

Direct effects of a biocontrol agent are greater than indirect effects through flower visitors for the alien plant Dalmatian toadflax (*Linaria dalmatica*: Scrophulariaceae)

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Abstract Herbivory and pollination are important determinants of female reproductive success in flowering plants. Plants must interact with herbivores and flower visitors simultaneously and interaction with one may alter the outcome of the interaction with the other. These indirect effects can have dramatic impacts on plant fitness. The purpose of this study was to examine whether the stem-boring weevil *Mecinus janthiniformis* (Curculionidae: Coleoptera) affects flower visitation rate and seed set of the exotic plant Dalmatian toadflax (*Linaria dalmatica* (L.) Mill. Scrophulariaceae). We compared the flower production, flower morphology, visitation rate, fruit production, and pollen limitation on Dalmatian toadflax plants with and without larval feeding by *M. janthiniformis*. Feeding by *M. janthiniformis* reduced the number of flowers and per plant visitation rate, and there was a significant interaction between herbivory and flower number suggesting that the change in visitation rate was not solely a function of a reduction in flower abundance. Herbivory also had direct

negative impacts on the reproductive success of Dalmatian toadflax. Total flower and fruit production decreased by over 30 % in plants attacked by *M. janthiniformis*. However, plants with *M. janthiniformis* were not more pollen-limited than those without *M. janthiniformis*. This suggests that herbivory had primarily direct effects female reproductive success.

Keywords Biocontrol · Multi-species interactions · Pollination · Herbivory · *Mecinus janthiniformis*

Introduction

Herbivory and pollination are important determinants of female reproductive success in flowering plants. Herbivory often directly reduces resource availability, survivorship and ultimately female reproductive success (Bigger and Marvier 1998) and this can affect plant populations (Maron and Crone 2006). In addition, nearly 90 % of flowering plant species globally are pollinated by animals (Ollerton et al. 2011). Increases in visitation rate by pollinators often directly increase pollen reception and subsequently seed set (Burd 1994; Ashman et al. 2004). Early research on plant–insect interactions has focused on these direct pair-wise relationships and has demonstrated that insects can have substantial direct effects on plant ecology and evolution (Bigger and Marvier 1998; Goodwillie et al. 2005).

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Plants simultaneously interact with multiple species and the interaction with one may affect the outcome of the relationship with another (Herrera et al. 2002; Morris et al. 2007). These indirect effects can take two forms. The first type of indirect effect occurs when one species changes the abundance of a second species with this change subsequently affecting a third species. This type of indirect effect known as an ‘interaction chain’ is predictable as it is simply a series of direct effects and is discernable by measuring each pair-wise interaction in isolation (Wootton 1993). For example, herbivory may reduce overall plant abundance and density (Maron and Crone 2006). If this leads to a decrease in the total number of flowers, this can affect pollinator visitation and pollinator communities (Roulston and Goodell 2011). Similarly, an herbivore may reduce the total flowers produced per plant and this may lead to a decrease in the number of pollinators visiting the plant (Strauss et al. 1996; Lehtila and Strauss 1997; Barber et al. 2012).

‘Interaction modifications’ are the second category of indirect effect (Wootton 1993). These occur when one species modifies the dynamics of the interaction between two other species. These interactions are more difficult to predict, as they are not solely a function of changes in abundance and are often evident only after experimental manipulation (Wootton 1993, 1994). For example, Kessler et al. (2011) found that while herbivores did not reduce the flower abundance of *Solanum peruvianum*, they did lead to the induction of plant volatiles. Pollinators avoided plants that produced these volatiles and this caused a decrease in visitation and seed production. Some of the most dramatic examples of interaction modifications occur due to florivory as it often directly results in changes in floral morphology or reward quality, and this may lead to a decrease in visitation rate independent of flower abundance (Johnson et al. 1995; Irwin and Brody 1998; Mothershead and Marquis 2000). Increasingly, studies using vegetative herbivory have also found changes in floral quality such as reward amount, flower size, and flower type and lead to decreases in visitation rate (Strauss et al. 1996; Mothershead and Marquis 2000; Hamback 2001; Halpern et al. 2010).

The interaction between herbivory and pollination may be particularly important for invasive, alien plants. Many exotic plants are introduced without the full suite of enemies found in their native range and

experience reduced herbivory in their invaded range (Liu and Stiling 2006). This lack of enemies is an important component of the Enemy Release Hypothesis (Keane and Crawley 2002) as well as the Evolution of Increased Competitive Ability Hypothesis (Blossey and Notzold 1995), and it underlies classical biological control programs. Furthermore, many exotic plants rely on flower visitors for sexual reproduction and native and exotic flower visitors readily visit introduced plants (Morales and Traveset 2009). Alien plants that are free from enemies may have more resources to devote to attracting mutualists such as pollinators. It might be expected that adding an herbivore may have not only direct effects on the fitness of an alien plant but also indirect effects through mutualists as well. Therefore, to address the actual impact of biocontrol agents, it is important to understand both their direct and indirect effects. Despite the ubiquity of using biological agents to control alien plants and the fact that many alien plants rely on or benefit from insect pollinators, relatively few studies have addressed how the effects of both herbivores and pollinators influence alien plants. Swope and Parker (2012) found that a bud-feeding biocontrol agent had slight reduction in pollinator visitation. In contrast, Swope and Parker (2010) found that an experimental addition of a fungal-pathogen had no effect on pollinator visitation by one pollinator.

The purpose of this study was to examine whether the exotic stem-boring weevil *Mecinus janthiniformis* (Germar, Curculionidae: Coleoptera) affects flower visitation and seed set of the exotic plant Dalmatian toadflax (*Linaria dalmatica* (L.) Mill. Scrophulariaceae). Both Dalmatian toadflax and *M. janthiniformis* are native to southwestern Eurasia (Toveški et al. 2011). Dalmatian toadflax is now invasive in North America and the biological control agent *M. janthiniformis* has been released to control its populations. This system provides an interesting template to examine these interactions. Dalmatian toadflax relies on insects for sexual reproduction as it is self-incompatible (Docherty 1982; Vujnovic and Wein 1997) and has a closed flower structure that makes wind pollination not possible. Dalmatian toadflax has a large floral display and was purposely introduced into North America in 1894 as an ornamental (Vujnovic and Wein 1997). *M. janthiniformis* was released in 1991 and a number of studies demonstrate that it has large impacts on Dalmatian toadflax (Peterson et al. 2005, Sing et al. 2005).

We addressed three questions: (1) Does herbivory by *M. janthiniformis* directly alter flower number and floral traits of Dalmatian toadflax? We predicted that *M. janthiniformis* would decrease flowers per plant and would change floral morphology. (2) Does herbivory affect visitation rate through changes in floral abundance or do changes in floral traits influence visitation independently of flower number? (3) Does herbivory decrease fruit set and increase pollen limitation due to decrease in visitation rate? We expected plants with *M. janthiniformis* would have greater pollen limitation than plants without herbivory.

Methods

Study species

Dalmatian toadflax is native to Mediterranean regions of Eurasia. It was introduced into the United States in the late seventeenth century as an ornamental and is now invasive in much of Canada and the western and northern United States (Alex 1962; Vujnovic and Wein 1997). It is a short-lived perennial that reproduces by both seed and rhizomes. Individual plants are made up of multiple stems that can each reach up to 1.5 m in height and produce a simple raceme of yellow, zygomorphic flowers (Whitson et al. 2002). Plants flower from May through early October. Each fruit can produce up to 300 seeds and individual Dalmatian toadflax plants can produce up to 500,000 seeds per growing season (Robocker 1974). Flowers are hermaphroditic, protandrous, and self-incompatible and rely on flower visitors for sexual reproduction (Docherty 1982; Vujnovic and Wein 1997). Corollas remain closed throughout the life of the flower and flower visitors must either pry open corollas or insert their proboscis between the petals to collect nectar contained in a spur. In other flowering plants, nectar robbing can reduce floral attractiveness and reward amount leading to a decrease in visitation and reproductive success (McCall and Irwin 2006 for review). Short-tongued bees pierce and rob flowers of Dalmatian toadflax (*Cariveau pers obs.*) and its congener yellow toadflax (Newman and Thompson 2005; Burkle et al. 2007). We did not observe any signs of robbing in this study (*Cariveau pers obs.*).

Mecinus janthiniformis is a univoltine stem-boring weevil that was intentionally released into North

America in 1991 as biological control agent of Dalmatian and yellow toadflax (DeClerck-Floate and Miller 2002). At the time of its introduction this species was named *M. janthinus*; more recent systematic work has determined this to be a separate, distinct species (*M. janthiniformis*) that develops exclusively on Dalmatian toadflax and closely related host plants (Toveški et al. 2011). Adults are active from early spring through June. They feed on flowers and leaves, and in the late spring and early summer, females chew small holes and oviposit into the stem where the larvae develop. Larval feeding results in reduced photosynthetic rates, transpiration rates, and stomatal conductance (Peterson et al. 2005). Larvae pupate in the stems, overwinter as adults, and emerge in the late spring the following year. *M. janthiniformis* is currently the most effective biological control agent for controlling populations of Dalmatian toadflax in North America (Sing et al. 2005).

Experimental design

At the Colorado State University campus in Fort Collins, Colorado USA, we grew 120 Dalmatian toadflax plants from seed and transplanted them into 10-L plastic pots. Approximately 4 months after germination, we placed 7 or 8 potted plants per cage into 16 cages covered with spunbonded polyester. This allowed for photosynthetic light to pass but was impenetrable to *M. janthiniformis*. These cages were kept outside in a shade house. We randomly assigned 8 cages as beetle-present and 8 cages as beetle-free. In May 2007, we released 10 *M. janthiniformis* adults per plant into the beetle-present cages for a total of 70 or 80 beetles per cage. We used *M. janthiniformis* adults that were extracted from Dalmatian toadflax stems that were collected the previous fall. Adults were left in cages for 6 weeks allowing them to feed, mate, and oviposit in the stems.

Six weeks after introducing *M. janthiniformis* (July 19), we took plants out of the cages and removed all adult *M. janthiniformis*. Plants in cages where *M. janthiniformis* were released on average had 44.9 ± 3.8 (max = 150 min = 3) larvae per plant. These numbers are within the range found in other field studies (DeClerck-Floate and Miller 2002; Norton unpublished data). Some *M. janthiniformis* did oviposit on 'M. janthiniformis free plants', but the average was much lower (2.1 ± 0.41 , max = 14, min = 0). *L. dalmatica*

is rarely attacked by other, generalist herbivores (Norton *pers. obs.*). In addition, the experimental site was isolated from other *L. dalmatica* populations and we did not detect other specialist herbivores on study plants.

We transferred the plants to the Colorado State Forest Tree Nursery located at an elevation of 1,560 m in Fort Collins, Colorado. The nursery is comprised of tree rows, fallow fields, and open grass meadows that contain a mixture of native and exotic species. The plants for this experiment were placed in the open grass meadows with no blooming *L. dalmatica* plants in the vicinity. There were few naturally blooming flowers present in the area and there were no known blooming Dalmatian toadflax populations within 1 km of the study site. We placed the plants in 10 rows of 12 plants using a completely randomized design, with each row and individual plants within each row separated by 3 meters. All plants were well watered and fertilized throughout the experiment thus reducing the impact of resource limitation on fitness or floral traits.

Does M. janthiniformis herbivory alter the number of flowers and floral traits?—Once a week from July 19 to September 6, we counted all open flowers on each Dalmatian toadflax plant to estimate the number of flowers open per day per plant. On Aug 2, we randomly chose 30 beetle-attacked and 30 beetle-free plants, and using calipers, we measured the size of three haphazardly chosen flowers per plant. We recorded corolla width, flower length, and spur length. From these data, we calculated flower area for each individual flower as the product of corolla length by corolla width. For all measurements, data were averaged for the 3 flowers from each plant, keeping plant as the experimental unit.

Does M. janthiniformis herbivory affect visitation rate to Dalmatian toadflax?—On August 7, 14, and 21, we observed each flowering plant for 10 min. The order of plant observations was randomized. As we had multiple observers, all plants with flowers were observed on each date. For consistency, we conducted all observations between 800 and 1,300. This was also the time of peak insect activity (Cariveau *per obs.*). We recorded a visit when any part of the flower visitor entered the flower corolla. The morphology of the flower is such that a pollinator that is able to enter the flower comes in contact with the reproductive parts of the flower. We calculated visitation rate as the number of visits received per plant per minute. The number of

flowers per plant was also counted to be used as a covariate in the analysis (see below).

Does M. janthiniformis herbivory decrease fruit set and increase pollen limitation in Dalmatian toadflax?—Once a week we counted all open flowers on each plant and collected and counted all ripe fruits. We then summed these values to obtain an estimate of the total number of flowers and fruits produced per plant. In addition, once a week from July 22 through Aug 16, we haphazardly chose six flowers each from 30 randomly-chosen beetle-present and 30 randomly-chosen beetle-free plants and brushed dehiscing anthers collected from flowers of non-study plants onto the receptive stigma. For each plant at each date we also marked open pollinated flowers to use as a control. If a plant had fewer than 6 flowers, we designated half of the flowers as hand pollinated and half as open pollinated. We used jewelry tags to mark the hand and open pollinated flowers. We collected the marked fruits before dehiscence and counted the number of seeds in each fruit.

Data analysis

Does M. janthiniformis herbivory alter the number of flowers and floral traits?—To assess whether *M. janthiniformis* feeding affected daily number of flowers produced by Dalmatian toadflax, we used repeated measures mixed model ANOVA. The response variable was the number of flowers open per plant for each date. Date, *M. janthiniformis* presence, and their interaction were fixed effects and plant was a random effect. To test differences in flower measurements between the two herbivory treatments, we used a *t* test with the assumption of unequal variances.

Does M. janthiniformis herbivory affect visitation rate to Dalmatian toadflax?—We used a repeated measures mixed model ANOVA with visitation rate as the response variable and plant as a random effect. Plants without blooming flowers were not included in the analyses. Fixed effects were date, daily flower number, the presence of *M. janthiniformis*, and the interaction between flower number and *M. janthiniformis* feeding. A significant effect of flower number but not *M. janthiniformis* herbivory indicates that flower visitors are responding to flowers and not herbivory. A significant interaction between herbivory and flower number indicates that flower visitors respond to flower number but this response depends on the presence of *M. janthiniformis*.

Does M. janthiniformis herbivory decrease fruit set and increase pollen limitation in Dalmatian toadflax?—To examine whether *M. janthiniformis* herbivory affected total number of flowers and total number of fruits per plant, we used a t-test with the assumption of unequal variances. We also used a mixed model ANOVA to examine whether *M. janthiniformis* presence affected pollen limitation. The response variable was seeds per fruit while pollen addition, *M. janthiniformis* presence, and their interaction were fixed effects. Plant was a random effect. We did not have enough power to adequately assess whether pollen limitation changed with date and therefore averaged seeds per fruit per plant over date for each plant.

We conducted all mixed model ANOVAs using the MIXED procedure in SAS (v9.2, SAS Institute 2008). We used the Kendall-Rogers adjustment for degrees of freedom in the mixed models. For all repeated measures analyses, we chose the variance–covariance structure that resulted in the lowest Akaike’s Information Criterion (AIC) value (Littel et al. 1996). All t-tests were analyzed using JMP (v7.0.2 SAS Institute 2007). All models were tested for normality and heteroscedasticity and as models met these assumptions, we did not transform response variables.

Results

Does M. janthiniformis herbivory alter the number of flowers and floral traits?—Dalmatian toadflax plants produced fewer flowers per day when attacked by

M. janthiniformis (Fig. 1; Table 1). The number of flowers in both treatments increased with date until the end of the season (Fig. 1; Table 1). There was a significant interaction between number of flowers and date (Fig. 1; Table 1), with the *M. janthiniformis* plants having more flowers in mid-August while differences between treatments were minimal at the beginning and end of the season (Fig. 1). Using a Bonferroni adjustment for multiple comparisons, we found fewer flowers on *M. janthiniformis* attacked plants on July 19 (26.4 ± 5.3 vs. 9.2 ± 2.1 , $t_{824} = 3.96$, $P < 0.001$), August 18 (53.6 ± 3.7 vs. 28.9 ± 3.6 , $t_{824} = 5.66$, $P < 0.001$), and August 26 (43.9 ± 3.9 vs. 68.0 ± 5.8 , $t_{824} = 5.51$, $P < 0.001$).

Floral morphology did not differ between *M. janthiniformis* present or absent treatments. Corolla length (25.94 ± 0.77 vs. 24.46 ± 1.2 , $t_{24.02} = -1.04$; $P = 0.31$), corolla width (8.60 ± 0.37 vs. 9.1 ± 0.48 , $t_{28.5} = 0.828$; $P = 0.41$), spur length (11.44 ± 0.48 vs. 10.07 ± 0.73 , $t_{24.7} = -1.57$; $P = 0.13$), and flower area (225.63 ± 13.3 vs. 229.59 ± 20.81 , $t_{22.3} = 0.16$; $P = 0.87$) was not affected by *M. janthiniformis* herbivory.

Does M. janthiniformis herbivory affect visitation rate to Dalmatian toadflax?—*Bombus* species and *Apis mellifera* comprised the majority of visitors (40.3 and 34.1 %, respectively). Diptera species made up 20.2 % of flower visitors and 5.4 % were solitary bees. We found evidence for an interaction chain as *M. janthiniformis* herbivory reduced flower number (Fig. 1; Table 1) and reduced flower number resulted in fewer overall visits (Fig. 2; Table 1). In addition,

Fig. 1 Number of Dalmatian toadflax flowers per day with and without *M. janthiniformis* herbivory. Clear bars represent plants without *M. janthiniformis* feeding. Filled bars represent plants attacked by *M. janthiniformis*. Error bars represent ± 1 standard error. Asterisk indicate $P < 0.001$ and are adjusted using the Bonferroni test for multiple comparisons

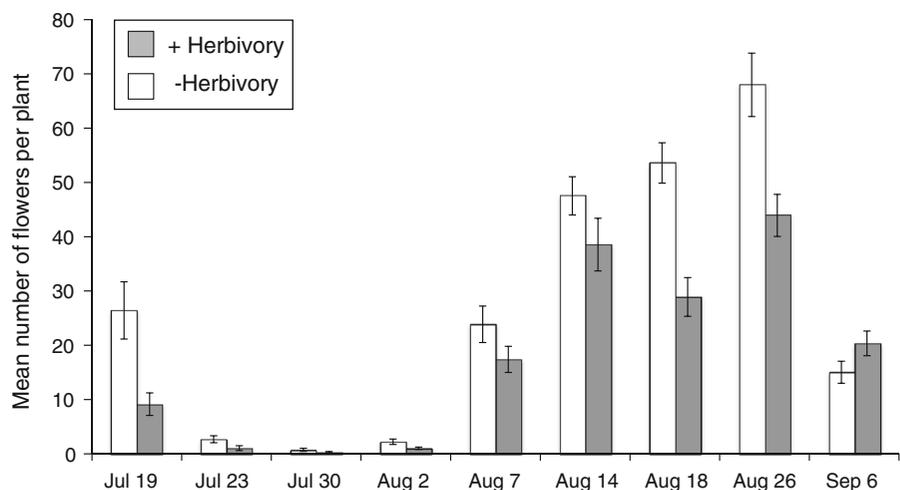


Table 1 Repeated measures and mixed model ANOVAs examining the effect of *M. janthiniformis* herbivory on flowers per day, visitation rate and seed per fruit per plant

Response variable	Effect	DF	F	P
Flowers per day	<i>M. janthiniformis</i>	1, 120	15.69	<0.001
	Date	8, 775	77.04	<0.001
	<i>M. janthiniformis</i> × Date	8, 775	7.29	<0.001
Visitation rate	<i>M. janthiniformis</i>	1, 202	3.33	0.069
	Number of flowers	1, 245	54.73	<0.001
	<i>M. janthiniformis</i> × flowers	1, 287	15.08	<0.001
	Date	2, 209	2.16	0.118
Seeds per fruit per plant	<i>M. janthiniformis</i>	1, 56	1.81	0.184
	Pollination treatment	1, 56	6.02	0.017
	Pollination × <i>M. janthiniformis</i>	1, 56	0.11	0.74

we found evidence for an interaction modification as plants without *M. janthiniformis* experienced a greater positive relationship between visitation rate and number of flowers (Fig. 2; Table 1). In this model, *M. janthiniformis* feeding by itself and date were not significant (Table 1). For both treatments, visitation rate increased with date but this effect was not significant (Table 1).

Does M. janthiniformis herbivory decrease fruit set and increase pollen limitation in Dalmatian toadflax?—Plants without *M. janthiniformis* produced 33 % more flowers and 38 % more fruits than those attacked by *M. janthiniformis* (Fig. 3a, b). We counted more fruits than flowers as we did not count flowers every day and thus missed a number of flowers. Plants with *M. janthiniformis* had fewer seeds per fruit than those without *M. janthiniformis* but this was not significant (Table 1).

We did not find evidence of an interaction between *M. janthiniformis* herbivory and pollen addition (Fig. 4; Table 1). However, hand-pollination of *M. janthiniformis* attacked plants significantly increased the number of seeds per fruit by 15.1 % (Fig. 4). Hand pollination also increased seeds per fruit in *M. janthiniformis* free plants (Fig. 4) however this difference was not significant (Fig. 4).

Discussion

The findings of this study demonstrate that larval feeding by the classical biological control agent, *M. janthiniformis*, has direct and indirect effects on

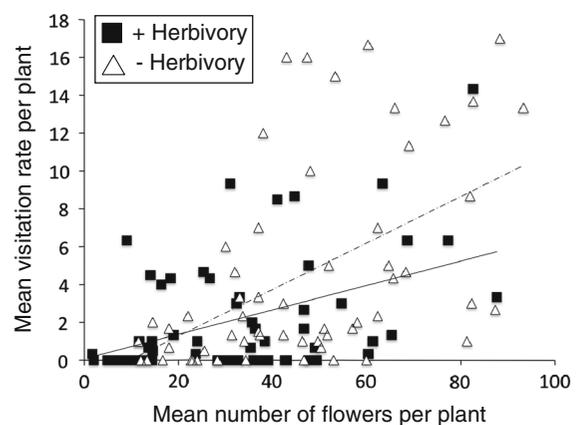


Fig. 2 The mean visitation rate and flower number for each plant. Clear triangles and dashed line represent plants without *M. janthiniformis* feeding. Filled squares and solid line represent plants attacked by *M. janthiniformis*

Dalmatian toadflax. Further, direct effects of the biocontrol had a stronger effect on female fitness than the indirect effect. Our results are comparable to those found in number of other studies using native plants (Strauss et al. 1996; Lehtila and Strauss 1997; Hamback 2001). For example, Hamback (2001) found that spittlebug (Cercopidae: Hemiptera) feeding reduced the number of flowers and number of flowers visited in *Rudbeckia hirta* (Asteraceae). In addition, Swope and Parker (2012) examined the interaction between seed predators, pollinators and an invasive plant. They found that a pre-dispersal seed predator had negative effect on visitation by one flower visitor (*A. mellifera*) but this effect was smaller than the direct effects (Swope and Parker 2012). In this study, larval

Fig. 3 The mean of the total number of (a) fruits and (b) flowers produced over the entire season. *Clear bars* represent plants without *M. janthiniformis* feeding. *Filled bars* represent plants attacked by *M. janthiniformis*. *Error bars* represent ± 1 standard error

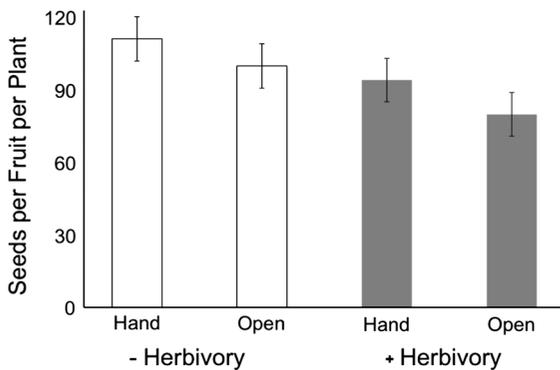
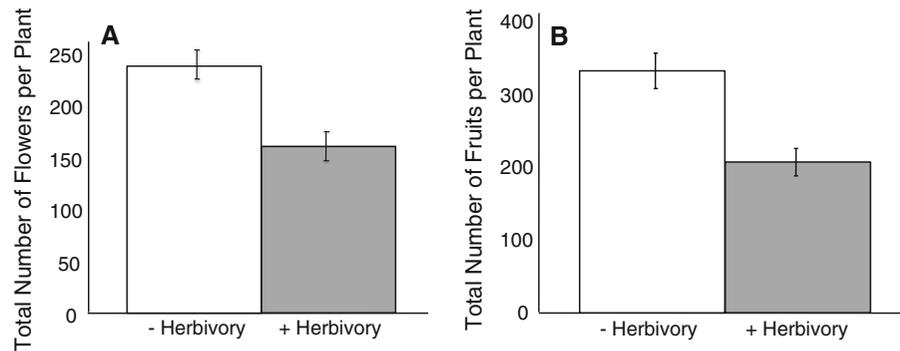


Fig. 4 Least squares means of seeds per fruit. *Clear bars* represent plants without *M. janthiniformis* feeding. *Filled bars* represent plants attacked by *M. janthiniformis*. *Error bars* represent ± 1 standard error

feeding reduced the total seasonal number of flowers and fruits per plant by 33 and 38 %, suggesting a direct effect of herbivory on female reproductive success. In addition, pollen addition increased seeds per fruit by 15 % in *M. janthiniformis* attacked plants however the effect was similar to plants without *M. janthiniformis*. Larval feeding by *M. janthiniformis* reduces photosynthetic rates, transpiration rates, and stomatal conductance of Dalmatian toadflax, and this likely leads to a decrease in the amount of resources available for flower production (Peterson et al. 2005). We did find some evidence of an indirect effect through an interaction chain as a decrease in the number of flowers resulted in concomitant decreases in visitation rate. This was expected as flower visitors often prefer plants with larger inflorescences (Hambäck 2001; Mitchell et al. 2004; Naug and Arathi 2007). However, in this experiment this reduction in visitation rate did not translate into detectable effects on fitness.

In addition, we also found evidence of an interaction modification as we found a significant effect of an interaction between *M. janthiniformis* feeding and flower number on per plant visitation rate. This result suggests that, in addition to reducing flower abundance, *M. janthiniformis* feeding altered one or more floral traits that are also important determinants of visitation rate. In some systems, vegetative herbivory alters the size and morphology of individual flowers and this leads to a decrease in visitation (Strauss et al. 1996; Mothershead and Marquis 2000). However, we found no evidence for an effect of *M. janthiniformis* feeding on individual Dalmatian toadflax flower measurements. Herbivory may also alter other floral characteristics important to visitation such as pollen production, nectar amount, and nectar quality (Strauss et al. 1996; Strauss et al. 2001; Adler et al. 2006). In addition, Kessler et al. (2011) found that bees use volatiles to avoid *Solanum peruvianum* attacked by foliar herbivores. While *M. janthiniformis* feeding may have affected these floral and plant traits, we did not measure these attributes in this study.

While this study suggests that indirect effects of this biocontrol agent are weaker than direct effects, indirect effects may still be important in a number of systems. In particular, different types of herbivores can have distinct impacts on a plant, and this may influence the magnitude of direct and indirect effects through flower visitors. For example, florivores can have dramatic effects on visitation as their damage results in a number of changes to floral displays and attractiveness to pollinators (reviewed in Strauss and Irwin 2004, McCall and Irwin 2006). We may have underestimated the indirect effects in our study as we focused on larval herbivory which takes place only in the stem. *M. janthiniformis* adults also feed on leaves

and flowers and this may result in a reduction of plant attractiveness to floral visitors (McCall and Irwin 2006). Finally, we measured only correlates of female fitness (i.e. seeds per fruit). Other work has demonstrated that herbivory may also affect male fitness such as by reducing the amount of pollen produced (Strauss et al. 1996; Schaeffer et al. 2013). Fewer insects visited plants with *M. janthiniformis* and this likely decreased the quantity of pollen exported per plant. A decrease in the overall pollen pool may also lead to an increase in pollen limitation (Campbell and Motten 1985). Therefore, to assess the total effect of feeding by biocontrol agents, multiple life history stages of the biocontrol agent and other components of plant fitness must be considered.

Ideally, biological control agents should have large impacts on the target plant to maximize the benefit to cost ratio of release (Pearson and Callaway 2003; Sing et al. 2005). Our findings of a >30 % reduction in flowers and fruits and additional indirect effects of herbivory mediated through flower visitors suggest that feeding by *M. janthiniformis* has negative effects on *L. dalmatica*. We did not test how this may affect population growth of *L. dalmatica* but results from other alien plant systems suggest that reductions of 70–99 % of seed production are needed to reduce population growth (Parker 2000). However, other studies looking at a broad range of effects have found that *M. janthiniformis* has considerable negative effects on Dalmatian toadflax populations (Sing et al. 2005; Peterson et al. 2005; Schat et al. 2011; Van Hezewijk et al. 2010). These results coupled with Breiter and Seastedt's (2007) finding that *M. janthiniformis* is highly host-specific in both greenhouse and field settings suggest that *M. janthiniformis* is likely an efficacious and safe management tool for controlling Dalmatian toadflax populations. In addition, *M. janthiniformis* may ameliorate the impacts of this exotic plant independent of its influence on population size. For example, exotic plants may affect native plants through competition for pollination services (e.g. Chittka and Schurkens 2001; Brown et al. 2002; Cariveau and Norton 2009). Exotic plants often have larger floral displays and rewards and these plants may draw away flower visitors from native plants. *M. janthiniformis* feeding reduced flower number and visitation rate to Dalmatian toadflax and this may translate into a reduction in the ability of the plant to compete with native plants for pollination services. A

more complete understanding of the negative and positive impacts of biological control on both the target exotic plants and native communities will greatly aid in successful management of invasive plants.

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