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Réponses des parties aérienne et souterraine de Populus nigra L. aux contraintes mécaniques observées sur la rivière Allier, France

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ABSTRACT

Pioneer riparian trees such as *Populus nigra* L. which establish on alluvial bars within dynamic riparian corridors strongly influence fluvial geomorphology by trapping sediments and constructing landforms during floods. The engineering effects (changes in the physical state of the habitat by organisms) of *P. nigra* on alluvial bars depend on its biomass and its exposure to mechanical stress. *P. nigra* has a strong phenotypic plasticity that enables individuals to adapt their morphological and biomechanical traits, according to the local hydrogeomorphic conditions. The comprehension and quantification of the variation of morphological and biomechanical response trait attributes of *P. nigra* populations according to their exposure to mechanical stress is fundamental to better understand why riparian plants are capable to impact fluvial geomorphology. In an empirical *in situ* study, we quantified the relation between response trait attributes of *P. nigra* and its exposure to three different levels of mechanical stress. At a highly exposed bar-head, plants clearly developed response traits such as small flexible stems and a strong root system which favour higher mechanical resistance, while at the less exposed bar-tail plants developed taller, less flexible stems and finer root systems. Plants that established in the lower reach of the chute channel developed some common trait attributes in comparison to the bar-tail population and some other trait attributes which were common to the bar-head population. Poplar plants which established on bar-tails favoured bioconstruction, and thus are potentially faster disconnected from hydrogeomorphic disturbances. These results further suggest that fine scale biogeomorphic feedbacks have an influence on larger scale processes within the fluvial corridor requiring hierarchical biogeomorphic bottom-up and top-down cross scale studies for a better understanding of complex biogeomorphic fluvial ecosystems.

Keywords: *Populus nigra* L., biogeomorphology, mechanical stress, trait, Allier River.

RÉSUMÉ

Des arbres riverains pionniers, tels que *Populus nigra* L., établis sur des bancs alluviaux au sein de corridors fluviaux dynamiques, influencent fortement la géomorphologie fluviale en piégeant des sédiments et en construisant des formes fluviales pendant les crues. L'effet ingénieur (changements dans l'état physique de l'habitat par les organismes) de *P. nigra* sur les bancs alluviaux dépend de sa biomasse et de son degré d'exposition à la contrainte mécanique. *P. nigra* a une plasticité phénotypique élevée qui lui permet d'adapter ses traits morphologiques et biomécaniques en fonction des conditions hydrogéomorphologiques locales. La compréhension et la quantification de la variation des traits de réponses morphologiques et biomécaniques au sein des populations de *P. nigra* en fonction de leur degré d'exposition à la contrainte mécanique est fondamentale pour mieux comprendre pourquoi et comment les plantes influent sur la géomorphologie. Dans une étude empirique *in situ*, nous avons quantifié la relation entre les traits morphologiques et biomécaniques de réponses de *P. nigra* et son exposition à différents niveaux de contrainte mécanique. En contexte très exposé, en tête de banc, les plantes ont développé des traits de réponse favorisant une plus grande résistance, notamment une tige flexible et basse et un système racinaire plus robuste. En contexte moins exposé, tel le cas de la queue de banc, les plantes ont développé des tiges plus longues et moins flexibles et un système racinaire plus fin. Les plantes établies dans le tronçon aval du chenal de chute alluviale ont développé certains traits communs avec la population de queue de banc et d'autres traits communs avec la population de tête de banc. Les peupliers établis en queue de banc ont favorisé la bioconstruction et donc potentiellement une déconnexion plus rapide des perturbations hydrogéomorphologiques. Nos résultats suggèrent que les processus biogéomorphologiques se produisant à l'échelle fine influent sur les processus à plus large échelle. Ce résultat pointe la nécessité de développer des études biogéomorphologiques hiérarchiques selon des approches ascendante (bottom-up) et descendante (top-down) pour une meilleure compréhension des écosystèmes fluviaux biogéomorphologiques complexes.

Mots clés : *Populus nigra* L., biogéomorphologie, stress mécanique, trait, rivière Allier.

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1. Introduction

Pioneer riparian trees such as *Populus nigra* L. which establish on gravel bars within dynamic riparian corridors strongly influence fluvial geomorphology by trapping sediments and constructing landforms during floods (Corenblit et al., 2007; Gurnell, 2014; Hortobágyi et al., 2017). Ecosystem engineers (Jones et al., 1994) are species which can significantly modify geomorphic processes, landforms and habitats, and thus control the availability of resources. Hortobágyi et al. (in press) showed on a laterally dynamic section of the Allier River, France, that after one to two years of growth, *P. nigra* saplings significantly influence sediment dynamics on gravel bars because they reached a sufficient biomass. This stage was defined as the “biogeomorphic feedback window” because the riparian plants and geomorphic processes strongly interact in a reciprocal way (Hortobágyi et al., in press). The authors showed that *P. nigra* populations which established on alluvial bars under low to intermediate levels of exposure (e.g. bar-tails) to mechanical stress caused by water flow and sediment transport developed a strong aerial biomass and efficiently trapped fine sediments. At the most exposed locations of alluvial bars (i.e. on bar-heads), *P. nigra* populations were able to resist mechanical stress but they did not develop an important aerial biomass, and thus they did not trap significant quantities of fine sediment. These results suggested that the morphological and biomechanical “traits” and related “attributes” of young *P. nigra* populations which colonize alluvial bars, change according to variations in exposure to mechanical stress (i.e. shear stress imposed by water flow; sediment transport) and that these changes result in varying aptitudes of the plants to trap fine sediments during annual floods. Plant traits are morphological, biomechanical, physiological and phenological characteristics of plants which can be measured at the individual level; the value or the modality taken by a trait is called an “attribute” (Violle et al., 2007). When the attribute of a trait varies in response to changes in environmental conditions (e.g. water flow, sediment erosion, transportation, deposition), the trait is called a “response trait”. Traits which affect environmental conditions (e.g. flow characteristics, geomorphic landforms), community or ecosystem properties, are considered as “effect traits” (Violle et al., 2007; Corenblit et al., 2015).

P. nigra has a strong phenotypic plasticity, i.e. individuals can adapt their morphological and biomechanical traits according to the local hydrogeomorphic conditions (Karrenberg et al., 2003; Chamailard, 2011; Corenblit et al., 2014). Such plasticity improves *P. nigra* individual’s probability to establish under harsh environmental conditions (e.g. exposed to flood disturbances) and eventually to reach their biogeomorphic feedback window (Eichel et al., 2015; Hortobágyi et al., in press). During establishment (i.e. first three years following germination), the sapling’s growth pattern is highly controlled by local hydrogeomorphic conditions, such as sediment texture, topographic level, hydrological regime and exposure to mechanical stress that act as a strong ecological filter (Cooper et al., 1999). Different authors have suggested that in order to increase their resistance to mechanical stress, saplings develop specific morphological and biomechanical attributes (Karrenberg et al., 2002; Bornette et al., 2008; Puijalon et al., 2011). Variation in trait attributes is supposed to be dependent upon the level of mechanical stress with a trade-off related to the function of anchorage and resource acquisition (Karrenberg et al., 2003; Read and Stokes, 2006; Pasquale et al., 2013).

The quantification of morphological and biomechanical variations of response trait attributes in *P. nigra* populations according to their location on alluvial bars is essential to understand why these ligneous

riparian plants are capable to impact fluvial morphodynamics and fluvial landforms. To our knowledge, very little is known about the *in situ* aboveground and belowground morphological and biomechanical response of saplings in their early stage of development on alluvial bars with the exception of very recent studies (Kui and Stella, 2016). We hypothesise that (i) when highly exposed to shear stress, saplings predominantly develop functional morphological and biomechanical traits increasing their resistance to uprooting, such as a reduced size and a strong flexibility which limits drag force, i.e. “avoidance traits”, and also other traits such as a strong root system that increases anchorage, i.e. “tolerance traits”; (ii) conversely, under less exposed situations, their morphology will predominantly be the expression of the function of resource acquisition, i.e. water and nutrient uptake, with varying root/shoots ratios but a weaker structural root system (the roots with a smaller diameter) and potentially a taller above-ground size under good growth conditions.

In this empirical *in situ* study, we will focus on the early stage of the widely (on the European continent) distributed *P. nigra* which is also an abundant species on the alluvial bars of the laterally dynamic Allier River, France. The main objective was to explore if contrasted morphological and biomechanical responses exist in-between the *P. nigra* populations in relation with exposure to mechanical stress. Three contrasting locations on alluvial bars were distinguished: (i) on the most exposed upstream location of the alluvial bar, hereafter called bar-head; (ii) on the less exposed downstream location of the alluvial bar, hereafter called bar-tail; and (iii) within the lower reach of a chute channel which is sheltered during low annual floods but more exposed to concentrated water flow during more important floods.

2. Methods

2.1. Study site and location of *P. nigra* populations

Populus nigra L. individuals were sampled in spring 2014 within a reach of the lower gravel bed Allier River, France, near Châtel-de-Neuvre (fig. 1) which is evolving from a transitional wandering style to a meandering style. This river reach within the “Réserve Naturelle Nationale du Val d’Allier” with a certain protection status and which experienced moderate anthropogenic impacts, is characterized by an active lateral erosion in the outer bends of meanders and point bar formation and migration in the inner bends (Petit, 2006; Dejaifve and Esquirol, 2011). The Allier River has a pluvial hydrological regime with strong seasonal and interannual variability and a mean annual discharge of $117 \text{ m}^3 \cdot \text{s}^{-1}$ (1986-2017; data: Banque Hydro <http://www.hydro.eaufrance.fr>). *P. nigra* individuals were sampled within three populations located on two alluvial bars juxtaposed in the downstream direction and within one chute channel. The three populations were mainly composed of *P. nigra* individuals chosen from the same local populations, however, some *Salix purpurea* L. and *Salix alba* L. individuals were also present within the sampled vegetation patches.

These three populations dating back to 2011 and 2012 were chosen in order to (i) obtain three different levels of exposure to mechanical stress with homogeneous sediment texture at the patch scale, (ii) and to maximise the probability that the populations originated from the same local population, and thus dispose of a close genotype. The first population (fig. 1C) is located on the highly exposed bar-head of the downstream alluvial bar; the second population on a less exposed bar-tail location of the upstream alluvial bar (fig. 1D) and the third population within the lower (downstream) reach of the chute channel of the upstream alluvial bar (fig. 1E).

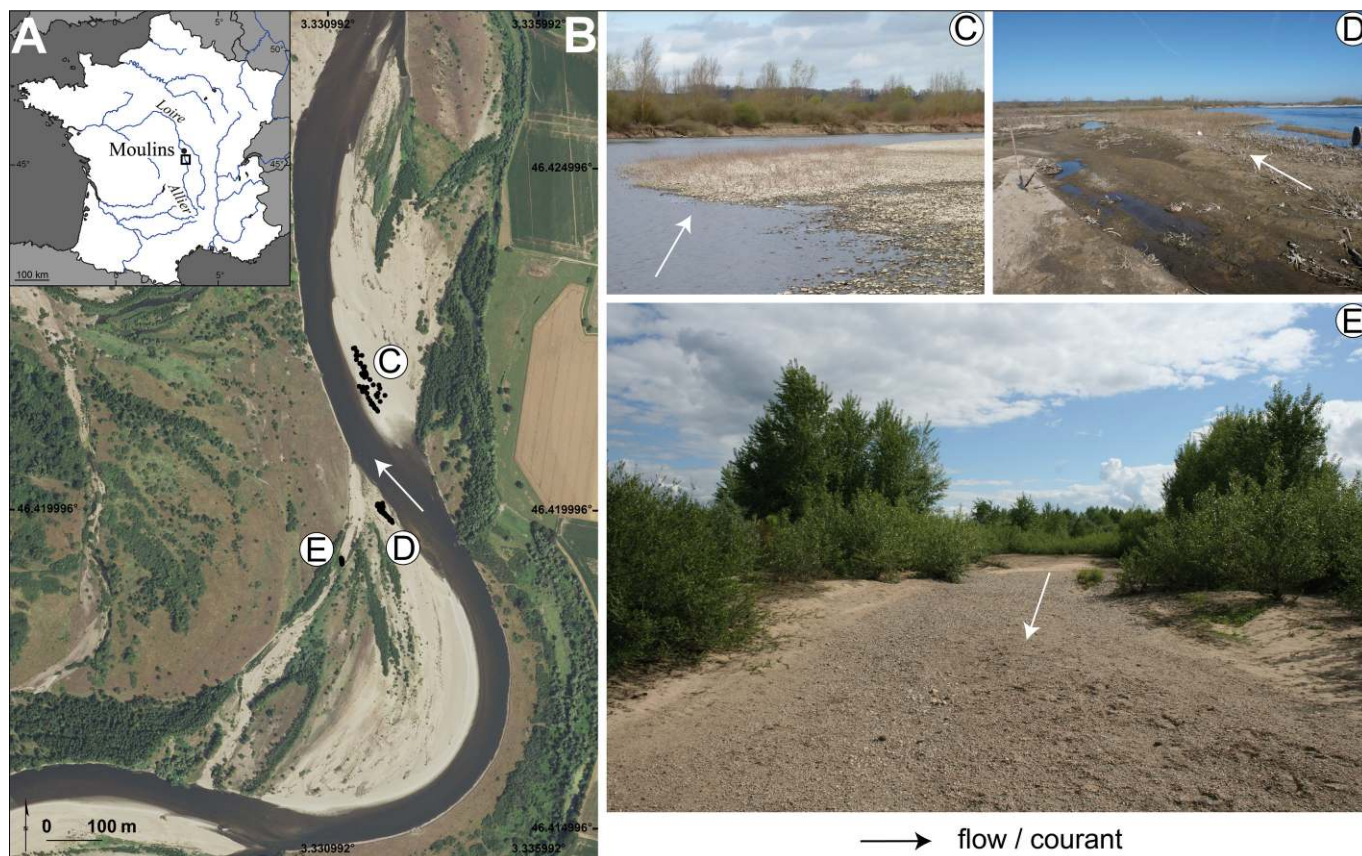


Fig. 1 – Localisation map.

A. Study site; B. Sampling sites on the Allier River. C. Bar-head; D. Bar-tail; E. Lower reach of chute channel

Fig. 1 – Carte de localisation.

A. Zone d'étude ; B. Sites d'échantillonnage sur la rivière Allier. C. Tête de banc ; D. Queue de banc ; E. Tronçon aval de la chute alluviale.

The flooding threshold of all three populations corresponds to a discharge of about $130 \text{ m}^3 \cdot \text{s}^{-1}$ (fig. 2). Total submersion time, determined from flow hydrographs, of the two year old *P. nigra* saplings was about 342 days. During the first year the saplings were exposed to two quasi-annual floods of 357 and $408 \text{ m}^3 \cdot \text{s}^{-1}$ (2-years return period: $580 \text{ m}^3 \cdot \text{s}^{-1}$) and to one flood of $729 \text{ m}^3 \cdot \text{s}^{-1}$ (5-years: $810 \text{ m}^3 \cdot \text{s}^{-1}$). During the second year after recruitment, three more floods of 610 , 364 and $375 \text{ m}^3 \cdot \text{s}^{-1}$ occurred. The first two floods occurred during autumn and winter when saplings were leafless and the third flood occurred during spring time when leaves had sprouted at the end of the dormancy. The last three floods occurred during spring time, full summer (maximum biomass) and winter (leafless period). Submersion time of one year old *P. nigra* saplings was around 69 days. These saplings were only exposed to the last three floods.

2.2. Field sampling

First, all selected poplar individuals were localised using a DGPS (Magellan PM500). One surface and one sub-surface sediment sample was taken in order to characterize overall sediment texture for each of the three populations. The subsurface sample was taken at the level where a clear transition in sediment texture was detected. Sediment texture was determined at the laboratory using standard sieving procedures (Rivière, 1977).

Vegetation parameters were measured *in situ*: the above ground height (cm), diameter (cm) at ground level and at 20 cm, inclination of the stem (degree) and flexibility (Newton). Initial stem inclination was measured along the channel upstream-downstream axis. Higher values than 90° indicate that the

stem is bent to the downstream direction. In order to quantify biomechanical properties of the individuals, the stem flexibility was measured with an electronic gauging force (Sauter FH 50; Newton range of 0.01-50): from its initial position, the stem was bent by an additional 10° along the upstream-downstream axis of the flow channel. High values indicated the necessity of applying a strong force to bend the stem, and therefore a low flexibility of the individual. Finally, plants were excavated using conventional shovels in order to measure parameters related to the belowground part of the plants: the length of buried stem (cm), the length (cm) and diameter (cm) of the taproot, diameter of the collar (cm), number of lateral and adventitious roots and the number of roots with a diameter of $>0.3 \text{ cm}$ which was chosen because it is suggested that it corresponds to the structural roots (Ding, 2014). Structural roots are more specifically related to the function of anchorage and fine roots to the function of nutrient uptake (Stokes et al., 1995; Read and Stokes, 2006). Between seedling recruitment and field sampling, the river deposited additional sandy sediment on the study sites during high water stages ($>130 \text{ m}^3 \cdot \text{s}^{-1}$). The length of the buried stem was measured between the root collar and the bar or chute channel surface. Roots growing on this part of the stem are *adventitious roots*, while *lateral roots* are growing from the original taproot. Additionally, we calculated the ratio between the aerial and the buried parts of the stem and also the total length of the plant (i.e. the above- plus the belowground part on the plant). In spring 2014, we excavated a total of 96 *P. nigra* individuals within the three populations, (bar-head [pop1]: 46 individuals; bar-tail [pop2]: 40; chute channel [pop3]: 10). From the 96 individuals, 62 individuals (respectively 23, 32 and 7) were excavated entirely without breakage of the tap root. Stems were cut and sanded at the

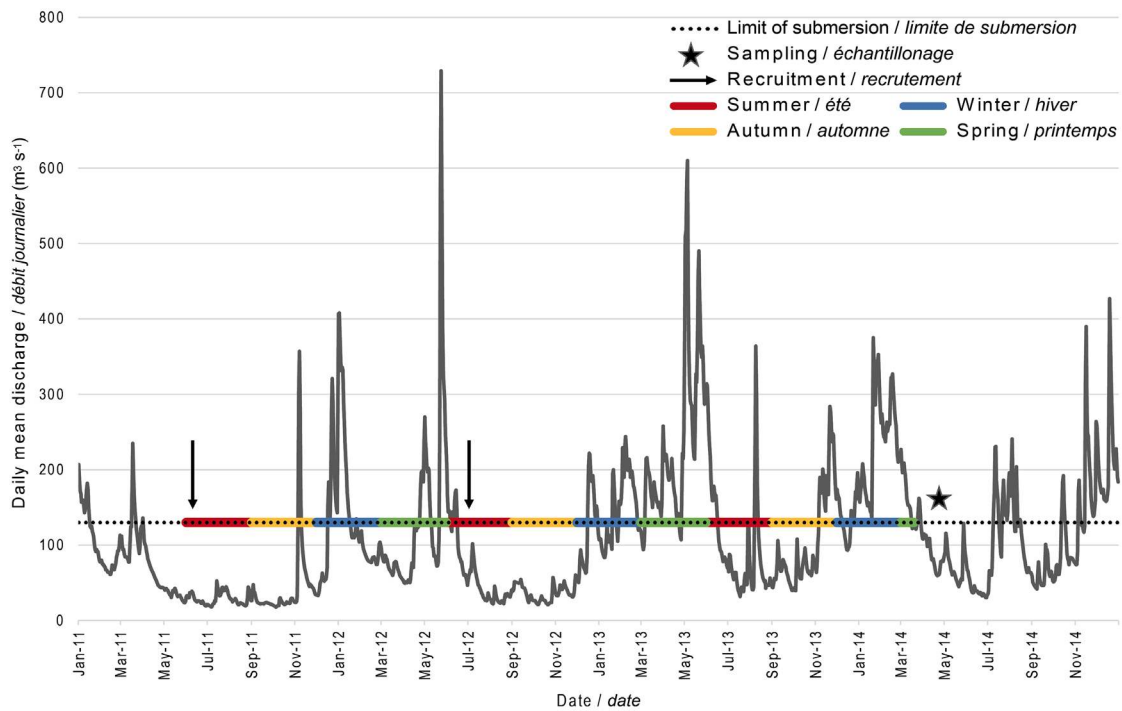


Fig. 2 – Daily mean discharges ($\text{m}^3 \cdot \text{s}^{-1}$) at the hydrological station of Châtel-de-Neuvre between 2011 and 2014 and possible recruitment periods of *P. nigra* populations (data. Banque Hydro <http://www.hydro.eaufrance.fr>; station code: K3400810).

Fig. 2 – Débits journaliers (m^3/s) à la station hydrologique de Châtel-de-Neuvre entre 2011 et 2014 et les périodes de recrutement possibles des populations de *P. nigra* (données. Banque Hydro <http://www.hydro.eaufrance.fr>; code de station : K3400810).

collar, then they were analysed with a binocular microscope and scanned at a high resolution. Annual growth rings were counted with a high precision. This dendrochronological analysis of each individual confirmed that the three populations had the same age, and that a statistical comparison of their morphological and biomechanical responses to mechanical stress could be carried out.

2.3. Data analysis

We used two datasets for the statistical analyses. The first dataset included all (in total 96), i.e. intact and broken (at tap root level), individuals. This dataset was used to study the aboveground response of *P. nigra* (pop1: 46; pop2: 40; pop3: 10 individuals). The second dataset included only the 62 intact individuals (pop1: 23; pop2: 32; pop3: 7 individuals). This dataset was used to study the belowground and the complex (above- and belowground) response of *P. nigra*.

2.3.1. Descriptive statistics

First, we used descriptive statistics and statistical tests in order to determine if plant response trait attributes varied in relation with the different levels of exposure to mechanical stress (bar-head, bar-tail, chute channel). We used Kruskal-Wallis non-parametric test with Steel-Dwass-Critchlow-Fligner multiple pairwise comparison procedure to identify which sites were responsible for rejecting H_0 . Letters are assigned to groups (i.e. A, B) indicating that the groups are significantly different. The analysis was undertaken with XLSTAT software.

2.3.2. Discriminant analysis

P. nigra individuals had known group membership (three distinct locations). After data standardisation, we applied discriminant

analysis to explain and predict the membership to several groups. This method allows (i) to check on a two-dimensional chart if the groups are well discriminated; (ii) to describe group properties using explanatory variables; and (iii) to predict to which group an observation belongs. Statistical tests were calculated, such as the Box test (Fisher's F asymptotic approximation) and the Wilks' Lambda test (Rao's approximation). The Box test is used to verify the assumption of equality for intra-class covariance matrices. The Wilks' Lambda test allows to test if the vector of the means for the various groups are equal or not. In addition, the confusion matrix was calculated showing the correctly and incorrectly assigned observations to groups based on the discriminant analysis. We have also undertaken a cross-validation to compensate for an optimistic apparent error rate. In cross-validation each observation one at a time is removed and the classification function is recalculated using the remaining data, and then the forecast is calculated for the omitted observation. The analysis was undertaken for the complete dataset (aboveground and belowground traits) within the XLSTAT software to better understand the response of the entire plant with a possibly correlated response between the aboveground and belowground traits to different levels of mechanical stress.

In the second part of the analysis, we have undertaken a cartographic analysis to study plant responses within each of the three locations (within-patch analysis). For each observation, its membership class was assigned by the discriminant analysis model, which is deduced by the membership probabilities. We mapped the probability values and the assigned group membership for each observation to determine where incorrectly assigned observations were localised. The cartographic work was undertaken in ArcMap™ using the probabilities and the membership classes of the cross-validation model, which is a more realistic model.

3. Results

3.1. Sediment texture and topography

The three locations differed according to sediment texture. The coarsest sediment texture was found on the bar-head and the finest on the bar-tail (fig. 3). There was a significant difference between the altitudes of the three populations. The population in the secondary channel was located at the highest mean elevation ($219.14 \pm 0.04\text{m}$), then the downstream population ($218.63 \pm 0.11\text{m}$) and finally the upstream one ($218.22 \pm 0.21\text{m}$). The relative altitudes of the three locations are respectively 1.65 m, 1.13 m and 0.81 m above the water level (frequency of 0.45).

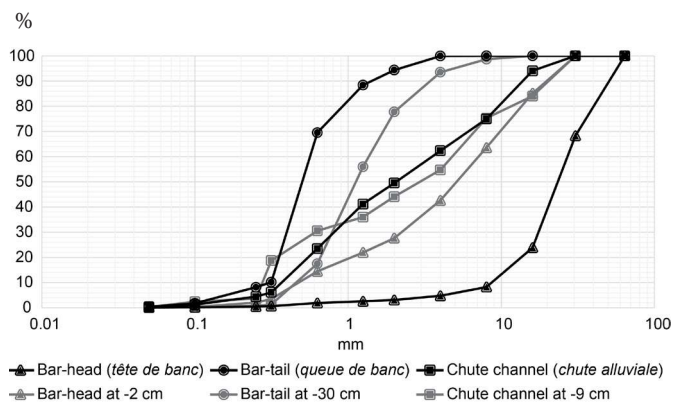


Fig. 3 – Surface and subsurface cumulated particle size distributions of the three sample sites.

Fig. 3 – Courbes granulométriques cumulées des trois sites à la surface et à la subsurface.

3.2. Age of patches

The dendrochronological analysis showed that the age of *Populus nigra* L. individuals within the three patches was comprised between one and three years. The mean age of the three populations including intact and broken individuals was 1.9 at bar-head, 1.6 at bar-tail and 2.3 years in the chute channel. For the dataset including only intact individuals the mean age was respectively 2, 1.6 and 2.2 years. There was no significant difference (tested with Mann-Whitney) concerning the height, the total length and the root collar diameter within groups between individuals of different age. Thus, age differences within populations did not induce a statistical bias for the in-between population analysis of differences related to response traits. A sign of mechanical impact was recorded between the first and the second ring of seven individuals within the upstream part of the bar-head population.

3.3. Populations' response traits: descriptive statistics

3.3.1. Aboveground response traits

For all aboveground response traits (height, flexibility, diameter at ground level and at 20 cm and inclination of the stem) the Kruskal-Wallis test rejected the H_0 . Thus, *P. nigra* trait attributes significantly varied between the three populations (tab. 1). The height of the plants was significantly different between all three locations (Steel-Dwass-Critchlow-Fligner multiple pairwise comparison) with the tallest individuals located in the chute channel and the smallest within the bar-head population. For all other aboveground traits a significant difference could be detected between the bar-head population and

the two others. At the bar-head location, plants had a more flexible stem with smaller diameters and a higher inclination than plants located at the bar-tail location and in the chute channel. However, the sampling size was reduced within the chute channel population and results must therefore be interpreted with caution.

3.3.2. Belowground response

Concerning the belowground response traits, the Kruskal-Wallis test showed significant differences related to the length of the buried stem, the taproot and root collar diameters and the number of structural roots with a diameter of >0.3 cm. No significant differences were observed regarding the length of taproot and the number of lateral and adventitious roots (tab. 1). The length of the buried stem was more important at the bar-head and bar-tail locations and was significantly shorter in the chute channel. The ratio of aerial and buried stem was close to the one within the bar-tail population demonstrating that the aerial part of the stem is equal to the buried one. Within the bar-head population the buried stem was longer, while in the chute channel population it was shorter than the aerial part. The total length (sum of the aerial, the buried stem and the taproot) of the plant was the longest on the bar-tail and the shortest at the bar-head population. The taproot and root collar diameters were the smallest at the bar-tail location and the largest on the bar-head and in the chute channel. The number of structural roots with a diameter of >0.3 cm showed the same pattern as the aboveground traits with a high similarity between the bar-tail and the chute channel populations. At these two locations *P. nigra* individuals exhibited a weaker proportion of structural roots than within the bar-head population.

3.4. Discriminant analysis: complex (above- and belowground) response of *P. nigra*

The Box test confirmed that we need to reject the hypothesis that the covariance matrices are equal between the groups and the Wilks' Lambda test confirmed that the difference between the mean vectors of the groups are statistically significant. The two-dimensional chart representing the observations on the factor axes confirmed that the tree populations are well discriminated (fig. 4A). Bar-head and bar-tail populations were discriminated along the first axis, while bar-tail and chute channel populations along the second axis. 100% of the variance is represented by the two factors. The correlation between the initial variables and the two factors are represented on Figure 4B. The factor F1 was the most correlated with the aboveground height, the inclination and the number of structural roots with a diameter of >0.3 cm; the factor F2 with the diameter of root collar and taproot and the length of the buried stem.

The upstream population (bar-head) was characterised by a small height, high inclination, a strong abundance of structural roots with a diameter of >0.3 cm, large root collar and taproot diameter and a long buried stem. The downstream population (bar-tail) was characterised by an important stem height, low inclination, low abundance of structural roots, small root collar and taproot diameter and a long buried stem. The population in the chute channel was characterised by an important stem height, low inclination, strong number of structural roots, large root collar and taproot diameter and a small buried stem. 100% of the observations were well classified and 80.65% of the observations were well predicted by the cross-validation (tab. 2). Only six individuals were classified by the cross-validation as individuals belonging to the downstream population instead of to the bar-head, four as belonging to the

Tab. 1 – Summary statistics and results of Kruskal-Wallis test ($\alpha = 0.05$) of aboveground and belowground *P. nigra* traits. Letters assigned to groups (i.e. A, B) are indicating that the groups are significantly different.

Tab. 1 – Statistiques sommaires et résultats du test de Kruskal-Wallis ($\alpha = 0,05$) des traits aériens et souterrains du *P. nigra*. Les lettres associées aux groupes (c.-à-d. A, B) indiquent que les groupes sont significativement différents.

Trait	Location	Sample nb.	Min.	Max.	Mean	Std. dev.	p-value	Groups
Height (cm)	Bar-head	46	18.00	63.00	37.63	11.80	< 0.0001	A
	Bar-tail	40	42.00	100.00	67.64	16.88		B
	Chute ch.	10	61.00	111.00	83.00	17.10		C
Flexibility (newton)	Bar-head	46	0.02	2.12	0.33	0.42	< 0.0001	A
	Bar-tail	40	0.04	2.30	0.83	0.53		B
	Chute ch.	10	0.30	2.40	1.20	0.70		B
\emptyset (cm; at ground)	Bar-head	46	0.30	1.20	0.59	0.19	0.0005	A
	Bar-tail	40	0.40	1.10	0.71	0.16		B
	Chute ch.	10	0.60	1.10	0.80	0.16		B
\emptyset (cm; at 20cm)	Bar-head	46	0.10	0.60	0.38	0.13	< 0.0001	A
	Bar-tail	40	0.30	0.80	0.55	0.11		B
	Chute ch.	10	0.40	0.60	0.53	0.09		B
Inclination (degree)	Bar-head	46	95.00	161.00	125.87	14.32	< 0.0001	A
	Bar-tail	40	78.00	128.00	105.94	10.24		B
	Chute ch.	10	85.00	112.00	101.60	7.29		B
Length of buried stem (cm)	Bar-head	23	55.00	102.00	74.48	13.45	0.0009	A
	Bar-tail	32	47.00	100.00	71.97	13.75		A
	Chute ch.	7	48.00	62.00	53.57	5.00		B
Ratio height / buried stem	Bar-head	23	0.19	1.15	0.57	0.20	< 0.0001	A
	Bar-tail	32	0.55	1.79	1.00	0.27		B
	Chute ch.	7	1.14	1.65	1.40	0.19		C
Total length (cm)	Bar-head	23	95.00	167.00	131.22	14.49	< 0.0001	A
	Bar-tail	32	110.00	198.40	160.18	21.79		B
	Chute ch.	7	125.00	185.00	148.57	18.06		B
Length of taproot (cm)	Bar-head	23	11.00	23.00	16.30	3.31	0.2269	A
	Bar-tail	32	5.00	46.00	18.34	9.44		A
	Chute ch.	7	13.00	25.00	19.86	3.93		A
\emptyset of taproot (cm)	Bar-head	23	0.40	1.10	0.74	0.21	0.0130	A
	Bar-tail	32	0.10	1.10	0.55	0.25		B
	Chute ch.	7	0.40	1.90	0.94	0.59		A
\emptyset of collar (cm)	Bar-head	23	0.60	1.70	1.10	0.29	< 0.0001	A
	Bar-tail	32	0.40	1.20	0.75	0.22		B
	Chute ch.	7	0.90	1.70	1.14	0.28		A
Nb. of lateral root	Bar-head	23	2.00	13.00	6.35	2.84	0.1361	A
	Bar-tail	32	1.00	34.00	10.69	7.94		A
	Chute ch.	7	3.00	22.00	10.00	8.04		A
Nb. of adventitious root	Bar-head	23	14.00	109.00	45.83	21.17	0.0617	A
	Bar-tail	32	9.00	101.00	45.59	24.79		A
	Chute ch.	7	7.00	48.00	25.43	15.95		A
Nb. of root $\emptyset > 0.3$ cm	Bar-head	23	0.00	6.00	2.87	2.14	0.0007	A
	Bar-tail	32	0.00	5.00	1.09	1.49		B
	Chute ch.	7	0.00	1.00	0.14	0.38		B

bar-head instead of belonging to the downstream population and two as belonging to the downstream population instead of to the chute channel.

The cartographic results suggest that between-patch, as well as within-patch gradients for plant responses were present (fig. 5). Some individuals of the most exposed bar-head location were assigned to lower exposed bar-tail location and conversely. The misclassified

individuals within the less exposed chute channel were assigned to the bar-tail group but not to the bar-head one. The misclassified individuals within the bar-head patch are rather located at the downstream part of this patch and the misclassified individuals within the bar-tail patch are rather located at the upstream part of this patch.

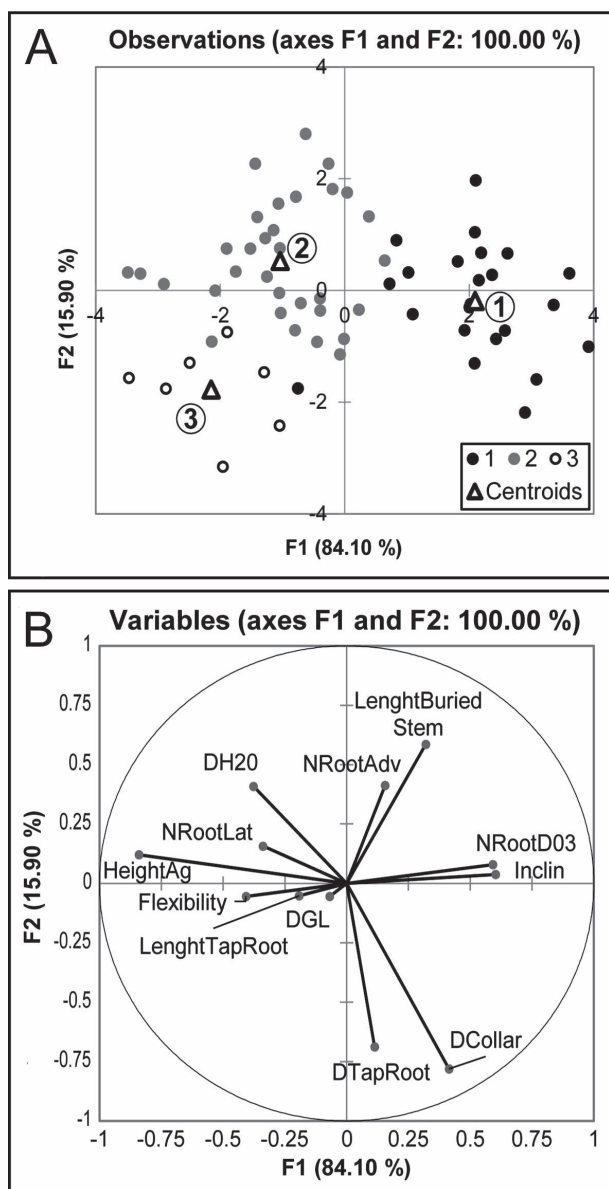


Fig. 4 – Discriminant analysis based on above- and belowground response traits.

A. Two-dimensional chart representing the observations on the factor axes; B. Correlation between the initial variables and the two factors. 1. Bar-head; 2. Bar-tail; 3. Lower reach of chute channel.

Fig. 4 – Analyse factorielle discriminante basée sur des traits aériens et souterrains.

A. Diagramme bi-dimensionnel représentant les observations sur les axes factoriels ; B. Corrélation entre les variables initiales et les deux facteurs. 1. Tête de banc ; 2. Queue de banc ; 3. Tronçon aval de la chute alluviale.

4. Discussion

In accordance with our first hypothesis that within exposed locations young poplar saplings increase their resistance to uprooting, the *Populus nigra* L. population located on the highly exposed bar-head responded to mechanical stress with a reduced size and a strong flexibility of stems (sections 3.3.1 and 3.4). The stems also showed an inclination in the downstream direction parallel to flow. The development of these two trait attributes related to stem size and flexibility was observed in experimental *in situ* (Puijalon and Bornette, 2004) and *ex situ* (Puijalon et al., 2008) studies, for

example on *Mentha aquatica* L. plants in response to mechanical stress related to water flow and for *Ulmus americana* L. plants subjected to flexural treatment in an *ex situ* greenhouse experiment (Telewski and Pruyn, 1998). These observed response trait attributes most likely correspond to avoidance trait attributes as defined by Puijalon et al. (2011): the plants reduce their above-ground size to limit mechanical damage and to prevent uprooting. As corollary of the reduced plant size, the limitation of the drag decreases the potential of the plants to trap large amounts of fine sediment. Hortobágyi et al. (in press) demonstrated on several alluvial bars of the Allier River within the same study reach (including the present bars) that such a limitation of engineer effects caused by mechanical stress in the most exposed locations on bars seems to reflect an inhibiting effect of niche construction by riparian plants. Sediment texture of the bar-head was constituted of coarse sediments, coarser than the chute channel and the bar-tail (fig. 6), suggesting a limitation of surface plant engineer effects and the occurrence of a dominantly physically-driven sedimentation process. Our results suggest that *P. nigra* plants which establish within exposed bar-head locations are able to resist strong mechanical stress (shear stress and coarse sediment transport and burial) by developing aerial avoidance traits, but they do not significantly contribute to sediment trapping because of their small size and low structural density. A trade-off based on the cost-benefit balance between the function of resisting mechanical constraints and improving resource storage must be found by the plants. Therefore, we argue that in the highly exposed contexts, short term sapling survival is the priority of the individual plant and that engineering effects remain non-significant.

Within the bar-head, we also observed that the buried part of the stem of all individuals sampled was proportionally greater than the part of the aerial stems (sections 3.3.2 and 3.4). Furthermore, the buried stems lay close to a horizontal position under a coarse sediment layer (fig. 6). These observations suggest a strong biomechanical impact of floods and especially bedload transport on the exposed saplings resulting in a high stem inclination and coarse sediment burial that could lead to the improvement of anchorage of the plants through specific adaptations. Stokes et al. (1995) showed that for trees exposed to wind stress, windward roots (i.e. roots growing towards the mechanical force, here the wind) are playing an important role in stability. We suggest that the buried stems of the observed *P. nigra* plants and their associated abundant and strong adventitious roots provide an increased anchorage capacity. The high share of buried stems leads to a smaller part of the plant being directly exposed to flow and shear stress and contributes to the further development of adventitious roots and thus to an additional increase of anchorage.

However, within the population of the bar-head, we did not observe any increase in tap root length compared to the two other populations (sections 3.3.2 and 3.4). This is in line with the results of Tamasi et al. (2005), who studied root response of *Quercus robur* L. plants to wind loading and did not observe significant difference in tap root length between wind loaded plants and the control group. It was suggested that plants are rather investing energy in lateral root growth because they provide the major component of anchorage strength in trees (Stokes et al., 1995). As expected, within the bar-head population, structural roots with a diameter of >0.3 cm were significantly more abundant, and collar and taproot diameters were more important than within the population of the bar-tail. This tolerance strategy (*sensu* Puijalon et al., 2011), which enables plants to reach a higher resistance to uprooting, was also observed in an *ex situ* glasshouse experiment comparing sunflower and maize seedling responses to mechanical stimulation in the form of stem flexing (Goodman and Ennos, 1996). In addition, the development of

Tab. 2 – Confusion matrix for the estimation sample and for the cross-validation.

Confusion matrix	from \ to	Bar -head	Bar -tail	Chute channel	Total	% correct
Estimation sample	Bar-head	23	0	0	23	100.00%
	Bar-tail	0	32	0	32	100.00%
	Chute channel	0	0	7	7	100.00%
	Total	23	32	7	62	100.00%
Cross -validation	Bar-head	17	6	0	23	73.91%
	Bar-tail	4	28	0	32	87.50%
	Chute channel	0	2	5	7	71.43%
	Total	21	36	5	62	80.65%

Tab. 2 – Matrice de confusion pour l'échantillon d'estimation et pour les résultats de la validation croisée.

such tolerance trait attributes (strong root system) certainly impacts geomorphology through the persistence of *P. nigra* individuals under highly exposed locations by increasing sediment cohesion, which is a widely recognized role of riparian vegetation (Abernethy and Rutherford, 1998; Polvi et al., 2014).

Adventitious roots that rapidly develop in freshly deposited sediments also improve the capacity of the plants to explore the substrate for water and nutrient uptake. This is especially important on the bar-head within a coarse and rather nutrient poor sediment environment. Therefore, and despite a small aboveground plant size, the adventitious roots contribute through an increase in anchorage and water and nutrient uptake to an improved capacity of the plants to survive under highly disturbed and stressful conditions and to resist mechanical destruction. A further advantage of the development of the adventitious root system lies in its potential response to changes in geomorphology, e.g. in relation to lateral channel migration or avulsion. Within a less disturbed and stressful environment the earlier developed belowground biomass (long buried stem with adventitious roots) can subsequently facilitate rapid aboveground biomass production.

In accordance with our second hypothesis that under less exposed situations plant morphology predominantly expresses the function of resource acquisition, saplings on the bar-tail and within the lower chute channel showed longer, larger, less flexible and less inclined stems (sections 3.3.1 and 3.4). The total plant length was maximal within the bar-tail population (tab. 1), suggesting that fine sediment burial under less exposed situations stimulates aboveground biomass production. Some woody plant species of coastal dunes (i.e. *Populus balsamifera* L. and *Salix cordata* Michx.) also respond with increased vertical shoot growth to burial stress (Dech and Maun, 2006). Thus, the positive growth response we observed in the bar-tail population seems clearly to be linked to the combination of the decrease in exposure to mechanical stress and the occurrence of fine sediment deposition, which provides nutrients and an improved moisture retention capacity during summer (Steiger and Gurnell, 2003; Francis et al., 2009). Furthermore, the correlation between fine sediment trapping and plant morphology attributes was studied in various contexts, such as in a flume experiment on marsh species (Bouma et al., 2013), in a gully erosion project (Erktan and Rey, 2013) and in riparian environments (Euler et al., 2014; Corenblit et al., 2015; Manners et al., 2015). Within the fluvial environment, higher plants that exhibit a larger biomass are expected to induce greater positive topographic changes (Kui et al., 2014; Diehl et al., 2017). The buried stems covered by fine sediment observed within the bar-tail population suggest such an effect of the *P. nigra* individuals on fine sediment trapping. Hortobágyi et al. (in press) highlighted

on the same alluvial bars of the Allier River, that *P. nigra* engineer effects on sediment trapping are indeed the most efficient when plants are exposed to intermediate and low mechanical stress, and, concurrently, develop a larger aerial biomass. Furthermore, a very high plant density was observed within the bar-tail population leading to a high roughness and thus a very efficient sediment trapping capacity.

Our results combined with the ones obtained by Hortobágyi et al. (in press) suggest that within the bar-tail population, changes in *P. nigra* morphological and biomechanical trait attributes on alluvial bars are not only a passive response to mechanical stress but that they result from induced fine sediment trapping and positive feedbacks between *P. nigra* plant growth and fluvial landform construction (Corenblit et al., 2007, 2015; Gurnell, 2014). Landform construction, as observed during *P. nigra* establishment on the Allier River, might be considered as a niche construction strategy leading to a progressive decrease of mechanical stress and modifications of habitat conditions that positively impact *P. nigra* survival and growth (Corenblit et al., 2014). Furthermore, the niche construction process, as observed during the present study, might be reinforced through the sheltering effect of plants growing within the most upstream and exposed areas of the studied vegetation patch. Corenblit et al. (2016) showed that on the alluvial bars of the channelized Garonne River, France, highly exposed *P. nigra* cohorts offer bioprotection for younger cohorts which establish just downstream. The sheltering effect of upstream established plants was also demonstrated in relation to the survival of seedlings and cuttings of *P. nigra*, *S. alba* and *S. elaeagnos* (Moggridge and Gurnell, 2009). Our within-site results (fig. 5) suggest that a plant sheltering effect exists from the beginning of establishment, i.e. during the first two years following recruitment, within the same patches composed of individuals of the same age or very close age forming dense stands. In such patches, individuals located downstream benefit from the protective effects of the upstream individuals (i.e. intra-specific facilitation). However, these exploratory results have to be confirmed by repeated sampling within a shorter time period to exclude any differences linked to the development of saplings.

The population located in the chute channel differed from the two others by its aboveground stem which was longest in the chute channel, and its buried stem which was shortest in the chute channel. The total plant length was shorter compared to the bar-tail population. This result emphasizes aerial biomass growth stimulation provided by fine sediment burial that increases the local potential of water and nutrient acquisition. Individual plants that establish in the lower reach of the chute channel developed some common trait attributes in comparison to the bar-tail population and

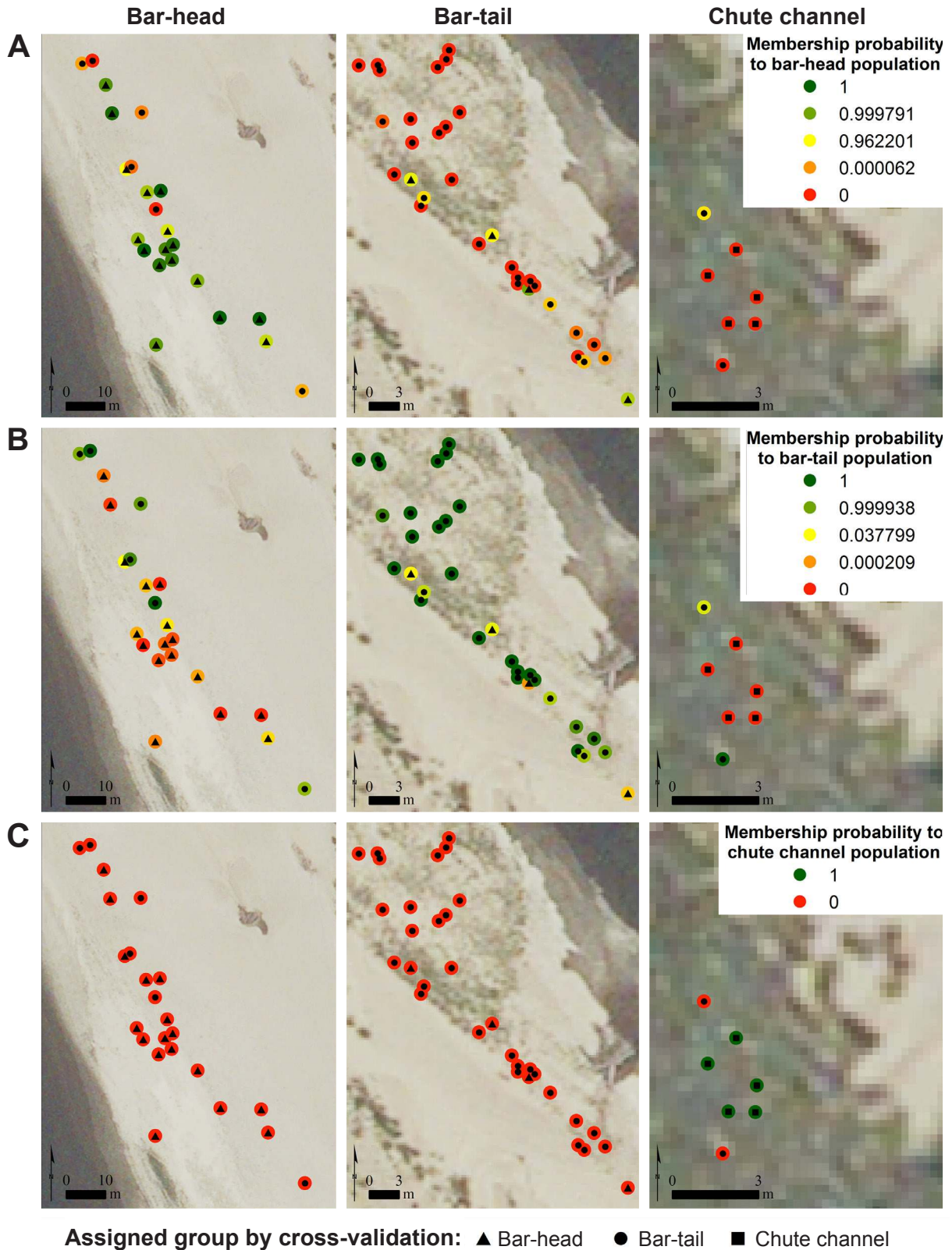


Fig. 5 – Membership probabilities and membership classes of observations deduced by the probabilities in cross-validation mode.

A. Membership probability to be assigned to the bar-head population; B. Membership probability to be assigned to the bar-tail population; C. Membership probability to be assigned to the chute channel population. Note that thresholds between classes are different for A, B and C (see legend).

Fig. 5 – Probabilité d'appartenance à un groupe et classes d'appartenance des observations déduites par les probabilités en mode de validation croisée.

A. Probabilité d'appartenance attribuée à la tête de banc; B. Probabilité d'appartenance attribuée à la queue de banc; C. Probabilité d'appartenance à être attribuée à la chute alluviale. Notez que les seuils de classes sont différents pour chaque site (voir légende).

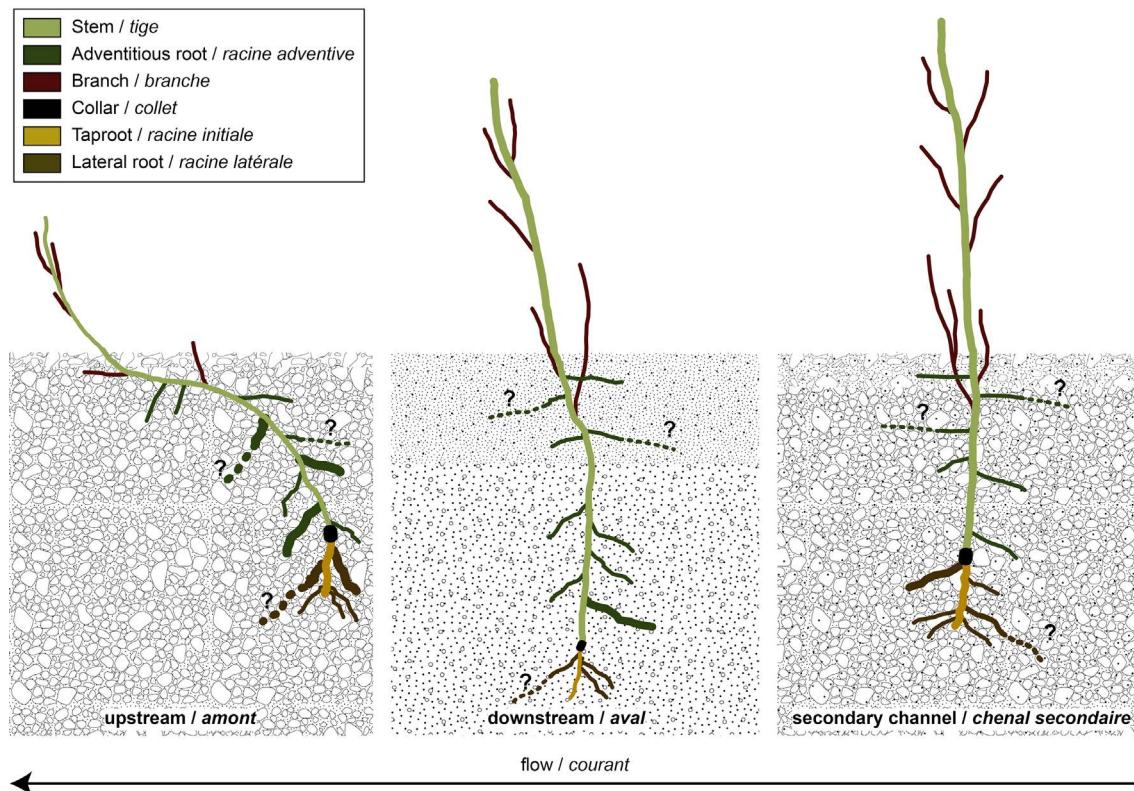


Fig. 6 – Schematic representation of *Populus nigra* L. exposed to different levels of mechanical stress. The length of adventitious and lateral roots remains unknown since they could not be excavated entirely. Question marks indicate that root lengths are unknown.

Fig. 6 – Représentation schématique de *Populus nigra* L. exposé au stress mécanique de différents niveaux. La longueur des racines adventives et latérales est inconnue, étant donné qu'elles n'ont pas été excavées dans leur intégralité. Les points d'interrogation indiquent le manque d'information sur la longueur des racines.

some other trait attributes which were common to the bar-head population. The long, large, less flexible and less inclined stems and the low abundance of structural roots with a diameter >0.3 cm were similar with the bar-tail population which was less exposed to mechanical stress. However, the larger collar and taproot diameter are common trait attributes in comparison with the bar-head population. This contrast within the same population may be related to the fact that (i) *P. nigra* plants growing within lower chute channels benefit from favourable habitat conditions (i.e. water and nutrients pools combined with a decreased exposure to mechanical stress during annual floods) thus favouring biomass production; (ii) they endure more mechanical stress during higher flows and floods because chute channels function as flood channels where water flow converges. The close resemblance concerning the collar and taproot diameter with the bar-head population might also be explained by the similarity in sediment texture (coarse sediment). An additional explanation which could not be further explored in the present study was given by Ennos (1993) who observed that plants compensate their aboveground growth to develop an optimal anchorage system.

Overall, our observations indicate that *P. nigra* populations can develop a set of variable morphological and biomechanical responses to contrasted hydrogeomorphic constraints, leading to functional diversity and an increased resistance of the plants at the scale of an alluvial bar. At the highly exposed bar-head location, plants rather developed avoidance and tolerance response traits without significantly affecting sediment trapping while at less exposed bar-tail locations effect traits seem to be operant resulting in a positive feedback between plant growth and fluvial landform construction.

5. Conclusion

In this biogeomorphic study we provided a quantitative understanding of the relation between response trait attributes of *Populus nigra* L. plants and their exposure to different levels of mechanical stress caused by flow and sediment transport. At the highly exposed location, plants developed both avoidance and tolerance response traits allowing a higher resistance to mechanical stress, while at the less exposed location plants developed response trait attributes allowing a better resource acquisition and higher growth rates thus favouring bioconstruction. These results support the hypothesis of a positive niche construction by riparian poplar plants within fluvial corridors (Corenblit et al., 2014). Our study, in addition to the one undertaken by Hortobágyi et al. (in press), suggests that differences in plant response trait attributes and their related effects on fluvial landform construction may lead to different biogeomorphic evolutionary trajectories on alluvial bars from a functional trait perspective. These findings highlight the importance of considering in more detail the role of fine scale biogeomorphic processes occurring at the micro-scale and at a short timescale (e.g. development of individual plant response traits to mechanical stress) on those occurring at larger spatio-temporal scales (e.g. construction of wooded pioneer fluvial islands, benches and floodplains; adjustment of the landscape mosaic). We also stress the need to further develop nested hierarchical biogeomorphic bottom-up and top-down cross scale studies within fluvial corridors to better understand complex biogeomorphic fluvial ecosystems.

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Version française abrégée

Les arbres riverains pionniers, tels que *Populus nigra* L., établis sur des bancs alluviaux au sein de corridors fluviaux dynamiques, influencent fortement la géomorphologie fluviale en piégeant des sédiments et en construisant des formes fluviales pendant les crues (Corenblit et al., 2007 ; Gurnell, 2014 ; Hortobágyi et al., 2017). L'effet ingénieur (changements dans l'état physique de l'habitat par les organismes) de *P. nigra* sur les bancs alluviaux dépend de sa biomasse et de son degré d'exposition à la contrainte mécanique. *P. nigra* a une plasticité phénotypique élevée qui sous-tend une grande variation de ses traits morphologiques et biomécaniques selon les conditions hydrogéomorphologiques locales. La compréhension et la quantification de la variation des traits de réponses morphologiques et biomécaniques au sein des populations de *P. nigra* en fonction de leur exposition à la contrainte mécanique est fondamentale pour mieux

comprendre pourquoi et comment les plantes sont capables d'influer sur la géomorphologie. Dans une étude empirique in situ, nous avons quantifié la variation des traits de réponses morphologiques et biomécaniques de populations de *P. nigra* selon trois niveaux différents de contrainte mécanique. En contexte très exposé (en tête de banc alluvial), les plantes ont développé des traits de réponses permettant une plus grande résistance, notamment une taille réduite, une tige flexible et inclinée et un système racinaire plus robuste (tab. 1, fig. 6). Néanmoins, ces réponses morphologiques et biomécaniques réduisent en même temps le potentiel « ingénieur » des plantes, c'est-à-dire la capacité de piégeage des sédiments fins. Hortobágyi et al. (sous presse) ont démontré sur la rivière Allier l'effet ingénieur limité du peuplier noir dans les zones les plus exposées, ce qui traduit un effet inhibiteur de la construction de niche par les contraintes mécaniques

liées à l'écoulement. En contextes moins exposés (en queue de banc et dans le chenal secondaire), les peupliers ont développé une tige plus large, plus longue, moins flexible et moins inclinée. Cette réponse exprime une fonction préférentiellement dédiée à l'acquisition des ressources et à la bioconstruction. Le fait que la longueur totale des plantes est maximale en queue de banc suggère que l'enfouissement par des sédiments fins stimule la production de la biomasse aérienne, celle-ci renforçant le potentiel photosynthétique. La construction des formes fluviales par le peuplier noir peut être considérée dans notre cas d'étude et de manière plus générale comme une stratégie de construction de niche conduisant à la diminution progressive des

contraintes mécaniques et à l'accumulation des sédiments fins, de la matière organique et des nutriments qui influencent de manière positive la survie et la croissance des peupliers (Corenblit et al., 2014). Nos résultats suggèrent que les processus biogéomorphologiques se produisant à une échelle fine ont une influence sur les processus à une échelle plus large. Cela pointe la nécessité de développer des études biogéomorphologiques hiérarchiques selon des approches ascendantes (bottom-up) et descendante (top-down) pour renforcer notre compréhension du fonctionnement des écosystèmes biogéomorphologiques fluviaux.