

6-19-2021

Intense Mowing Management Suppresses Invader, but Shifts Competitive Resistance by a Native to Facilitation

David U. Nagy

Martin Luther Universitat Halle-Wittenberg, davenagy9@gmail.com

Emily Rauschert

Cleveland State University, e.rauschert@csuohio.edu

Ragan M. Callaway

University of Montana

Tamas Henn

City Government of Komlo Varoshaz Tér 1, Komlo,

Rita Filep

University of Pécs

See next page for additional authors

Follow this and additional works at: https://engagedscholarship.csuohio.edu/scibges_facpub

 Part of the [Biology Commons](#)

[How does access to this work benefit you? Let us know!](#)

Recommended Citation

Nagy, David U.; Rauschert, Emily; Callaway, Ragan M.; Henn, Tamas; Filep, Rita; and Pal, Robert W., "Intense Mowing Management Suppresses Invader, but Shifts Competitive Resistance by a Native to Facilitation" (2021). *Biological, Geological, and Environmental Faculty Publications*. 250.
https://engagedscholarship.csuohio.edu/scibges_facpub/250

This Article is brought to you for free and open access by the Biological, Geological, and Environmental Sciences Department at EngagedScholarship@CSU. It has been accepted for inclusion in Biological, Geological, and Environmental Faculty Publications by an authorized administrator of EngagedScholarship@CSU. For more information, please contact library.es@csuohio.edu.

Authors

David U. Nagy, Emily Rauschert, Ragan M. Callaway, Tamas Henn, Rita Filep, and Robert W. Pal

RESEARCH ARTICLE

Intense mowing management suppresses invader, but shifts competitive resistance by a native to facilitation

Dávid U. Nagy^{1,2,3} , Emily S. J. Rauschert⁴ , Ragan M. Callaway⁵, Tamás Henn⁶, Rita Filep⁷, Robert W. Pal⁸ 

Interactions among native and invasive species may affect management outcomes and goals. We implemented different mowing regimes to control the invasive *Solidago gigantea* and restore natural diversity, and also examined interactions between *Solidago* and a European native competitor, *Tanacetum vulgare* in the context of these regimes. Experimentally planted *Tanacetum* suppressed *Solidago* by 79% without management, and a suite of mowing management regimes reduced the density of *Solidago* by 80–98% when *Tanacetum* was absent. But, when *Tanacetum* was added, the density of the invader was not reduced by mowing. Put another way, in mowed plots with *Tanacetum*, *Solidago* was twofold to over fivefold denser than in mowed plots without *Tanacetum*. It is not clear why the effect of *Tanacetum* shifted from competition in the absence of disturbance to facilitation with intense management-associated disturbance, but other studies suggest that *Tanacetum* may create plant–soil feedbacks that favor *Solidago*. Evidence shows similar shifts from competition to facilitation under mowing regimes for other species, but these are not mechanistically clear either. We speculate that mowing reduced competition from *Tanacetum* while leaving belowground facilitative effects unchanged, shifting the net effect of *Tanacetum* to facilitation. When single-year mowed plots were abandoned for just 1 year, *Solidago* was twofold denser than in the control, thus maintaining treatments over time was important for successful management. Our results indicate that mechanical control may substantially alter biotic resistance gained from native competition.

Key words: biotic resistance, disturbance, diversity, invasion management, mechanical control, *Solidago gigantea*, *Tanacetum vulgare*

Implications for Practice

- Our study indicated that a single mowing in 1 year can reduce the density of *Solidago gigantea* for at least 2 years.
- Consistent with previous findings, extending the management of *Solidago gigantea* beyond 1 year had a more positive effect on species diversity and longer suppression of the invader, thus the most effective application may require long-term maintenance of management regimes.
- Facilitation by a native competitor, in the context of intense management-related disturbance, should be considered in a holistic context of invasive plant management. For example, if good competitors are abundant at a target management site, the overall effectiveness of mowing should be evaluated.

affect recreational activities, resulting in significant economic losses (Pimentel et al. 2005). Thus, there is a need to understand the mechanisms and outcomes of management approaches for

Author contributions: DUN, RWP, ESJR conceived the ideas and designed methodology; DUN, RWP, TH, RF collected the data; DUN analyzed the data; DUN, RMC led the conceptual development and writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

¹Institute of Geobotany/Plant Ecology, Martin-Luther-University, Halle, Große Steinstraße 79/80, Halle (Saale), D-06108, Germany

²Cochrane Hungary, Medical Centre University of Pécs, József Attila u. 7, Pécs, 7623, Hungary

³Address correspondence to D. U. Nagy, email davenagy9@gmail.com

⁴Department of Biological, Geological, and Environmental Sciences, Cleveland State University 2121 Euclid Avenue, Cleveland, OH 44115-2214, U.S.A.

⁵Division of Biological Sciences and the Institute on Ecosystems, University of Montana, Missoula, MT 59812, U.S.A.

⁶József Attila Library and Museum Collection, City Government of Komló Városház Tér 1, Komló, 7300, Hungary

⁷Department of Pharmacognosy, Faculty of Pharmacy, University of Pécs, Rókus u. 2, Pécs, 7624, Hungary

⁸Department of Biological Sciences, Montana Technological University, 1300 Park Street, Butte, 59701, U.S.A.

© 2021 The Authors. Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

doi: 10.1111/rec.13483

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13483/supinfo>

Introduction

Invasive plant species are among the most important factors driving local species extirpation and the transformation of native communities (Hejda et al. 2009; Vilà et al. 2011). They also reduce agricultural, forestry, and industrial production, and can

exotic invasive plant species, and how to best resist invasion and restore native communities and ecosystem functions (An et al. 2007).

Most management of invaders comes in the form of intensive disturbance, including hand-pulling, herbicide, and mowing. In the majority of cases, the intent is to shift the balance of competition so that natives are favored and invaders are not. In that context, a form of potential weed management that does not involve disturbance is the use of highly competitive native species (MacDougall et al. 2009; Davis et al. 2010; Leger & Espeland 2010; Byun & Lee 2017; Germain et al. 2020) or diverse seed mixes of natives (Maron & Marler 2008; Byun et al. 2013). However, disturbance can alter or reverse competitive outcomes such as sought in competition/diversity-based management (Walker 1999; Besaw et al. 2011; Laurent et al. 2017), or even shift the direction of interactions to facilitation (Callaway et al. 2005; Michalet et al. 2014). For example, Maalouf et al. (2012) found that in undisturbed European grasslands, in the absence of disturbance plant, interactions among target species were mostly competitive or neutral, but when disturbance via mowing was applied, competition switched to facilitation for some species (also see Le Bagousse-Pinguet et al. 2012). Furthermore, the competitive abilities of species in managed plant communities can influence how communities respond to management (Schooler et al. 2010). Thus, it is important to understand plant–plant interactions when planning and conducting invasive plant management.

Solidago gigantea is a rhizomatous perennial herb that is native to North America but has become highly invasive throughout Europe and Asia (Weber & Jakobs 2005). In its non-native range, it exerts a negative impact on native communities by decreasing species richness and diversity, apparently due to its intense competitive effects (Botta-Dukát & Dancza 2012; Pal et al. 2015; Lucero et al. 2020), rapid growth (Jakobs et al. 2004), and its positive interactions with resident soil biota (Majewska et al. 2017). It is challenging to control in its non-native ranges because of its tolerance to a variety of biotic and abiotic stressors (Shibel & Heard 2016) and its rapid vegetative propagation (Nagy et al. 2018). The most common management techniques used against *Solidago* include periodic flooding, mowing, mulching, grazing, and herbicide application (Botta-Dukát et al. 1998; Guo et al. 2009; Cservenka et al. 2017). Nagy et al. (2020) found that mowing just once a year can reduce the density of the invader. Szépligeti et al. (2017) reported that mowing during both the growing and flowering periods can have stronger effects than a single mowing.

To test the effect of competition from natives on *Solidago* in the contexts of different management regimes, we experimented with *Tanacetum vulgare*, potentially an important source of native competitive biotic resistance to exotic invasion (Power & Vilas 2020) in habitats invaded by *Solidago*. *Tanacetum vulgare* is native to Eurasia, but invasive in parts of North America (LeCain & Sheley 2014). There, management activities to control the plant include grazing, mowing, and herbicide (Jacobs 2008). *Tanacetum vulgare* appears to be a very effective competitor against *S. canadensis*, both in *Tanacetum*'s native

and non-native range (Schittko & Wurst 2014; Lucero et al. 2020). Even so, Szymura and Szymura (2016) found that *Solidago* can outcompete *Tanacetum* in European common garden experiments, but they argued that disturbance might alter this outcome.

Here, we investigated the mechanisms for how *Tanacetum* influences the effects of 1- and 2-year mowing regimes on *Solidago*. To test this, a common garden experiment was performed in a Hungarian mesic meadow with plots planted with *Solidago* or *Solidago* with *Tanacetum*. At the end of the 5-year experiment, we assessed the effect of different mowing regimes on the stem density and height of *Solidago*, and community-level diversity and species richness. We explored the following questions: (1) does mowing alter competitive resistance to invasion from a native competitor? (2) Do differences in the applied mowing regimes impact *Solidago* performance? and (3) do the effects of mowing regimes interact with a strong competitor to affect native diversity?

Methods

Seed Collection

For the common garden experiment, seeds were collected from six Hungarian *Solidago* populations and two Hungarian *Tanacetum* populations (Table S1). For each species, the minimum distance among populations was 3 km and the maximum was 131 km. Collection sites were in the same climatic region as the experimental sites, with similar humidity (continental type), temperature (hot/warm summer subtype), and intermediate soil moisture. There was no canopy shading, and both target species were relatively abundant at the collection sites. Seed heads with mature seeds were collected in the field from 10 randomly chosen individual shoots per population from each species (i.e. seed family). Individuals within a population were located at least 10 m apart from another to reduce the risk of resampling the same clones. After collection, seeds for each population were bulked.

Propagation of Experimental Plant Species

Seeds were chosen randomly from each population and seed family for germination in Petri dishes, and seedlings were randomly chosen for transplanting. Seedlings were transplanted into 120-mL rocket pots filled with 1:1 mixture of potting soil and sand, and grown in a greenhouse in the Botanical Garden of the University of Pécs (Hungary) at 18–25°C temperature and under 12-h light periods, with 70 $\mu\text{Em}^{-2} \text{s}^{-1}$ of PAR and 60–70% relative humidity. Pots were watered daily, based on their need for 4 months.

Study Site and Experimental Design

The experimental site was established in a mesic meadow with mixed shrubs and other herbaceous species, in Pellérd, Hungary (46.03°; 18.13°), where *Solidago* was present but not in large stands. The site had not been previously managed for *Solidago*.

One day before experimental planting, vegetation was mowed in a 12×12 -m area using a string trimmer to provide as similar initial conditions as possible, reduce site-based variation in priority effects (Fukami 2015), and to facilitate planting. The small size of the experimental site allowed us to minimize heterogeneity in topography, vegetation, and land use. Fifty 50×50 -cm plots were established in five blocks in a randomized complete block design. The distance was 50 cm among plots and 100 cm among blocks. In May 2010, when the seedlings in the greenhouse reached an average height of 5 cm, single-stem seedlings were planted in the common garden. Half of the plots contained six *Solidago* seedlings (*Solidago* plots) and half of the plots contained three *Solidago* and three *Tanacetum* seedlings (*Solidago* + *Tanacetum* plots), with seedlings planted alternately. The arrangement of the plots was randomized. After planting, seedlings were allowed to interact with the native vegetation at the site for 2 years, without any manipulation or intervention. After 2 years, we conducted a baseline survey and measured cover values of each species and the number of *Solidago* stems. This was to evaluate post-treatment differences among each management regimes independently from baseline differences. Immediately after the baseline survey, we began the management regimes (see below). In the next year, only half of the plots were managed (2-year plots), while the other half were not (1-year plots), which allowed us to compare the efficacy of 1-year long management with 2-year long

management. In the next (third) year, we conducted final data collection. For clarity, the experimental design is presented in Figure 1.

Boundary effects can be strong in long-term common garden experiments with invasive species, especially in small experimental areas, thus we tried to minimize these effects from the beginning of the experiment. The surrounding 5-m area of the experimental site was mowed every year and the vegetation surrounding the sites was periodically grazed by sheep, but not the experimental site. The treatment combinations were placed randomly in the common garden, the odds of all combinations to be at the border or in the center was the same. These results should have been affected minimally by disproportionate boundary effects. Based on our previous common garden experiments (Lucero et al. 2020; Pal et al. 2020), the plot size and the distance among plots and blocks appeared to prevent vegetative cross-spreading among plots over the experiment. Finally, flowerheads were clipped every year of the experiment to prevent reproductive cross-spreading among plots and to prevent the escape of *Solidago* from the experimental site.

Management Regimes

In the common garden, three factors (competition, mowing frequency, and duration of management) were tested with each of two levels in a full factorial design: with versus without

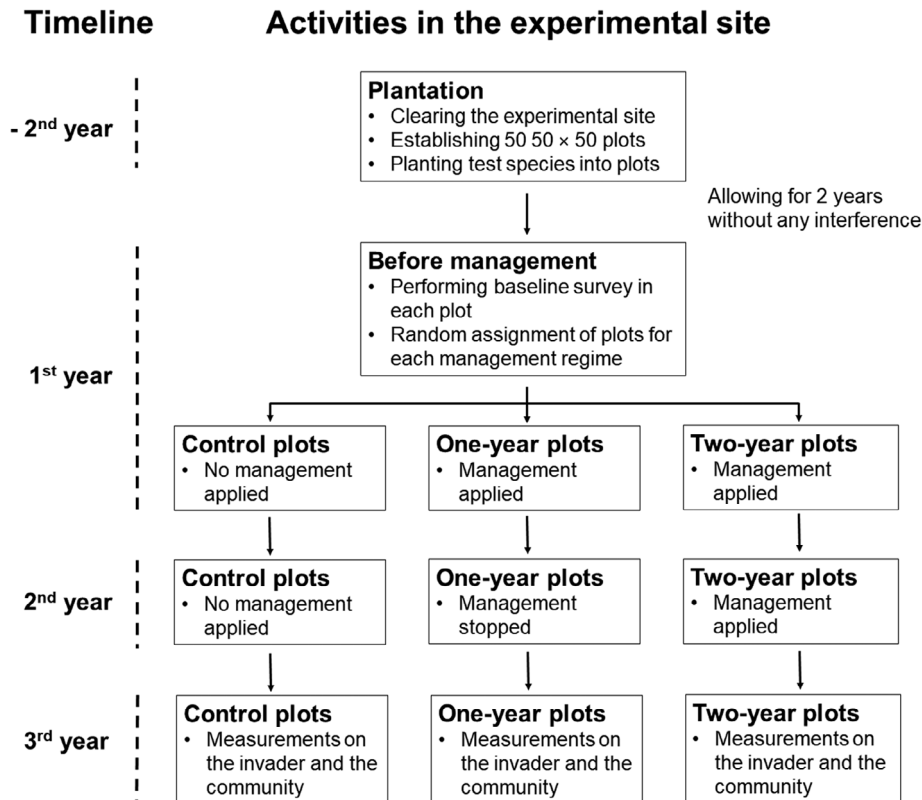


Figure 1. Flow chart describing the experimental design. In the control plots, no management was applied throughout the study, in the 1-year plots management was abandoned after 1 year, in the 2-year plots management was carried out for 2 years. In the managed plots, two different mowing regimes were applied: Half of the plots were mowed once a year and the other half were mowed twice a year.

Tanacetum; mowing once a year versus mowing twice a year; and managing for 1 year versus managing for 2 years. This design resulted in 10 differently managed plots within a block (two competition \times two mowing regimes \times two durations + two controls). The arrangement of plots was randomized within each of the five blocks. This resulted in $n = 5$ for each combination of treatments.

Mowing was performed with a hand clipper—the above-ground plant growth of all species was cut 5–10 cm above soil surface, and the biomass was removed. In both years, mowing treatments were carried out in June, during the most active aboveground growing phase for both species. This was intended to reduce vegetative growing potential. For one set of treatments, mowing was carried out again in September, before fruit ripening to prevent pollen and seed production. In both years, the once-a-year mowing treatment was carried out only in June.

Data Collection and Statistical Analyses

After 2 years of management, the absolute percent cover was estimated for each vascular plant species by two investigators in each plot to evaluate the community impact of management regimes. Cover values of each species were rounded to the nearest 5%, except for species below 10% cover where the estimation was 2.5 or 0.1%. The number of *Solidago* stems and height of the 10 tallest stems were recorded to quantify the effect of each management regime on the invader. Shannon diversity was calculated in PAST 3.11 (Hammer et al. 2001) using the absolute cover of all species, including the planted *Solidago* and *Tanacetum*.

Statistical analyses were performed using R, version 3.5.3 (R Development Core Team 2019). Two separate models were run: one for the baseline survey (pre-treatment) and one for the survey at the third year (post-treatment). *Solidago gigantea* stem number, height, species richness (total number of species), and Shannon diversity of the plots were analyzed with generalized linear mixed models (stem number) using Poisson family and linear mixed models (height, species richness, and Shannon diversity) using the lme4 package (Bates et al. 2014). This tested the effect of the following fixed factors: (1) management regime (control, mowing once, mowing twice treatments, and their 1-year vs. 2-years mowing), (2) competition status (with or without *Tanacetum*), and (3) the management regime \times competition status. Blocks were treated as a random factor. The normal distribution and the residuals of the models were evaluated graphically (after Crawley 2014). Homogeneity of variances of models was assessed using Levene's test. Significance of models was tested with chi-square tests using the drop-term function (Venables & Ripley 2002). For pair-wise comparisons, Tukey post-hoc tests were conducted with the multcomp package (Hothorn et al. 2008) to compare each treatment to the controls and to compare all treatments to each other.

To test how species composition varied across managed plots and/or competition status, we performed a multivariate abundance analysis on our community data using mvabund package (Wang et al. 2012). In the model (1) management regime, (2) competition status, and (3) the management

regime \times competition status of the plots and their effect on the percent cover of all identified species in the third year were tested. The model hypothesis testing was performed with the analysis of variance (ANOVA).

Results

Management Effects on *Solidago* Planted with *Tanacetum*

In our baseline, pre-treatment survey, there were no differences among the plots assigned to different management regimes, but in *Solidago* plots, pre-treatment *Solidago* density was 31.4 ± 1.39 vs. 19.2 ± 1.00 (Tables S2 and S3) in *Solidago* + *Tanacetum* plots. In *Solidago* plots, pre-treatment species richness was 15.6 ± 0.40 vs. 14.7 ± 0.39 (Tables S2 and S3) in *Solidago* + *Tanacetum* plots. Pre-treatment Shannon diversity was 1.6 ± 0.03 in *Solidago* plots versus 1.7 ± 0.04 in *Solidago* + *Tanacetum* plots (Tables S2 and S3). Thus, post-treatment difference in management regimes should have not been due to pre-treatment biases.

Tanacetum vulgare suppressed the density of *Solidago* by 79% ($z = 6.285$; $p < 0.001$; see Table S4 for results of linear mixed models), but not height ($z = 2.476$; $p = 0.256$) in control plots (Fig. 2). However, this relationship switched to facilitation in some of the management treatments. When *Tanacetum* was present, *Solidago* was two to three times denser in mowed plots than when *Tanacetum* was absent, with the exception of when the 1-year plots were mowed twice (Fig. 2A). *Tanacetum* affected *Solidago* height only when mowing was once a year for 2 years, and this case *Tanacetum* increased height by 40% compared to the *Solidago* plots ($z = 3.222$; $p < 0.036$; Fig. 2B).

Management Effects on *Solidago* Planted without *Tanacetum*

Two-year mowing regimes decreased *Solidago* stem density by 97–98% (mowing once: $z = 5.388$; $p < 0.001$; mowing twice: $z = 5.873$; $p < 0.001$) and 1-year regimes decreased *Solidago* stem density by 80–86% (mowing once: $z = 6.285$; $p < 0.001$; mowing twice: $z = 6.686$; $p < 0.001$) compared to the control (Fig. 2A). However, mowing once versus twice a year did not affect density (2-year mowing: $z = 0.444$; $p = 0.999$; 1-year mowing: $z = 1.209$; $p = 0.964$). Mowing once was almost three-fold more effective ($z = 3.105$; $p = 0.047$) on *Solidago* density in 2-year treatment plots than in 1-year treatment plots, but there was no differences between mowing once versus twice ($z = 2.464$; $p = 0.252$). *Solidago* height was decreased by all mowing regimes (35–46%) without differences among mowing regimes (Fig. 2B).

Management Effects on Diversity and Composition

Overall, 80 species were identified in the plots during the experimental period. The multivariate abundance analysis showed a significant interaction effect between management regime and competition status on community composition, and there was a direct effect of management regime on species composition. Competition status alone had no effect on composition (Table S4). The average changes in species cover in plots with

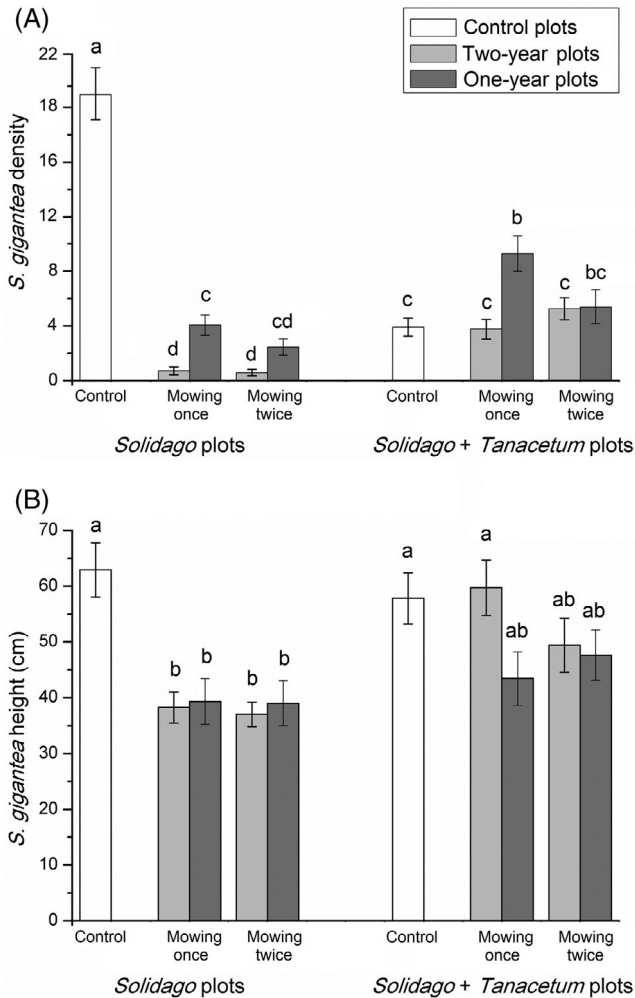


Figure 2. Effects of the management regimes on the density (A) and height (B) of *Solidago* in the 0.25 m² plots, after 2 years. In *Solidago* plots, *Solidago* was planted alone, whereas in *Solidago* + *Tanacetum* plots it was planted with the native competitor *Tanacetum* to simulate increased competition. Control plots refer to the unmanaged plots, 2-year plots refer to plots where management occurred for 2 years, while 1-year plots refer to plots where management was only in the first year. Shared letters represent means that do not differ significantly, based on Tukey post-hoc tests. Error bars represent ± 1 SE.

different management regimes, compared to controls, are summarized in Table S5.

With no mowing, experimental planting of *Tanacetum* decreased the Shannon Index of diversity by 19% ($z = 3.187$; $p = 0.046$), but did not decrease species richness ($z = 1.165$; $p = 0.977$). *Tanacetum vulgare* also altered the effect of mowing on diversity (Fig. 3). Compared to the control, 2-year mowing regimes increased diversity by 28–35% (mowing once: $z = 3.789$; $p = 0.006$; mowing twice: $z = 4.685$; $p < 0.001$), and mowing once increased species richness by 44% ($z = 3.496$; $p = 0.017$). Furthermore, 1-year mowing regimes increased diversity by 34–37% (mowing once: $z = 4.564$; $p < 0.001$; mowing twice: $z = 5.089$; $p < 0.001$) and mowing twice increased

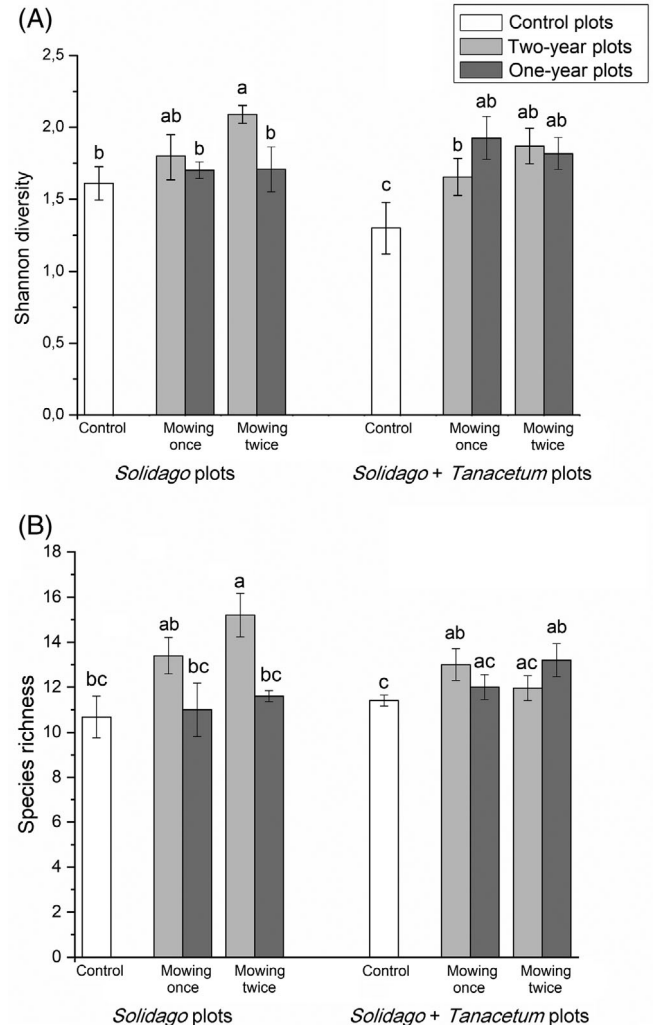


Figure 3. Effects of the management regimes on the Shannon Diversity Index (A) and species richness (B) of treated plots after 2 years. In *Solidago* plots, *Solidago* was planted alone, while in *Solidago* + *Tanacetum* plots *Solidago* was planted with the native competitor *Tanacetum*. Control plots refer to unmanaged plots, 2-year plots refer to plots where management was for 2 years, while 1-year plots refer to plots where management was only in the first year. Shared letters represent means that did not differ significantly, based on Tukey post-hoc tests. Error bars represent ± 1 SE.

species richness by 46% ($z = 3.330$; $p = 0.030$) compared to the control. There were no significant differences in the Shannon Diversity Index or in species richness when comparing the same management regime in the presence or absence of *Tanacetum* (Fig. 3). However, with *Tanacetum* added, the abundance of *Poa pratensis*, *Vicia angustifolia*, *Medicago falcata*, *Hypericum perforatum*, and the exotic *Erigeron annuus* increased with mowing (Table S5).

In plots without *Tanacetum*, mowing twice in the 2-year management regime increased the Shannon Diversity Index by 30% ($z = 4.037$; $p = 0.002$) and species richness by 46% ($z = 3.996$; $p < 0.01$), compared to the control, whereas the other treatments had no effects (Table S2, Fig. 3). The frequency of mowing had

no effect on the Shannon Diversity Index or richness in 2-year (Shannon: $z = 2.516$; $p = 0.259$; richness: $z = 1.998$; $p = 0.600$) or 1-year treatments (Shannon: $z = 0.132$; $p = 1.000$; richness: $z = 0.449$; $p = 1.000$). All mowing regimes decreased the dominance of *Verbascum thapsus*, *Arrhenatherum elatius*, and *Lythrum salicaria*; and increased the dominance of *Medicago lupulina*, *Trifolium repens*, *Poa pratense*, and *Erigeron annuus* (Table S5).

Discussion

In response to our first question, management by mowing suppressed *Solidago*, but reduced competitive biotic resistance by *Tanacetum* to the invader. In plots with experimentally planted *Tanacetum*, but no mowing, *Solidago* was highly suppressed, relative to plots without *Tanacetum*. When these same species combinations were managed by mowing, this interaction was reversed. In plots with *Tanacetum*, *Solidago* was much denser than in plots without *Tanacetum*. In other words, intense competitive biotic resistance in the absence of management via disturbance, shifted markedly to facilitation by the same species that otherwise provided biotic resistance. This shift from competition to facilitation in response to disturbance has precedence in the literature. But, this is generally manifest when plant species that are able to tolerate disturbance create stable and protected environments that facilitate species that are not tolerant of disturbance (Callaway 2007). For example, some plant species are able to stabilize shifting sand dunes or cobble beaches which creates habitat for other species (Bruno & Kennedy 2000; Toft & Elliot-Fisk 2002). For example, *Carex nudata*, or torrent sedge, is common in northern California rivers and is highly tolerant to violent spring runoffs. Levine (2000) found that most plant species in these riparian habitats were found highly associated with the *Carex* tussocks where they appeared to be facilitated.

Our results are limited due to the design of the common garden experiment. The experiment was conducted in only one habitat type and at only one site. Thus, we cannot fully extrapolate our results to other environments. Nonetheless, our results draw attention to a potentially important shift from competition to facilitation in the management of invasions, thus suggesting future protocols for similar experiments and possible re-evaluations of past studies.

The mechanisms described above for disturbance-associated facilitation, and related literature in general (Callaway 2007) involve physical protection of some species by others, which was not the case in our study where *Tanacetum* did not protect *Solidago* from clipping. But similar to our results, in the absence of disturbance, Maalouf et al. (2012) found primarily competitive and neutral interactions in a European grassland, depending on water stress. But, with management, these interactions shifted to neutral and facilitation (for a range of reactions to mowing also see Rasran et al. 2007; Le Bagousse-Pinguet et al. 2012; Zhou et al. 2019).

We do not know mechanisms that might drive the sort of shift from competition to facilitation that we and others have observed. One possibility might involve plant–soil feedbacks. Schittko and Wurst (2014) found that the growth of *Tanacetum*

increased in soil from *S. canadensis* root zones compared with soil from the root zones of *Tanacetum*. In contrast, Lucero et al. (2020) conducted plant–soil feedback experiments with these species, but did not find that soils from *Tanacetum* improved the growth of *S. canadensis*. If soil biota cultured by *Tanacetum* is beneficial for *Solidago*, mowing may decrease aboveground competition from the former, allowing net competitive effects to possibly be more influenced by soil biota (see Lekberg et al. 2018). This could promote compensatory responses from *Solidago* (Ramula et al. 2019). Compensatory responses to damage might enable *Solidago* to better withstand frequent disturbance as Liao et al. (2016) observed, but they did not test the effect of soil biota on this response. Other studies indicate that soil biota may increase compensatory responses in general (He et al. 2014; Allsup & Paige 2016). In addition, soil biota may interact with neighbors to improve such compensation (Kula et al. 2005). For example, Callaway et al. (2001) found that a native grass promoted the compensatory response of the exotic invasive *Centaurea melitensis* to clipping, but only in the presence of soil biota. The facilitation of *Tanacetum* we observed might also be indirectly mediated by soil biota. Overcompensation by *Solidago* might be caused by increased endoreduplication (localized polyploidy) as a result of apical damage, as shown with *Arabidopsis thaliana* (Scholes & Paige 2014). Endoreduplication increases cell size (along with body size), as well as the number of gene copies, and thus gene expression or shifts through metabolic pathways, and this may induce a rapid response to stress (Van de Peer et al. 2020). In addition, damage-mediated endoreduplication can supply intermediate compounds into the shikimate pathway for secondary metabolite production promoting increased regrowth and reproduction success (Paige 2018), and this could also induce changes in soil biota (Mesa et al. 2017). Thus, this mechanism may directly benefit *Solidago* or indirectly through soil biota and *Tanacetum* in ways that overcompensate in response to mowing.

To be clear, our experimental design lacks density controls in the \pm native competitor treatments. In the non-native treatment, we planted six *Solidago* individuals, but in the *Solidago* + *Tanacetum* treatment, there are only three *Solidago* individuals. This was to control total density, a necessity for other aspects of the experiment. Thus, the low density of *Solidago* with *Tanacetum* could have been due to lower initial densities and the increase in density in mowed plots could be explained by reduced intraspecific competition once the native is mowed. Without controlling for these differences in *Solidago* density, it is difficult to parse out all possible mechanisms.

We found that shifts to facilitation with disturbance might degrade a native community's biotic resistance to invasion, but facilitation is often a crucial component of ecological restoration when abiotic conditions limit plant growth (Bradshaw 1983; Maestre et al. 2001; Padilla & Pugnaire 2006). In some cases, invasive plant species may facilitate native species, such as the invasive *Tamarix* sp. facilitating the native *Acer negundo* in riparian habitats, by providing early protection for the young saplings (DeWine & Cooper 2010). Also, native species can facilitate invasive species through the altering abiotic conditions

in ways that can be exploited by the invaders (e.g. Maron & Connors 1996; Siemann & Rogers 2003; Badano et al. 2007; Cavieres et al. 2008; Lucero et al. 2020).

With respect to our second question, in plots without *Tanacetum* all mowing regimes suppressed the density of the invader by 80–98% and its height by 35–46%. Similar studies with *Centaurea stoebe* (Rinella et al. 2001) and *Heracleum sosnowskyi* (Klima & Synowiec 2016) have shown large decreases in density with longer term but similar management. We found that only 1–2 years were needed to strongly suppress *Solidago*, possibly due to differences in physiology, life form, sensitivity to the applied methods, and prevailing habitat conditions.

We found no differences in invader density or height, whether or not mowing was conducted once versus twice a year. In contrast, plant diversity increased only when mowing occurred twice a year and applied in this way for 2 years. Thus, moderate disturbance can increase species diversity (Hughes et al. 2007; Sheil & Burslem 2013). Improving species richness and diversity is a critical aspect of restoring community function after invasion ceases, to reduce the potential risk of re-invasion. Therefore, successful management should balance the trade-off between the reduction of invader density with changes in the diversity of other species (see Nagy et al. 2020). Specifically, we found that mowing regimes increased the dominance of perennial forbs and grasses, as did Nagy et al. (2016). This may be particularly important for biotic resistance if these types of species possess traits that allow them to outperform invaders (Catford et al. 2012; Bulleri et al. 2016). Our results also emphasize the importance of maintaining management treatments over time. Our 1-year, mowing-once regime increased *Solidago* density, compared to the 2-year, mowing-once regime. The abandonment of restoration treatments too quickly may eliminate the positive results (see Visnyovszky 2017).

With respect to our third question, *Tanacetum* outcompeted *Solidago* in undisturbed plots, but this natural resistance had its cost. Diversity was also reduced by 30% compared to control plots without *Tanacetum*. Thus, the same species that provides biotic resistance against invasion appeared to be responsible for higher biodiversity loss than caused by the invader by itself. Two highly competitive species may have increased competition for resources (Aschehoug et al. 2016), increased total biomass (Güsewell et al. 2006), or produced allelopathic compounds (Hodişan & Csep 2010; Pal et al. 2015) in ways that eliminated species other than our test species. But, all mowing regimes increased diversity and two regimes increased species richness compared to the control, whereas in plots without *Tanacetum* only 2 years of mowing twice-per-year treatments increased diversity and richness. We suggest that mowing regimes reduced strong competition from *Tanacetum* and *Solidago* on other species, consistent with Le Bagousse-Pinguet et al. (2012) and Maalouf et al. (2012). In addition, plants in highly disturbed communities tend to invest more into reproduction, allowing them to rapidly react to opportunities provided by disturbance (Tilman 1994). This is consistent with strategies along gradients of disturbance, with the appearance of ruderal species with high dispersal abilities (like *Erigeron annuus*) soon after disturbance and stress-tolerant species (like *Medicago falcata* or *Hypericum*

perforatum) long after disturbance (Grime 1973). Our findings suggest that increased competition from a native species and an invasive species might influence native diversity, and this might affect the success of restoration approaches.

Application

Our study indicated that even short-term management efforts can decrease the density of *Solidago*, similar to previous findings (Nagy et al. 2020). Continuous mowing regimes suppressed the density of the invader to a more sustainable level (around four stems per m²) and preserved or even improved diversity. A twice-a-year mowing regime (during June and September) was more advantageous, consistent with Szépligeti et al. (2017), due to its positive effect on species diversity and its longer-term effect on suppressing the invader. Effective application may require long-term maintenance of mowing regimes.

Tanacetum vulgare provides competitive resistance to *Solidago* invasion, but as a side effect, this native species increased biodiversity loss. However, when *Tanacetum* was present, mowing regimes were ineffective against the invader. Moreover, mowing once in only 1 year increased the density of the invader in the presence of *Tanacetum*. In contrast, all applied regimes helped to restore community diversity. This indicates that initial status of vegetation should be taken into consideration before management, since mowing might shift competitive interactions to the facilitation of *Solidago* and thus resist management efforts.

Acknowledgments

The project was supported by the European Union, co-financed by the European Social Fund Grant no.: EFOP-3.6.1.-16-2016-00004 entitled by Comprehensive Development for Implementing Smart Specialization Strategies at the University of Pécs (D.U.N.). The project was subsidized by the People Programme (Marie Curie Actions) of the European Union's under REA grant agreement number 300639 (R.W.P.). The authors also acknowledge the support of TÁMOP-4.2.2.B-15/KONV-2015-0011 and a Fulbright Scholar grant (E.S.J.R. and R.W.P.). R.M.C. thanks the National Science Foundation EPSCoR Cooperative Agreement OIA-1757351 for support.

LITERATURE CITED

- Allsup CM, Paige, KN (2016) Belowground fungal associations and water interact to influence the compensatory response of *Ipomopsis aggregata*. *Oecologia* 180:463–474. <https://doi.org/10.1007/s00442-015-3470-8>.
- An SQ, Gu BH, Zhou CF, Wang ZS, Deng ZF, Zhi YB, Li HL, Chen L, Yu DH, Liu YH (2007) *Spartina* invasion in China: implications for invasive species management and future research. *Weed Research* 47:183–191
- Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM (2016) The mechanisms and consequences of interspecific competition among plants. *Annual Review of Ecology, Evolution, and Systematics* 47:263–281
- Badano E, Villarreal E, Bustamante RO, Marquet PA, Cavieres LA (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology* 95:682–688
- Bates D, Maechler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48

- Besaw LM, Thelen GC, Sutherland S, Metlen K, Callaway RM (2011) Disturbance, resource pulses and invasion: short-term shifts in competitive effects, not growth responses, favour exotic annuals. *Journal of Applied Ecology* 48:998–1006
- Botta-Dukát Z, Dancza I (2012) Magas aranyvessző (*Solidago gigantea* Ait.), Kanadai aranyvessző (*Solidago canadensis* L.). In: Csiszár Á (ed) *Inváziós növényfajok Magyarországon. Nyugat-magyarországi Egyetem Kiadó, Sopron, Hungary*
- Botta-Dukát Z, Dancza I, Szabó I (1998) A kaszálás és az avar eltávolításának hatása a *Solidago gigantea* Ait. növekedésére. *Természetvédelmi Közlemények* 7:65–73
- Bradshaw AD (1983) The reconstruction of ecosystems. *Journal of Applied Ecology* 20:1–17
- Bruno J, Kennedy C (2000) Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. *Oecologia* 122:98–108
- Bulleri F, Benedetti-Cecchi L, Jaklin A, Iveša L (2016) Linking disturbance and resistance to invasion via changes in biodiversity: a conceptual model and an experimental test on rocky reefs. *Ecology and Evolution* 6:2010–2021
- Byun C, Lee EJ (2017) Ecological application of biotic resistance to control the invasion of an invasive plant, *Ageratina altissima*. *Ecology and Evolution* 7:2181–2192
- Byun C, de Blois S, Brisson J (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology* 101:128–139
- Callaway RM (2007) Interaction between competition and facilitation. In: *Positive interactions and interdependence in plant communities*. Springer, Dordrecht, Netherlands
- Callaway RM, Newingham B, Zabinski CA, Mahall BE (2001) Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. *Ecology Letters* 4:429–433
- Callaway RM, Kikodze D, Chiboshvili M, Khetsuriani L (2005) Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86:1856–1862
- Catford JA, Daehler CC, Murphy H, Sheppard AW, Hardesty BD, Westcott DA, et al. (2012) The intermediate disturbance hypothesis and plant invasions: implications for species richness and management perspective. *Perspectives in Plant Ecology, Evolution and Systematics* 14:231–241
- Cavieres LA, Quiroz CL, Molina-Montenegro MA (2008) Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? *Functional Ecology* 22:148–156
- Crawley MJ (2014) *Statistics: An introduction using R*. 2nd edition. John Wiley and Sons, Chichester, United Kingdom
- Cservenka J, Magyari M, Petróczi I, Békássy G (2017) The control of giant goldenrod in the Felső-Kongó meadows by Szigliget. In: Csiszár Á, Korda M (eds) *Practical experiences in invasive alien plant control*. 2nd revised and expanded edition. Rosalia Handbooks. Duna – Ipoly National Park Directorate, Budapest, Hungary
- Davis KW, Nafus AM, Sheley RL (2010) Non-native competitive perennial grass impedes the spread of an invasive annual grass. *Biological Invasions* 12:3187–3194
- DeWine JM, Cooper DJ (2010) Habitat overlap and facilitation in tamarisk and box elder stands: implications for tamarisk control using native plants. *Restoration Ecology* 18:349–358
- Fukami T (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23
- Germain RM, Srivastava D, Angert AL (2020) Evolution of an inferior competitor increases resistance to biological invasion. *Nature Ecology & Evolution* 4:419–425
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Guo SL, Jiang HW, Fang F, Chen GQ (2009) Influences of herbicides, uprooting and use as cut flowers on sexual reproduction of *Solidago canadensis*. *Weed Research* 49:291–299
- Güsewell S, Jakobs G, Weber E (2006) Native and introduced populations of *Solidago gigantea* differ in shoot production but not in leaf traits or litter decomposition. *Functional Ecology* 20:575–584
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:9
- He M, Ding J, Lu X (2014) Increased compensatory ability of an invasive plant to above- and below-ground enemies in monocultures. *Plant Ecology* 215:253–260
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97:393–403
- Hodişan N, Csep N (2010) Research on the allelopathic effect among the species *Tanacetum vulgare* and some agricultural crops. *Acta Agraria Debreceniensis* 39:105–109
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363
- Hughes RA, Byrnes JE, Kimbro DL, Stachowicz JJ (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters* 10:849–864
- Jacobs J (2008) *Ecology and management of common Tansy (Tanacetum vulgare L.)*. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington D.C.
- Jakobs G, Weber E, Edwards P (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions* 10:11–19
- Klima K, Synowiec A (2016) Field emergence and the long-term efficacy of control of *Heracleum sosnowskyi* plants of different ages in southern Poland. *Weed Research* 56:377–385
- Kula AAR, Hartnett DC, Wilson GWT (2005) Effect of mycorrhizal symbiosis on tallgrass prairie plant–herbivore interactions. *Ecology Letters* 8:61–69
- Laurent L, Märell A, Korboulewsky N, Saïd S, Balandier P (2017) How does disturbance affect the intensity and importance of plant competition along resource gradients? *Forest Ecology and Management* 391:239–245
- Le Bagousse-Pinguet Y, Gross EM, Straile D (2012) Release from competition and protection determine the outcome of plant interactions along a grazing gradient. *Oikos* 121:95–101
- LeCain R, Sheley R (2014) *Common tansy (Tanacetum vulgare)*. MontGuide MT199911AG. Montana State University-Extension, Bozeman, Montana
- Leger EA, Espeland EK (2010) PERSPECTIVE: coevolution between native and invasive plant competitors: implications for invasive species management. *Evolutionary Applications* 3:169–178
- Lekberg Y, Bever J, Bunn R, Callaway RM, Hart M, Kivlin S, et al. (2018) Relative importance of competition and plant soil feedbacks, their synergy, context dependency and implications for coexistence. *Ecology Letters* 21:1268–1281
- Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854
- Liao H, Gurgel PCS, Pal RW, Hooper D, Callaway RM (2016) *Solidago gigantea* plants from nonnative ranges compensate more in response to damage than plants from the native range. *Ecology* 97:2355–2363
- Lucero JE, Arab NA, Meyer ST, Pal RW, Fletcher R, Nagy DU, Callaway RM, Weisser WW (2020) Escape from natural enemies depends on the enemies, the invader, and competition. *Ecology and Evolution* 10:10818–10828
- Maalouf JP, Le Bagousse-Pinguet Y, Marchand L, Touzard B, Michalet R (2012) The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Annals of Botany* 110:821–828
- MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. *Journal of Ecology* 97:609–615
- Maestre FT, Bautista S, Cortina J, Bellot J (2001) Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* 11:1641–1655
- Majewska M, Rola K, Zubek S (2017) The growth and phosphorus acquisition of invasive plants *Rudbeckia laciniata* and *Solidago gigantea* are enhanced by arbuscular mycorrhizal fungi. *Mycorrhiza* 27:83–94
- Maron JL, Connors PG (1996) A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312

- Maron JL, Marler M (2008) Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology* 96:1187–1197
- Mesa JM, Scholes DR, Juvik JA, Paige KN (2017) The molecular interdependence of plant resistance and tolerance. *Ecology Special Feature* 98:2528–2537
- Michalet R, Maalouf JP, Choler P, Clément B, Rosebery D, Royer JM, Schöb C, Lortie SJ (2014) Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography* 38:335–345
- Nagy DU, Henn T, Waller LP, Pal RW (2016) How initial composition affects the later development? – a secondary successional study in differently managed agricultural sites. *Applied Ecology and Environmental Research* 14:281–295
- Nagy DU, Stranczinger S, Godi A, Weisz A, Rosche C, Suda J, Mariano M, Pal RW (2018) Does higher ploidy level increase the risk of invasion? A case study with two geo-cytotypes of *Solidago gigantea* Aiton (Asteraceae). *Journal of Plant Ecology* 11:317–327
- Nagy DU, Rauschert ESJ, Henn T, Cianfaglione K, Sz Stranczinger, Pal RW (2020) The more we do the less we gain? Balancing effort and efficacy in managing *Solidago gigantea* invasion. *Weed Research* 60:232–240
- Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* 4:196–202
- Paige KN (2018) Overcompensation, environmental stress, and the role of endoreduplication. *American Journal of Botany* 105:1–4
- Pal RW, Chen S, Nagy DU, Callaway RM (2015) Impacts of *Solidago gigantea* on other species at home and away. *Biological Invasions* 17:3317–3325
- Pal RW, Maron J, Nagy DU, Waller L, Tosto A, Liao H, Callaway RM (2020) What happens in Europe stays in Europe: apparent evolution by an invader does not help at home. *Ecology* 101:e03072
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288
- Power G, Vilas JS (2020) Competition between the invasive *Impatiens glandulifera* and UK native species: the role of soil conditioning and pre-existing resident communities. *Biological Invasions* 22:1527–1537
- R Development Core Team R (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Ramula S, Paige KN, Lennartsson T, Tuomi J (2019) Overcompensation: a 30-year perspective. *Ecology* 100:e02667
- Rasran L, Vogt K, Jensen K (2007) Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient. *Folia Geobotanica* 42:271–288
- Rinella MJ, Jacobs JS, Sheley RL, Borkowski JJ (2001) Spotted knapweed response to season and frequency of mowing. *Journal of Range Management* 54:52–56
- Schittko C, Wurst S (2014) Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*. *Biological Invasions* 16:1465–1479
- Scholes DR, Paige KN (2014) Plasticity in ploidy underlies plant fitness compensation to herbivore damage. *Molecular Ecology* 23:4862–4870
- Schooler SS, Cook T, Prichard G, Yeates AG (2010) Disturbance-mediated competition: the interacting roles of inundation regime and mechanical and herbicidal control in determining native and invasive plant abundance. *Biological Invasions* 12:3289–3298
- Sheil D, Burslem DFRP (2013) Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. *Trends in Ecology & Evolution* 28:571–572
- Shibel Z, Heard SB (2016) Synergistic and additive effects of drought stress and simulated herbivory on two goldenrods, *Solidago altissima* L. and *Solidago Ait.* *Botany* 94:635–642
- Siemann E, Rogers WE (2003) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology* 91:923–931
- Szépligeti M, Kun R, Bartha S, Bodoncz L, Szentirmai I (2017) Experience gained from the control of giant goldenrod in the Őrség National Park. In: Csizsár Á, Korda M (eds) Practical experiences in invasive alien plant control. 2nd revised and expanded edition. Rosalia Handbooks. Duna – Ipoly National Park Directorate, Budapest, Hungary
- Szymura M, Szymura TH (2016) Interactions between alien goldenrods (*Solidago* and *Euthamia* species) and comparison with native species in Central Europe. *Flora* 218:51–61
- Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16
- Toft C, Elliot-Fisk D (2002) Patterns of vegetation along a spatiotemporal gradient on shoreline strands of a basin desert lake. *Plant Ecology* 158:21–39
- Van de Peer Y, Ashman TL, Soltis PS, Soltis DE (2020) Polyploidy: an evolutionary and ecological force in stressful times. *The Plant Cell* 33:11–26
- Venables WN, Ripley BD (2002) Modern applied statistics with S. 4th edition. Springer, New York
- Vilá M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708
- Visnyovszky T (2017) The conservation management of Canadian goldenrod in the Aggtelek National Park. In: Csizsár Á, Korda M (eds) Practical experiences in invasive alien plant control. 2nd revised and expanded edition. Rosalia Handbooks. Duna – Ipoly National Park Directorate, Budapest, Hungary
- Walker LR (1999) Ecosystems of disturbed ground. Elsevier Science, Amsterdam, Netherlands
- Wang Y, Naumann U, Wright ST, Warton DI (2012) Mvabund - an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3:471–474
- Weber E, Jakobs G (2005) Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* 200:109–118
- Zhou JQ, Wilson GWT, Cobb AB, Yang GW, Zhang YJ (2019) Phosphorus and mowing improve native alfalfa establishment, facilitating restoration of grassland productivity and diversity. *Land Degradation & Development* 15:647–657

Supporting Information

The following information may be found in the online version of this article:

Table S1. Locations of seed sampling sites.

Table S2. Results of the linear mixed-effect model analyses testing the interaction of the management regime and competition status (presence of *Tanacetum*) on *Solidago* and community diversity before management (pre-treatment baseline survey).

Table S3. Results of the baseline survey (before any management treatments), evaluating differences among plots within each management regime.

Table S4. Results of the linear mixed-effect model analyses (*Solidago* stem number, height, Shannon diversity, and Species richness) with chi-square hypothesis testing, and multivariate abundance analysis (Species composition).

Table S5. Mean changes in absolute species cover in each management regime compared to the unmanaged control plots.