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Optimization of restoration techniques: In-situ transplantation experiment of an endangered clonal plant species (*Typha minima* Hoppe)

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ABSTRACT

In the current context of biodiversity erosion, ecological restoration is sometimes the only way to reinforce plant population and preserve them from the deterioration of their natural habitat. Dwarf bulrush (*Typha minima* Hoppe) is an endangered pioneer clonal plant, which grows in frequently disturbed habitats along Eurasian temperate piedmont rivers. In the Alps, its population has decreased by 85% over the last century and numerous pressures (e.g. river works) continue to threaten its remnants. The main objective of this study is to identify an adapted ecological engineering protocol for field transplantation of *T. minima* in order to maximize restoration success. Several transplantation experiments were implemented between 2013 and 2016 along a French alpine river, the Isère. Five distinct transplantation protocols were tested by individually varying the following parameters: bank type (redesigned bank and embankment protection), transplantation height above water level (5 levels between +0.45 m and + 1.55 m above the average water level), initial biomass transplanted (high, medium and low), initial plot shape (linear strip or square plots) and species association (without or with Salicaceae or Poaceae). During the first two or three years, several clonal traits relative to the spatial monopolization and colonization abilities of *T. minima* were monitored and analyzed. Our analysis showed that *T. minima*'s ability to colonize was optimal on natural banks, at medium transplantation heights and in linear strip plots. In addition, spatial monopolization and colonization speed, through both sexual and vegetative reproduction, were maximized with a higher initial biomass. Lastly, species association did not affect the colonization ability of *T. minima*. Our study provides valuable information for future conservation plans and restoration projects for *T. minima*.

1. Introduction

Restoration through ecological engineering is often a necessary conservation tool for endangered plant populations (Dobson et al. 1997). This is particularly the case in urban and peri-urban areas, where plant extinction has drastically increased over the last two centuries due to artificialization and the subsequent loss of natural habitats (McDonald et al., 2020).

However, the success of a population restoration is not guaranteed; indeed, several studies have highlighted numerous failures which are often underestimated (Godefroid et al. 2011; Silcock et al. 2019).

To limit restoration failures, enhanced knowledge of the target species' ecology is necessary (Menges et al. 2016). Field experiments based on plant ecology theories and scientific knowledge can help optimize ecological engineering success by testing hypotheses in-situ (Falk et al., 1996; Gellie et al. 2018).

A crucial preliminary step in restoration project is the identification of suitable sites for collecting the initial plant material and for subsequent transplanting. The selected sites must be environmentally similar to the historical species habitat and close to remnant populations of the target species to enable sufficient gene flow (Proft et al. 2018). In riparian areas, widespread human activities such as diking, bank artificialization and damming, often make it difficult to identify historical habitats (IUCN, 2016).

Once donor and transplanting sites have been found, a second step is the collection of initial plant material. Collection and growth can be

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challenging for endangered plant species and transplanted biomass should be optimized. For instance, clonal plant species can produce genetically identical ramets using vegetative propagation, making it easier to restore and conserve local populations (Baldwin et al. 2009). Providing a higher amount of biomass could favor transplanting success: clonal plant stem and root production (regeneration) increases with the quantity of initial rhizome biomass transplanted (Cordazzo and Davy 1999; Luo and Zhao 2015; Wang et al. 2016). Indeed, greater carbohydrate reserves and more meristems are contained in a larger rhizome biomass, and this can positively affect clonal plant regeneration in the early stages (Klimešová et al. 2018; Ott et al. 2019).

After transplantation, some factors likely to affect restoration success in these early stages are specific to riparian habitats. For example, vegetation is subjected to disturbance regimes such as flooding or erosion and important feedback loops occur between vegetation and water and sediment flows (Vervuren et al. 2003; Corenblit et al. 2009). Riparian clonal-plant restoration projects should therefore take into account the hydrogeomorphological processes at work. Riparian species are distributed along a gradient of distance to water table depth (Allen-Diaz 1991; Shafroth et al. 2000; Chen et al. 2008;). Moreover, floods, erosion and burial by sediments induce a high turnover in riparian vegetation in the most exposed areas (Arscott et al. 2002; Gurnell et al. 2012).

Junk et al. (1989) introduced the “flood pulse concept” to describe the close interactions between biological and hydrogeomorphological processes along the river corridor. On the one hand, hydrogeomorphological processes drive ecological dynamics through population destruction and propagule dispersion (Boedeltje et al. 2004). On the other hand, biological dynamics also affect hydrogeomorphological processes through bank stabilization and propagule trapping induced by engineer species (Kuzovkina and Volk 2009). This could explain the positive effect of young Salicaceae and herbaceous species in the maintenance and survival of pioneer riparian communities that Corenblit et al. (2009) observed.

The Dwarf bulrush (*Typha minima* Hoppe) is a clonal pioneer plant species growing on gravel bars and riverbanks (Csencsics et al. 2008; Prunier et al. 2010; Jaunatre et al. 2018). Over the last century, *T. minima* has suffered a drastic decline, estimated at 85% in the Alps, due to river containment and floodplain drainage (Prunier et al. 2010).

In this study, we used a large-scale project with multiple transplanting sites of Dwarf bulrush (*Typha minima* Hoppe) to address the following question: How can we improve transplanting protocols for this clonal pioneer plant species of riparian habitats?

Our first specific question was: What kind of riverbank and transplanting height above water would optimize the clonal expansion and survival of *T. minima*? We hypothesized that: (1) *T. minima* would root and expand more easily on a managed riverbank that was physically and biologically close to a natural riverbank; (2) the optimal height above water for survival and expansion would provide a compromise between water availability and exposure to disturbance.

Our second question was: In view of the limited initial living material available, how could *T. minima* transplantation, spatial monopolization and colonization (asexual and sexual reproduction) be optimized through initial biomass and plot shape. We hypothesized that: (3) higher initial biomass, i.e. a higher initial amount of rhizomes transplanted, would speed up colonization due to greater clonal expansion; (4) a large-perimeter transplantation plot would maximize clonal expansion by offering a larger open space for clonal expansion.

Our third and final question was: How could association with a pioneer species improve *T. minima* clonal expansion though facilitation? We hypothesized that: (5) association with other pioneer species could improve *T. minima* clonal expansion and survival through facilitation interactions.

2. Methods

2.1. Study site

The study site was located in France along the Isère River, a tributary of the Rhône River, between Pontcharra and Grenoble (Southeastern France) in the Alps (Fig. 1). During the nineteenth century, major embankment works were undertaken along the river to drain the floodplain and control flooding (Girel et al. 2003; Girel 2010). Today, over the 60 km covered by the study area, the Isère River flows in a single embanked channel (contrary to the ancient braided river) with a slope of 0.1% on average (Allain-Jegou 2002). The space between the dikes (channel width: 70 m to 130 m) includes a few gravel bars and vegetated islands (Vautier et al. 2002). Dominant vegetation types comprise pioneer communities (*Calamagrostis pseudophragmites* (Haller f.) Koeler*, Phalaris arundinacea* L., *Typha minima* Hoppe, *Salix spp., Populus* spp. and *Alnus spp.*), hardwood communities (*Fraxinus excelsior* L., *Robinia Pseudacacia* L.) and intermediate stages i.e. post pioneer communities (Vautier et al. 2002). A snowmelt and rainfall regime characterizes the river hydrology (Vivian, 1969; Jourdain et al., 2015) and causes annual spring and fall floods (the average flow in Grenoble is 120 m^3/s while annual flood flow is 420 m^3/s) (EauFrance, 2020).

2.2. Typha minima Hoppe

The habitat of the Dwarf bulrush (*Typha minima* Hoppe) is characterized by sandy-silty moist substrates on gravel bars and riverbanks frequently disturbed by floods, which are crucial to maintaining its population dynamics (Werner 2010; Baur et al. 2017). New habitat colonization is possible by clonal expansion, rhizome fragment dispersal (vegetative reproduction) and seed dissemination (sexual reproduction) through anemochory or hydrochory (Csencsics et al. 2008). The species is fugacious in the sense that it has a high population turnover (Trabaud and Lepart 1980) with continuous local extinctions and new colonization processes related to the high disturbance rate of its habitat (Till-Bottraud et al. 2010). According to the UICN species red-list (https://www.iucnredlist.org/), *T. minima* is considered extinct in Germany (Greulich 2017), critically endangered (CR) in Austria and endangered (EN) in Switzerland. In France, the species is still classified as of Least Concern (LC, IUCN) but has been listed as endangered at the regional scale, making its populations a major conservation focus in the Alps.

2.3. Transplanting experiments

Between 2013 and 2016, clones of *T. minima* were transplanted along the Isere River in the context of compensatory measures associated with flood protection works (between 2004 and 2021) (Jaunatre et al. 2018). These transplantations were used as a basis for experiments and were carried out at six sites within the study area (Fig. 1, A). Initially, 7140 different ramets were collected at three locations within the study area and multiplied in a nursery. Then, the rhizomes were transplanted in situ during leaf-off season, following five distinct experimental protocols detailed below.

2.3.1. Bank type effect

The aim of this first experiment was to determine *T. minima*’s capacity to take root and spread after transplanting according to the type of riverbank. Indeed, several riverbank types, arising from the flood protection works, are present in the study area and were tested for transplantation: 1) redesigned bare banks; 2) mixed-technique banks with riprap (civil engineering) and vegetation components (soil bioengineering); and 3) dikes protected by riprap. The riprap is composed of a coarse substrate (rocks and blocks) whose gaps are filled by a silty-sand substrate deposited by floods, whereas the bare banks are entirely composed of a fine substrate. In 2015, three sites with differing bank

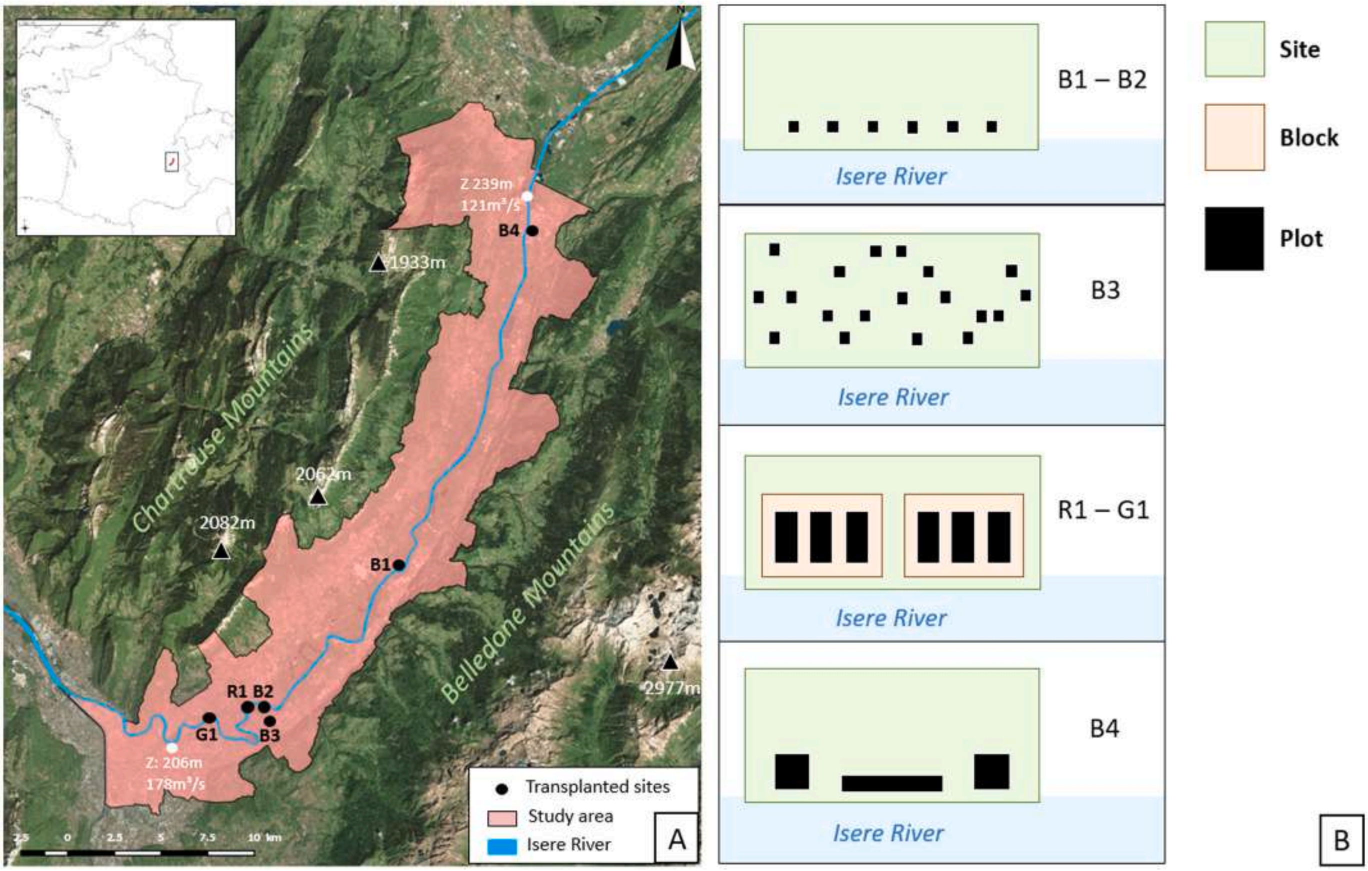

Fig. 1. **A -** Map and location of the study area with transplantation sites on the Isere River (southeastern France). Average river flows and altitude values are from the downstream and upstream hydrological stations (in white on the map). **B -** Schematic protocols implemented in the study area. First, bank type effect was tested on a redesigned bare bank (B3), mixed-technique banks (G1) and riprap (R1) with bucket transplants. Then 5 heights above the water level and 2 species associations were tested on a redesigned bare bank (B3) with container transplants. Third, initial biomass effect was tested on 2 redesigned bare banks (B1 and B2) with containers, buckets and bare root transplants. Finally, plot shape effect was tested on a redesigned bare bank (B4) with direct transplantation.

designs (redesigned bare banks (B3), mixed-technique banks (G1) and riprap (R1)) were transplanted with 100 plots each (300 plots). The transplants were of contained in medium biomass (mb) buckets (9 cm*9 cm) at each plot and the buckets were spaced four meters apart: (R1 - G1 and B3, Fig. 1, B).

2.3.2. *Transplanting height above water*

A second experiment, implemented in 2015, was designed to test the effect of height above the water line on *T. minima* clonal expansion and survival rate. Previous studies in the same area had shown that *T. minima* was naturally located between 0.45 m and 1.55 m above the average river level (Jaunatre et al. 2018). Following these results, 372 plots were randomly dispersed along five height lines relative to the average river water level (l1: +0.45 m x12, l2: +0.75 m x92, l3: +1 m x148, l4: +1.30 m x96, l5: +1.55 m x24). Along a given height line, the plots were separated from each other by at least 4 m; between two height lines, the plots were separated by at least 1 m (B3, Fig. 1, B).

2.3.3. *Initial biomass effect*

A third experiment consisted of transplantations with different initial biomass amounts to determine which one best optimized *T. minima* spatial monopolization and speed of colonization (sexual and vegetative). The experiment was implemented at two sites (B1 - B2, Fig. 1, B) on redesigned bare banks between 2013 and 2014. At site B2, ten blocks of three 2x8m plots each were selected and *T. minima* was randomly transplanted among the three plots at a high initial biomass ("hb": 44 containers of 30 L per plot), a medium biomass ("mb": 84 buckets of 9 × 9 cm per plot) and a low biomass ("lb": 82 bare roots per plot) (B2, Fig. 1, B). At site B1, five blocks were set up, each composed of one plot (2 × 8 m) at high biomass ("hb": 30 containers of 30 L per plot) and two plots (2 × 8 m) at low biomass ("lb" 130 bare roots per plot).

2.3.4. *Plot shape effect*

A fourth experiment was designed to determine the best plot shape to maximize *T. minima* colonization. Two simple easy-to-implement shapes were chosen: linear strips and squares. Rhizomes with their soil (without containers) were directly transplanted from nurseries in fall 2016 on redesigned flat bare banks in ten linear strip plots ("lp": 0.3 × 20 × 0.5 m, 1.26m^3, perimeter = 42.6 m) and ten square plots ("sp": 2.5 m × 2.5 m × 0.5 m, 1.26m^3, perimeter = 10 m) randomly dispatched along the banks (B4, Fig. 1, B). The square and linear strip plots were separated from each other by 5 (minimum) to 10 m (maximum). The same initial volume (1.26m^3 of rhizomes + soil) was transplanted to each plot; consequently, *T. minima* biomass was considered to be similar among plots.

2.3.5. *Species association effect*

A final experiment tested the species association effect on *T. minima* expansion and survival rate. In 2015, high biomass containers (30*L*) of *T. minima* were randomly transplanted on redesigned bare banks (B3, Fig. 1, A) according to three treatments: one with *T. minima* alone ('hb': 118 control) and two with species associations: *T. minima* + Poaceae species (randomly chosen between *Calamagrostis pseudophragmites* (Haller f.) Koeler and *Phalaris arundinacea* L.) (84 "hbh")); and *T. minima* + Salicaceae species (randomly chosen between *Salix alba* L. and *Salix triandra* L.) (76 "hbs")). The species-association plots had one central container of *T. minima* surrounded by four *Salix* spp. cuttings (“hbs”) or four tussocks of Poaceae species (‘hbp’) (B3, Fig. 1, A and B).

2.4. Functional traits monitored

Primack and Drayton (1997) suggested that restoration success could be considered a success when plant populations had achieved the following: i) patchy expansion and new colonization and ii) seed production and dispersal related to self-persistence over time. To evaluate our experiments in terms of success, we monitored the functional traits representative of these capacities as follows: spatial monopolization (frequency) and colonization ability (patch expansion, vegetative and sexual reproduction).

We monitored *T. minima* traits related to competition and regeneration, to evaluate the effects of the different transplantation protocols in our experiment area. First, we used *T. minima* frequency to assess species abundance, as related to spatial monopolization and the plant’s subsequent capacity to monopolize natural resources (Van Groenendael and de Kroon 1990; Klimes et al. 1997). Second, we measured the internode length (length of the rhizomes between two connected ramets) and clonal expansion (from plot measurements taken both perpendicularly and parallel to the river) to assess the dispersal distance attained through vegetative multiplication (Klimes et al. 1997; Herben et al. 2014). Lastly, we counted the number of inflorescences to assess the potential for short- and long-distance dispersal through sexual reproduction (Pywell et al. 2003; Godefroid et al. 2011).

2.5. Data acquisition and extrapolation

All the transplanted sites had been monitored annually from their implementation and until the plots had merged and covered all open space (between 2 and 3 years). *T. minima* frequency was estimated by the pinpoint contact method (at least 100 points) implemented along two transects through the initial plots B1, B2 and B4, perpendicular and parallel to the river through the plot center. The internode length between two ramets was measured on ten rhizomes on each of plots B1 and B2. We randomly selected 10 ramets on each treatment by threwing a stone into a *T. minima* patch, dug down and extracted the first rhizome available and measured it. Clonal expansion was assessed through direct measurement of “plot width” perpendicular to the river and “plot length” parallel to the river at all the transplanted sites. Finally, the total number of inflorescences per plot was counted at sites B1 and B2. Area and clonal expansion data were calculated from plot dimension measurements. Plot area was approximated by multiplying the plot width and length of the square plots (B1, B2, B4). For the strip transplantations (B3, R1 and G1), a proxy for plot area was obtained by calculating an ellipse to better match the plot shape. Lastly, inter-annual clonal expansion was calculated in terms of plot area, plot width and plot length for all the transplanted sites (Expansion $X^t = X^t - X^{t-1}$). Supporting data are available in supplementary material (Table S1).

2.6. Statistical analyses

We used the R software (version 3.5.1) to process the statistical analyses. We applied mixed models with transplantation protocol (bank type, transplantation height, initial biomass, plot shape, species association) and monitoring year as fixed factors, and site as a random factor. Following (Hervé 2018), we used either LMM or GLMM with different error distribution families or link functions. For all continuous variables, we built LMMs (Table S2) with a Gaussian error distribution (default) for five explanatory variables: area expansion (at sites G1, R1 and B3), width and length expansion (at site B3, for the height and species association protocols), width and length expansion (site B4) (I only see five variables: area exp., width exp., length exp., height and species). We built GLMMs with a Gamma error distribution and a logarithm link [lme4 package, (Bates et al. 2015)] for the continuous and strictly positive variables: internode length (B1-B2 site) and plot area (B3 site, elevation and association protocols; Table S2). We built two GLMMs with a Quasi-binomial error distribution and logit link for species frequency of occurrence (B1-B2 and B4 site; Table S2) [Matrix package, (Bates and Maechler 2012)]. Lastly, for over-dispersed count data, the number of inflorescences, we built a GLMM with a negative binomial error distribution (B1-B2 site; Table S2) [MASS package, (Venables and Ripley 2002)]. Due to the limited number of replicates available for the lowest height above water line (l1: 0.45 m) at site B3 (Table S2), it was excluded from the analyses. We validated our models by assessing the independence between the model residuals and fitted values.

To assess the significance of each factor, we performed F-tests (for the linear models) or a Wald chi-square test (for the generalized models) [car package (Fox and Weisberg, 2019)]. If the fixed effect was significant (p value <0.05), the mixed models were then assessed with a post-hoc multi-comparison test [multcomp package (Hothorn et al. 2008) and emmeans package (Lenth et al. 2018)] with 0.05 as the p-value threshold.

3. Results

3.1. Transplanting location

3.1.1. Bank-type effect

The riverbank type strongly affected the clonal expansion of *T. minima* ($X^2 = 10.08$, $df = 2$, $p = 0.006$). One year after completion, transplanting on redesigned bare banks (741 ± 274 cm^2) resulted in better vegetative colonization than on riprap (167 ± 54 cm^2) or on mixed-technique sites (78 ± 28 cm^2).

3.1.2. Effect of height above water line

Transplanting height did not affect the area occupied by *T. minima* for either monitoring year, whatever the elevation (from +0.45 m to +1.55 m above average water level). Only a year effect was found, with a larger area colonized the second year ($X^2 = 361.52$, df = 1, $p < 0.001$).

Nonetheless, expansion in width was affected by height above water line ($X^2 = 8.96$, $df = 3$, $p = 0.03$), monitoring year ($X^2 = 193.29$, Df = 1, $p < 0.001$) and their interaction ($X^2 = 8.97$, $df = 3$, $p = 0.03$) (Fig. 2). The greatest expansion in width was obtained for transplantations at plot l3: +1 m and the effect of height above water line was even more pronounced after two years (39 ± 3 cm, Fig. 2).

Similar trends were measured for expansion in length, which showed a significant effect of transplantation height ($X^2 = 10.06$, $df = 3$, $p = 0.02$) and monitoring year ($X^2 = 193.45$, $df = 1$, $p < 0.001$) at site B3. One year after implementation, greater length expansion was obtained for transplantations at plots l3: +1 m (86 ± 10 cm) and l4: +1.30 m (88 ± 10 cm). Two years after implementation, the pattern was the same but no longer significant. Height above average water level also affected transplants survival ($X^2 = 17.72$, $df = 4$, $p = 0.001$). Survival mostly increased with height (17% at plot l1, +0.45 m and 71% at l5: +1.55 m; Fig. 3).

3.2. Transplantation optimization

3.2.1. Initial-biomass effect

Initial biomass transplanted ($X^2 = 47.19$, $df = 2$, $p < 0.001$), monitoring year ($X^2 = 23.05$, $df = 1$, $p < 0.001$) and the interaction of the two ($X^2 = 10.77$, $df = 2$, $p = 0.005$) affected *T. minima* frequency at sites B1 and B2 (See Fig. 4). Frequency increased with initial biomass during the two monitoring years though the increase was not significantly different between medium and high initial-biomass transplantations in year two.

Initial biomass ($X^2 = 39.47$, $df = 2$, $p < 0.001$) and monitoring year ($X^2 = 27.56$, $df = 1$, $p < 0.001$) also affected the number of inflorescences: higher initial biomass produced a larger number of inflorescences than did medium biomass for both monitoring years. In addition, the number of inflorescences increased between the two

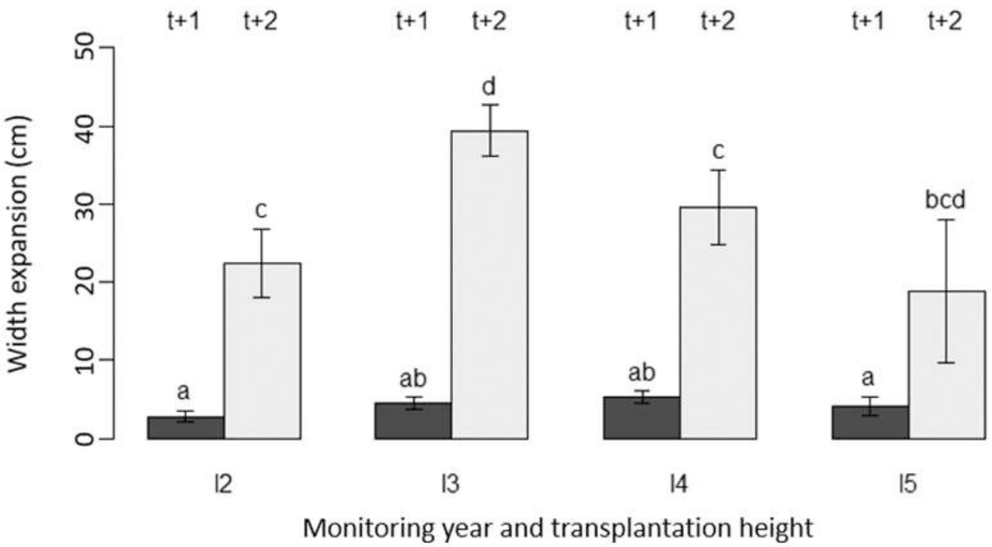

Fig. 2. Effect of four transplantation heights (l2: 0.75 m, l3: 1 m, l4: 1.30 m and l5: 1.55 m above the average water level, $X^2 = 8.96$, df = 3, p = 0.03), monitoring year ($X^2 = 193.29$, df = 1, $p < 0.001$) and the interaction between the two ($X^2 = 8.96$, df = 3, $p = 0.02$) on *T. minima* clonal expansion in width monitored over 2 years (t + 1, t + 2) at site B3. Plot represents average width expansion and monitoring year with standard errors. Bars sharing a common letter are not significantly different ($p < 0.05$).

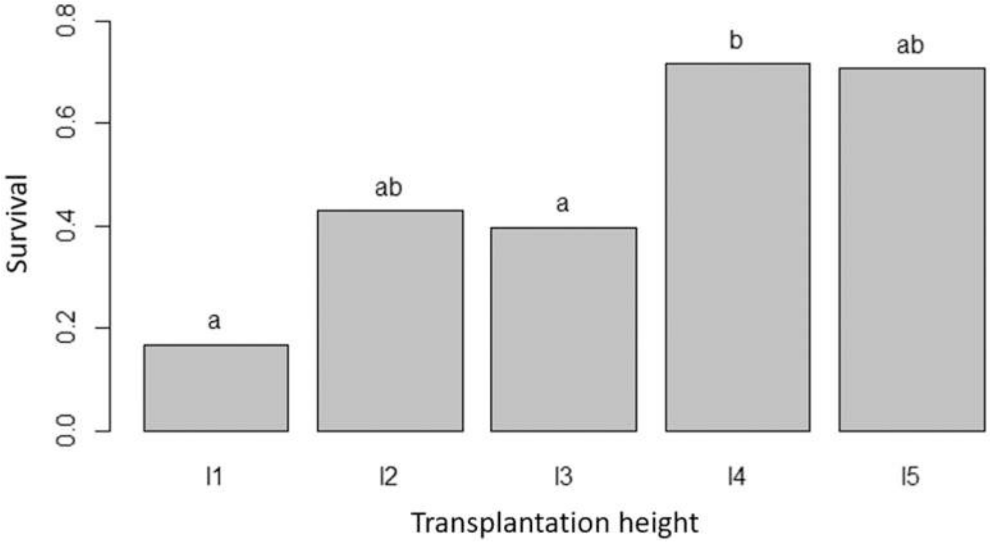

Fig. 3. Effect of transplanting height (l1: +0.47 m, l2: +0.75 m, l3: +1 m, l4: +1.30 m and l5: +1.55 m above average water level) on *T. minima* survival rate (% of total) for the first monitoring year at site B3 (ANOVA, $X^2 = 3.53$, df = 3 p = 0.001). Bars sharing a common letter are not significantly different.

monitoring years, for the high (t + 1 = 16.13 ± 5.55; t + 2 = 195.79 ± 53.66) and medium initial biomass treatments (t + 1 = 0.10 ± 0.10; t + 2 = 24.10 ± 12.28).

Finally, initial biomass ($X^2 = 9.39$, $df = 2$, $p = 0.009$) and monitoring year ($X^2 = 4.23$, $df = 1$, $p = 0.03$) had a significant effect on internode length: two years after transplantation, longer internode lengths were found for a high initial biomass (20 ± 4 cm) than for an initial low biomass (5 ± 1 cm). Moreover, internode length decreased with time for the low initial biomass (t + 1: 15.31 ± 1 cm, t + 2: 5.54 ± 0.5 cm).

3.2.2. Plot shape effect

Initial plot shape ($X^2 = 5.90$, $df = 1$, $p = 0.01$), monitoring year ($X^2 = 49.22$, $df = 2$, $p < 0.001$) and their interactions ($X^2 = 24.30$, $df = 2$, $p < 0.001$) affected expansion in width (perpendicular to the river) at site B4 (Fig. 5). The second year, linear strip width expansion was higher (127 ± 21 cm) compared to other monitoring years and to the square plot shape (Fig. 5). Nevertheless, plot width dropped the third monitoring year, both for linear strip plots (−36 ± 20 cm) and for square plots (−21.11 ± 20 cm), due to bank erosion.

Clonal expansion in length (parallel to the river) was only influenced by year ($X^2 = 10.66$, $df = 2$, $p = 0.005$). Finally, *T. minima* frequency was only affected by monitoring year ($X^2 = 12.47$, $df = 2$, $p = 0.002$) and the interaction between year and plot shape ($X^2 = 10.85$, $df = 2$, $p = 0.004$). However, due to the unbalanced data, the post hoc test did detect trends toward a higher *T. minima* frequency in square plots over time.

3.2.3. Species-association effect

Transplanting *T. minima* in association with other species did not affect plot area ($X^2 = 0.88$, $df = 2$, $p = 0.64$), plot width expansion ($X^2 = 0.08$, $df = 2$, $p = 0.96$) or plot length expansion ($X^2 = 2.13$, $df = 2$, $p = 0.34$). Only a year effect was detected for plot area ($X^2 = 456.24$, $df = 1$, $p < 0.001$), plot width expansion ($X^2 = 204.35$, $df = 1$, $p < 0.001$) and plot length expansion ($X^2 = 127.14$, $df = 1$, $p < 0.001$), with greater clonal expansion the second monitoring year. Moreover, no significant difference in survival rate was detected with species association ($X^2 = 3.47$, $df = 2$, $p = 0.18$).

4. Discussion

The restoration success of transplanting a given species by

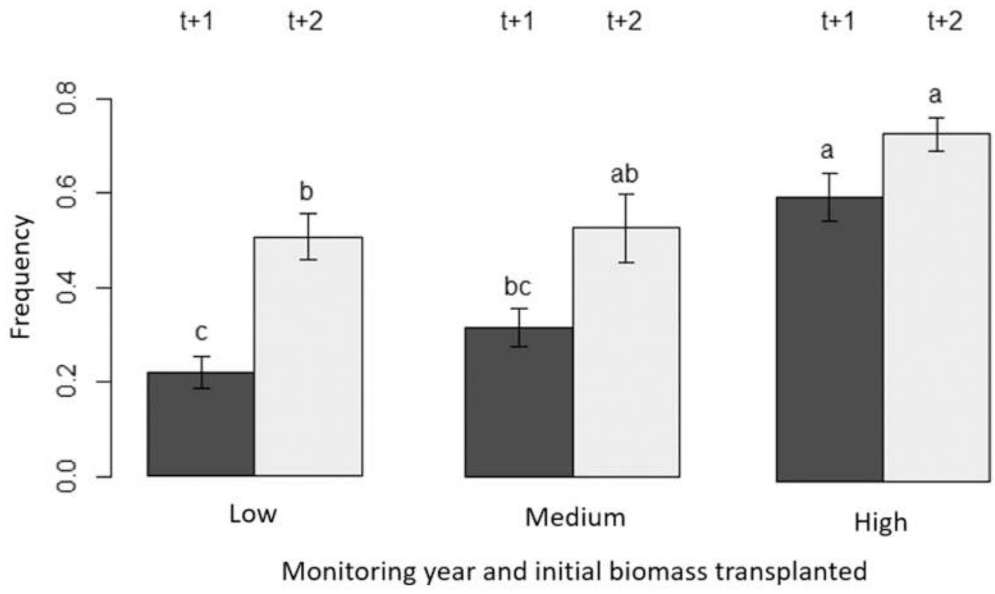

Fig. 4. Effect of three different amounts of initial biomass (high, medium and low, $X^2 = 47.19$, df = 2, $p < 0.001$), monitoring year (t + 1 and t + 2, $X^2 = 23.05$, df = 1, $p < 0.001$) and their interaction ($X^2 = 10.77$, df = 2, $p = 0.005$) on *T. minima* frequency at sites B1 and B2. Plot represents average frequency per initial biomass and monitoring year with standard errors. Bars sharing a common letter are not significantly different ($p < 0.05$).

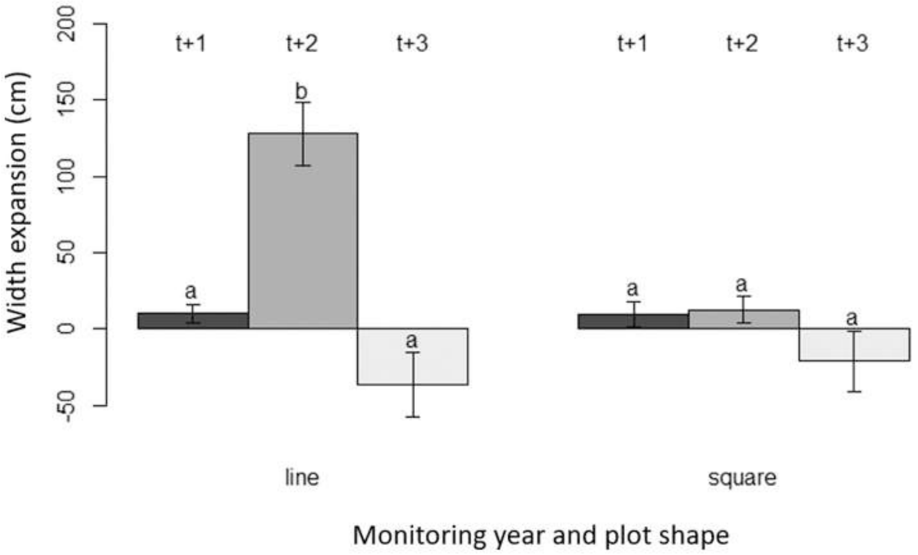

Fig. 5. Effect of two different initial plot shapes (linear strip or square) ($X^2 = 5.90$, df = 1, p = 0.01), monitoring year ($X^2 = 49.22$, df = 2, $p < 0.001$) and their interactions ($X^2 = 24.30$, Df = 2, $p < 0.001$) on *T. minima* expansion in width monitored over 3 years (t + 1, t + 2, t + 3) at site B4. Plot represents average expansion in width, per plot shape and monitoring year with standard errors. Bars sharing a common letter are not significantly different ($p < 0.05$).

transplanting depends on the ability of the species to grow and reproduce effectively shortly after transplantation. Our results highlight that the spatial monopolization, colonization ability and the survival rate of *Typha minima* Hoppe could be optimized by adapting the transplanting protocol. Indeed, bank type, transplantation height above water, initial transplanted biomass and plot shape all significantly affected *T. minima* restoration, as reflected through certain clonal traits, during the early years after implementation.

4.1. Transplantation location

We found that *T. minima* colonization was higher on the most natural banks (redesigned flat bare banks) compared to mixed-technique banks and riprap, this validates our first hypothesis. Therefore, natural or redesigned bare banks should be preferred for transplanting. Our results are consistent with the findings of Guerrant Jr and Kaye (2007), who showed that restoration site selection must be based on historical species habitat to maximize transplantation success. Among the three bank types we selected, the redesigned natural banks were the closest to historical *T. minima* habitat due to higher fine sediment cover available for vegetative colonization. However, we found that *T. minima* clonal expansion and maintenance were still possible on riverbank protection structures (mixed-technique banks and riprap), though with less success. Still, riverbank protection structures can serve as refuge zones for riparian plant species on urbanized rivers (Cavaillé et al. 2013), as evidenced by the restored *T. minima* patches that grew on all three bank types and by spontaneous settlement observed on other riverbank protection structures where fine sediment deposition occurred.

Concerning the riparian elevation gradient, we showed that *T. minima* colonization by clonal expansion was optimal for medium heights above the water level as expected in our second hypothesis. Transplanting at higher levels did not lead to higher *T. minima* mortality despite a potentially higher competition for resources with later successional species (Janssen et al. 2020) or drier abiotic conditions (Shafroth et al. 2000). Flood submergence and erosion could explain the survival rate gradient we observed. Along the riparian corridor, flood exposure drives vegetation turnover through erosion, accretion and immersion (Arscott et al. 2002; Junk et al. 1989) affecting riparian species expansion and survival rates (Tealdi et al. 2013).

4.2. Optimizing biological material

We found that a high initial amount of transplanted biomass maximized spatial monopolization and colonization for *T. minima* from the first year after restoration; this confirmed our third hypothesis. More metabolic resources led to more space being colonized by *T. minima* during the first year, which undeniably enhanced the plant's ability to compete with other pioneer species that usually colonize riparian habitat (Tealdi et al. 2013). Two years later, stem production was equivalent for both medium and high transplanted biomass. Both amounts of biomass both improved vegetative colonization through the production of longer internodes. However, higher transplanted biomass also boosted inflorescence production and therefore improved colonization through sexual reproduction. In clonal plants, rhizomes act as storage organs besides serving in vegetative reproduction (Klimešová et al. 2018; Ott et al. 2019). Our results are consistent with previous studies, which have highlighted the positive feedback between initial rhizome biomass and clonal plant regenerative abilities (e.g. ramet number, survival) during vegetation recovery (Luo and Zhao 2015; Wang et al. 2016). Our results suggest using high initial biomass transplantation to optimize both clonal and sexual colonization, and using medium biomass to optimize clonal colonization only and to reduce costs (1115€ per 100m^2 vs 2580€ - 3870€ per 100m^2).

Plot shapes also played a key role in *T. minima* colonization: greater clonal expansion occurred on linear strips with longer sides and more open habitat available for ramets. It has been acknowledged that ramet production and expansion in clonal plants are driven by resource availability (Kettenring et al. 2016; Reijers et al. 2020). We found that spatial monopolization (frequency) by *T. minima* was similar on linear strips and square plots during the first two years but regressed in width due to severe riverbank erosion the third year. Similar habitat destruction also occurred in the height experiment, especially at the lowest height above water. Frequent floods induce significant idiosyncratic significant bank erosion (Gurnell et al. 2012; Janes et al. 2018). Flooding occurrence should be therefore taken into account in the spatial designs for riparian species transplantation. Spreading the transplantations at different suitable heights and in multiple sites may constitute a bet-hedging strategy for successful transplantations (Doherty and Zedler 2015).

No facilitation effect by other pioneer riparian species on *T. minima* was evidenced in our results. Previous studies have demonstrated facilitation by Salicaceae or Poaceae species through their role in fine sediment accretion, stabilization and erosion resistance (Corenblit et al. 2009; Gurnell et al. 2012). Salicaceae species could also have a facilitation effect on riparian pioneer vegetation though phytohormone production (i.e. abscisic acid (ABA) and gibberellins (GAs)) are involved in plant dormancy and growth (Olsen 2006)). Although the presence of these phytohormones in the immediate vicinity could improve seed germination and root growth (Egorova et al. 2019), our results did not allow us to detect this effect with *T. minima*.

To conclude, one limitation all of our transplanted banks had in common was that the initial environmental conditions were never exactly the same as those found on natural banks. The redesigned natural banks were artificially created for restoration purposes, some were sown to limit the arrival of exotic species and others were strongly affected by flow erosion due to a geomorphological imbalance with flow velocity (Hagerty et al. 1981). These restored banks can therefore be considered hybrids, or novel ecosystems, as the biotic conditions there were degraded and the ecological processes may be different from historical habitats (Hobbs et al. 2006).

4.3. Perspectives for *T. minima* restoration

A lack of perspective and insufficient long-term monitoring often plague restoration projects (Menges et al. 2016). The next step toward improving *T. minima* restoration will be the long-term monitoring of restored patches, which will provide information on long-term population dynamics and ecological processes. Previous studies have shown that *T. minima* restoration can fail at the medium-term (5–10 years) (Ansermet 2009; Werner 2010). Nevertheless, *T. minima* being a riparian pioneer species, local extinctions are part of its natural population dynamics. Future work could focus on these long-term dynamics, including patch extinctions and emergence in natural sites related to the flood pulse concept (Junk et al. 1989; Boedeltje et al. 2004). Moreover, another important issue is that most of the restored patches come from vegetative propagation of only a few clones. Connectivity between restored and natural patches should therefore be explored in terms of genetic structure and exchanges through sexual reproduction (Proft et al. 2018).

5. Conclusion

Our results confirm that multiple hydrogeomorphological parameters affect riparian pioneer clonal plants (*Typha minima* Hoppe) and must be taken into account in restoration operations. We show that greater colonization by clonal expansion and sexual regeneration was achieved on redesigned bare banks compared to more artificial banks (riprap and mixed-technique banks). Transplanting at high and medium levels above the water line led to greater clonal expansion (in width and length) during the first years of growth, and initially higher biomass made it possible to maximize spatial occupancy (frequency) and colonization speed (number of inflorescences, internode length). To optimize biological material, linear strips proved to be the most suitable plot shape; they allowed greater vertical clonal expansion on the riverbank compared to square plots. We hope these results will help managers and conservationists to design better restoration protocols and maximize restoration success.

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Credit author statement

Conceived and designed the experiments: MB, ED, AE and RJ. Implemented the experiment: MB and ED. Collected data: NP, GF, AE and RJ. Analyzed data: NP, YP and RJ. Wrote the manuscript NP. Contributed to draft versions: NP, YP, AE and RJ. Revised and approved the final version of the manuscript: all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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