 1999). At these locations, established trees are easily undermined and eroded through lateral and vertical bank excavation (Abernethy and Rutherford, 2000). The presence of rip rap currently prevents the formation of high exposed, non-cohesive banks along the channelized river Garonne, and so lateral erosion is limited. At the same time, our spatial analysis has revealed extremely strong resistance of the studied biogeomorphic units to erosion, despite the occurrence of morphogenic floods with a return period of over 2 years in the interval between 2000 and 2010 (Figure 11). Our recent (i.e. in the years 2014 and 2015) field observations on the two study sites following our study indicate that the wooded bars remained intact following two large floods with an occurrence of about 10 and 20 years which occurred respectively in June 2013 and January 2014 (Figure 11). Even the most exposed zone at the point bar head has remained largely stable at both study sites. We explain this by the fact that, conversely to dynamic meandering (e.g. river Ain, France; Lassetre *et al.*, 2007), wandering (e.g. river Allier, France; Petit, 2006) or island braided rivers (e.g. river Tagliamento; Surian *et al.*, 2014), lateral erosion of high non-cohesive banks is currently active in very restricted areas in the channelized section of the river Garonne.

The GIS analysis indicates that when *P. nigra* cohorts establish on low-lying topographical surfaces, the threshold for complete destruction by flow is very difficult to achieve, even during floods with a recurrence interval of 20 years (e.g. June 2000; Figure 11), and so the threshold of wooded bar remobilization remains unknown, but possibly requires a minimum of a 50 year flood as was the case on the river Garonne in 1952. Such a threshold of biogeomorphic remobilisation may not be an exception in the context of sediment deficit when woody vegetation successfully establishes (Corenblit *et al.*, 2010).

Within the oldest cohorts located at the upstream face of the point bars, relative surface elevation and fine sediment thickness remain low (Figure 3), although the basal bar elevation of the coarse sediment surface is up to 0.4 m above the low water level. This indicates that gravel and pebbles are deposited in this location during large floods, but fine sediment are regularly flushed away. Furthermore, we observed that old trees are often broken and partly buried at this location and so tend to remain multi-stemmed with intermediate stem diameters and canopy heights (Figure 3). This is consistent with many *in situ* observations of poplars that are not growing on elevated non-cohesive banks, which confirm that they are highly resistant to hydrodynamic forces and are efficient in vegetative regeneration and propagation (Karrenberg *et al.*, 2003; Barsoum *et al.*, 2004; Francis *et al.*, 2004; Lytle and Poff, 2004; Moggridge and Gurnell, 2009).

It appears that the resistance threshold of *P. nigra* to total destruction may not be related to intrinsic biomechanical properties of individual plants that are able to combine tolerance (highly resistant tissues) and avoidance (flexible stems reconfiguring their morphology in the fluid) to hydrodynamic forces. Instead, it may be related to the complex relation between drag (which varies with the morphology and biomechanics of the plants and the vegetation patchiness) and sediment cohesiveness (which varies with sediment texture and structure). On the river Garonne, even if poplars are regularly damaged and partly buried in the frontal area of point bars, they resist total destruction and have a vigorous recovery, thus maintaining an active sheltering effect for downstream cohorts. This suggests that the general physiognomy of early poplar cohorts exposed to high shear stress at the front of the point bar represents a functional response that increases within-site resistance to breakage and uprooting and also enhances downstream bioprotection for younger cohorts (Corenblit *et al.*, 2014).

Upstream cohorts facilitate P. nigra recruitment downstream the point bar

Flood deposited fine sediment and moisture are crucial for the development of new cohorts of poplars within river channels (Stromberg, 1993; Johnson, 2000; González *et al.*, 2010; Stella *et al.*, 2011), and the recruitment pattern defines the locations where pioneer ligneous vegetation will engineer fluvial landforms and dynamics (Gurnell *et al.*, 2012). Sexual regeneration of *P. nigra* frequently occurred on low-

lying alluvial bars of the study reach prior to flow regulation and river channelization (Langlade and Décamps, 1995; Guillois *et al.*, 2002; Muller *et al.*, 2002). Our analysis demonstrates how this process has continued and how building and stabilizing of fluvial landforms along the present channelized river allows black poplars to be considered as ecosystem engineers (*sensu* Jones *et al.*, 1994) because they enhance the creation and maintenance of new sheltered, open, fine sediment surfaces, suitable for seedling recruitment downstream of the biogeomorphic nucleus (Gurnell *et al.*, 2005; Moggridge and Gurnell 2009). Poplar seedlings that germinate at low elevations on bare moist alluvial surfaces are only likely to survive during the first year of growth if (i) they do not face significant hydrological stress during the dry season (Guillois *et al.*, 2012) and (ii) they are not too exposed to shear stress and scour during winter high-flows (Mahonney and Rood, 1998). Bioprotection by older plants contributes to meeting criterion (ii).

Conceptual model of landform construction by P. nigra

The formation of the initial bare surface at both study sites during the late 1990s, was probably a consequence of the end of gravel extraction from the river channel. Our analysis shows that the biogeomorphic accretion nuclei at both sites grew (i) mainly longitudinally in a downstream direction within the area protected by previously recruited cohorts, and also to a lesser degree, (ii) laterally towards the centre of the channel (Figure 12). Vertical construction related to sandy sediment accretion within the wooded stands predominantly occurred between 2000 and 2010, with new generations of sediment deposition downstream of the wooded nuclei being quickly colonized by new, dense cohorts of *P. nigra*. Each new cohort trapped sediment, aggraded the bar surface and thus diverted the flow towards the opposite bank while providing shelter for fine sediment deposition and vegetation recruitment even further downstream.

Based on our observations on the river Garonne, biogeomorphic units on point bars in channelized rivers may continue to grow progressively laterally and downstream until they reach a limit imposed by the plan geometry of the stabilized channel. When this limit is attained, perhaps after 20 to 30 years, which is almost the present case on the river Garonne, the kinetic energy of floods may remain concentrated within the main channel but also the chute channel because the meander cannot translate laterally. Stella *et al.* (2011) noted that in unchannelized conditions, secondary channels (e.g. chutes) tend to be colonized by dense cohorts of *Populus* or *Salix* spp. and become incorporated into the floodplain. Our results show that in a channelized context the initial chute channel remains connected and free of vegetation for at least the first 20 years of bar evolution.

The present observations are useful for understanding channel and bar dynamics within a sinuous, channelized river. Three functional sub-units of the wooded point bar can be distinguished (Figure 13a): (i) the initial biogeomorphic nuclei forming on

the point bar head a dissipative structure and a shelter for the next generations of cohorts which (ii) established just downstream of the initial nuclei and favour (iii) downstream fine sediment deposition and thus the creation of a suitable habitat for further recruitment. The non-protected bare alluvial surfaces which forms during summer low-water levels within the immediate channel margins are also suitable for recruitment but they are less protected than the downstream (i.e. engineered) niche of regeneration of *P. nigra*. This non-engineered unit may be functional for recruitment only if no significant floods occur during the first year of growth.

The observed establishment pattern of the pioneer cohorts and related landform construction in the transverse and longitudinal directions controls meander shape and translation (Figure 13b). In our proposed conceptual model, the emergence and development of the biogeomorphic units follow four fundamental steps: (i) initial formation of a point bar following a large flood; (ii) initial recruitment on the point bar according to a suitable 'recruitment box' (*sensu* Mahoney and Rood, 1998); (iii) activation of the biogeomorphic positive feedback of landform construction and vegetation recruitment and growth; (iv) development and stabilization of the biogeomorphic units until they are reset by an exceptionally large flood in a channelized context and additionally by meander translation in a natural context. This model is consistent with flume experiments showing that vegetation establishing on point bars increases bank cohesion while diverting flow towards the opposite bank (Bennett *et al.*, 2002; Tal and Paola, 2010). It is also consistent with the conceptual model proposed by Edwards *et al.* (1999) in which *Salix* spp. and *P. nigra* establishing on point bars shape fluvial morphology and meander dynamics.

Can the biogeomorphic units be considered functional from an ecological perspective?

Fisher *et al.* (1999) suggested that feedbacks between form (i.e. at the landscape scale) and function may exist in riparian ecosystems. Recently, several authors have expressed a similar view, proposing that specific feedbacks between geomorphology and organisms may lead to the emergence of functional biogeomorphic units at the landscape scale (Phillips, 2009; Corenblit *et al.*, 2011; Steiger and Corenblit, 2012; Bätz *et al.*, 2014). 'Functional' here means that geomorphic changes under biotic control increase (i) growth performance and the chances of *within site* individuals to reach sexual maturity in good condition and (ii) sexual regeneration in the protected area created by upstream cohorts. Here, functionality implies that the biogeomorphic unit improves its resistance and resilience through characteristic feedback mechanisms between geomorphic and biological processes.

We suggest that form and function are coupled in a lagged way at the scale of the studied biogeomorphic units on the river Garonne. The biogeomorphic shift in topography and vegetation physiognomy is well illustrated by the multivariate exploratory analysis (PCA) we conducted on the geomorphic and biologic variables.

Surface aggradation and raised elevation under the control of engineer plants is accompanied by progressive disconnection from the influence of annual floods (Bendix and Hupp, 2000), and the wooded surface tends to achieve a higher elevation than would be possible without vegetation. Indeed, Bertoldi *et al.* (2011) noticed a significant difference in the river bed elevation frequency distribution among reaches of the river Tagliamento, Italy, according to the vegetated area, with the highest areas of the river channel associated with the oldest and most extensive riparian tree cover. Such divergence of the topography from its purely physical state could be considered a possible functional signature of life in the landscape (Corenblit *et al.*, 2010, 2014). Furthermore, these engineered landforms and related physiochemical changes (e.g. Bätz *et al.*, 2014, 2015) may also be functional for the engineer species, here *P. nigra*, and potentially for other plants, micro-organisms and fauna (Corenblit *et al.*, 2014).

Concluding remarks

This diachronic two and three dimensional study of two wooded point bars in combination with topographical, sedimentary and dendrochronological measurements permitted to highlight the rapid colonization of point bars by riparian woods, mainly *P. nigra* and its high resistance and resilience capacity despite a flow disturbance regime with frequent morphogenic floods as well as potentially destructive low frequent high magnitude floods. Thus, flow regulation which is well known to favour woodland expansion within river channels was not at the origin of this evolution. Here, river channelization and the stabilization through bank protections stopped the natural process of meander translation and therefore also stopped related natural process of destruction of mature stands of vegetation in the concavity of the meanders. Due to channel incision and despite a significant sediment accretion within the biogeomorphic units, i.e. wooded point bars, the latter did not reach the floodplain level but remain in-channel landforms.

Furthermore, our study suggests that these biogeomorphic units can be considered functional from an ecological perspective which implies that the biogeomorphic unit improves its resistance and resilience through characteristic feedback mechanisms between hydrogeomorphic and biological processes and that within river systems *P. nigra* can be considered as a native 'ecosystem engineer' (*sensu* Jones *et al.*, 1994) favoring its own capacity to survive and reproduce. The next step will consist in an investigation of the creation, modulation and adjustment of landforms involving physical ecosystem engineers such as *P. nigra* and its effects on natural selection pressures on organisms through niche construction with positive or negative evolutionary consequences (Corenblit *et al.*, 2014). The evolutionary dimension will permit to further develop what Steiger and Corenblit (2012) coined 'evolutionary geomorphology' and to go a step beyond the study of biogeomorphological dynamics at the contemporary timescale.

Acknowledgments

We acknowledge the French research projects (i) AAP-MSH 'CONSILPOP' financed by 'La Maison des Sciences Humaines' (MSH USR CNR 3550), Clermont-Ferrand, France and (ii) 'Waters & Territories. Water of the territory and territory of water: the restitution of fluvial dynamics and natural services provided to society at stake - GALE&T', financed by the French Ministry of Ecology, Environment, Sustainable Development and Planning (MEEDDAT) and the French National Centre of Scientific Research (CNRS). We thank the 'Syndicat Mixte d'Etude et d'Aménagement de la Garonne' (SMEAG), EPTB-Garonne (France) for their financial support during the year 2010. We also thank all the Master students of the University Blaise Pascal, Clermont-Ferrand - Master 'Géoenvironnement'^(a) of the University Paris Diderot – Master 'Espace, environnements dynamiques et risques'^(b) and of the University Paul Sabatier, Toulouse – Master 'Terre et planètes'^(c) who contributed enthusiastically to this project as part of their Master theses: (a) E. Bibolet; D. Ding, E. Takeo-Kane; R. Soursas; B. Márton (b) S. Sayad; J. Dousseau; A. Pilard; (c) S. Mader.

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Table 1. Properties of the IGN (French National Institute of Geographical and Forestry Information) used in the present analyses. P = panchromatic, D = digital, C = color.

Date	Mission number	Photos N°	Type	Scale
23/05/2000	CA00S00842_2000_fd4682_250	46 – 47	P, C	1 :27000
12/06/2002	CP02000212_2002_fd0031_250_c	91 - 93	P, C	1 :26000
17/07/2006	CP06000212_FD003x013	511 – 512	D	1 :5000
25/06/2010	10000021_FD82x28	05194 – 05198	D	1 :25000

Table 2. The statistical significance of longitudinal and transverse gradients in physical and biological properties assessed using Kruskal-Wallis tests.

Site/Gradient	Relative elevation	Fine sediment thickness	Basal elevation	Number of stems	Stem diameter	Canopy height
Site 1 / longitudinal	H = 23.04 P = 0.0017	H = 23.00 P = 0.0005	H = 30.61 P < 0.0001	H = 16.21 P = 0.0232	H = 35.67 P < 0.0001	H = 39.50 P < 0.0001
Site 1 / transverse	H = 44.94 P < 0.0001	H = 37.28 P = 0.0001	H = 25.54 P = 0.0007	H = 43.54 P < 0.0001	H = 31.75 P < 0.0001	H = 26.17 P = 0.0061
site 2 / longitudinal	H = 30.27 P < 0.0001	H = 19.34 P = 0.007	H = 30.44 P < 0.0001	H = 21.61 P = 0.0030	H = 24.82 P = 0.0008	H = 33.51 P < 0.0001
site 2 / transverse	H = 15.86 P = 0.0698	H = 18.62 P = 0.0286	H = 7.31 P = 0.6041	H = 6.6400 P = 0.6749	H = 11.41 P = 0.2488	H = 11.76 P = 0.2270

Table 3. Physical and biological characteristics (mean \pm sd) of the five biogeomorphic groups identified by agglomerative, hierarchical cluster analysis using Ward's cluster algorithm. Kruskal-Wallis tests assess the degree to which each characteristics shows statistically significant differences across the five groups.

Group	Relative elevation (m)	Fine sediment thickness (m)	Basal elevation (m)	Number of stems	Stem diameter (cm)	Canopy height (m)	Age (years)
G1	0.41 \pm 0.34	0.47 \pm 0.45	-0.06 \pm 0.30	10.20 \pm 6.79	6.06 \pm 3.05	6.14 \pm 3.16	7.01 \pm 1.68
G2	0.33 \pm 0.17	0.30 \pm 0.23	0.03 \pm 0.20	36.44 \pm 13.60	4.17 \pm 2.27	7.48 \pm 4.77	6.01 \pm 1.22
G3	0.72 \pm 0.42	0.47 \pm 0.34	0.25 \pm 0.44	10.28 \pm 4.68	7.99 \pm 3.22	15.97 \pm 2.23	8.00 \pm 1.54
G4	1.21 \pm 0.39	0.88 \pm 0.41	0.33 \pm 0.47	2.95 \pm 1.78	18.85 \pm 4.73	20.93 \pm 3.87	11.80 \pm 1.31
G5	1.35 \pm 0.12	0.62 \pm 0.24	0.73 \pm 0.19	1.71 \pm 1.25	45.02 \pm 3.43	22.67 \pm 3.55	16.39 \pm 2.24
Kruskal-Wallis test	H = 58.20 P < 0.0001	H = 31.29 P < 0.0001	H = 28.32 P < 0.0001	H = 71.34 P < 0.0001	H = 89.60 P < 0.0001	H = 85.58 P < 0.0001	H = 88.99 P < 0.0001

Table 4. Gain versus loss of wooded area at the two study sites between 2000 and 2010.

Site / Period	Gain (m ²)	Loss (m ²)	Ratio (m ²)
Site 1			
2000-2002	+2 509	-203	+2 306
2002-2006	+8 841	-373	+8 468
2006-2010	+6 079	-171	+5 908
Total 2000-2010	+17 429	-747	+16 682
site 2			
2000-2002	+844	-293	+551
2002-2006	+3 299	-84	+3 215
2006-2010	+3 111	-415	+2 696
Total 2000-2010	+7 254	-792	+6 462

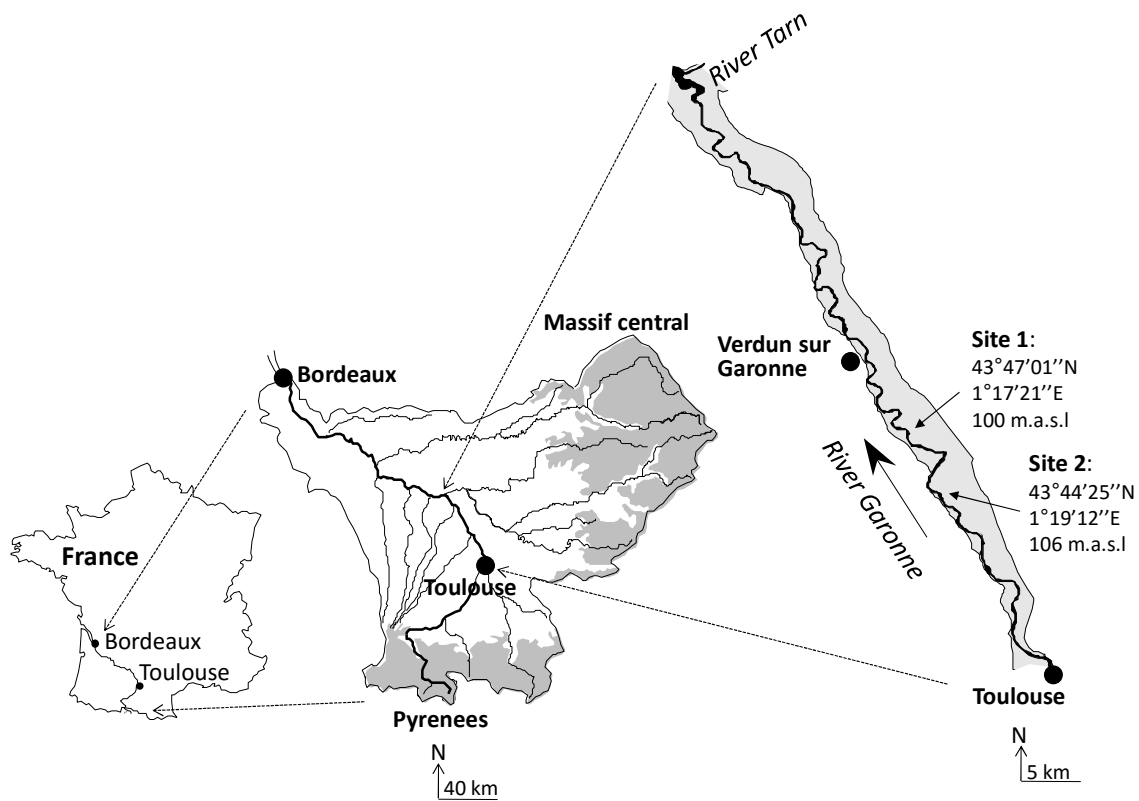


Figure 1. Location of study sites 1 and 2 on the river Garonne, France.

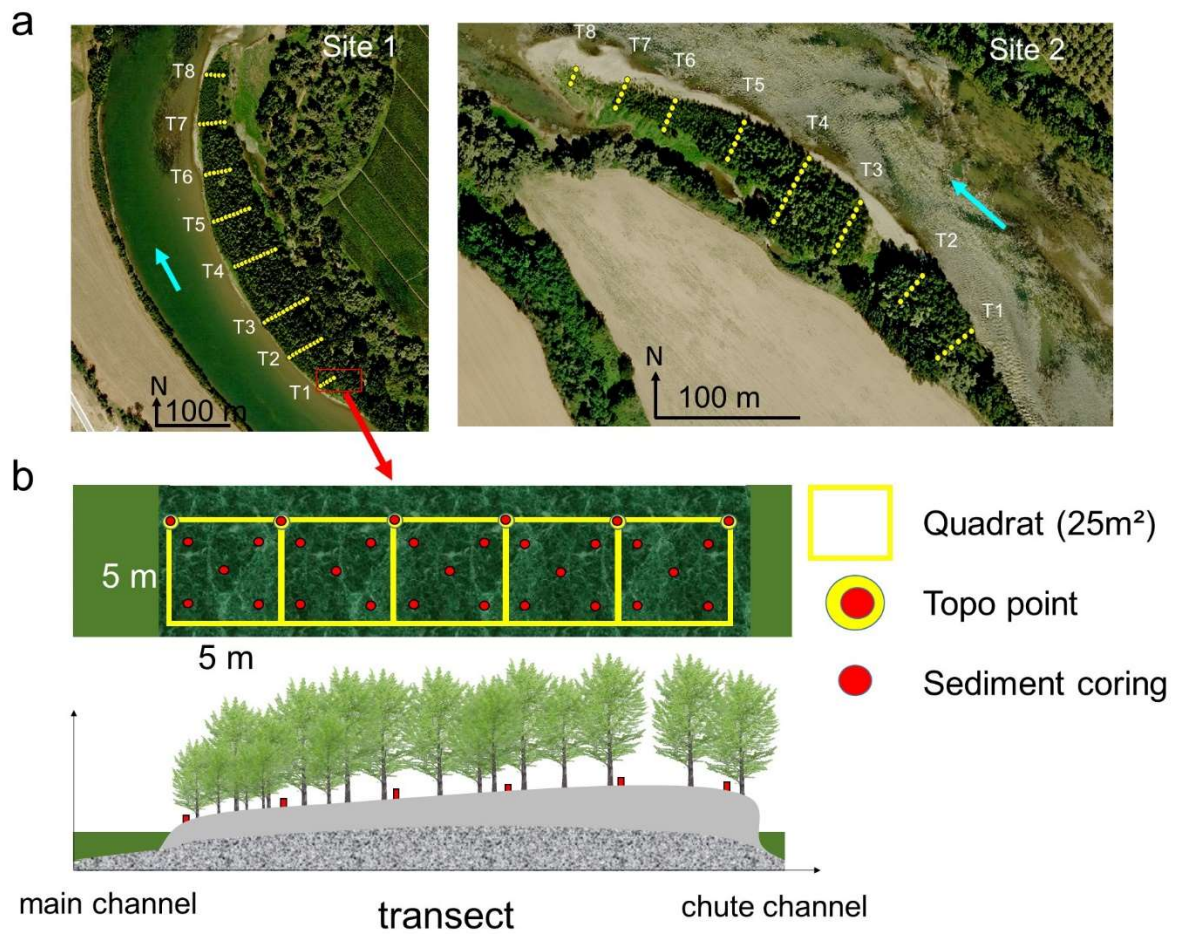
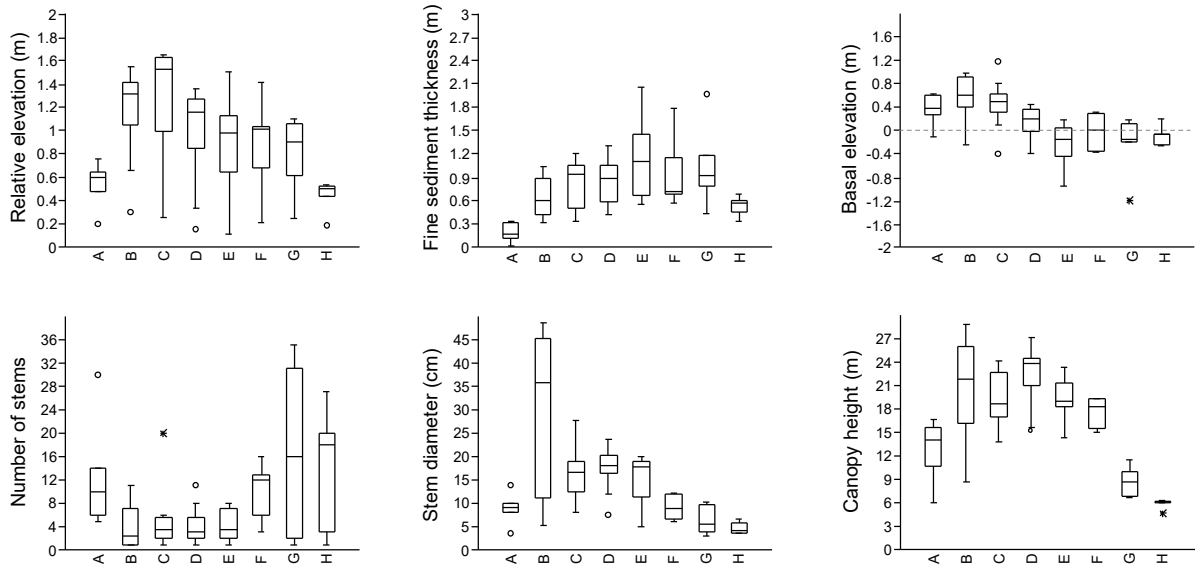


Figure 2. Sampling design. (a) Location of the transects and plots on Site 1 and site 2. (b) Location of the measurement points within the plots.

Site 1



Site 2

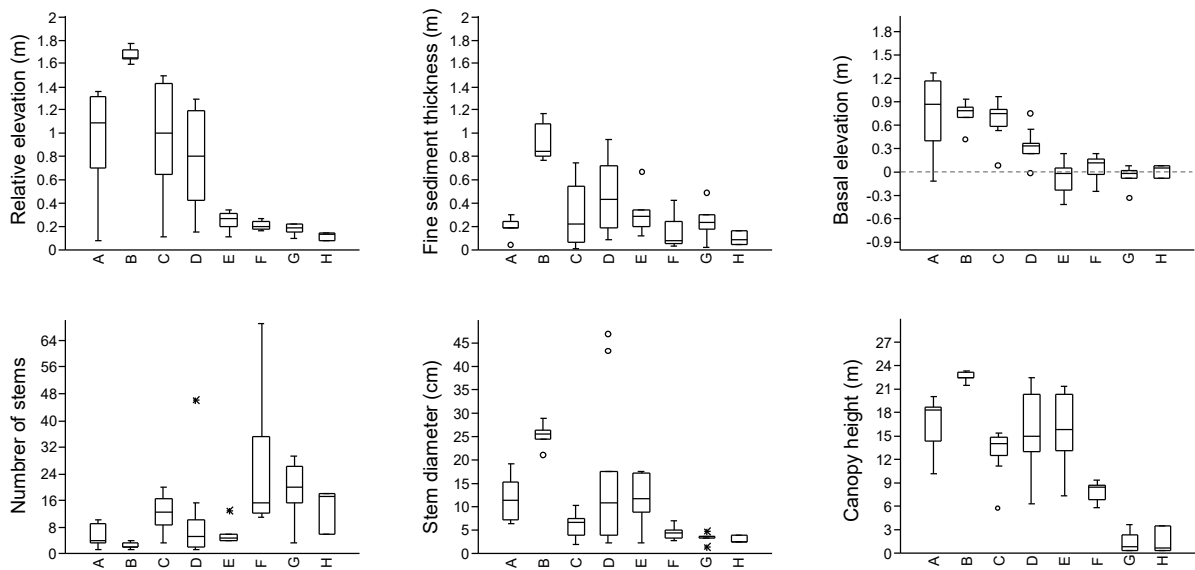
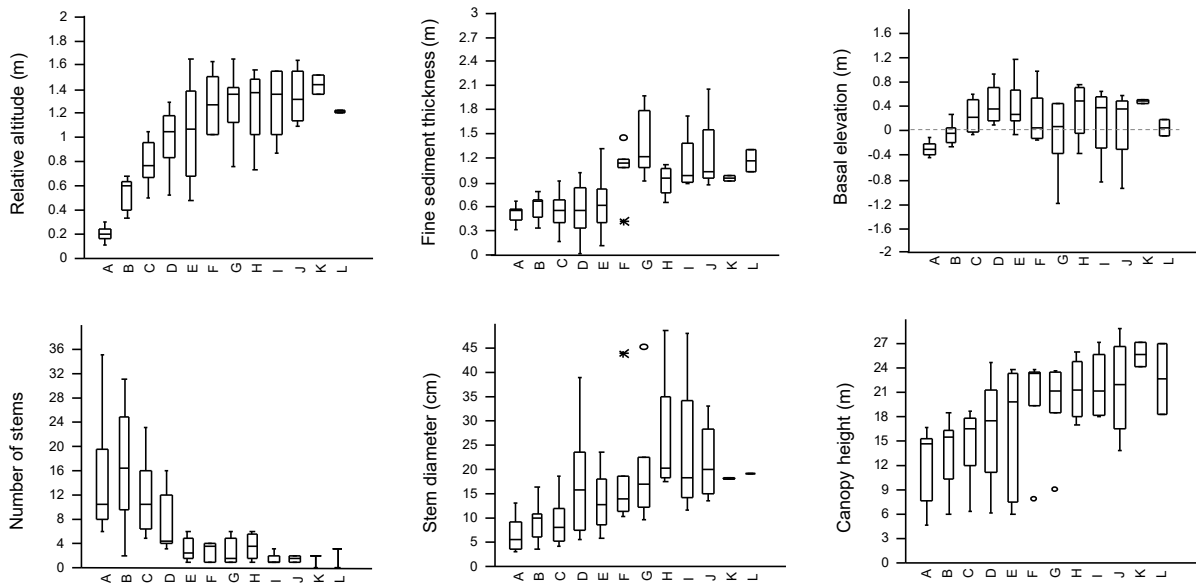


Figure 3. Variation of geomorphic and biological variables longitudinally from upstream to downstream along the point bar. A to H represent the 8 transects along the point bar from 1 (upstream) to 8 (downstream). In each box and whisker plot, the box marks the 25 and 75 percentiles; the horizontal line within the box is the median; the whiskers show the range from minimum to maximum values, apart from outliers which are marked with small circles.

Site 1



Site 2

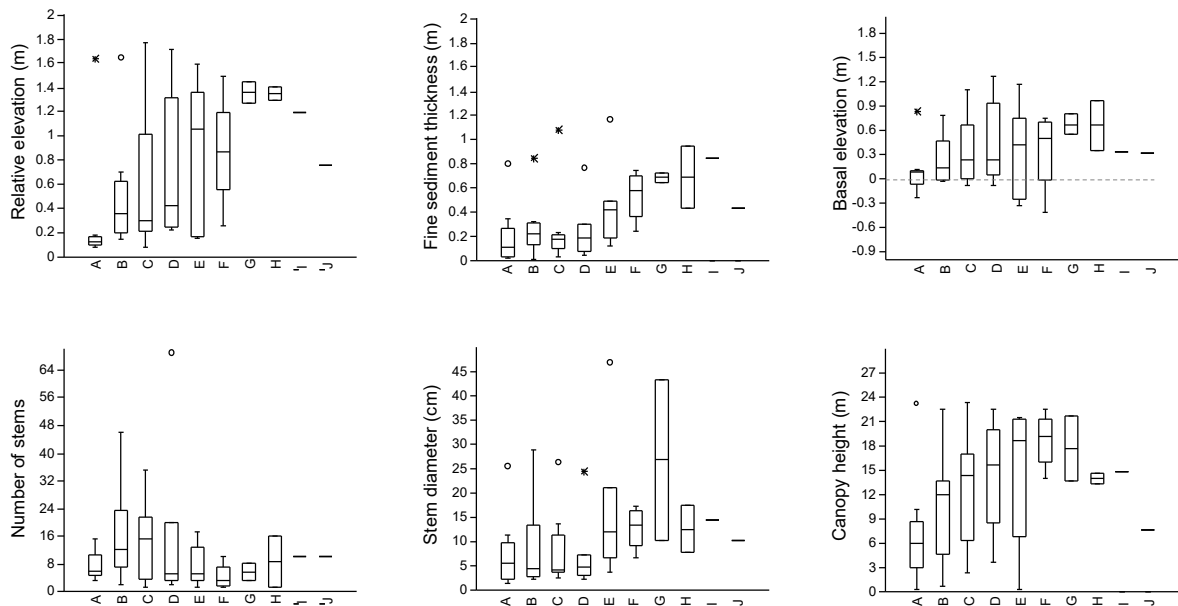


Figure 4. Variation of geomorphic and biological variables transversely from the main channel to the chute channel across the point bar. A to J represent the lines of plots from A next to the main channel to L (Site 1) and J (site 2) next to the chute channel. In each box and whisker plot, the box marks the 25 and 75 percentiles; the horizontal line within the box is the median; the whiskers show the range from minimum to maximum values, apart from outliers which are marked with small circles.

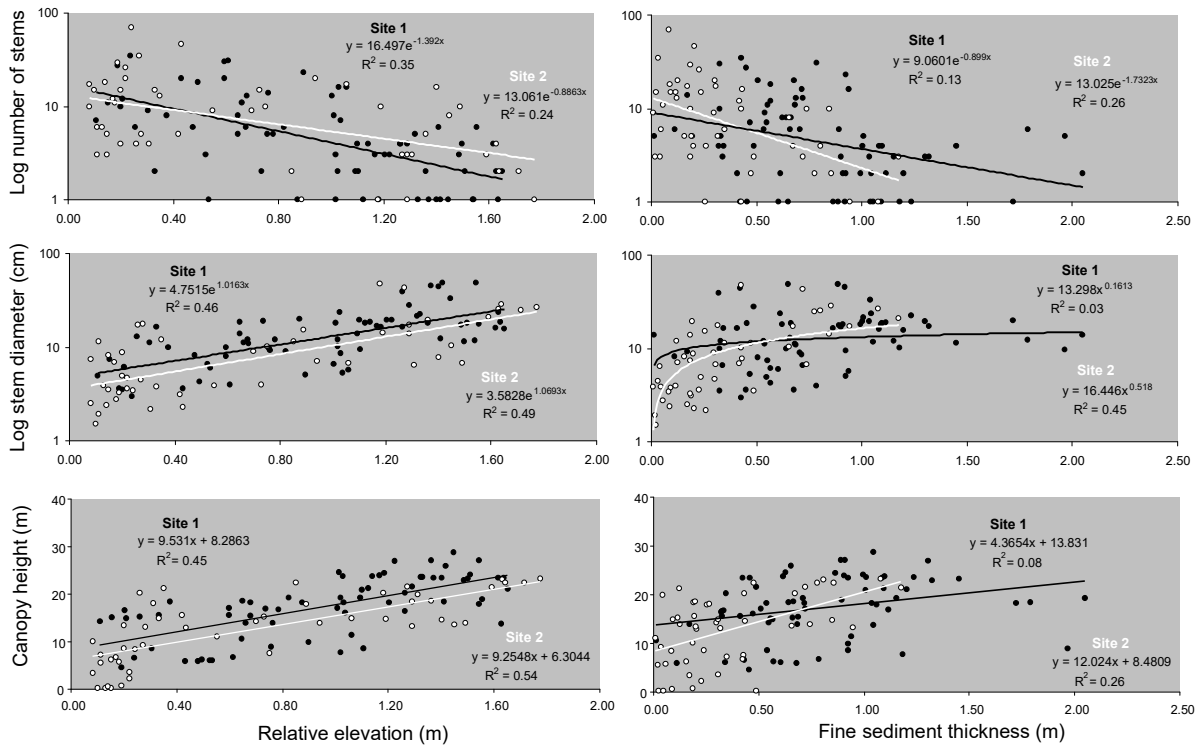


Figure 5. Linear and non-linear regression models estimated between the key biological (y) and geomorphic (x) variables.

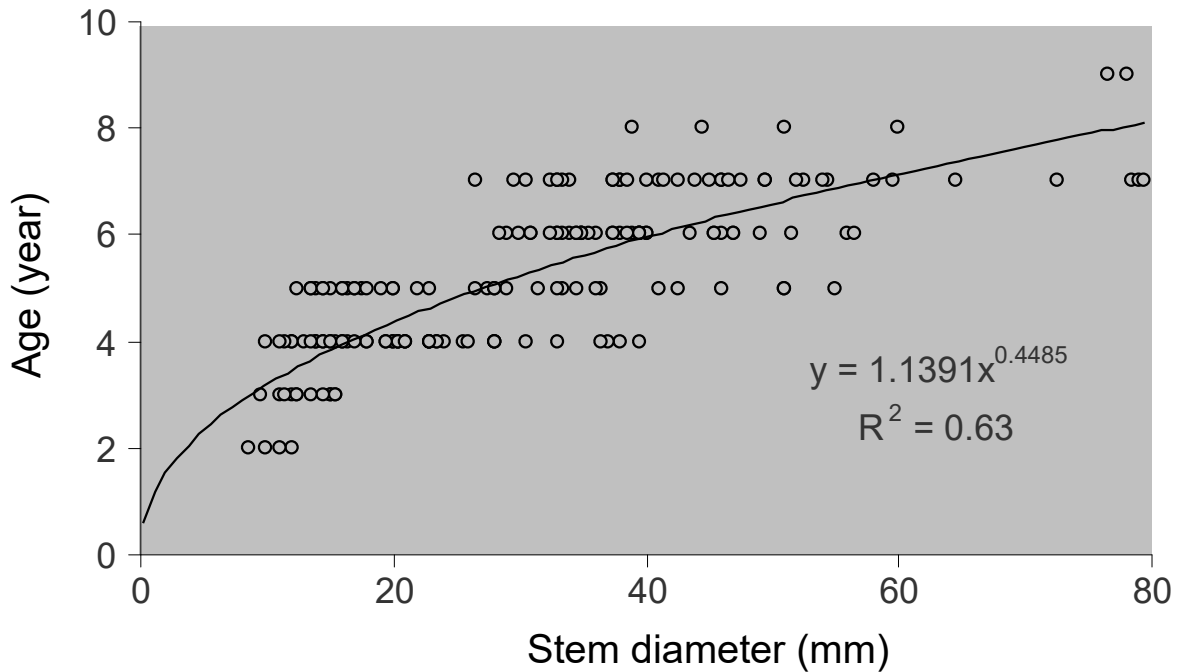


Figure 6. Power model of poplar age according to basal stem diameter (N = 180).

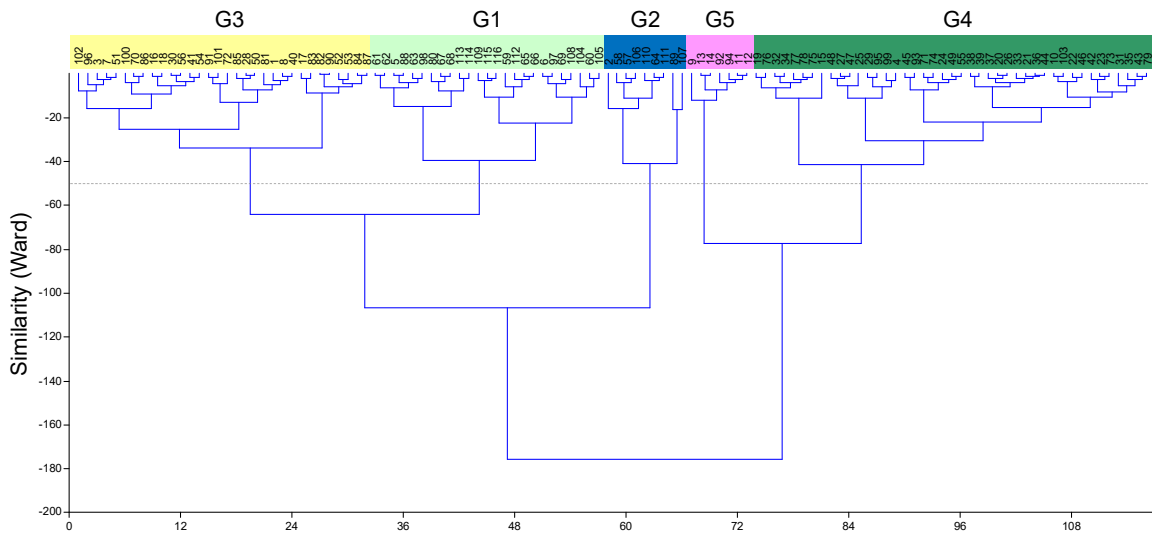


Figure 7. Hierarchical cluster analysis (HCA employing Ward's similarity index) on the 6 key geomorphic and biological variables. The grey dotted line defines the separation of the five groups that were chosen for further analysis.

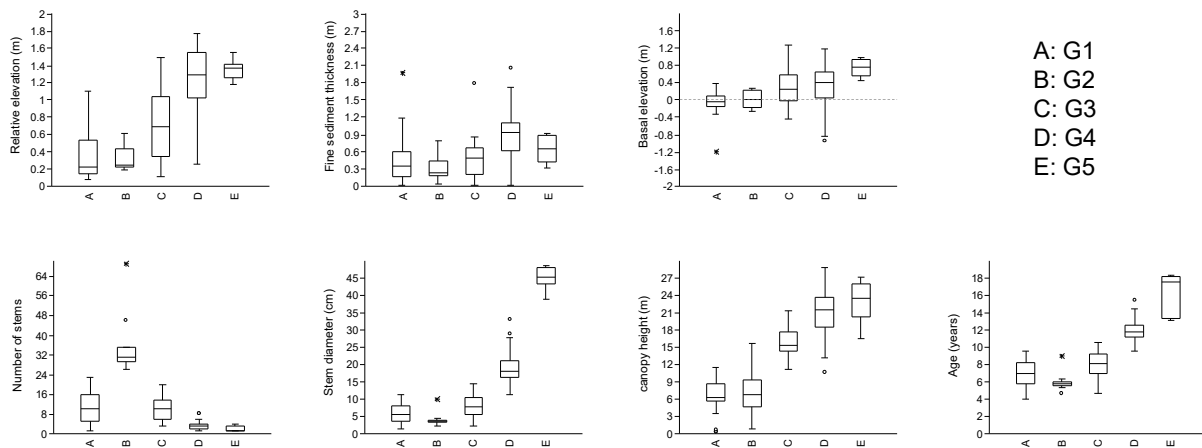


Figure 8. Box and whisker plots illustrating differences in the six physical and biological variables according to the five groups identified by HCA (Figure 7; Table 3). A = G1; B = G2; C = G3; D = G4; E = G5.

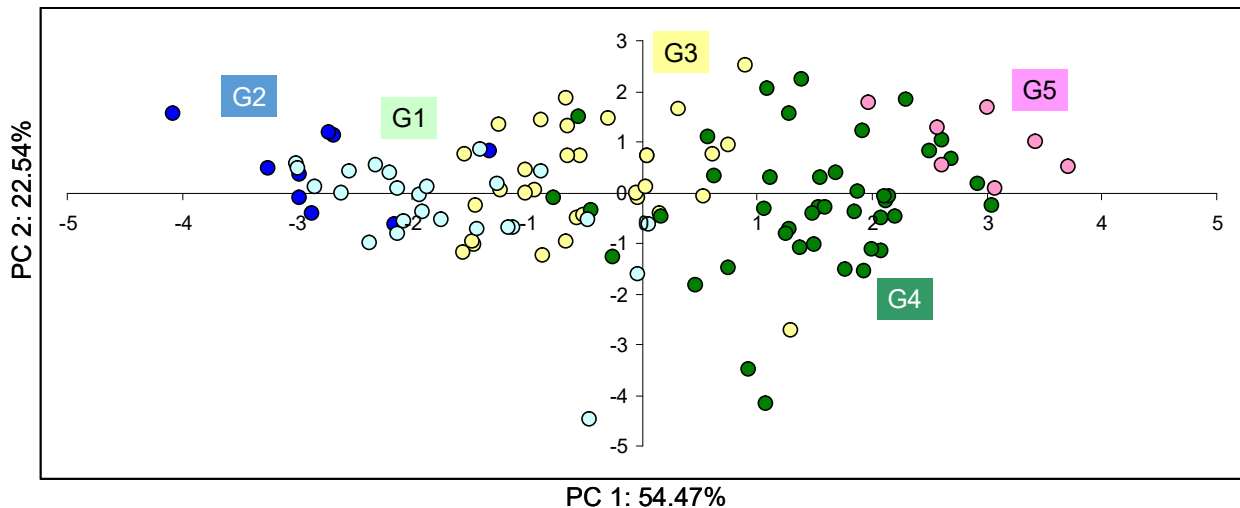


Figure 9. Principal Components Analysis (PCA) on the geomorphic and biological key variables. PC 1 represents a gradient of size related to the process of biogeomorphic maturation; PC 2 represents a gradient of ‘form’ related to the relation between fine sediment thickness and basal elevation. PC 1 variable loadings: relative elevation: 0.50284; basal elevation: 0.27282; fine sediment thickness: 0.31422; number of stems: -0.36953; stem diameter: 0.45395; canopy height: 0.48101. PC 2 variable loadings: relative elevation: 0.079593; basal elevation: 0.72834; fine sediment thickness: -0.65333; number of stems: 0.17672; stem diameter: 0.071446; canopy height: -0.0011908.

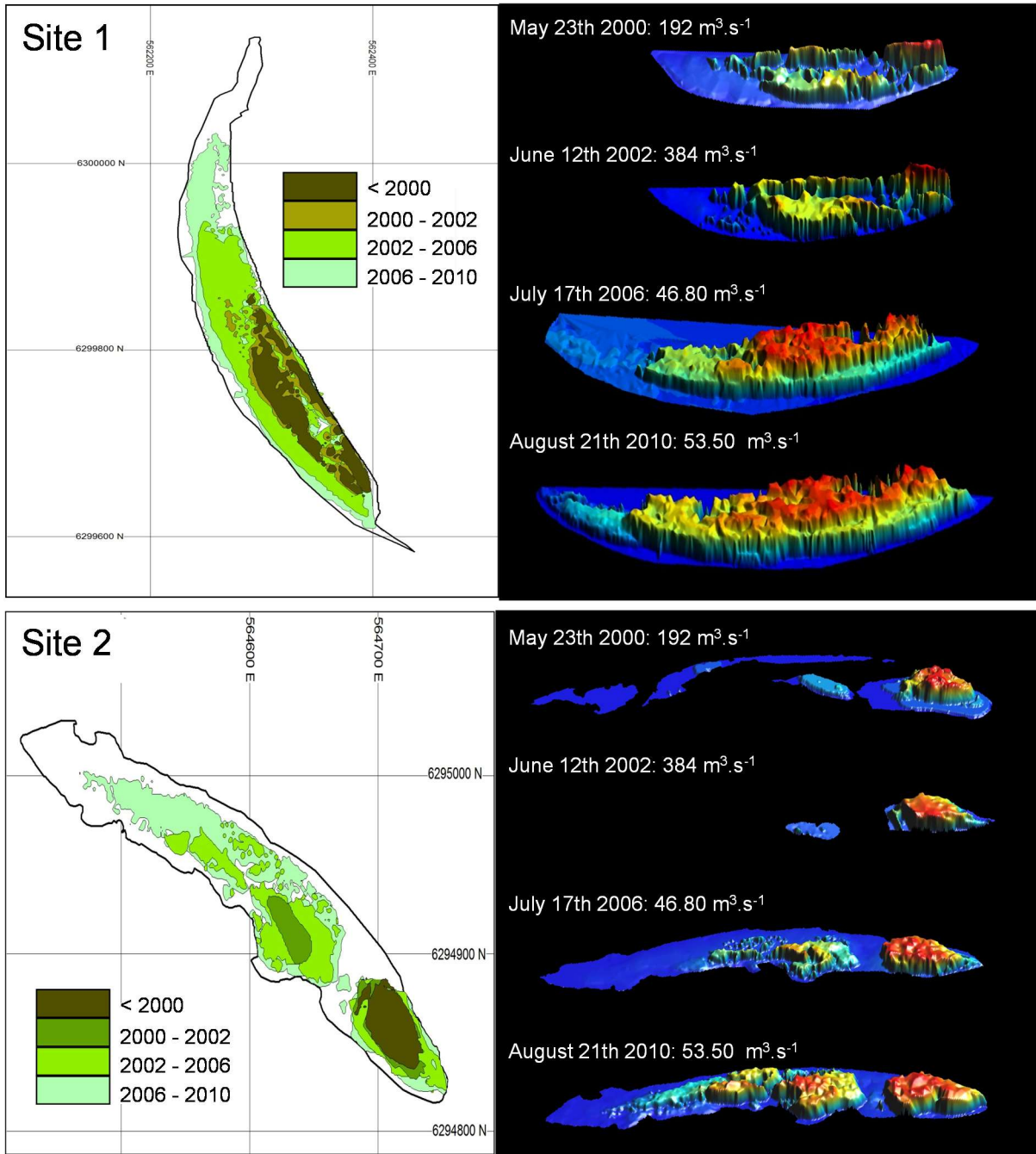


Figure 10. Two (GIS analysis) and three (Photogrammetric analysis) dimensional patterns of biogeomorphic construction on Sites 1 and 2.

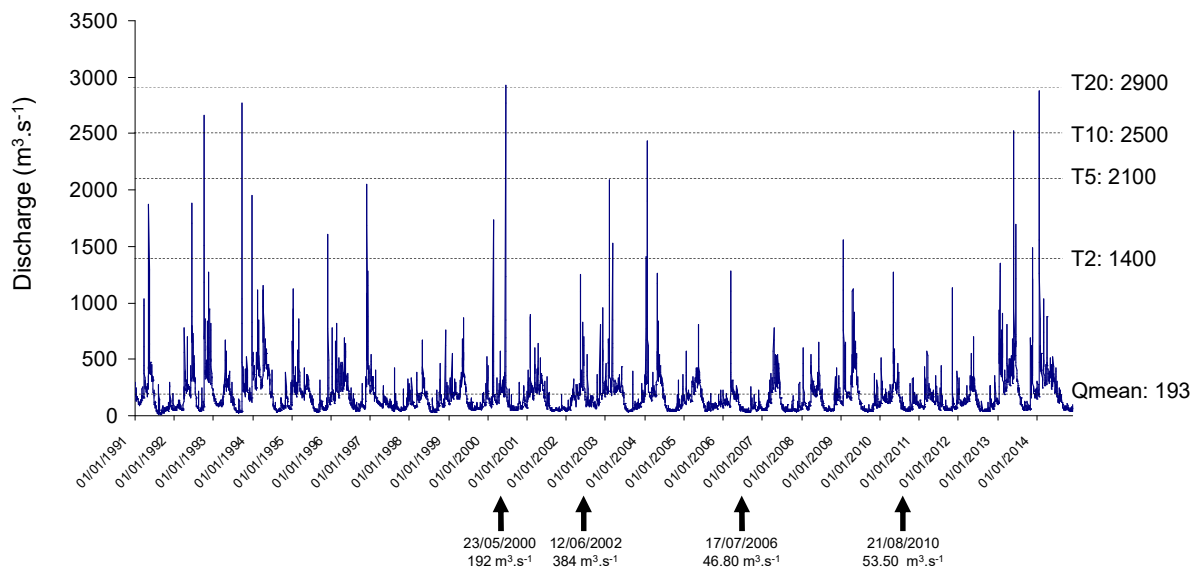


Figure 11. Daily mean discharge ($\text{m}^3 \text{s}^{-1}$) at the DREAL Midi-Pyrénées hydrological station of Verdun-Sur-Garonne between 1995 and 2014 (station code: O2620010); basin area: 13 730 km^2 ; altitude a.s.l.: 96 m; coordinates (extended Lambert II): X = 511908 m, Y = 1873173 m. Mean annual discharge (Q_{mean}) and return period (T_x) are indicated by horizontal lines. The dates of capture of the four photographs and corresponding daily discharges are indicated by arrows.

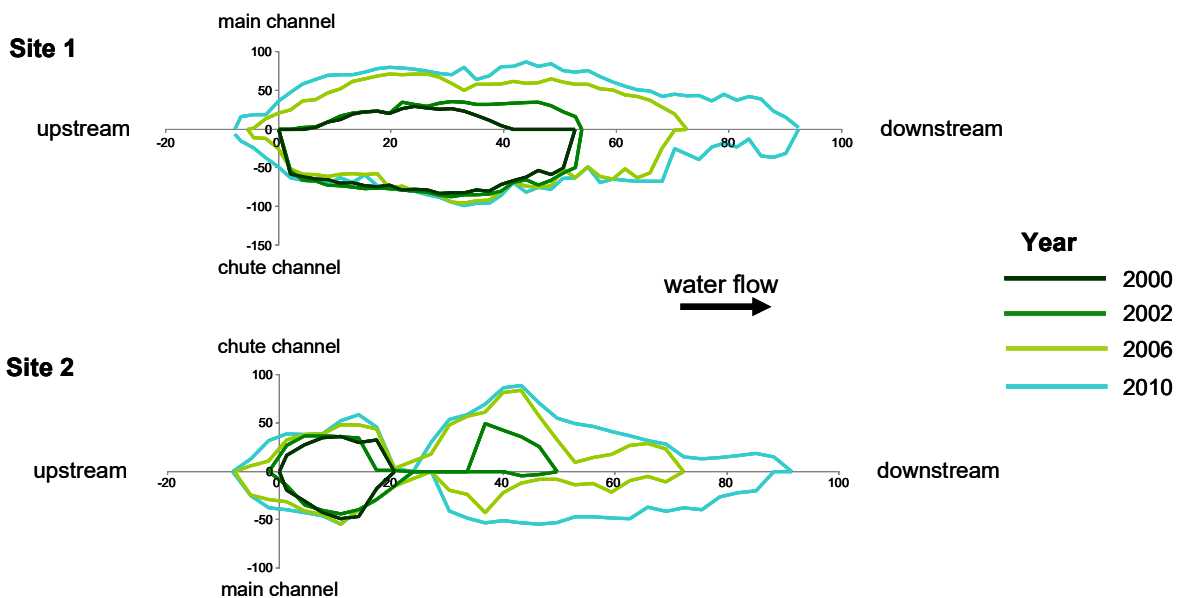


Figure 12. Relative percentage biogeomorphic extension at the two study sites between 2000 and 2010 in four directions: upstream, downstream, towards the main channel; towards the chute channel.

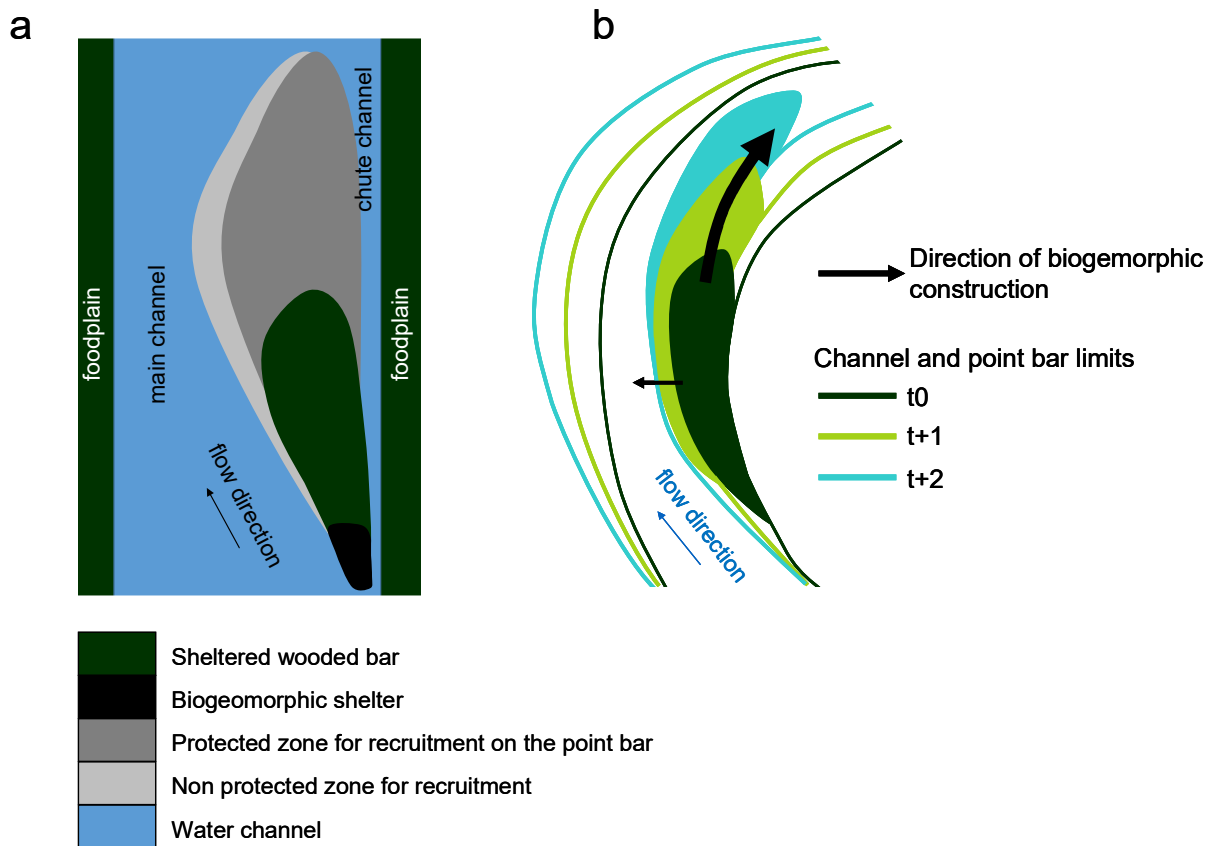


Figure 13. Conceptual model of biogeomorphic construction and related meander dynamics. (a) Functional biogeomorphic sub-units; (b) model of meander formation associate to feedbacks between vegetation and geomorphology on point bars.