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Black poplar establishment on alluvial bars: seed rain homogeneity over a few kilometres

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Abstract: The Black poplar is a pioneer tree species occurring along many river courses across Europe. Seedlings establish at very high density and experience various stresses (e.g., hydric, mechanical). In a previous study conducted in 2017 on the same population we described the fine-scale genetic structure (FSGS) of three age cohorts (5, 10 and > 20 years old) and found a significant SGS in the younger cohort. In this study, we aim to determine the FSGS in Black poplar cohorts of one-year-old seedlings, which is the most informative about seed dispersal. We used microsatellite markers to explore the FSGS of four different patches of Black poplar seedlings from two riverbanks in the Val d’Allier National Natural Reserve (France). We found a high genetic diversity and detected no FSGS in any of the four sampled seedlings patches. The absence of SGS at the seedling stage suggests that in this natural population, seeds from different mother trees are widely dispersed, well mixed and are deposited homogeneously on the various germination sites available over few kilometres.

Keywords:

List of abbreviations: SGS – spatial genetic structure, FSGS – fine-scale spatial genetic structure

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Introduction

The Black poplar (*Populus nigra* L., Salicaceae) is a pioneer tree species with a good tolerance to submersion, sediment burial and high temperatures occurring along many river courses across Europe (Chamaillard, 2011). The species is dioecious, and a female tree produces each year millions of short living seeds which are transported by both wind and water (Barrat-Segretain, 1996; Karrenberg et al., 2002). Seeds germinate immediately after arrival on suitable bare moist alluvial bars (Barsoum & Hughes, 1998; Guillois-Froget et al., 2002). During favourable years, Black poplar seedlings generally establish in

very high density (e.g., > 4000/m²; Braatne, 1996) at the immediate margins of the main or secondary channels. Suitably positioned seedlings on alluvial bars near the channels generally form elongated recruitment bands or patches composed of individuals of the same age (cohort) (Guillois-Froget et al., 2002; Corenblit et al., 2009; 2016). As a pioneer species, the eco-hydrological conditions for regeneration include freshly disturbed, competitor-free sediments and it is highly dependent on water table level fluctuations (Mahoney & Rood, 1998; Corenblit et al., 2014). Harsh summer (drought) and winter (submersion, erosion and/or burial) conditions on alluvial bars allow seedlings to establish only during restricted

time periods and years (Barsoum & Hughes, 1998; Mahoney & Rood, 1998; Stella & Battles, 2010; Guillois et al., 2011). The relatively long period of seed production of Black poplar (2-3 months according to Braatne, 1996; Guillois-Froget et al., 2002) combined to the variability of dispersal conditions (i.e., wind and hydrological regimes, location and number of father- and mother-trees, geomorphological configuration) may lead to strong intra- and inter-annual variability in seedling relatedness on the colonization sites. Patterns of dispersal of pollen and seeds have important consequences for the spatial distribution of genotypes at the colonisation stage (Banks et al., 2013).

The spatial genetic structure (SGS), defined as the non-random distribution of genotypes, characterizes the relationship between relatedness of individuals and their physical proximity within population (Loiselle et al., 1995; Hardy, 2003). The presence of a significant SGS may be the result of historical founding events and/or population expansion, selection pressures and, limited or structured gene dispersal (Vekemans & Hardy, 2004). In pioneer tree species, investigating the SGS helps improve our understanding of dispersal and colonisation patterns, and the subsequent development of the woodland ecosystems they inhabit (Jones et al., 2006). Moreover the comparison of SGS between different age cohorts or at different spatial scales allows to make inferences about gene flow (pollen and seed dispersal) and, therefore, valuable for the conservation of threatened species (Gaudeul & Till-Bottraud, 2008; Batista Leite et al., 2014). Studies of SGS in trees generally address large geographic areas; at the river reach scale (Imbert & Lefevre, 2003; Jelić et al., 2015; Kettenring et al., 2019; González-Robles et al., 2020) or from kilometres (Pospíšková & Šálková, 2006; Born et al., 2008; Wójcikiewicz et al., 2019) to hundreds of meter (Rathmacher et al., 2010; Sagnard et al., 2011; Deng et al., 2020). However, sampling often neglects the very fine scale, at less than a meter. Hereafter, we will use “fine-scale spatial genetic structure” (FSGS) to refer to scale of a meter or less which correspond to the distance at which individuals interact with each other (i.e., including the zone of interaction among immediate neighbours at fine spatial scales as defined by Fajardo et al., 2016). FSGS has been studied in trees in an agricultural setting (Baldauf et al., 2014; Sjölund et al., 2015; Ramos et al., 2016), and also in woodland environments (Till-Bottraud et al., 2012; Bessega et al., 2016; Fajardo et al., 2016; Kitamura et al., 2018), but to our knowledge, very few have explored FSGS of Black poplar within river corridors (Mazal et al., 2021).

In a previous study we described the FSGS of three cohorts (5, 10 and > 20 years old individuals) in the

Allier and the Garonne rivers and found a significant FSGS for the young cohort (5 years old individuals) but not in older cohorts (Mazal et al., 2021). However, we did not investigate the FSGS for seedlings of the year, which are the most informative about seed dispersal. Investigating the evolution of FSGS in populations across different developmental stages can provide a better understanding of their local patterns of dispersal and colonization and could provide valuable information on Black poplar’s ability to colonize alluvial bars within the fluvial corridor. Following our previous results, we hypothesised that during dispersion seeds may get aggregated into clumps of related seeds and form micro-patches of related seedlings on the alluvial surfaces, resulting in FSGS for the seedlings of the year. The goal of this paper was to study the FSGS in cohorts of seedlings in the same natural population studied previously in order to improve our understanding of seed dispersal and spatial genetic structuration during recruitment. We used microsatellite markers to explore the FSGS of four different patches of black poplar seedlings from two riverbanks distant by at most 1.2 km in a natural reserve of the Allier River (France) and discussed our previous results obtained in 2017 on older cohorts from the same population (Mazal et al., 2021) in the light of these results.

Material and Methods

Study site and sampling strategy

The study site is located along the lower reaches of the Allier River in the Val d’Allier National Natural Reserve, near Châtel-de-Neuvre (46°25’06.5”N, 003°19’43.2”E; 220 m a.s.l.) in central France. This site is the same as described and studied in Mazal et al. (2021). The area benefits from a certain degree of protection and has experienced moderate anthropogenic impacts (e.g., few bank protections or rip rap) (Petit, 2006; Dejaifve & Esquirol, 2011). This reach of the Allier River is characterized by active lateral erosion on the outer bends of meanders, with point bar formation and migration on the inner bends within the Réserve Naturelle Nationale du Val d’Allier (Garófano-Gómez et al., 2017). The progressive

Table 1. Summary of the characteristics of the four patches sampled for *P. nigra* seedlings along the Allier River.

Patch	Patch area (m ²)	Number of individuals sampled	Density (ind./m ²)
A	1	90	90
B	0.3	93	310
C	2	93	47
D	1.04	92	89
Mean	1.09	92	134

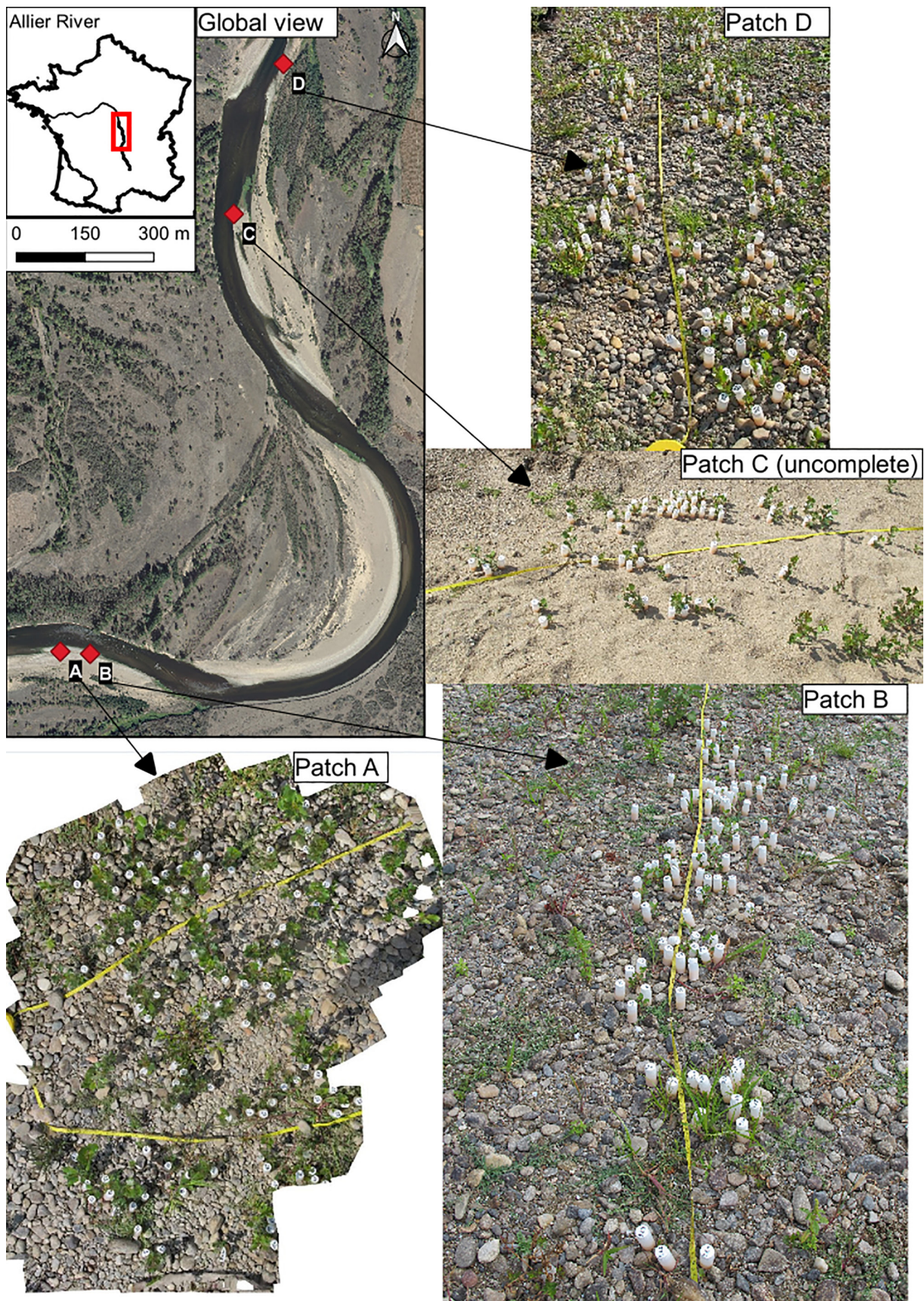


Fig. 1. Aerial photograph of the Allier River study site, showing the position of the Black poplar patches (A, B, C and D) sampled along the two gravel bars. River flow direction is from South to North. In the four patches, the white vials (6 cm high) are positioned next to each sampled individual

shifting of the river channel allows for periodic recruitment events on many germination sites on alluvial bars, resulting in different aged cohorts of *P. nigra* recruits growing in elongated bands parallel to the main channel (Hortobágyi et al., 2017).

In August 2019, we sampled seedlings of 1 year old in four patches on two alluvial bars. We chose two patches of seedlings in each bar and collected approximately 90 individuals in each patch (Table 1, Fig. 1). Density was very high in the four patches (mean density = 133 ± 59.61 individuals/m²) and the patches sampled were relatively small (1 m²). Patches were distant by at most 1.2 km. Table 1 lists the number of black poplar seedlings, patch area, and patch plant density. For each patch, we built a distance matrix between each pair of individuals at a centimetre scale using pictures on which we digitized the location of each individual (ArcGis™ v.12.4). The studied patches were located in similar conditions, including the proximity and elevation relative to the channel. Numerous adult trees are present close to our studied site. A few km downstream from our site, Wendelgaß (2016) found approximately 130 adult trees (> 20 years-old, based on tree-ring counts) out of 330 measured over an area of 11,500 m². This indicate that more than 20,000 adult trees are present in the Reserve.

DNA extraction and genotyping

Total DNA was extracted from leaves using the NucleoSpin 96 Plant Core Kit extraction kit (Macherey Nagel™) according to the manufacturer instructions. We used 12 unlinked (Gaudet et al., 2007) nuclear microsatellites markers to genotype individuals (see details in Table S1): WPMS06, WPMS07, WPMS09, WPMS13, WPMS14, WPMS16, WPMS20, WPMS22, PMGC93, PMGC2578, PMGC14, and ORPM221 (Smulders et al., 2002; Van Oosterhout et al., 2004; Chenault et al., 2011; Faivre-Rampant et al., 2016). Markers were arranged in three PCR-multiplex reactions. Multiplex1: ORPM221, WPMS07, WPMS13, WPMS22; Multiplex2: PMGC14, PMGC93, PMGC578, WPMS14; Multiplex 3: WPMS06, WPMS09, WPMS16, WPMS20. We used indirect tagging with M13-tailed primer method (Oettingts et al., 1995). In this method, instead of synthesizing one specific fluorescently labelled primer for each SSR marker, only a dye labelled M13 primer is needed. Marker amplification was performed according to Mazal et al. (2021). Analysis of The PCR products were performed in a 3750xl Genetic Analyser (Applied Biosystems™) with GeneScan™ 500 LIZ® internal size standard. Genotypes were scored using Geneious™ v.2020.1.1. and confirmed manually.

Genetic analyses

Three markers did not amplify (WPMS06, WPMS07, WPMS22) and were removed from the analysis. Loci were tested for null allele frequencies with Brookfield's methods (Brookfield, 1996) using Microchecker v2.2.3 (Van Oosterhout et al., 2004) low DNA concentrations and primer-site mutations may result in the incorrect assignment of microsatellite genotypes, potentially biasing population genetic analyses. MICRO-CHECKER is WINDOWS®-based software that tests the genotyping of microsatellites from diploid populations. The program aids identification of genotyping errors due to nonamplified alleles (null alleles. Three markers (PMGC14, WPMS09 and WPMS16) presented a high null-allele frequency and were therefore removed from the dataset. To estimate the discrimination power of the dataset, we calculated the probability of sampling two different genotypes with the same multilocus SSR phenotype (probability of identity) with one to six markers using GenAIEx v6.5 (Peakall & Smouse, 2012). This probability decreased from 2.9×10^{-02} with one marker, and reached a plateau around 7.5×10^{-07} with four markers suggesting a high discrimination power of our six markers combination.

We estimated allele frequencies, total and effective number of alleles, expected and observed heterozygosities and inbreeding coefficient using SPAGeDi 1.5 (Hardy & Vekemans, 2002). Genetic structure was analysed using the STRUCTURE 2.3.4 (Pritchard et al., 2000) with a burn-in period of 100,000 iterations followed by 200,000 additional MCMC iterations. The analysis was based on the admixture model and uncorrelated allele frequencies with the recessive alleles option. Twenty independent runs for each number of groups (K), ranging from 1 to 5 were used. The best number K was estimated and visually verified as the highest value of Ln(P) following Puechmaille (2016) because the ΔK method does not evaluate $K=1$ causing an overestimation (Evanno et al., 2005).

Spatial genetic structure and relatedness

We checked for the absence of clonality using the GenAIEx (Peakall & Smouse, 2012). FSGS was assessed within patches using the SPAGeDi. Loiselle multilocus kinship coefficients, R_{ij} (Loiselle et al., 1995), were calculated between each pair of individuals. Because R_{ij} is a kinship coefficient relative to the population mean, negative values can result, meaning that two individuals are less related on average than randomly selected individuals from the population (Hardy, 2003). Kinship coefficient values were averaged within distance classes (d), giving $F(d)$ and plotted against geographical distances. Ten distance

classes were defined manually. Significance of $F(d)$ for each distance class was tested by running permutations of the spatial position of individuals 10,000 times, yielding a 95% confidence interval for $F(d)$ for each distance class. To test for SGS, we tested the significance of the regression of R_{ij} values on the spatial distance (d) (Vekmans & Hardy, 2004). The spatial positions of the individuals were permuted 10 000 times in order to get the frequency distribution of the slope under the null hypothesis that R_{ij} and d were uncorrelated (Hardy 2003).

To determine whether patches originated from different groups of related seeds, we tested if kinship coefficients (R_{ij}) between individuals from the same patch were higher than between individuals from different patches. Pairwise R_{ij} are not independent when individuals are related to each other within patches. Consequently, we sampled randomly all independent R_{ij} 's within patches and we compared the R_{ij} distributions (within and among patches) with a Wilcoxon rank test. We repeated this procedure 9,999 times. Because of multiple comparison tests, we corrected the p-values of the different tests with the Benjamini–Hochberg method (Benjamini & Hochberg, 1995). To test the significance of the comparisons, we used the average corrected p-value and the percentage of tests passing the significance level ($\alpha = 0.05$) after correction.

Results

Genetic structure

As expected for seedlings, we found no identical multilocus genotypes in different samples in our dataset. The multilocus inbreeding coefficient was low ($F_{is} = 0.007$) and does not show deviation from Hardy-Weinberg equilibrium (p-value = 0.441) indicating no population sub-structure. The absence of population subdivision was confirmed by the STRUCTURE analysis that indicates $K=1$ as an optimal genetic cluster (Fig. S1). Moreover, all pairwise comparisons between patches showed low and not statistically significant values of genetic differentiation (F_{ST} ranging from 0 to 0.007; Table S2).

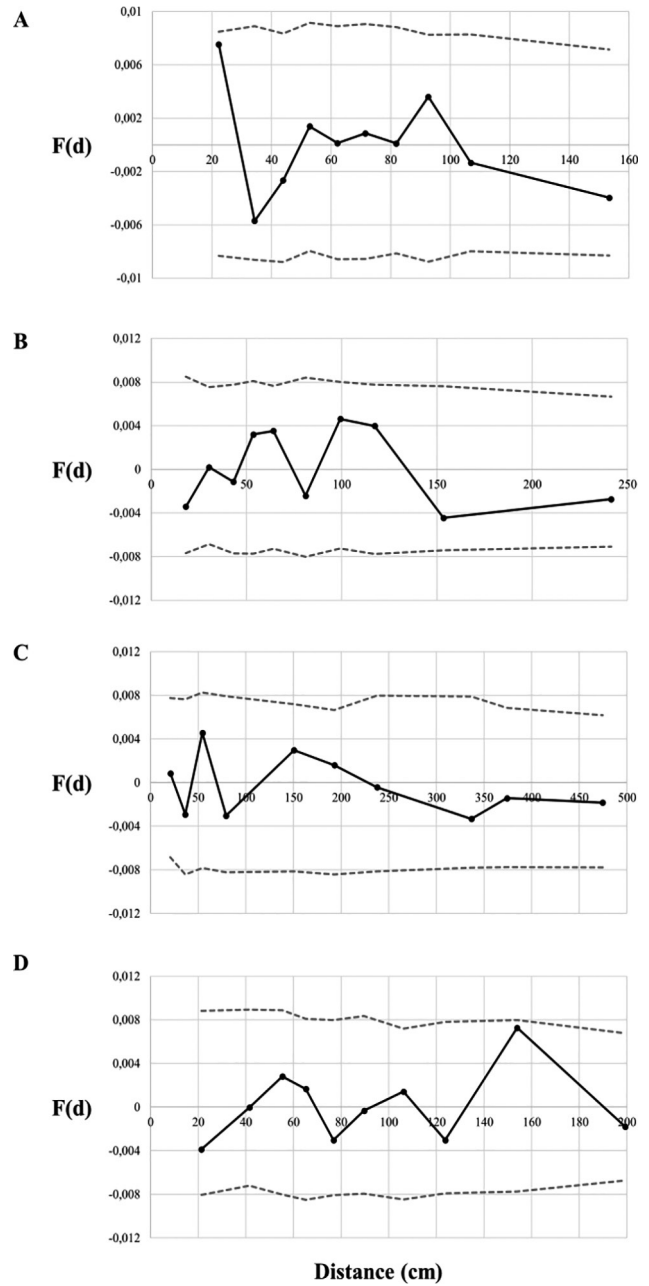


Fig. 2. Spatial autocorrelation plots for the four patches (A, B, C and D). The average kinship coefficient $F(d)$ is plotted against geographical distance between individuals. Confidence intervals (95%) are indicated by dashed lines. All values within the confidence interval are not significantly different from 0 ($\alpha = 0.05$)

Table 2. Population genetic parameters (multilocus) for each patch sampled. N = number of individuals; N_a = total number of alleles; N_{ae} = effective number of alleles (Nielsen et al., 2003); H_e and H_o = expected and observed heterozygosities, respectively; F_{is} = inbreeding coefficient; $P(F_{is} \neq 0)$ = the p-value of the permutation test

Patch	N	N_a	N_{ae}	H_e	H_o	F_{is}	$P(F_{is} \neq 0)$
A	90	12.00	5.83	0.805	0.807	-0.002	0.956
B	93	13.50	5.84	0.808	0.828	-0.024	0.175
C	93	12.50	7.05	0.854	0.827	0.032	0.084
D	92	12.33	6.39	0.822	0.837	-0.018	0.341
All	368	15.33	6.37	0.822	0.816	0.007	0.441

We found a high genetic diversity for the whole population ($He = 0.822$; Table S3) and in each patch (Table 2). Moreover, these value of genetic diversity were similar to the ones we found in our previous study ($He = 0.859$ and $Ho = 0.850$ Mazal et al., 2021).

Regressions between R_{ij} values and the spatial distance were never significant, indicating no spatial genetic structure in any of the four sampled patches along the 1.2 km river reach (Fig. 2). Kinship coefficient (R_{ij}) between pairs of seedlings ranged between -0.31 and 0.55 , indicating that some full-sibs are present in the sample (within and among patches in the same alluvial bar). However, when sampling randomly all independent pairwise relatedness coefficients R_{ij} s within patches, we found no differences between intra-patch and inter-patch mean R_{ij} (mean intra = 0.00419 ± 0.00104 SE; mean inter = -0.00265 ± 0.00102 SE; average = 0.472 ; average corrected = 0.907). Only 0.06% of our p-values were inferior to the 0.05 threshold (Fig. S2), further confirming the absence of genetic structure over our sampling area.

Discussion

We found a high level of genetic diversity for the studied population (for comparison with other published data on Black poplar, see Mazal et al (2021). Furthermore, the level of genetic diversity detected for the seedlings in this study is similar to the one found in the later life stages of the same population (Mazal et al., 2021). Similar level of genetic diversity between different life stages were also reported by Wójcikiewicz et al. (2019). The authors proposed that the maintenance of high genetic variation through the generations is essential for long term stability of populations maintaining a balance between genetic drift and mutation. The high genetic diversity found here confirms that in the current state, the hydrogeomorphological and ecological conditions in the study reach of the Allier River are suitable for the preservation of the genetic resources of the Black poplar.

We did not detect any significant FSGS for the four patches of the one-year-old seedlings we studied in the Allier River, and also genetic structure across the patches. The results indicate that primary seed dispersal did not create an initial FSGS pattern during recruitment in 2019. In plants in general, the dispersal curves show a maximum of seed dispersal relatively close to the source (Nathan, 2006; Nathan et al., 2008). Black poplar seeds are generally deposited within only a few hundred meters of the mother tree (Braatne, 1996). In a previous study, we found a significant FSGS in five-year-old cohorts, but not for older cohorts in both the Allier and Garonne Rivers (Mazal et al., 2021). Following

the idea of a short-distance dispersion, and our previous results, we proposed that across short dispersal distances seeds from different mother trees were not homogeneously dispersed and could lead to an initial FSGS pattern after germination. The present study does not verify this hypothesis. Moreover, the studied population is located in a natural reserve that experiences moderate anthropogenic impacts and no barrier to gene flow were identified (Petit, 2006; DeJaifve & Esquirol, 2011). Mature trees are abundant in this reserve. Thus, the absence of FSGS we observed, indicated that seeds from numerous and different parent trees (both mothers and fathers) are widely dispersed by wind and water and are deposited homogeneously on the various germination sites available along a few kilometres. This result shows that when reproductive trees are in high density in a river reach, the diverse genotypes spatially cover the whole span of local habitat variability thanks to an efficient mixing of seeds during dispersal only over few km. Such phenomena may lead to an improved capacity of the population to reach each year a suitable recruitment window in a highly variable and shifting mosaic of habitat conditions. Our results however suggest that seeds from one mother tree can disperse at relatively short distances as evidenced by the fact that some pairs of highly related individuals (high R_{ij} values) were found in the same patches and by the FSGS found in the five-year-old cohort (Mazal et al., 2021). All together, these observations could indicate multiple pathways of seed dispersal resulting in patches with or without FSGS at the recruitment stage. The interannual variability of the hydrological regime combined with the possibility for *P. nigra* seeds to disperse by wind and/or water would explain the proposed pattern of seed dispersal.

FSGS was found in young cohorts of Black poplars (five-years old) in the Allier and the Garonne rivers but not in older cohorts (Mazal et al., 2021). The previous significant FSGS we observed in the five-years old cohorts in the Allier and the Garonne Rivers may be the result of a singular group dispersal event, leading to the formation of patches of related individuals (Mazal et al., 2021). The change in FSGS between cohorts (i.e. from seedlings to five-years old) could also be caused by similar microhabitat requirements between related individuals, which could lead to differential mortality. Similarly, Berens et al. (2014) showed in *Prunus africana*, that SGS was stronger in adults than in late juveniles. The authors propose that similar microhabitat requirements between related individuals, along with spatial heterogeneity in abiotic conditions, could allow the survival of related individuals in later life stages, resulting in a higher SGS in adults stages.

In our previous study, we did not find global genetic structuring (Mazal et al., 2021). Therefore, for

the present study, we chose only a limited number of patches. In addition, to ensure repeatability of our analysis, we chose our patches from two different alluvial banks. The results of the present study confirm this lack of structure. However, since the individuals sampled in this study are not the same as those sampled in our previous study, it is not possible to establish a direct relationship between the patterns of FSGS found in the different aged cohorts in our two studies.

Concluding remarks

The present results on FSGS complement those of our previous study in which the seedling stage was missing. The absence of FSGS at the seedling stage suggests that seed dispersal was homogeneous in the sampled natural population. Further studies, such as cohort monitoring approach from establishment to the mature stage, would be promising for precisely understanding how riparian successions unfold and to point to potential factors that would explain the changes in FSGS observed between the different life stages in the Black poplar. Moreover, we chose to study a site located in a natural reserve where the flow regime is unregulated, river morphodynamics are only moderately impacted by human activities and that harbours a large number of adult trees. This situation where natural processes are largely undisturbed make it suitable for *P. nigra* regeneration. In this site, genetic diversity was high, similar to, or even higher than, most data available for European rivers. This site is thus a valuable asset for the conservation of *P. nigra* genetic diversity.

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Compliance with ethical standard

The authors declare that they have no conflict of interest.

Data archiving statement

Genotypes and R script used in this study are currently being submitted to Zenodo open-access repository (<https://about.zenodo.org/>).

Authors' contributions

All authors contributed to the study conception and design. Sampling, material preparation, data collection and analysis were performed by Lucas Mazal, Irène Till-Bottraud and Boris Fumanal. Lucas Mazal led the writing of the article to which all authors contributed. All authors read and approved the final manuscript.

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