# Seeding dynamics from a local seed mixture on a bioengineered riverbank protection structure

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**Abstract**

Restoration of riverbanks through soil bioengineering techniques allows managers to combine riverbank stability and riparian ecosystem functioning. This restoration often involves the sowing of a seed mixture, which helps develop herbaceous vegetation. This development and sufficient vegetation cover are essential for protection against erosion and for hosting biodiversity, two of the main goals of riverbank bioengineering. Restoration aims at recreating ecosystems closer to an undisturbed state; choosing seed mixtures of local provenance is therefore encouraged. In this study, we investigated the local seed mixture sown on bioengineered riverbanks and the conditions influencing the first steps of plant development, so as to delineate the setting favoring restoration. We focused on the composition of the seed mixture and germination capacity as well as the effect of sowing density and soil quality on vegetation cover and diversity. We tested four sowing densities: 5, 10, 15 and 30 $g.m^{-1}$. The seed mixture presented considerable diversity and germination rates were heterogeneous. Sowing density had a positive impact on vegetation cover and diversity, and high cover up to 100% was rapidly reached. Soil quality did not affect vegetation diversity but had a significant effect on vegetation cover, with the nutrient content, notably nitrogen, most probably involved.

 

**Keywords**: ecological restoration, bioengineered riverbanks, seed mixture, local provenance, seedling establishment

## Introduction

Riparian ecosystems include the biotic communities along stream and lake shorelines (Naiman et al. 1993). They bind aquatic and terrestrial environments and have a key role as ecotones. They provide many functions such as nutrient control and bank stabilization and they create an ecological corridor and a biodiversity reservoir (Naiman and Decamps 1997). Riverbank modification (channelization, embankment) set up to protect against stream erosion or flooding, or to facilitate human exploitation of the river system (hydropower production, irrigation etc.), has jeopardized riparian ecosystem functioning (Naiman et al. 2010). Although stream management is crucial to protect human infrastructures, it may be possible, through ecological restoration, to combine riverbank stabilization and most of the main riparian ecosystem functions. Ecological restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). It is today recognized as an efficient way to repair damage caused by human activities. However, the reference state to which restoration aims to return an ecosystem has not met with consensus (Dufour and Piégay 2009). The biological feasibility of restoration to a historical state is declining (Jackson and Hobbs 2009), and historical fidelity is considered as insubstantial to define today's restoration goals (Benayas et al. 2009, Rohwer and Marris 2016). Restoration often results in the emergence of novel ecosystems with novel species combinations that deviate from those found in classic reference systems (Hobbs et al. 2009); therefore, trying to reach precise goals such as a target plant community composition is a useful way of evaluating its success afterward (Ruiz-Jaen and Mitchell Aide 2005).

 

Riverbank bioengineering can be defined as the inclusion of grasses, shrubs, trees, and other types of vegetation – living or inert – into engineering design for riverbank restoration, consisting of several ecological and structural engineering components combined into an integrated system that provides protection to the entire bank (Evette et al. 2012). This inclusion can be partial and combined with concrete structures or total in the case of pure bioengineering. It aims at improving and protecting hill slopes, embankments, and structures from the problems associated with erosion and other types of shallow slope failure (Clark and Hellin 1996). Riverbank restoration and protection can be achieved through partial or pure bioengineering techniques (Li and Eddleman 2002, Li et al. 2006, Cavaillé et al. 2015). Rebuilding riverbanks through bioengineering has two main objectives. The first objective is to protect riverbanks against erosion. Riverbank protection is provided by sufficient vegetation growth and cover (Beeson and Doyle 1995, Adam et al. 2008). However, ecological restoration international standards require this vegetation to be diverse, native, and local (SER 2004, McDonald et al. 2016). The second objective is therefore to allow the riparian ecosystem to recover with a diverse set of local native species. Implanting local plants integrates the restoration into its landscape better and does not make restoration a disturbing factor of population genetic structures (McKay et al. 2005). Moreover, local plants have a better chance of successfully settling on a restoration site because they are adapted to the environment (Bischoff et al. 2006, Breed et al. 2013, Bucharova et al. 2017). Two important criteria for riparian ecosystem restoration success when combined with riverbank protection are therefore a high vegetation cover and a mostly local provenance of the species provided.

Herbaceous vegetation on riverbanks plays an important role of erosion prevention and biodiversity hosting (Micheli and Kirchner 2002). Seed mixture sowing is an essential part of a riverbank's restoration because it accelerates herbaceous vegetation development

 

where colonization is too low and quickly provides resistance against erosion. Sowing success depends on the number of propagules reaching the site, which would correspond to seed sowing density in restoration, and on the different filters they encounter (Keddy 1992, Cristofoli and Mahy 2010). Seedling establishment is affected by biotic and abiotic factors, especially soil characteristics such as fertility, but also its structure including porosity, aggregation level, texture, and water availability (Chambers 1995, Shiels et al. 2008). The study of soil fertility involves the assessment of soil nutrient content, especially carbon and nitrogen.

The local provenance of seeds sown on a riverbank restoration site is currently of major concern and sowing success is an important issue. Although the local provenance of these seeds is now recognized as an important part of restoration works (Vander Mijnsbrugge et al. 2010, Bucharova et al. 2017) and local species or wild seed mixtures are more frequently used in restoration (Koch et al. 2015), the use of local seeds still presents uncertainties, e.g. regarding germination rates. Thus seed sowing conditions, including sowing density and the diversity of mixtures, have not met with consensus in technical recommendations (Zeh 2007, Adam et al. 2008).

The aim of this study was to investigate the composition of a local seed mixture and the appropriate sowing conditions for vegetation development in a restoration context. This was addressed *ex-situ* through the first two steps of plant development: germination and seedling development. The study used a seed mixture that had been sown on a bioengineered riverbank structure on the Romanche River in the French Alps that was carried out after the construction of a hydroelectric dam. The seed mixture sown on the site came from mechanical harvest in local hay meadows; its composition and the germination capacity of seeds were mostly unknown. To ensure that the two objectives for bioengineered riverbanks were fulfilled – erosion protection and riparian ecosystem recovery – we explored the

 

processes involved in these initial steps of community succession and assembly (Young et al. 2001) and identified some of the abiotic and biotic factors influencing them. The understanding of plant colonization and the success of the local seed mixtures sown in relation to soil fertility is essential for riverbank management and future restoration work in the region. The soil used for the bioengineered riverbank structure was very poor, albeit soil fertility is a key issue for plant riverbank restoration success as a quick plant cover and a fast growth of species are needed to rapidly protect the bank against erosion (Schiechtl and Stern 1997). To understand how improvement in the fertility of the soil would change the success of the first steps of plant development, different soils were tested.

The objectives of this study were to (1) determine the composition of the seed mixture, (2) test the germination capacity of the seeds, (3) investigate the effect of sowing density in fertile soils, and (4) examine the effect of soil quality on vegetation (cover and diversity).

## Materials and Methods

### Study area

The Romanche River is an alpine stream flowing from the Massif des Ecrins (glacier above 3700 m and spring located at 2143 m a.s.l.) to the Drac River (257 m a.s.l.). It has a drainage basin surface of 1000 $km^2$ and a mean annual discharge of 37.40 $m^3\ s^{-1}$ (W2764010 La Romanche station in Bourg-d'Oisans). A check dam was constructed at 700 m a.s.l. to provide a water intake for a new hydropower plant; 1.6 km of bioengineered riverbanks were built on both sides of the dam. A sown seed mixture was mechanically harvested in seven hay meadows surrounding the infrastructure, the furthest being 15 km away in the same valley.

 

**Seed mixture**

An experiment was conducted in the Irstea Research Center, in Grenoble, France, during spring 2017. The experimentation site has approximately the same climatic conditions as the restoration site except its elevation is 500 m lower. The seed mixture was provided by the company Zygene and was made up of seeds harvested in meadows surrounding the check dam during the summer of 2016. The whole seeds were carefully mixed by the company to ensure maximum homogeneity. Zygene provided 1.5 kg of seeds and we used 500 g to perform the composition and germination tests. We consider 1.5 kg as representative of the seed mixture; however, it may affect the detection of some rare species.

**Composition test**

The composition of the mixture was studied in two phases with a stereoscopic microscope. Seeds were identified to the genus or species level with atlases (Cappers et al. 2012, CBNA 2017) and the assistance of the National Alpine Botanical Center (CBNA).

First, the relative abundance and relative mass of these seeds in the mixture were determined with three 5-g samples. The mass of pure seeds was estimated by isolating the seeds from the detritus and weighing the mass of pure seeds. The seeds were then identified, and each taxon was separated from the others, weighed, and the seeds were counted. The relative abundance of taxa in the seed mixture was determined as the mean number of seeds of each taxon in the three 5-g samples. The relative mass of taxa was determined as the mean mass of each taxon in the three 5-g samples.

Second, the rest of the mixture was studied to detect rare taxa: All the different seeds observed were isolated.

**Germination test**

The germination rate of the 26 most abundant taxa in the seed mixture (14 families) was tested; the other taxa were not present in sufficient abundance. For each taxon three

 

samples of 100 seeds were placed on filter paper in a Petri dish, except for those for which an insufficient number of seeds were isolated: *Leucanthemum vulgare* Lam. (three times 70 seeds) and *Ranunculus repens* L. (three times 40 seeds). They were then put in a growth chamber in standard conditions: 20–25°C, 70% humidity, and a light cycle of 12 h total darkness and 12 h light (Vallée et al. 1999, GENMEDOC 2006). They were checked daily and the seeds were counted and removed as soon as the hypocotyl appeared.

**Experimental sowing**

The seed mixture was then sown in pots in an outdoor experimental garden. The pots were 60 cm long, 40 cm wide, and 15 cm deep. The experiment explored the effect of sowing density at nonlimiting fertile conditions and of soil quality. We did not intend to test their interaction.

**Sowing density**

The effect of sowing density on plant growth and diversity were tested with four sowing densities: 5, 15, 30, and 60 g $m^{-2}$ (15 g $m^{-2}$ corresponding to the sowing density applied to the bioengineered riverbank). Twenty-five pots of horticultural compost were prepared, 20 of them were sown (five at 5 g $m^{-2}$, five at 15 g $m^{-2}$, five at 30 g $m^{-2}$, and five at 60 g $m^{-2}$) and five were left unsown as control (Table 1).

**Soil quality**

The effect of soil quality on plant growth and diversity was tested with three different soils: soil sampled on the riverbanks (RB), soil sampled on the riverbanks and sterilized for 24 h at 200°C (Trevors 1996, Thompson et al. 1997) (RBS), and horticultural compost (HC). Sterilization aimed at neutralizing the soil's seed bank. Ten pots of each soil were prepared, five were sown with the seed mixture at a density of 15 g $m^{-2}$ and five were left unsown as



 

control (Table 1). Moreover, soil tests were performed to determine the C/N ratio of RB and RBS soils. Three samples per pot were taken, making 60 samples overall (3 × 10 pots of RB = 30 and 3 × 10 pots of RBS = 30). These tests were performed by a laboratory specialized in agronomical soils (CESAR Laboratory, France).

| | 0 g $m^{-2}$ | 5 g $m^{-2}$ | 15 g $m^{-2}$ | 30 g $m^{-2}$ | 60 g $m^{-2}$ |
|---|---|---|---|---|---|
| RB | ×5 | | ×5 | | |
| RBS | ×5 | | ×5 | | |
| HC | ×5 | ×5 | ×5 | ×5 | ×5 |

Table 1: 45 pots as combinations of the three different soils (RB = riverbank, RBS = riverbank sterilized, HC = horticultural compost) and the four sowing densities; density of 0 g $m^{-2}$ represents the control pots.

Two months after sowing, we surveyed vegetation cover and community composition. The vegetation cover was evaluated by visually estimating the percentage of soil covered by vegetation. During vegetation surveys, the pots were examined to determine the community composition, in order to assess species diversity (total number of taxa) and cover using several floras (Aeschimann and Burdet 2005, Eggenberg and Mohl 2013, Tison and Foucault 2014).

**Statistical analysis**

**Germination test**

The germination rate of a sample was measured as the percentage of seeds germinated in the sample over 30 days (GENMEDOC 2006). The germination rate of a species is the mean of the three sample germination rates. At the family level, germination rates of the two most abundant families, *Fabaceae* (six taxa tested) and *Poaceae* (six taxa tested), were



 

compared using analysis of variance (ANOVA). When residuals did not present a normal distribution or homoscedasticity was not respected, a Wilcoxon test was conducted.

**Sowing density and soil quality**

Differences between the four sowing densities (5 g $m^{-2}$, 15 g $m^{-2}$, 30 g $m^{-2}$, 60 g $m^{-2}$) and differences between the three soils (RB, RBS, HC) on vegetation cover and diversity as well as the differences in the C/N ratio were evaluated using analysis of variance (ANOVA). When assumptions of ANOVA were not respected (normal distribution of residuals and homoscedasticity), a Kruskal–Wallis test was conducted. If the null hypothesis was rejected, a pairwise *t*-test, or pairwise Wilcoxon test if assumptions were not respected, with a Bonferroni adjustment was performed to compare all the groups.

All these analyses were performed using R software version 3.3.0 with RStudio software version 1.1.463 (R Core Team 2016).

## Results

### Composition of the seed mixture

Of all the taxa isolated, 45 were identified at the species level, 15 at the genus level, and three remained undetermined. The seed mixture included at least 63 taxa, and we considered with certainty that there was not redundancy in taxa undetermined at the species level. A total of 20 families were present in the mixture; nevertheless, 44% of the species are members of the *Asteraceae*, *Fabaceae,* and *Poaceae* families.

The mean mass of pure seeds was 4.00 ± 0.03 g in 5 g of seed mixture, meaning four fifths of the sown mixture were actual seeds and the rest impurities. We found 2430, 5593, and 5298 seeds in the first, second, and third sample, respectively; the mean number of seeds

 

in 5 g of mixture was 4440 ± 1747 (about 888 seeds per gram). These results show a high variability of seed number per sample. There were on average 46 ± 3 taxa in 5 g of seed mixture and we found 49 different taxa in the three 5-g samples overall. It can therefore be considered that a 15-g sample of seed mixture contained about 49 taxa.

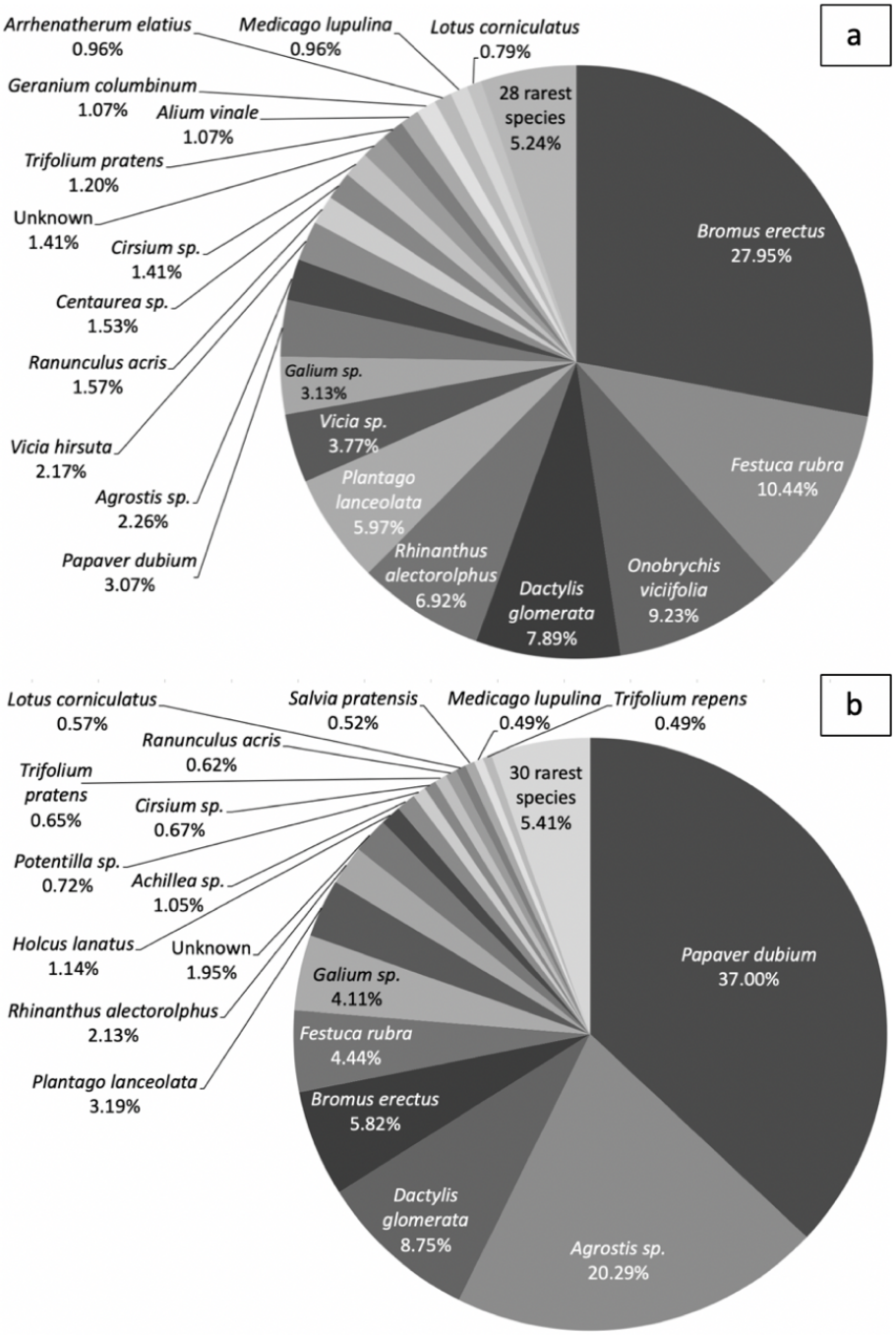


**Fig. 1** Average over the samples of (a) the proportion of each taxa in the total mass of pure seeds and (b) the proportion of each taxa in the total number of seeds.



 

The mass of the seed mixture was dominated by *Poaceae* (Fig. 1a). The three species *Bromus erectus* Huds., *Festuca rubra* L., and *Dactylis glomerata* L. accounted for 46.18% of the pure seed mass. Of the 49 species that were present in samples, 17 accounted for 90.00% of the total mass and 14 of them made up 1.06% of the total mass. Mean specific seed masses of taxa varied from 0.02 g (*Onobrychis viciifolia* Scop.) to less than 0.01 µg (*Papaver dubium* L., *Deschampsia cepitosa* (L.) P.Beauv., *Cerastium sp.*), showing high variability.

The total number of seeds in the sample was dominated by *P. dubium* and *Agrostis* sp. (Fig. 1b), which made up 56.80% of the seeds. Moreover, *Poaceae*, which were dominant regarding mass, were also dominant regarding the number of seeds. *Agrosti*s sp., *D. glomerata*, *B. erectus,* and *F. rubra* made up 38.96% of the total number of seeds. Of the 49 species present in the samples, only 13 of them made up 90.00% of the total number of seeds and 16 species accounted for less than 1.00% of the total number of seeds. Similar to mass, the contribution of each species to the total number of seeds was disparate.

**Germination test**

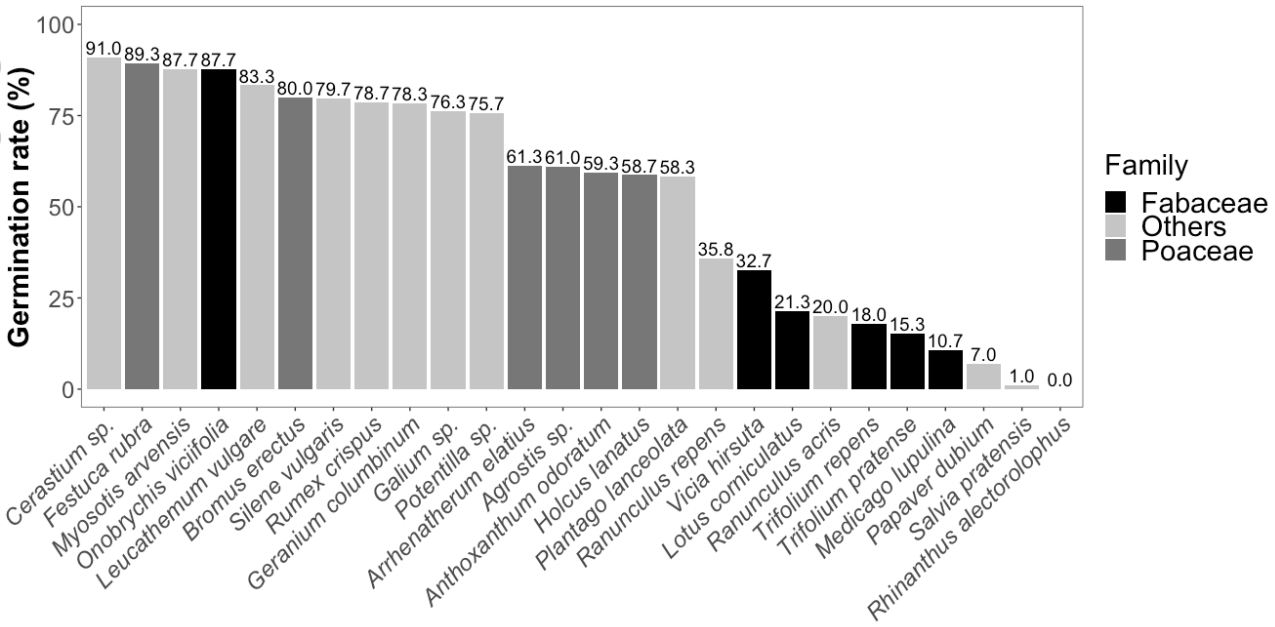


 

**Fig. 2** Germination rate of 26 of the most abundant taxa from the seed mixture.

There was substantial heterogeneity in the germination rate of taxa found in the seed mixture (Fig. 2). The lowest rate was for *Rhinanthus alectorolophus* (Scop.) Pollich and the highest was for *Cerastium* sp. Regarding differences among families, the germination rate of *Fabaceae* (31.0% on average) was significantly lower than the *Poaceae* germination rate (68.3% on average) ($p_{Wilcoxon} = 0.041$).

**Effect of sowing density on vegetation cover and species diversity**

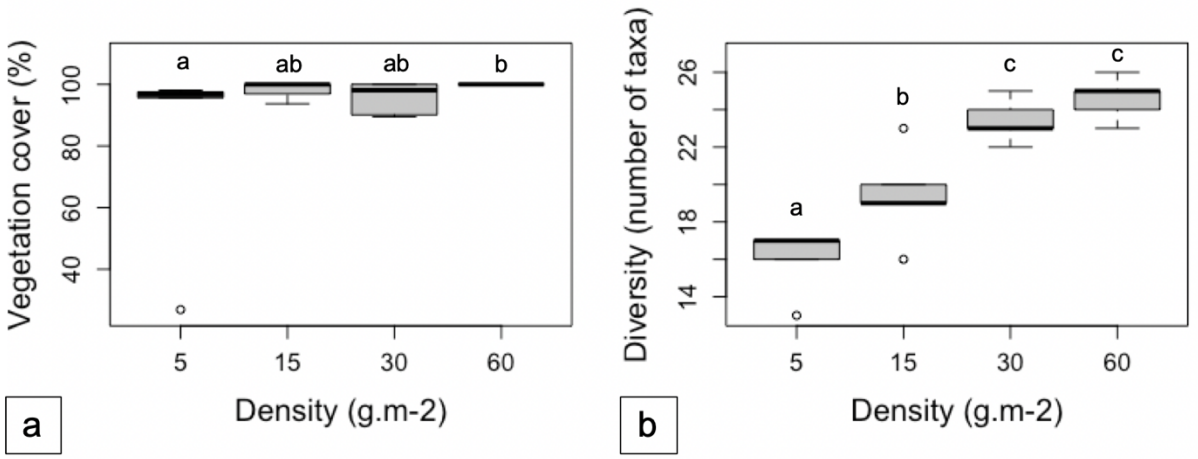


**Fig. 3** Effect of sowing density on (a) vegetation cover and (b) vegetation diversity in pots of HC (horticultural compost) 10 weeks after sowing ($n$ = 5 pots per treatment). Boxes with the same letter are not significantly different (pairwise $t$-test or pairwise Wilcoxon test with Bonferroni adjustment; $p > 0.05$).

High vegetation cover was obtained with every sowing density. Median values of 96.6% and 98.1% were reached with sowing densities of 5 g $m^{-2}$ and 30 g $m^{-2}$, respectively, and 100% with sowing densities of 15 g $m^{-2}$ and 60 g $m^{-2}$ (Fig. 3a). A sowing density effect

 

on vegetation cover was detected, however ($p_{Kruskal–Wallis}$ = 0.046). The pairwise Wilcoxon test indicated that a sowing density of 5 g $m^{-2}$ generated a vegetation cover significantly lower than did a density of 60 g $m^{-2}$ (median: 96.6% and 100.0%, respectively). Considerable differences in sowing density did not generate high vegetation cover differences.

Since there were on average 4440 ± 1747 seeds in 5 g of seed mixture, we could then estimate that a sowing density of 15 g $m^{-2}$ amounted to 13,320 seeds $m^{-2}$, 30 g $m^{-2}$ to 26,640 seeds $m^{-2}$, and 60 g $m^{-2}$ to 53,280 seeds $m^{-2}$. The median number of taxa per pot varied from 17 (sowing density, 5 g $m^{-2}$) to 25 (sowing density, 60 g $m^{-2}$) (Fig. 3b). Sowing density had a significant positive effect on vegetation diversity ($p_{anova}$ < 0.001). A greater number of seeds seems to increase diversity; however, this effect appears to lessen when increasing density above 26,640 seeds $m^{-2}$.

**Effect of soil quality on vegetation cover and species diversity**

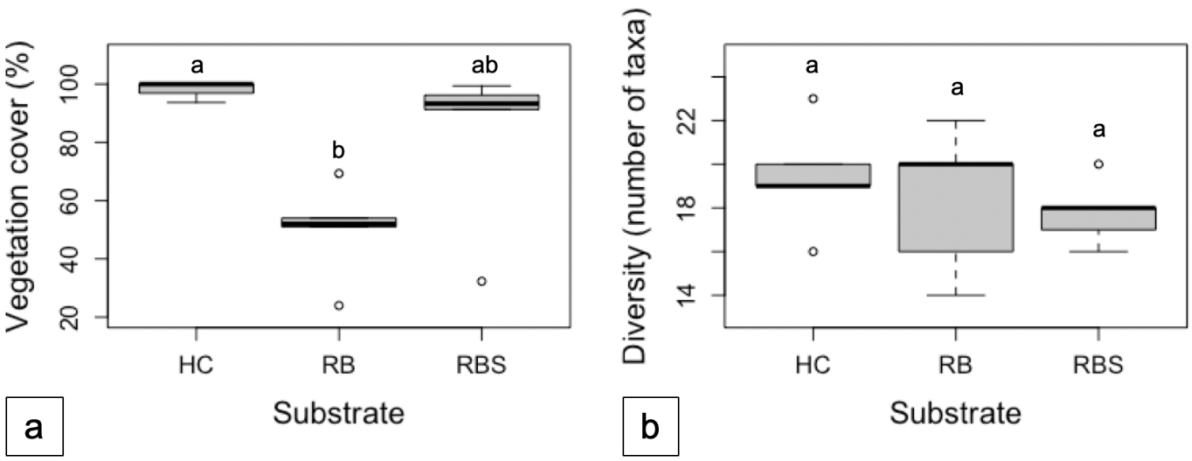


**Fig. 4** Effect of soil quality on (a) vegetation cover and (b) vegetation diversity 10 weeks after sowing ($n$ = 5 pots per treatment). HC: horticultural compost, RB: riverbank soil, RBS: sterilized riverbank soil. Boxes with the same letter are not significantly different (pairwise Wilcoxon test with Bonferroni adjustment; $p$ > 0.05).



 

Vegetation cover close to 100% was reached in the HC and RBS pots. RB median vegetation cover was 52.0% (Fig. 4a). Soil quality had a significant effect on vegetation cover ($p_{\text{Kruskal–Wallis}} = 0.009$), but there was no significant vegetation cover difference between HC and RBS. Vegetation cover on RBS was higher than on RB. The median number of taxa varied: 18.0 in RBS, 19.0 in HC, and 20.0 in RB (Fig. 4b). Nevertheless, no effect of soil quality on vegetation diversity was detected.

Some species were only detected in RB pots, notably *Agrostis stolonifera* L. and *Tussilago farfara* L. It is worth noting that almost only Poaceae were present on the surface of RBS pots, especially *F. rubra* (53.33% cover from 10.44% of sown seed mass and 4.44% of sown seeds), and *D. glomerata* L. (6.50% cover from 7.89% of sown seed mass and 8.75% of sown seeds), while RB and HC did not present such distinction. RB pots were dominated by *A. stolonifera* (48.1% cover from seed bank) and *Plantago lanceolata* L. (14.2% cover from 5.97% of sown seed mass and 3.19% of sown seeds). HC pots presented a similar dominance, independently of sowing density, of *F. rubra* (42.46% cover from 10.44% of sown seed mass and 4.44% of sown seeds) and *P. lanceolata* (16.70% cover from 5.97% of sown seed mass and 3.19% of sown seeds), and to a lesser extent *Papaver* sp. (6.45% cover from 3.07% of sown seed mass and 37.00% of sown seeds) and *Holcus lanatus* L. (4.68% cover from 0.51% of sown seed mass and 1.14% of seed sown). The taxa dominating the mixture in terms of the number of seeds (Fig. 1b) also dominated the pot of established plants, except for *Agrostis* sp. that was absent and *B. erectus* that was present but not dominant (2.76% cover).



 

Carbon and nitrogen tests performed on RB and RBS soil revealed substantial differences (Fig. 5). The C/N ratio was significantly higher in RB pots (median value: 12) than in RBS pots (median value: 10) ($p_{anova} < 0.001$).

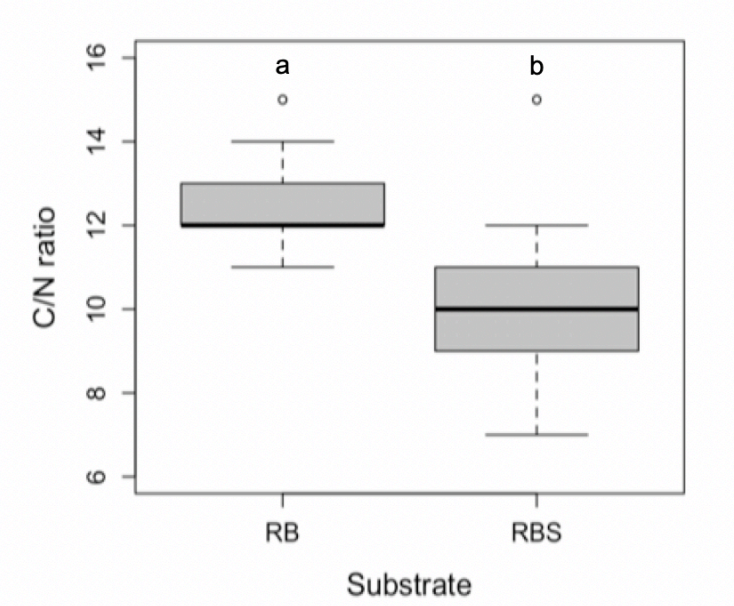


**Fig. 5** C/N ratio of RB and RBS pots. RB: riverbank soil, RBS: sterilized riverbank soil. Boxes with the same letter are not significantly different (pairwise Wilcoxon test with Bonferroni adjustment; $p > 0.05$).

## Discussion

The composition of seed mixture, the germination of seeds, and the sowing conditions are decisive elements for the success of herbaceous restoration. In a local seed mixture, more than 60 taxa were detected, and the seeds presented heterogenous germination rates. Ex-situ sowing experiment showed that greater sowing densities increased plant diversity.

### Uneven germination performance

The seed mixture used in our experiments was harvested on local hay meadows, and the seeds were therefore not certified (in France an Interprofessional Organization is

 

appointed by the Ministry for Agriculture to certify commercial seeds). Certified seeds are widely used both for legal reasons and because of their quality (Conrad and Tischew 2011, Koch et al. 2015). They undergo a selection process that guarantees germination performance, but they can lack genetic diversity and local adaptation (Bischoff et al. 2010). The use of a local seed mixture may be a good alternative to certified seed to reach ecological restoration with a community composed of local ecotypes of native species. We tested the germination rates of 26 taxa of local seeds. Although not certified, some seeds presented excellent germination performance, but on the contrary, some seeds did not germinate at all. Our rates (median value of 60.2%) are sufficient, but higher rates are desirable, as Koch (2015) estimates that revegetation success is compromised if a mixture has a germination rate of less than 50% and Demonty (2014) considered 70% as the desirable rate. Performance heterogeneity could stem from a number of sources including differences between seeds given that larger seeds tend to have better germination rates (Chatain and Payany 1994) as well as temperature and light (Walck et al. 2005, Finch-Savage and Leubner-Metzger 2006). Besides environmental conditions, phenology is also critical, since some species have very precise germination and dormancy timing depending on seasonality (Walck et al. 2005). The factors influencing germination might have played a role in explaining the significant germination rate variation among taxa tested.

**Adequate diversity of the seed mixture**

We found that the mixture contained a considerable diversity of taxa compared with other seed mixtures used for restoration purposes (Table 2).

| | Number of mixtures | Number of species | Origin of the mixtures | Context |
|---|---|---|---|---|
| Vécrin et al. 2002 | 1 | 4 | Non-local | Floodplain meadow restoration |

 

| | | | | |
|---|---|---|---|---|
| Lencová and Prach 2011 | 1 | 8 | Non-local | Hay meadow restoration |
| Lepŝ et al. 2007 | 2 | 4 and 15 | unknown | Semi-natural grassland restoration |
| Staab et al. 2015 | 6 | 23 | Non-local and local | Road verge bioengineering |
| Jongepierová et al. 2007 | 1 | 27 | Local | Hay meadow restoration |
| Conrad and Tischew 2011 | 3 | 17, 22 and 37 | Non-local | Grassland restoration |
| Kirmer et al. 2012 | 2 | 3 and 51 | Non-local and local | Surface mined-land restoration |
| Kiehl et al. 2010 | 17 | Between 15 and 51 | Local | Semi-natural grassland restoration |

Table 2: Characteristics of seed mixtures used for restoration purposes.

It should be highlighted, however, that most studies concern grasslands. And to our knowledge there is no study examining this issue on restored riverbanks, although it is a key issue in bioengineering works for riverbank protection. Indeed, since conditions on riverbanks are not homogeneous, the seed mixture sown for restoration should contain sufficient diversity. A minimum of 10–15 species is recommended in seed mixtures for all microsites to be covered (Adam et al. 2008). Thus, the 63 taxa detected in the whole seed mixture and the 49 found in 15g suggest a desirable diversity.

When considering established plants, diversity is lower than the one found in the seed mixture, since 10 weeks after sowing in 0.25 $m^2$ pots there were on average 24.6 taxa when sown at 60 g $m^{-2}$ and 19.4 taxa when sown at 15 g $m^{-2}$. But even if the seed mixture had been carefully mixed before sowing, it is likely that the total number of species sown in each pot would be somewhat different because the seed mixture samples might had differed at least for some rare species. Previous studies on semi-natural grassland revealed a low transfer rate of rare species (Rydgren et al. 2010); in their experiment only half of the entire species pool was expressed in the sown plots, which is consistent with our results. Moreover, *Agrostis* sp. and *B. erectus*, although presenting a considerable number of seeds (20.29% and 5.82%, respectively, of total seed number) and a good germination rate (36.1% and 80.0%,

 

respectively), did not dominate pot communities (mean cover of 0% and 2.76%, respectively). Therefore, alongside rarity there are other elements affecting transfer, which may include factors affecting germination and intra- and inter-species interactions (Cristofoli and Mahy 2010), most notably competition (Keddy 1992, Mouquet et al. 2004). Moreover, an overview of Palearctic grassland diversity showed that in Central Europe (Germany and Italy) the mean vascular plant richness on 0.1-$m^2$ plots is between 3.0 and 25.0 species, while on 1-$m^2$ plots it is between 3.9 and 37.0 species (Dengler et al. 2016). Our values are within these orders of magnitude, and it is the case also considering riverbank rather than grasslands. Studies of seed banks reporting on the number of species in riverbanks natural seed banks show a high variability ranging from less than 40 species (Gioria and Osborne 2009, White and Stromberg 2011) to more than 100 (Gurnell et al. 2006, Cockel and Gurnell 2012, O'Donnell et al. 2014).

**A seed mixture of local provenance suitable for restoration**

Seed mixtures sown should be designed for the environment in which they are implanted (Staab et al. 2015) and the hay meadows where our seeds were harvested can be considered as a meso-hygrophilous environment, suiting riparian zones well. It should be noted that in some contexts, such as severe disturbance, local seed mixtures have shortcomings, and other species or genotypes could be better adapted (Lesica and Allendorf 1999). This is also the case for the climate change context (Harris et al. 2006); for instance, using plant material composed of species less sensitive to temperature variation and more likely to adapt to different temperatures may enhance the probability of restoration success (Grady et al. 2011). Nevertheless, local seed mixtures benefit restoration sites in many other ways. Various restoration techniques of the sagebrush community showed that non-local seed sowing could result in less diversified vegetation than local seed sowing (Newman and

 

Redente 2001). On alpine grassland, recruitment of native seedlings after restoration is greater when noncertified local seeds are sown because they are less competitive (Hagen et al. 2014). The nature of the seeds sown and their characteristics are essential for the first steps of vegetation establishment (Stockey and Hunt 1994, Staab et al. 2015), and they are also crucial over the long term given that two decades after a restoration intervention, species present in the seed mixture sown are still dominant on some restored sites (Newman and Redente 2001, Hagen et al. 2014).

**Sowing density and soil quality affect cover more than diversity**

We tested the effect of sowing density on the early development of vegetation given that the recommended density of the seed mixture sown on bioengineered riverbanks has not reached consensus. Wide ranges of seed mixture density are suggested in riverbank bioengineering technique guides, for instance, Zeh indicates 5–20 g $m^{-2}$ (2007) while Adams recommends 25–30 g $m^{-2}$ (2008); for grassland restoration, Scotton used seed densities ranging from 0.75 g $m^{-2}$ to 9.28 g $m^{-2}$ (Scotton 2016). Raising seed density increases the probability that seeds will find suitable conditions for their development (Sheley and Half 2006). However, raising the quantity of seed sown also increases the cost of restoration. We showed that on horticultural compost, raising the sowing density becomes irrelevant in increasing vegetation cover: Sowing 5 g $m^{-2}$ of seed mixture already provides a cover close to 100%. The quality of horticultural compost is better than riverbank soil; nevertheless, studies of dry grassland restoration and road verges showed that a sowing density of 5 g $m^{-2}$ was enough to obtain sufficient vegetation cover (Staab et al. 2015). Sowing density had a positive effect on vegetation diversity, but the differences between densities were not considerable. We can therefore recommend that practitioners limit seed density to 5 g $m^{-2}$ in fertile conditions.

 

Soil quality, however, did not affect vegetation diversity, but seemed to have a great impact on vegetation cover. Topsoil has an impact on long-term site recovery by seed sowing (Rydgren et al. 2011, Rydgren et al. 2013), and it appears that effects can be detected over the short term as well. Interestingly, after 10 weeks of growth, vegetation sown on riverbank soil had developed half as much vegetation as on horticultural compost and sterilized soil. In contrast to the two other soils, riverbank soil may contain a seed bank as well as mycorrhizae and microorganisms. Soil seed banks developed in riverbank soil pots – sown and control – since they contained species absent under other treatments (notably *Tussilago farfara*, *Oxalis* sp., and *A. stolonifera*). This could have impacted sown vegetation development by competing with it (Hölzel et al. 2003). On the other hand, mycorrhizae and microorganisms are known to have a positive impact on herbaceous vegetation (Kardol et al. 2007, Münzbergová 2012). However, seeds from both seed banks and seed mixture were characterized by low vegetation growth in riverbank pots, indicating broad unfavorable development conditions. The high vegetation cover on sterilized soil was surprising and sterilization can have many impacts on soil such as affecting the structure of the soil component (Berns et al. 2008). It is also reported to increase nutrient content, including nitrogen, in soils (Jensen and Jakobsen 1980, Chambers and Attiwill 1994) and uptake by vegetation (Troelstra et al. 2001, Miransari et al. 2009). Since the C/N ratio is higher in unsterilized soil, we can assume that sterilization modified the nutrient content of the soil, which explains the differences in vegetation performance at least partially. The results suggest that soil quality requires specific attention and that fertilization is needed on poor soils if a quick vegetation cover is required for erosion control. But if erosion control is not an issue, it can be interesting to allow a slow natural successional process to occur with local pioneer species.

 

## Conclusion

In the present study, we showed that a locally harvested seed mixture destined for riverbank restoration presented fair diversity. Despite the absence of certification, the seed sample that was tested presented good germination capacity. The seed mixture studied seemed appropriate to meet the main goals of seed sowing in restoration, namely, soil protection against erosion and accelerated return of local vegetation. The latter goal is more likely to be achieved with the use of local seeds. Regarding development conditions, we demonstrated that seed addition and the quality of soil significantly affected the early stages of vegetation. Our results suggest that plant diversity could be more influenced by sowing density and vegetation cover by soil quality.

Seed mixtures of different composition, different origin, and different sowing treatments result in very different early development of vegetation. They must therefore be considered with caution and also on a case-by-case basis, since restoration sites may present different conditions, regarding soil quality for instance. Moreover, since these initial inputs have impacts over time as well, long-term surveys are essential to increase our understanding of vegetation development and to ensure that restoration goals are met.

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