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Plant cover restoration to inhibit seedling emergence, growth or survival of an exotic invasive plant species

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ABSTRACT

We conducted a mesocosm restoration experiment to test the efficacy of early summer sowing of seed mixtures for inhibiting the emergence, growth and/or survival of giant hogweed (*Heracleum mantegazzianum*) seedlings. *H. mantegazzianum* is invasive in Europe and North America, where it has a negative effect on plant diversity and represents a serious health hazard, due to the photodermatitis it may cause. We tested five plant mixtures comprising a selection of North American native or naturalized non-invasive plant species. Compared to the unseeded control mesocosm, all plant covers reduced seedling emergence, growth and survival of *H. mantegazzianum*. There were large differences between mixtures regarding inhibition effects. The nature of the effects depended on species composition, with one mixture more effective in preventing establishment, another essentially affecting seedling growth and survival. Total plant cover, irrespective of seed mixtures, appeared to have a major effect on *H. mantegazzianum*. Other factors that may have played a role included the litter from the seeded plants and the allelopathic effect of Canada goldenrod (*Solidago canadensis*). Our study adds to the growing body of evidence promoting the restoration of a plant cover as a means to prevent reinfestation by invasive species following a control operation.

RÉSUMÉ

Nous avons mené une expérience de restauration en mésocosmes afin de tester l'efficacité de l'ensemencement d'un couvert végétal en début d'été pour inhiber la germination, la croissance ou la survie des semis de la berce du Caucase (*Heracleum mantegazzianum*). *H. mantegazzianum* est envahissante en Europe et en Amérique du Nord, où elle a un effet négatif sur la diversité végétale et représente un risque pour la santé en raison de la photodermatite qu'elle peut provoquer. Nous avons testé cinq mélanges de semences comprenant une sélection d'espèces non invasives indigènes ou naturalisées d'Amérique du Nord. Par rapport au mésocosmes témoins non ensemencés, tous les couverts végétaux réduisent l'émergence, la croissance et la survie des semis de *H. mantegazzianum*. Il y avait cependant de grandes différences entre les mélanges concernant les effets d'inhibition. La nature des effets dépendait de la composition des espèces, un mélange étant plus efficace pour empêcher l'établissement, un autre affectant essentiellement la croissance et la survie des semis. La couverture végétale totale, indépendamment des mélanges de semences, semblait avoir un effet majeur sur *H. mantegazzianum*. La litière provenant des plantes ensemencées et l'effet allélopathique de la verge d'or du Canada (*Solidago canadensis*) ont également joué un rôle. Notre étude s'ajoute au nombre croissant de démonstrations de l'importance de la restauration du couvert végétal pour prévenir la réinfestation par des espèces envahissantes suite à une opération de contrôle.

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Introduction

Considerable efforts have been directed toward the search for appropriate methods to control invasive plants, depending on the species and circumstances. The most common methods include the use of herbicides, mowing, hand-pulling, mechanical cultivation, tarping and biological agents (Tu et al. 2001). A successful control operation may, however, create the conditions for reinfestation by the invader (Schuster et al. 2018). Risks of reinvasion are particularly high for the many invasive species that are known to establish after a disturbance (Jauni et al. 2015). The establishment phase represents the most vulnerable stage for several invasive plant species (Fraser and Karnezis 2005; Byun et al. 2018). In this context, rapidly restoring a competitive plant community that can interfere with invasive plant establishment should be part of integrated management strategies (Pyke et al. 2013; Schuster et al. 2018).

Ecological theory and experimental evidence have provided some guidelines for creating a competitive

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plant cover that will interfere with the establishment of invasive plant species (Blumenthal et al. 2005; Byun et al. 2018). The niche theory, for example, states that introducing a plant species most similar to the invader (habitat requirements, growth form, etc.) may be effective in preventing reinvasion because the niche of the invader is then fully occupied (Bakker and Wilson 2004; MacDougall et al. 2009). Deriving from the niche theory, there is growing evidence that greater plant diversity leads to stronger biological resistance to invasion, presumably because a high diversity offers a better chance to fill the invader's niche (Shea 2002). These evidence suggest that a plant cover with high species or functional diversity should be used for restoration (Kennedy et al. 2002; Nemec et al. 2013; Larson et al. 2013). A priority effect may also occur when earlier emergence or arrival provides a competitive advantage over later-arriving invasive plants (Byun et al. 2013; Hess et al. 2019). The main mechanisms of priority effect are 'niche preemption' (reduction of available resources by the early colonizers) and 'niche modification' (change in available niches by the early colonizers) (Fukami 2015). Seeding fast-growing species that may form a dense cover quickly is one approach to exploiting the priority effect in a successful revegetation to inhibit invasive plant species (Schuster et al. 2018).

These hypotheses are not mutually exclusive, and a combination of strategies may, over the long term, succeed in preventing an invader's resurgence. Controlling an invasion requires an understanding of its underlying mechanisms, which vary depending on the environment and taxa. Species selection is a critical aspect of revegetation to suppress invasive plant species, and factors such as early growth, origin (native or non-invasive exotic), and diversity must all be considered (Schuster et al. 2018). Restoration case studies with different plant covers at different sites are therefore needed, in order to evaluate how these strategies based on ecological theory may be applied in any particular context (Byun et al. 2018).

Giant hogweed (*Heracleum mantegazzianum* Sommier & Levier) is a large monocarpic herbaceous plant from the Apiaceae family. It originates from the Caucasian mountains of Eurasia, and was introduced in Europe and North America for horticultural purposes, later becoming invasive (Jahodová et al. 2007; Lavoie 2019). It negatively affects local plant diversity in old fields and on riverbanks, essentially because of its fast and very early (spring) growth and large size (Pyšek and Pyšek 1995; Thiele and Otte 2007). *Heracleum mantegazzianum* may also alter chemical and biological characteristics of soils (Jandová et al. 2014). More importantly, severe photodermatitis may result from skin contact with the sap and subsequent exposure to ultraviolet rays, making it a serious health hazard (Chan et al. 2011; Lavoie 2019).

Herbicides, uprooting and root cutting are the most common methods used for controlling *H. mantegazzianum* (Nielsen et al. 2005; Pyšek et al. 2007; Rajmis et al. 2016). When soil is left bare after a successful control operation, it becomes extremely vulnerable to reinvasion by large *Heracleum* species (Ravn et al. 2007). *H. mantegazzianum* does not thrive or spread in dense forests, grasslands, or sedge meadows, suggesting that competition from the existing community may inhibit seedling establishment or growth (Page et al. 2006). Thus, revegetation is a promising strategy to prevent its reestablishment. However, to be effective, the seeded species have to be carefully selected considering the large reproduction of *H. mantegazzianum* and its strong competitive potential. This species does not spread vegetatively but produces a large amount of seeds (several thousand per individual) that may easily disperse from nearby populations or along brooks and rivers (Trottier et al. 2017). Most seeds germinate in the following spring, but a small proportion may remain viable in the seed bank for up to three years (Krinke et al. 2005; Moravcová et al. 2006). The large seeds provide abundant resources for seedlings, favoring their rapid growth in spring (late April to early May). Developing a plant cover to prevent reinvasion by seeds thus represents a challenge.

Ravn et al. (2007) conducted a field experiment to test the effect of sowing a native plant cover on reinvasion by another closely related and very similar invasive large hogweed (Sosnowsky's hogweed; *Heracleum sosnowskyi* Manden.). Sowing grass mixtures did not reduce the density of *H. sosnowskyi* seedlings compared to unseeded control areas. The failure of the plant cover in preventing *H. sosnowskyi* establishment was attributed in part to the timing for sowing (Ravn et al. 2007).

The objective of our study was to test the performance of plant covers in preventing the emergence, growth or survival of *H. mantegazzianum* seedlings in a mesocosm experiment. We assumed that a successful approach would begin with complete removal of the adults and seedlings, immediately followed by sowing a mixture of herbaceous species. In our experiment, where the timing of sowing reproduced this approach, we tested five different plant mixtures, in addition to an unseeded control.

Materials and methods

Experimental set-up

The experiment was conducted at the Montréal Botanical Garden (QC, Canada). It consisted of 48 plots divided into eight blocks. Each plot of 1.2 by 1.2 m was delimited with wood planks emerging 0.3 m above ground, filled with 0.2 m of seed-free gardening soil put directly on top of the existing soil of the site.

A standard control operation and subsequent seeding for revegetation would result in *H. mantegazzianum* seedlings emerging concurrently with those of the seeded mixture in the following spring. Because *H. mantegazzianum* germinates in early spring and has large seeds that provide ample resources to the seedlings, it is highly competitive against other plant species, threatening the success of the revegetation. To counter this and optimize chances of success, our experiment assumed an additional control operation on *H. mantegazzianum* seedlings, conducted prior to sowing the plant mixture. The entire operation comprised the following steps: a control of *H. mantegazzianum* individuals in summer or fall (root extraction, herbicide); a period with no intervention in early spring to allow all *H. mantegazzianum* seedlings to emerge, either from seeds produced the preceding year (fresh seeds) or from older seeds (dormant seeds); a control operation on seedlings (manual uprooting, light plowing); sowing the plant mixture on the bare ground. This procedure allows the sowed mixture one full growing season (year 1) to establish before the next cohort of *H. mantegazzianum* emerges the following spring (year 2). It is effective because, as we observed, all *H. mantegazzianum* seeds germinate in early spring, with no subsequent germination during the rest of the season from either fresh and dormant seeds. Citing unpublished data, Page et al. (2006) also report a pot experiment showing a full halt in germination in summer.

Five different plant mixtures were used in addition to an unseeded control (Table 1). The species used in each treatment were a mixture of annuals and perennials, with North American native or naturalized non-invasive plant species. Plant richness in mixtures varied from three (SO1 and SO2) to eleven (RE2) species. The first two mixtures, RE1 and RE2 (for REstoration), composed of graminoid species, were selected because they are commercialized specifically for site restoration, and are thus easily accessible for site managers. RE1 was *Herbio stabilization* seed mixture from Gloco Inc. (Montréal, QC, Canada), and RE2 was a modified version of *Mica* seed mixture, from Horticulture Indigo Inc. (Ulverton, QC, Canada), enriched with additional three species to include a high diversity mixture in our experimental design: fox sedge (*Carex vulpinoidea* Michx.), soft rush (*Juncus effusus* L.) and fowl bluegrass (*Poa palustris* L.). All species used in RE1 and RE2 are readily available and reasonably priced. SO1 and SO2 (for SOlidago) were homemade mixtures containing Canada goldenrod (*Solidago canadensis* L.) with annual ryegrass (*Lolium multiflorum* Lam.) as a shelter species, and either red fescue (*Festuca rubra* L.) or red clover (*Trifolium pratense* L.) for SO1 and SO2, respectively. *Solidago canadensis* is a highly competitive forb with a presumed capacity to produce allelopathic substances that inhibit other plant species (Butcko and Jensen 2002; Abhilasha et al. 2008; Pisula and Meiners 2010), and thus is a good candidate for creating long-term stable plant covers resistant to invasion (De Blois et al. 2002, 2004). EUP (for EUPatorium) was a homemade seed mixture containing a high proportion of bonesets (spotted Joe-Pye weed; *Eupatorium maculatum* L.; common boneset; *E. perfoliatum* L.), because we observed dense stands of them in sites invaded by *H. mantegazzianum*, suggesting they could be good competitors. Seeds of *S. canadensis, E. maculatum* and *E. perfoliatum* were collected from nearby locations in southern Québec, while the other seeds used in SO1, SO2 and EUP were of commercial origin. The five plant mixtures and the control were randomly distributed within each block, yielding eight replicates per treatment.

Table 1. Composition of the bulk seed mixtures used in the Heracleum mantegazzianum experiment, in percentages of seeds per species, based on bulk seed density, within a treatment (seed mixture). For SO1 and SO2, seed numbers and percentages are only rough estimates, since the minute seeds of *Solidago canadensis* were not separated from the vegetative parts of the infructescence.

Mixture	RE1	RE2	SO1	SO2	EUP
Bulk seed density ($n \times 1{,}000$ m^{-2})	60	21	~30	~27	2
Species					
Agrostis gigantea	–	19	–	–	–
Agrostis scabra	48	–	–	–	–
Andropogon gerardii	–	7	–	–	–
Bidens cernua	–	–	–	–	15
Calamagrostis canadensis	–	8	–	–	–
Carex vulpinoidea	–	2	–	–	–
Elymus canadensis	1	7	–	–	–
Elymus virginicus	1	–	–	–	–
Eupatorium maculatum	–	–	–	–	72
Eupatorium perfoliatum	–	–	–	–	9
Festuca rubra	20	23	<8	–	–
Juncus effusus	–	8	–	–	–
Lolium multiflorum	–	17	<1	<1	4
Panicum virgatum	–	2	–	–	–
Poa palustris	30	5	–	–	–
Solidago canadensis	–	–	>91	>98	–
Spartina pectinata	–	2	–	–	–
Trifolium pratense	–	–	–	<1	–

The total number of seeds sown in each mixture was estimated in order to achieve a complete plant cover at the end of the season (Table 1). For RE1, the number of seeds sown followed the recommendation of the company. For RE2, the number of seeds was based on that used in a previous field experiment on *H. mantegazzianum* (Boivin and Brisson 2015), and the company's recommendation. For *S. canadensis* (SO1 and SO2), seeds were prepared by collecting and blending entire mature infructescences. The resulting blended mixture thus contained vegetative plant parts in addition to the very small *S. canadensis* seeds, making seed count difficult. Based on past field tests and experiments (e.g., Boivin et al. 2005), we estimated that 42 g m^{-2} of the dried blended infructescences was necessary to produce a complete plant cover. In contrast, for EUP, seed density sown for both *Eupatorium* species was low because their seeds are large, and a test we conducted showed a high germination rate (unpublished data). Bulk seed density varied from 2,300 to 60,000 seeds m^{-2} depending on the treatment. Because the exact percentage of seed germination was not available for all species, seed density is presented in this paper in terms of bulk seed density rather than pure live seed density. Plant mixtures were seeded on 27 June 2014. In the first week of the experiment, each plot was covered with a sheet to prevent birds from eating seeds. During the summer, plots were watered as needed, but never more than once a week. Plant species other than those that were seeded were removed as they appeared, and control plots were kept free of plants.

Heracleum mantegazzianum seeds were collected in September 2014 from 20 individuals at Saint-Isidore-de-Beauce (QC, Canada; see Trottier et al. 2017 for details). In October 2014, 250 seeds were regularly distributed on the surface of each plot, mimicking a fall seed rain and/or the presence of dormant seeds. Viability rate of the seeds was later estimated at 50%, based on laboratory tests (Trottier et al. 2017), so approximately 125 of the 250 seeds sown in each plot were potentially able to germinate the following spring. It should be noted that seedling emergence, rather than seed germination, was measured in the plot the following spring: seeds may germinate but not produce a viable seedling detectable during weekly surveys.

Data collection

From April 28 (first appearance of *H. mantegazzianum* seedlings) to 17 September 2015, percentage foliar cover for each plant species and for litter and bare soil was noted on a weekly basis using seven cover classes: <1%; 1% to 5%; 6% to 10%; 11% to 25%; 26% to 50%; 51% to 75%; >75%. Seedlings of *H. mantegazzianum* were counted and mapped at the same frequency. From June 15 to 17 September 2015, the width of the largest leaf of each *H. mantegazzianum i*ndividual emerging in the plots was estimated weekly using eight width classes: 2 to 4 cm; 4 to 5 cm; 6 to 7 cm; 8 to 10 cm; 11 to 15 cm; 16 to 20 cm; 21 to 30 cm; 30 to 40 cm. Because *H. mantegazzianum* is acaulescent during its first year, measuring the width of the largest leaf was a more reliable non-destructive estimation of plant size than plant height. For the analyses, we used the median of the leaf size cover classes.

Statistical analyses

The effect of plant mixture on *H. mantegazzianum* seedling emergence and survival was tested using a mixed-model ANOVA, with the block factor as a random variable, after assessments of normality and homoscedasticity had been verified. When significant main effects were found ($p < 0.05$), we compared means using Tukey's HSD multiple comparison test. Seedling emergence was the total number of seedlings found in a plot. Seedling survival was the percentage of seedlings in a plot that survived until the end of the growing season. The effect of plant mixtures on average seedling growth was tested with an ANCOVA using the number of *H. mantegazzianum* seedlings in each plot as a covariable. Average seedling growth was determined as the average width of the largest leaf of each individual in a plot. For leaf size, we used data collected on 2 September 2015, because no changes in leaf size were noted after this date.

The effect of total plant cover on *H. mantegazzianum* seedling emergence, irrespective of plant mixture, was tested using linear regression. Total plant cover was estimated as the sum of the median of the cover class for each individual species. This estimation of total plant cover may exceed 100% due to possible overlap between species. For this analysis, we used total plant cover measured on 26 May 2015, because maximum emergence for *H. mantegazzianum* was attained at this date, and no new seedlings were found subsequently. We tested the effect of plant cover on *H. mantegazzianum* seedling survival and average seedling growth in the same manner, using plant cover measured at the end of the growing season (2 September 2015). All analyses were conducted with version 3.1.2 of R software (R Foundation 2019), and results were considered statistically significant at $P < 0.05$.

Results and discussion

Cover composition

If we exclude EUP, all treatments had a relatively high plant cover, at both the beginning (from 59.2% to 87.5% plant cover) and the end of the 2015 season (from 55.3% to 91.1% plant cover) (Table 2). Plant cover was low in the early season for EUP (17.6%) but reached 51.7% at the end of the growing season. Several species from RE1 and RE2, seeded in 2014, were no longer present in spring 2015, i.e., at the time of *H. mantegazzianum* emergence. RE1 was then dominated by a dense cover of very

Table 2. Mean percentage of cover per species (average of eight plots per treatment) for each plant mixture and for the unseeded control treatment used in the *Heracleum mantegazzianum* experiment in spring (May 26) and early fall (September 2) 2015. The value for total plant cover excludes giant hogweed. The sum of all covers (seeded plants, *H. mantegazzianum*, litter and bare ground) is not expected to add up to 100%, due to possible overlap between species and because of imprecision in individual plant cover measurements (median value of cover classes).

Species	Spring (26 May 2015)						Early Fall (2 September 2015)					
Mixture	UNS	RE1	RE2	SO1	SO2	EUP	UNS	RE1	RE2	SO1	SO2	EUP
Agrostis gigantea	–	–	0.4	–	–	–	–	–	–	–	–	–
Agrostis scabra	–	–	–	–	–	–	–	76.6	–	–	–	–
Bidens cernua	–	–	–	–	–	2.3	–	–	–	–	–	5.7
Elymus canadensis	–	–	–	–	–	–	–	–	4.6	–	–	–
Eupatorium maculatum	–	–	–	–	–	9.4	–	–	–	–	–	18.8
Eupatorium perfoliatum	–	–	–	–	–	2.6	–	–	–	–	–	18.2
Festuca rubra	–	–	–	9.8	–	–	–	–	13.4	22.2	–	–
Heracleum mantegazzianum	4.9	0.1	11.4	0.4	1.1	1.4	61.6	–	39.4	2.2	3.9	17.5
Juncus effusus	–	–	–	-	–	–	–	–	–	–	–	–
Lolium multiflorum	–	–	–	0.6	4.8	3.3	–	–	24.4	2.6	3.9	9.0
Poa palustris	–	–	–	–	–	–	–	–	8.2	–	–	–
Solidago canadensis	–	–	–	48.8	38.1	–	22.3	–	–	66.3	63.1	–
Spartina pectinata	–	–	0.1	–	–	–	–	–	4.7	–	–	–
Trifolium pratense	–	–	–	–	17.5	–	–	–	–	–	21.9	–
Unidentified grasses	-	87.5	1.6	–	–	–	–	–	–	–	–	–
Litter	–	1.9	76.9	24.8	33.1	65.6	7.8	5.6	35.7	9.8	15.0	22.5
Bare soil	87.5	2.3	1.9	3.2	6.5	8.3	–	2.2	12.9	5.5	9.4	15.0
Total plant cover	–	87.5	79.0	59.2	60.4	17.6	–	76.6	55.3	91.1	88.9	51.7

small, graminoid seedlings that were mostly rough bentgrass (*Agrostis scabra* Willd.). At the end of the 2015 growing season, only *A. scabra* remained (Table 2). At the beginning of 2015, litter from the previous year covered an important part of the plots of RE2, with seeded species slow to emerge. By the end of the summer of 2015, five of the eleven species seeded shared approximately 50% of the total plant cover, excluding *H. mantegazzianum*. All species seeded in SO1, SO2 and EUP were still present in 2015. As expected, the shelter species *L. multiflorum* in SO1 and SO2, abundant the previous year, showed low cover in 2015, leaving *S. canadensis* as the dominant species, accompanied by *F. rubra* in SO1, and *T. pratense* in SO2. In EUP, all the four seeded species emerged through the dense litter from the previous year, and at the end of the summer of 2015, the two boneset species showed an almost equal 20% cover. Excluding RE1, all seeded treatments had a significant amount of litter from the previous year at the beginning of the 2015 growing season (from 25% to 75% cover). Despite a high cover of seeded plants and litter, there was the presence of bare ground in every seeded treatment (from 1.9% to 15.0% cover), even toward the end of the growing season (Table 2).

Impact on Heracleum mantegazzianum

Average *H. mantegazzianum* seedling emergence varied from 0% to 4% in the seeded plant mixtures, but reached 10% in the unseeded control (Figure 1), strongly suggesting that competition from seeded plants had a negative effect on *H. mantegazzianum* establishment. RE1, which had the highest seeded plant cover in spring, also had the lowest *H. mantegazzianum* emergence rate. Of all the 40 seeded plots, seven showed total inhibition of *H. mantegazzianum* seedling emergence, six of which were from RE1. The effect of plant mixtures on *H. mantegazzianum* emergence appeared to be related to the total plant cover measured in spring, since there was a negative linear relationship between establishment rate and plant cover ($R^2_{adj} = 0.196$, $P < 0.01$; Figure 1).

For the effect of plant mixture on seedling survival and growth, the number of seedlings monitored varied between treatments depending on the establishment. RE1 was discarded from this analysis because there were too few seedlings to be considered further. Results pertaining to the effect of mixtures on *H. mantegazzianum* seedling survival rates fell into two groups. In one, *H. mantegazzianum* survival was high in unseeded control and in RE2 and EUP (respectively 94%, 97% and 88%; Figure 1). In the other group, both plant mixtures with *S. canadensis* (SO1 and SO2) resulted in higher *H. mantegazzianum* mortality, with a survival rate averaging 40% of the seedlings. All seeded plant mixtures negatively affected *H. mantegazzianum* seedling growth compared to the unseeded treatment, but there were large differences between mixtures (Figure 1). The negative effect on seedling growth was maximal within the *S. canadensis* mixtures, with an average largest leaf width of 3 and 5 cm (SO1 and SO2, respectively), compared to 26 cm in the unseeded control UNS. The

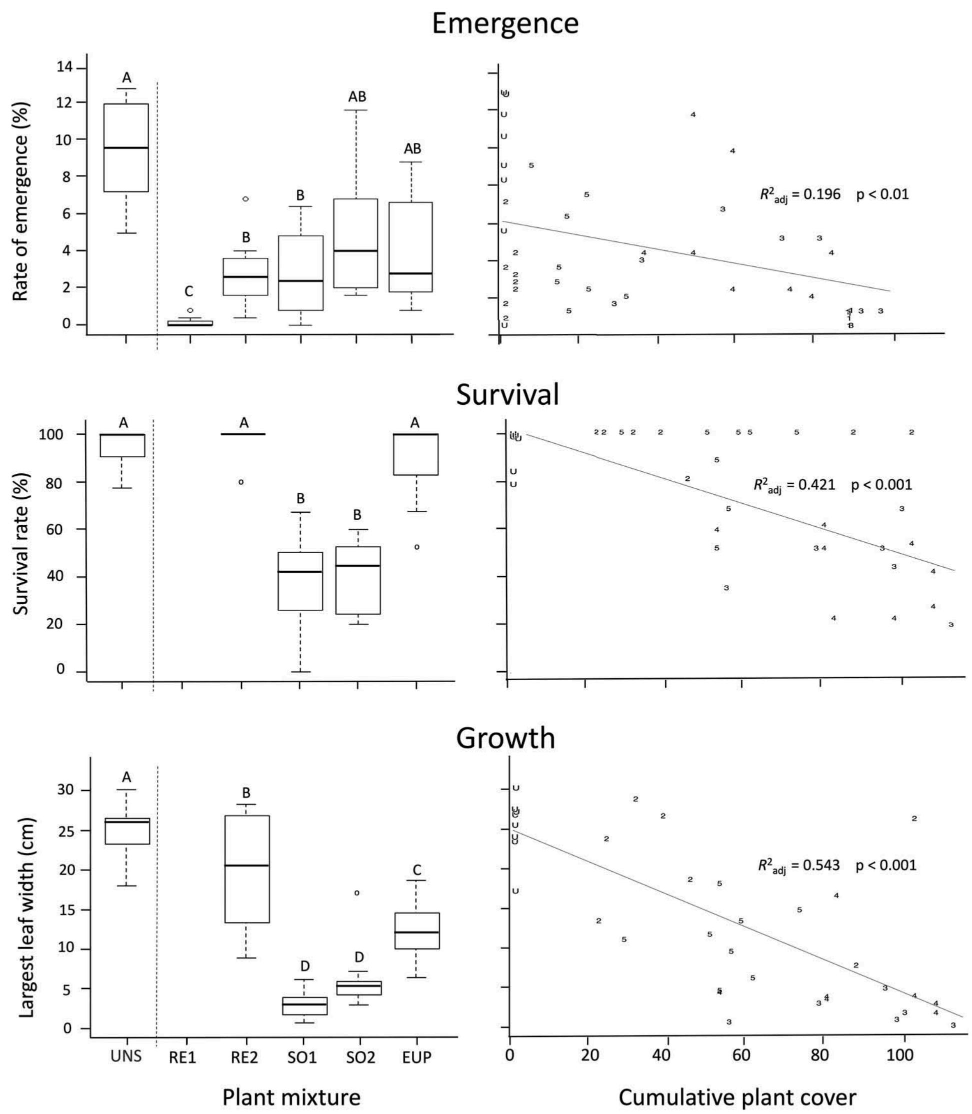

Figure 1. Rate of emergence, survival and growth of Heracleum mantegazzianum seedlings according to plant mixtures and total plant cover. The rate of emergence is the percentage of seeds that produced a seedling. The effects of plant mixtures with the same letter were not significantly different ($P < 0.05$). Total plant cover was evaluated in spring for the effect on seedling emergence, and in early fall for seedling survival and growth.

graminoid RE2 had a weak negative effect on growth, while the *Eupatorium* cover (EUP) had an intermediate effect between RE2 and the *S. canadensis* SO1 and SO2. The effect of plant mixture on seedling survival and growth appeared to be related to late-season plant cover, with a significant negative linear relationship between survival and plant cover, and between growth and plant cover, irrespective of treatments (survival: $R^2_{adj} = 0.421$, $P < 0.001$; growth: $R^2_{adj} = 0.543$, $P < 0.001$; Figure 1).

Plant invasion is a complex process that is determined by propagule pressure, abiotic components of the invaded system and biotic characteristics of the recipient community, including biotic resistance (Catford et al. 2009). Restoration practices that address these mechanisms on plant community assembly rules could help to delay or inhibit reinvasion (Byun et al. 2018). In our experiment, propagule pressure was set constant but high, and the soil and water conditions were designed to be highly favorable to *H. mantegazzianum* establishment. Our experiment suggests that, under these conditions, restoring a competitive plant cover following a late spring operation to remove *H. mantegazzianum* will at least partially inhibit its reinvasion. Compared to the unseeded control mesocosm, all plant covers reduced seedling emergence. Growth and survival of established *H. mantegazzianum* seedlings were also negatively affected by the presence of a plant cover. There were large differences between mixtures in terms of their effects, suggesting that the composition of the seeded plant cover had an impact on its inhibition efficiency. Moreover, the nature of the most negative impact also depended on the composition, with one mixture more effective in preventing establishment, while another had a greater effect on seedling growth and survival. The design of the experiment, with only five different treatments, did not make it possible to distinguish definitively which of the different factors, such as plant cover richness or plant identity, had a greater impact for preventing reinvasion. However, total plant cover, irrespective of treatment, appeared to be an important factor in inhibiting *H. mantegazzianum*, since it was correlated to all effects. In a review on the effect of revegetation in preventing reinvasion, Schuster et al. (2018) found that more diverse mixtures were less prone to invasion. In our experiment, RE2, which was by far the most diverse mixture, was not the most efficient in preventing *H. mantegazzianum* establishment, nor in inhibiting its growth and survival.

In the field experiment by Ravn et al. (2007), the absence of any effect of native plant cover on reinvasion by the hogweed *H. sosnowskyi* was attributed to sowing the grass mixtures at the wrong time. The results of our experiment support this assessment: a dense plant cover seeded in late spring or early summer, just after a successful operation to control *H. mantegazzianum*, could be successful in preventing reinvasion the following year. In our experiment, a seed mixture composed of five graminoid species (RE1) completely prevented *H. mantegazzianum* seedling establishment in six of the eight replicates. Because the plant cover was established from seeds sown the previous year (year 1), it rapidly produced a dense cover early in the growing season (year 2), during *H. mantegazzianum* germination, suggesting that a priority effect may have played an important role in inhibiting *H. mantegazzianum* establishment. The important quantity of litter produced at year 1 may also have been detrimental to *H. mantegazzianum* establishment at year 2, by reducing light level, but also by lowering soil temperature, to which giant *H. mantegazzianum* germination is particularly sensitive (Moravcová et al. 2006). Much of this litter came from the annual species that were dominant in year 1.

Seeded plant cover also had a negative impact on the growth and survival of *H. mantegazzianum* seedlings that succeeded in establishing. *Heracleum mantegazzianum* is shade intolerant (Tiley et al. 1996; Pyšek et al. 2007), and since it only forms a rosette during its first growing season, it may be outcompeted by a dense plant cover composed of erect plants. While the percentage of plant cover, irrespective of seeded plant composition, was correlated to a decrease in *H. mantegazzianum* growth and survival, the cover that included *S. canadensis* was clearly more effective in this respect. While an average of 40% of the seedlings emerging in early spring survived to the end of the season in the *S. canadensis* mixtures, they were much smaller than those in the unseeded treatment, so that further mortality of these seedlings could be expected to occur in the years to follow. Shading or competition for soil resources may explain the negative effect on *H. mantegazzianum*, since the *S. canadensis* mixtures were also those with the largest total plant cover.

The negative effect of *S. canadensis* may also be the result of allelopathic substances. This species is one of the plants that has been studied the most for allelochemical properties (Chen et al. 2017), and its success in becoming invasive in Europe, Asia and Australia has largely been attributed to these properties (Fisher et al. 1978; Werner et al. 1980; Butcko and Jensen 2002; Jin et al. 2004; Bing-Yao et al. 2006; Abhilasha et al. 2008; Yuan et al. 2013; Wang et al. 2016). Even within its native range, *S. canadensis* may form dense near-monospecific populations that are stable over time, delaying successional changes by inhibiting tree establishment (Fisher et al. 1978; Werner et al. 1980). This characteristic has made the species desirable in restoration operations under electric utility rights-of-way, in order to delay and reduce tree control operations and associated costs (De Blois et al. 2002, 2004). However, despite its presumed allelopathic properties, *S. canadensis* reduced but did not prevent *H. mantegazzianum* seedling establishment in our experiment. This may be due to the fact that *S. canadensis* emerges late and develops slowly over the course of the season. In spring, during *H. mantegazzianum* germination, it may not yet have a significant negative effect. However, as summer progresses, *S. canadensis* plant size and density increase to become dominant, with an associated impact on *H. mantegazzianum*.

Invasive plant control operations without appropriate restoration measures may, over time, exacerbate problems associated with invaders (Rinella et al. 2009). Relying entirely on passive, natural succession to re-establish a plant community following the removal of an invasive plant species is often inadequate in preventing re-invasion (Bauer and Reynolds 2016; Schuster et al. 2018). Our study adds to the growing body of evidence promoting the restoration of a plant cover as a means to prevent reinfestation (Sheley et al. 2006; Rinella et al. 2012; Pyke et al. 2013; Barak et al. 2015; Schuster et al. 2018). Insufficient sources of propagules, the legacy effect of invasive plant species or natural succession promoting species combinations that have a weak biotic resistance toward the exotic species are all possible reasons why restoration via revegetation is necessary (Shuster et al.

2018). A seed mixture with several species covering a broad spectrum of site conditions may contribute to this objective by preventing the formation of an uneven plant cover on heterogeneous sites. Furthermore, it is also important to establish a durable plant community that will persist over the years. Annual species in the seed mixture often result in fast establishment soon after seeding, protecting against erosion or other plant invasion during year 1, and also producing a litter that may inhibit *H. mantegazzianum* establishment in year 2. The presence of perennial species in the mixture that could dominate in the long run is necessary to ensure a more durable resistance to invasion. Compared to standard revegetation using mixtures to suppress invasive plant species, our experiment assumed an additional spring control operation on *H. mantegazzianum* seedlings, increasing the costs of the overall operation. A light plowing, when possible, would be the best method, because it would not only kill *H. mantegazzianum* seedlings, but would also favor the establishment of the seeded cover. *H. mantegazzianum* frequently invades habitats that may lend themselves to plowing, such as roadsides, grasslands and old fields (Page et al. 2006). While plowing as part of a control operation for an invasive plant species appears radical, it may well be justified considering the health threat posed by the species, especially near inhabited areas.

Finally, no restoration campaign using seeded plant cover can totally prevent invasive plant establishment. Even the sparse establishment of a few invasive individuals may, over time, undermine the goal pursued by a restoration operation (Hopfensperger et al. 2019). It is thus necessary to monitor a site, at least until the plant cover is well developed, and punctually eliminate invasive plant individuals that may successfully establish soon after the site has been restored.

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