Native seed addition as an effective tool for post-invasion restoration

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Abstract

Invasive plant species reduce biodiversity, alter ecosystem processes, and cause economic losses. Control of invasive plants is therefore highly desired by land managers and policy makers. However, invasive plant control strategies frequently fail, partly because management often concentrates only on the eradication of invasive plants and not on revegetation with native species that use the available resources and prevent reinvasion. In this study, we focused on the intracontinental invader *Rumex alpinus* L., which was introduced by humans from the Alps to the lower mountains of Central Europe, where it has spread to semi-natural meadows, suppresses local biodiversity, and reduces the quality of hay used as cattle fodder. The species can be effectively removed using herbicide, but this leaves behind a persistent seed bank. Without further treatment, the invader rapidly regenerates and reinvades the area. We supplemented the herbicide treatment by adding the seeds of native grasses. Addition of native-seed effectively suppressed the regeneration of the invader from the seed bank, reduced its biomass, and consequently, prevented massive reinvasion. While the invader removal was successful, the restored community remained species-poor because the dense sward of native grasses blocked the regeneration of native forbs from the seed bank. Nevertheless, the addition of native seed proved to be an effective tool in preventing reinvasion after the eradication of the invasive plant.

Keywords: alien species; invasive plant control; herbicide; seed bank; revegetation invader; Rumex alpinus; seed limitation.

Introduction

Biological invasions cause ecological and economic impacts around the globe, including biodiversity losses (Hejda, Pyšek, & Jarošík, 2009; Vilà et al., 2011), changes in ecosystem processes and services (Liao et al., 2008; Pejchar & Mooney, 2009), and economic losses (Pimentel, 2002). Biological invasions have been recognized as one of the main drivers of habitat degradation, and the scientific community is calling for management actions (IPBES, 2018). The management of invasive species includes the prevention and early detection of new invasions, the eradication or mitigation of already existing invasive species, and subsequent restoration of the habitat (Pyšek & Richardson, 2010).

If a habitat is degraded through the invasion of an alien plant species, its restoration can be challenging (Meyerson & D'Antonio, 2002). Many invasive plants are long-lived, perennial plants with high ability of vegetative propagation (Liu et al., 2006; Lowe, Browne, Boudjelas, & De Porter, 2000), and after mechanical eradication, they are able to regrow from the small vegetative fragments of rhizomes, roots, or stolons that have been left behind (e.g., Klimeš, Klimešová, & Osbornová, 1993; Kollmann, Brink-Jensen, Frandsen, & Hansen, 2011; Weber, 2011). Even when the removal of vegetative plants is successful, for example after herbicide treatment, many invasive plants leave behind a legacy that challenges restoration, for example in the form of physical or chemical alterations to the habitat or a buried seed bank (Corbin & D'Antonio, 2012; Loydi, Donath, Eckstein, & Otte, 2015). As the seeds of invasive plants generally survive longer in the soil than seeds of native congeners, soil seed banks contain a high proportion of invasive species (Drake, 1998; Gioria, Pyšek, & Moravcová, 2012). Thus, seeds buried in the soil can be the source of a rapid reinvasion of the space freed by the removal of vegetative plants. Management of seed banks is usually not effective (Cohen et al., 2018), so post-invasion restoration requires the filling of the space that was emptied by the removal of the invader, optimally by active revegetation with native species (Bakker & Wilson, 2004; Kettenring & Adams, 2011).

In ecological restoration, native species are frequently introduced in the form of seeds (Hölzel, Buisson, & Dutoit, 2012). Seed addition has proven to be an effective tool in post-mining restoration (Ballesteros et al., 2012; Kirmer, Baasch, & Tischew, 2012), the reestablishment of the semi-natural grasslands on former croplands (Coiffait-Gombault, Buisson, & Dutoit, 2012; Mitchley, Jongepierová, & Fajmon, 2012), or as a supplement to planting in forest restoration (Ceccon, González, & Martorell, 2016). On the other hand, seed addition in post-invasive restoration has had mixed success (Petrov & Marrs, 2000; Pyke, Wirth, & Beyers, 2013; Wilson & Pärtel, 2003), suggesting that this is a critical area for research in order to promote establishment of native species and prevent repeated invasions (Kettenring & Adams, 2011).

We focused on an intracontinental invader *Rumex alpinus* (also known as Alpine dock), a species native to high European mountains, such as the Alps and Carpathians, but introduced by humans to lower Central European mountains, such as the Krkonoše Mountains or Orlické Mountains, at the beginning of the 17th century, probably as a medicinal plant and vegetable. It typically grows on wet, nutrient-rich soils along mountain streams and above the tree line or at anthropogenic areas around mountain chalets or cattle shelters (Šťastná, Klimeš, & Klimešová, 2010). Even in its native range, the species is considered a weed (Leuschner & Ellenberg, 2018), but it has become especially troublesome in its introduced range, where it grows at lower altitudes and is more vigorous (Šťastná, Klimešová, & Doležal, 2012). In the Krkonoše Mountains, the species invades semi-natural meadows under the tree line, where it creates large stands. These meadows were created by humans centuries ago as grasslands traditionally used for hay production or grazing, and as such, they depend on mowing or grazing in order to prevent natural succession towards forest. Such meadows are an inherent part of the cultural landscape of Europe, and they typically host vast biodiversity and have a high a conservation value (Bengtsson et al., 2019). The current large stands of *R. alpinus* in the Krkonoše Mountains originated after World War II, when many mountain meadows were abandoned due to societal changes (Šťastná,

Klimeš, & Klimešová, 2010). Additionally, mountain chalets still lacked proper sewage treatment; their vicinities were rather wet and nutrient-rich, and as such, the environment was optimal for the establishment of dense stands of *R. alpinus*. Although the nutrient input decreased several decades ago (Rehder, 1982), stands of *R. alpinus* persist and strongly suppress native biodiversity (Delimat & Kiełtyk, 2019; Hejda, Pyšek, & Jarošík, 2009). As the species is avoided by cattle (Bohner, 2005), the stands are useless for mountain farmers who may wish to mow the meadows for hay or as a pasture. Consequently, there is a high demand for invasive plant control and restoration of native vegetation. The target of such restoration is twofold: the reduction of the invader and the restoration of native biodiversity. While suppressing the invader will make the meadows once again suitable for haymaking or grazing, restoring community composition and native biodiversity will recreate the conservation value of these habitats.

Once *R. alpinus* has established a dense stand on a former grassland, restoration of the area is problematic. The first necessary step is the return of traditional management practices for semi-cultural mountain meadows because its cessation was among the main causes of the invasion. However, simply returning to traditional management is insufficient because R*. alpinus* has large storage rhizomes that allow its rapid regeneration after the removal of aboveground biomass (Klimeš, Klimešová, & Osbornová, 1993). Burning, topsoil removal, chemical treatment, or very frequent mowing suppresses *R. alpinus* (Šilc & Gregori, 2016), but the species rapidly regenerates from a massive seed bank (Handlová & Münzbergová, 2006). Although seedlings of large docks are generally weak competitors and they are sensitive to mowing (Hujerová, Pavlů, Hejcman, Pavlů, & Gaisler, 2013; Zaller, 2004), seed banks contain only a limited number of native seeds twhich are not sufficient for the rapid re-establishment of native vegetation (Handlová & Münzbergová, 2006). Thus, seed addition could be a possible tool for post-invasion restoration.

In this study, we tested whether the addition of native grass seed is a possible tool for restoring mountain meadows after the eradication of *R. alpinus*. We hypothesized that (1) grass seedlings will suppress *R. alpinus* seedlings, resulting in grass dominance on the restored plots and, thus, an increase of biomass quality as fodder, and that (2) suppressing *R. alpinus* via seed addition will increase native plant biodiversity.

Materials and mathods

The experiment was carried out at two sites in the Czech Republic's Krkonoše Mountains: Černá Voda (N 50°44'04"N, 94 15°48'40"E), 950 m above sea level, and Klínovky (50°42'32"N, 15°39'18"E), 1,200 m above sea level. At each site, we selected vegetation with near 100% *R. alpinus* coverage. In early May 2000, we set up four pairs of experimental plots per site. Because a run-off from the neighbouring slope damaged two pairs of plots at the Černá Voda site, we established an additional four pairs in 2001. In total, the experiment comprised of ten pairs of plots. Each pair consisted of two 1.5 m x 1.5 m plots next to each other with 1 m of spacing. In June 2000 (2001 for the replacement plots), the stands of *R. alpinus* were treated with a glyphosate-based herbicide (Roundup, Monsanto, concentration 5%), which completely destroyed the vegetation on the plots. Three weeks after the herbicide treatment, we added grass seed to one random plot from each pair, while the other one remained without seed addition as a control. The seeds were collected the previous year in the neighbourhood of the plots. Specifically, we used a mixture of *Alopecurus pratensis*, *Festuca rubra*, and *Agrostis capillaris* in the densities of 500, 560, and 6,500 viable seeds per m^2, respectively. We selected these species because they are common at the sites and have easy-to-collect seeds, and the different densities were determined by seed availability. The total seeding density approximately corresponds to high seed density recommended for restoration in difficult conditions (https://www.rieger-hofmann.de).

We monitored the vegetation for three consecutive years (two for plots established in 2001), always in June. We used the core 1 m x 1 m of each plot to avoid edge effects and divided it into to 3x3 subplots. For each subplot, we recorded all species of vascular plants and estimated their coverage using the Braun-Blanquet scale. For the data analysis, we used the mean percentage cover of each unit ("r,+" = 0.5%; "1" –=3%; "2" = 15%; "3" = 37.5%; "4" = 67.5%; "5" = 87.5%). At three randomly selected subplots, we clipped the biomass 3 cm above ground, separated it to grass, forbs, and *R. alpinus*, dried it for 48 hours at 70 °C, and weighed it. We collected the biomass from the same subplots in all three years of monitoring (two for plots established in 2001). The rest of the plot and the surrounding vegetation were mown and the biomass was removed, as mowing is the traditional management necessary to maintain the target community in semi-natural mountain meadows.

Data analysis

In the first step, we evaluated the effect of seed addition on vegetation cover and biomass composition of the restored grasslands. We related (1) the proportion of biomass and (2) the cover of *R. alpinus* per subplot to the seed addition treatment, the year since plot establishment, and the interaction of the two variables in a linear mixed model. To account for the non-independency of the samples, we fitted site, year of establishment, plot pair, and plot identity as nested random factors. As the variances within the factors “seed addition” and “years since establishment” were not homogeneous (Levene test), we estimated variance separately for each level of the respective factor using the function varComb of the R package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2018). We did not specifically test for the differences between sites because we did not have enough independent replicates for such an analysis. Instead, we kept site as a random factor and focused on the main effect of seed addition. We also ran the same model for grass biomass (cover) and forb biomass (cover) as response variables.

In the second step, we evaluated the effect of seed addition on plant biodiversity, represented by the richness of native species. We related the number of native species per plot to seed addition, years since establishment, and their interaction in a model with the same structure as above. To illustrate to what degree the diversity difference was driven by sowing species, we also ran the same model for native species, excluding the sown grasses.

Results

Seed addition had a profound impact on the vegetation of the plots. Without sowing, *R. alpinus* massively regenerated from the seed bank and constituted the majority of the biomass. In the first year, the unsown plots were rather variable and were dominated by native forbs and *R. alpinus*, whle forb biomass decreased over time. After three years, *R. alpinus* comprised 60–90% of the biomass (Fig. 1, Table 1). On the plots with seed addition, the sown grasses effectively suppressed *R. alpinus* and other forbs, and grasses comprised more than 90% of the total biomass in all three years (Fig. 1, Table 1). Although the biomass proportion of *R. alpinus* increased over time in the sown plots, it rarely reached more than 5–10% of the total plot biomass. Interestingly, the proportion of grasses increased in plots without seed addition as well (Fig. 1.). Results based on vegetation coverage largely confirmed the pattern observed for biomass (Fig. S1, Table S1).

We did not detect any effect of seed addition on the number of native species per plot. However, seed addition affected how species richness developed in time. While the number of species did not change over time in the unsown plots, it decreased in the plots with seed addition (Fig. 2 Table 1). Moreover, the majority of the native species in plots with seed addition were the sown grasses that suppressed almost all naturally regenerating native species (Fig. S2, Table S2).

Discussion

173 Invasive plant control often fails, partly because the removal of the invader is not followed by active
174 revegetation with native plants (Kettenring & Adams, 2011). Here, we showed that an addition of native
175 grass seeds after herbicide application can effectively suppress invader regeneration and restore the
176 target community. Without seed addition, the invader regenerated from the seed bank and formed 60–
177 90% of biomass after three years, but seed addition reduced this number to less than 10%. This method
178 is definitely the most effective control of *R. alpinus* (Šilc & Gregori, 2016). Moreover, such success
179 exceeds the average reported in other studies on plant invasion control (Kettenring & Adams, 2011). On
180 the other hand, the restored community was species-poor because sown grasses created dense sward
181 that suppressed other native species.
182
183 *Invader suppression*
184 There are three possible reasons why the control of invasive plant species was so effective in
185 this study. First, we focused on a biological invasion with a known underlying change in abiotic
186 conditions: in this case, cessation of traditional management. It was relatively straightforward to
187 reintroduce mowing and reestablish abiotic conditions as the prerequisite of any successful restoration
188 (McDonald, Gann, Jonson, & Dixon, 2016). Second, we combined two suppression methods, i.e.,
189 herbicide treatment and seed addition. While this combination is relatively common in invasive species
190 control, a success such as that in the present study is rare (e.g., Mahmood et al., 2018; Sheley, Mangold,
191 & Anderson, 2006). Generally, a combination of methods is usually more successful than a single
192 method (e.g., Averill, DiTommaso, & Morris, 2008; Baer & Groninger, 2004; Dodson & Fiedler, 2006;
193 Kilbride & Paveglio, 1999). Third, detailed knowledge of the biology of both the invader and the target
194 community allowed us to design a restoration strategy that took advantage of the weaknesses of the
195 invasive species and the strengths of the native species. While adult *R. alpinus* plants are competitively
196 strong, its seedlings are weak and sensitive to mowing (Hujerová et al., 2013; Zaller, 2004). In contrast,

197 European grasses, as dominants of semi-cultural meadows, have faced extensive mowing or grazing for
198 centuries and adapted to this type of disturbance. When clipped or mown, they often produce more
199 tillers, spread clonally, and form a dense ground cover that is competitively strong (Alexander &
200 Thompson, 1982; Pecháčková, Hadincová, Münzbergová, Herben, & Krahulec, 2010). This mechanism
201 allowed the sown grasses to suppress the seedlings of *R. alpinus* that regenerated from the seed bank.
202 Although seed addition significantly contributed to the suppression of *R. alpinus*, some plants
203 did regenerate, but they stayed rather small. In fact, the proportion of *R. alpinus* increased over time on
204 plots with added seeds. The question remains whether the few established dock plants will eventually
205 suppress the grasses and form dense stands. We believe such a scenario is unlikely as long as the
206 meadows are mown. The seedlings may still die due to competition from grasses, as mortality of dock
207 seedlings in a mown grassland is highest among plants that are three to four years old (Hongo, 1989).
208 Even if the dock plants survive, they are unlikely to spread. Historically, *R. alpinus* grew for two centuries
209 in small, isolated stands in the Krkonoše Mountains and was relatively harmless as long as the meadows
210 were managed (Šťastná, Klimeš, & Klimešová, 2010), while it started spreading after that management
211 stopped. Such a scenario may recur, and the cessation of mowing of the restored grassland may trigger
212 a reinvasion from the persistent seed bank (Handlová & Münzbergová, 2006). Indeed, this happened to
213 the study plots when management was terminated with the end of the experiment in 2003. After a few
214 years without mowing, the restored 1.5 m x 1.5 m grasslands were again taken over by a dense stand of
215 *R. alpinus* (A. Bucharova, personal observation).
216
217 *The effect on native biodiversity*
218 While seed addition suppressed *R. alpinus*, it did not have any positive effect on native
219 biodiversity. On the contrary, the sown grasses were competitively strong and thus prevented the
220 establishment of other species from the seed bank or seed rain. This is a common problem when grasses

221 are seeded in high densities (Dickson & Busby, 2009). A possible solution would be a more diverse seed
222 mixture. In this study, we collected seeds manually, and we restricted ourselves to the most common
223 grasses with easy-to-collect seeds. The more suitable alternative could be species-rich seed mixtures
224 produced by threshing local hay or commercial regional mixtures that are increasingly available
225 throughout Europe and other parts of the world (e.g., Bucharova et al., 2019; Breed et al., 2018, Kiehl,
226 Kirmer, Shaw, & Tischew, 2014; Mitchley, Jongepierová, & Fajmon, 2012). Another reason for the strong
227 grass dominance may be a high content of available nutrients in the soil. As *R. alpinus* produces a lot of
228 biomass that accumulates in the topsoil, the substrate is rich in humus and, thus, available nitrogen
229 (Bohner, 2005). Together with a possible legacy of increased phosphorus due to historical
230 eutrophication, the nutrient content in the soil could have allowed the grasses to be more productive
231 and to outcompete forbs (Hájek et al., 2017). With regular mowing and removal of biomass, the nutrient
232 content will decrease over time, althoght it may take decades (Oelmann et al., 2009). However, even in
233 that case, the addition of a species-rich seed mixture may be necessary to restore a diversity
234 comparable to the reference habitat of a species-rich mountain meadow (Stampfli & Zeiter, 1999).
235

236 **Conclusion**

237 We have shown that the addition of native seeds is a powerful tool for post-invasive habitat restoration,
238 as the sown vegetation reduces reinvasion from the seed bank . It restores native vegetation cover and
239 ecosystem services in form of biomass suitable as cattle fodder. The success of this restoration measure
240 depended on the expert knowledge of the biology of both the invasive and native species, which
241 allowed us to design a method that used the weaknesses of the invader and the strengths of the local
242 species. This highlights the importance of research on invasive plants because lack of information on
243 species biology resulting in suboptimal management can be among the reasons why control invasive
244 plants and subsequent restoration often fail (Kettenring & Adams, 2011).

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Fig. 1. The effect of seed addition on the proportion of biomass of *Rumex alpinus*, grasses and forbs, and its development over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Colored dots represent biomass values per subplots. Significant effects are shown in Table 1.

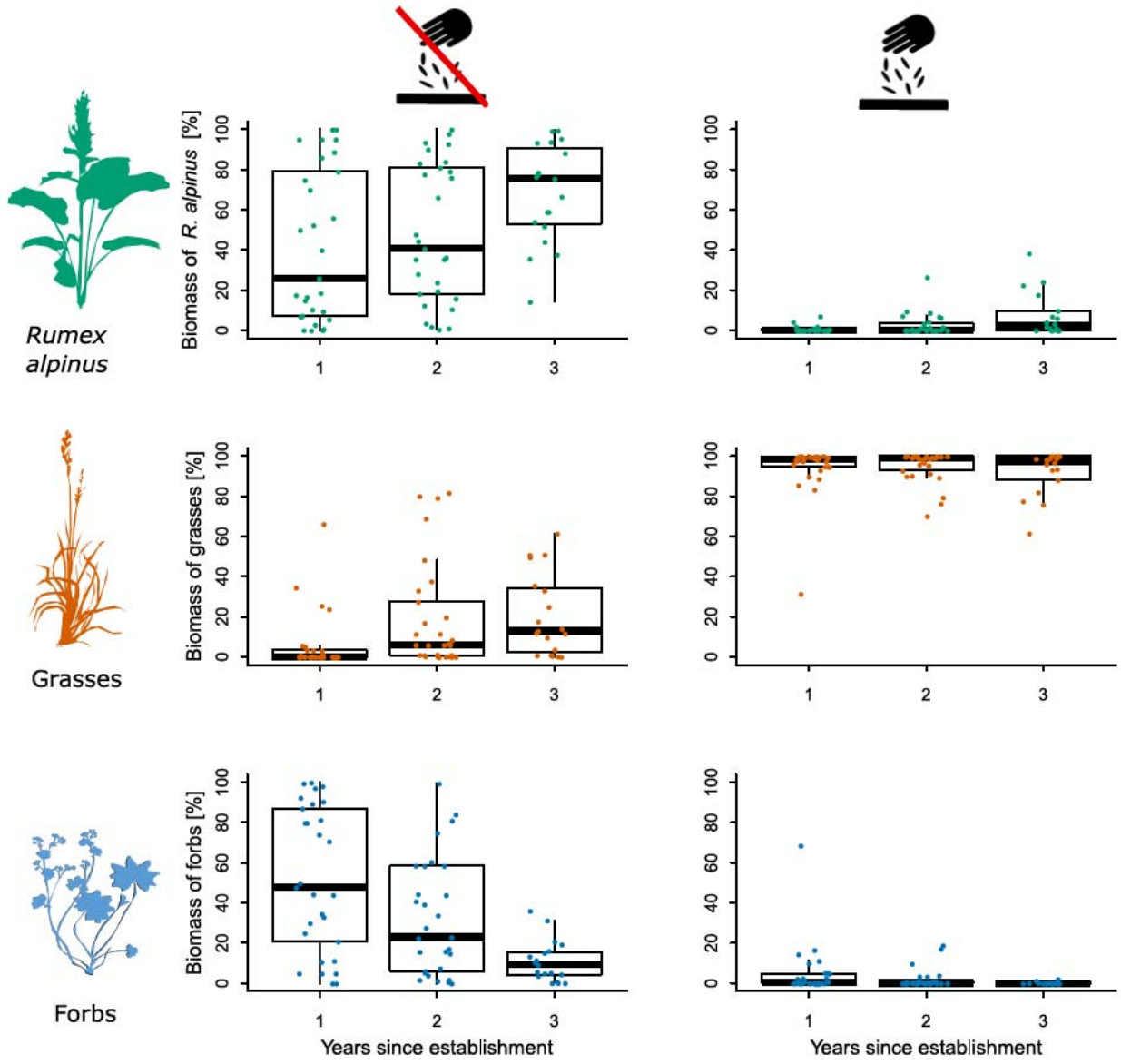

Fig. 2. The effect of seed addition on native plant species richness, and the development of species richness over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Dots represent species numbers per subplots. Significant effects are shown in Table 1.

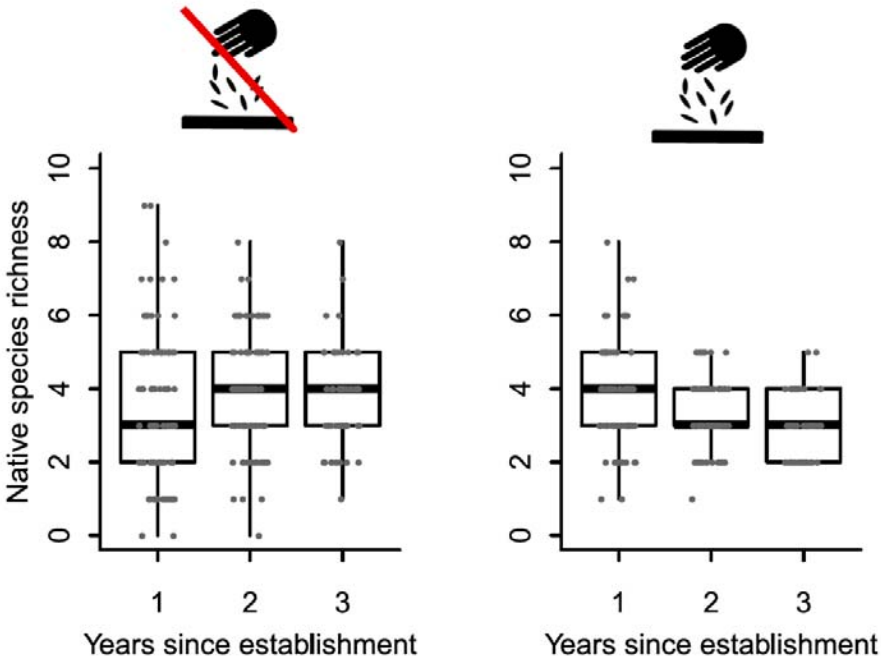

Table 1. The effect of seed addition and time since plot establishment on the proportion of biomass of *Rumex alpinus*, grasses and forbs, and the richness of native species. Results of ANOVA of linear mixed models, terms fitted sequentially, significant values ($P < 0.05$) are in bold.

	Proportion of biomass								Native species richness			
			R. alpinus		Grasses		Forbs					
	Num DF	Den DF	F	*P*	F	*P*	F	*P*	Num DF	Den DF	F	*P*
Intercept	1	91	4.87	**0.030**	256.80	**<0.001**	12.32	**<0.001**	1	281	25.10	**<0.001**
Seed addition	1	9	47.09	**<0.001**	676.70	**<0.001**	66.00	**<0.001**	1	9	4.13	0.073
Years since establishment	2	91	6.50	**0.002**	0.84	0.433	7.50	**<0.001**	2	281	1.09	0.337
Seed addition × Years	2	91	0.57	0.570	5.35	**0.006**	11.30	**<0.001**	2	281	31.99	**<0.001**

FigureS1: The effect of seed addition on the cover of *Rumex alpinus*, grasses and forbs, and its development over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Dots represent cover per subplots. Significant effects are shown in Table S1.

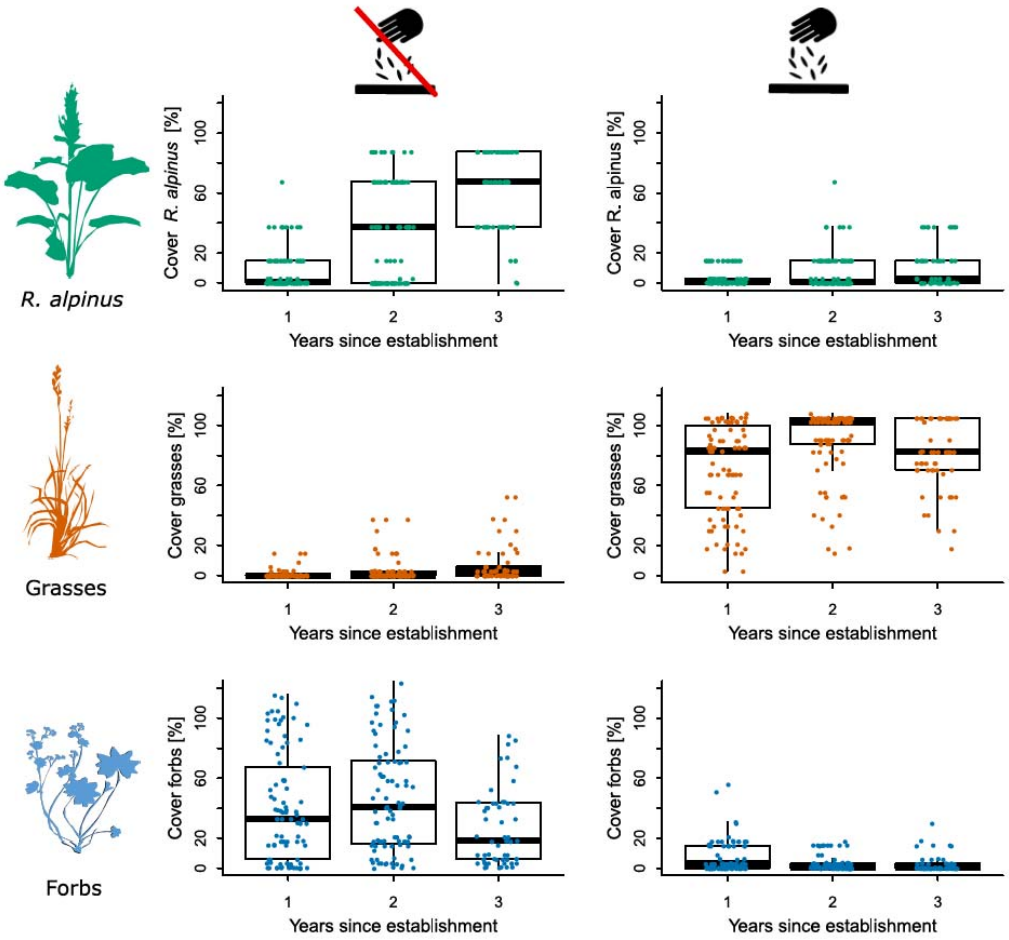

Figure S2: The effect of seed addition on the species richness of native plants regenerating from the seed bank, and the development of species richness over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Dots represent species number per subplot. Significant effects are shown in Table 1.

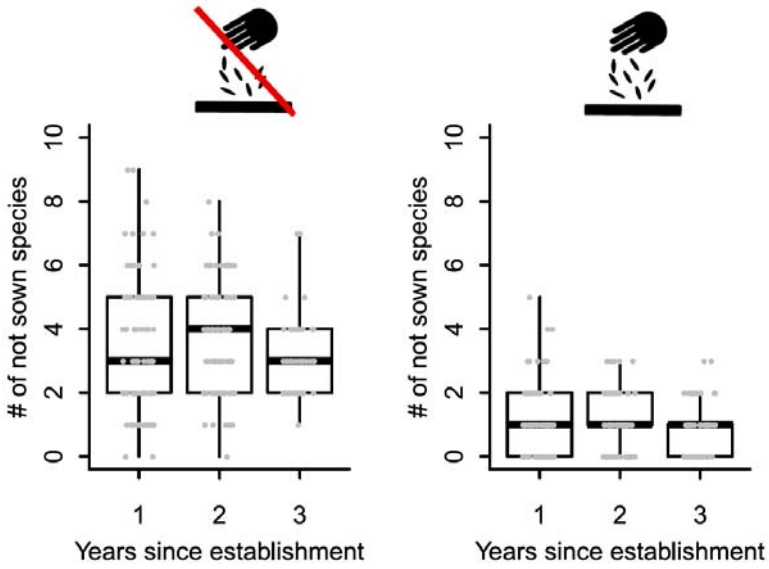

Table S1: : The effect of seed addition and the time since plot establishment on the cover of *Rumex alpinus*, grasses and forbs, and the richness of native species regenerating from the seed bank. Results of ANOVA of linear mixed models, terms fitted sequentially, significant values (P<0.05) are in bold.

	Cover								Native species richness (sown species excluded)			
			R. alpinus		Grasses		Forbs					
	Num DF	Den DF	F value	*P* value	F value	*P* value	F value	*P* value	Num DF	Den DF	F value	*P* value
Intercept	1	281	5.02	**0.026**	18.56	**<0.001**	2.92	0.089	1	281	9.89	**0.002**
Seed addition	1	9	15.40	**0.003**	237.00	**<0.001**	24.17	**<0.001**	1	9	51.71	**<0.001**
Years since establishment	2	281	52.61	**<0.001**	25.54	**<0.001**	3.52	**0.031**	2	281	0.04	0.961
Seed addition × Years	2	281	64.57	**<0.001**	16.86	**0.006**	8.82	**<0.001**	2	281	0.78	**<0.001**