

Establishment of the biological control agent *Aphalara itadori* is limited by native predators and foliage age

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Abstract

The knotweed psyllid, *Aphalara itadori*, is a biological control agent for invasive knotweed species in North America and Europe. Initial releases were conducted in Canada in 2014 but establishment has been slow, seemingly as a result of low nymphal survival. We conducted two field experiments in Ontario, Canada, to explore the effects of native predators and the age of knotweed (*Fallopia japonica*) foliage on nymphal survival in *A. itadori*. Survival of *A. itadori* nymphs was significantly reduced on potted plants that were exposed to native predators in the field, compared to plants from which predators were excluded. The number of surviving nymphs was also significantly reduced on older *F. japonica* foliage, compared to recent regrowth after a summer cutting treatment. We discuss our findings in the context of biological invasion theory and emphasize the potential for increased overlap between the fields of invasion ecology and biological control. Finally, we advocate the use of *A. itadori* in combination with other control measures as part of an integrated pest management programme, rather than as a solitary measure. Specifically, we recommend that future releases of *A. itadori* be concentrated shortly after cutting or herbicide treatments in order to maximize the availability of young tender foliage.

KEYWORDS

Fallopia japonica, integrated pest management, Invasion ecology, knotweed, predation, psyllid

1 | INTRODUCTION

When a classical biological control agent is released, there are a host of reasons why the agent may fail to establish successfully in the introduced range. Among the most common reasons are factors relating to climate, a lack of alternate hosts for the introduced agent in the case of parasitoids and the activity of native or introduced antagonists (Goeden & Louda, 1976; Heimpel & Mills, 2017; Stiling, 1993). In the case of weed biological control, invasive plants may also contribute to the inhibition of introduced agents through interactions with native mutualists such as ants or bacteria (Chalcoff, Lescano, & Devegili, 2019; Sorokan, Rummyantsev, Benkovskaya, & Maksimov, 2017). While

many biological control programmes endeavour to conduct post-release monitoring to track the establishment and efficacy of released agents (Havens, Jolls, Knight, & Vitt, 2019; Winston et al., 2014), generally fewer resources are available to investigate the factors that might provide impediments to agent establishment (Schulz, Lucardi, & Marsico, 2019). Such investigation can be useful in fine-tuning agent release programmes and contribute to a deeper understanding of invasion ecology. Here, we describe two experiments designed to examine the effects of native predators and host-plant foliage age on the survival of the knotweed psyllid, *Aphalara itadori* Shinji (Hemiptera: Psyllidae), a recently released biological control agent for the control of invasive knotweed species in North America.

Japanese knotweed, *Fallopia japonica* (Houtt.) Ronse Decr., is one of a complex of invasive knotweed species that are widespread in Europe and North America (Barney, 2006). The complex also consists of the closely related giant knotweed, *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, as well as Bohemian knotweed, *Fallopia × bohemica* (Chrtěk & Chrtěková) J. P. Bailey, which is a hybrid of Japanese and giant knotweed. Introduced to North America in the late 19th century for ornamental purposes (Bailey & Wisskirchen, 2006; Barney, 2006; Weston, Barney, & DiTommaso, 2005), the knotweed complex is now present in at least 41 states in the United States (U.S.) and in eight Canadian provinces (Bourchier, Grevstad, & Shaw, 2013; USDA NRCS, 2011), with considerable potential to spread. For example, based on analyses of temperature and precipitation thresholds, 53% of the land in southern Ontario is potentially suitable for Japanese knotweed growth (Bourchier & Van Hezewijk, 2010; Gaskin et al., 2014). *F. japonica* is a herbaceous perennial that forms extensive monoclonal stands (Dommanget et al., 2019). The plant's bamboo-like stems sprout in early spring and quickly reach heights of up to 3 m (Bailey, Bímová, & Mandák, 2009). The species, therefore, affects native diversity through intense light competition (Maurel et al., 2010) and leaf litter accumulation (Aguilera, Alpert, Dukes, & Harrington, 2010). The plant is also thought to inhibit native plants through allelopathy (Dommanget et al., 2014). While capable of growing in diverse habitats, *F. japonica* is a particular problem along the banks of rivers, where it contributes to increased soil erosion, affects stream nutrients (Urgenson, Reichard, & Halpern, 2009) and negatively affects native fauna (Beerling & Dawah, 1993; Gerber et al., 2008; Maerz, Blossey, & Nuzzo, 2005; McIver & Grevstad, 2010). Additionally, the vigorous root system can cause damage to infrastructure and, in some cases, affect property values (Wilde, 2019). From mid-summer onwards, *F. japonica* transfers photoassimilates to robust underground rhizomes (Aguilera et al., 2010; Price, Gamble, Williams, & Marshall, 2002). As a result, the plant is capable of rapid regrowth after seemingly successful chemical or mechanical control (Shaw, Bryner, & Tanner, 2009). The ability of *F. japonica* to recover quickly from traditional control methods, along with the inaccessibility of many of the infestations, suggests that eradication of the species is not a realistic goal. The use of chemical control is further complicated by the proximity of many infestation to rivers and streams. Classical biological control provides our best option for achieving long-term, sustainable reduction in *F. japonica* populations, at relatively low cost. Among members of the knotweed complex, *F. japonica* is a particularly good candidate for biological control, as its population in North America is known to be clonal (Gaskin et al., 2014), expanding primarily through non-sexual means (Hollingsworth & Bailey, 2000) except in cases of hybridization (Gammon, Baack, Orth, & Kessili, 2010). Plants that reproduce asexually are expected to be more susceptible to biological control (Burdon & Marshall, 1981; Crawley, 1990), because they are less able to evolve resistance or tolerance to arthropod attack.

Foreign exploration for potential biological control insects focused on the native range for the knotweeds, which encompasses southern Japan, Korea and the Kurile and Sakhalin Islands

(Burckhardt & Lauterer, 1997). The knotweed psyllid, *A. itadori* Shinji (Hemiptera: Psyllidae), was identified as the agent with the highest potential based on its narrow host range, and its ability to inflict significant damage to *F. japonica* even in low numbers (White, 2007). Two biotypes of the insect were collected, one from Kyushu in southern Japan (southern biotype), which performs better on *F. japonica*, and the other from the northern Japanese island of Hokkaido (northern biotype), which performs better on *F. sachalinensis* (Grevstad et al., 2013; Shaw et al., 2009). Both biotypes of *A. itadori* were found to be specific to *F. japonica* and *F. sachalinensis* in host range testing (Grevstad et al., 2013). In 2010, the southern biotype was released in the United Kingdom (UK), becoming the first biological control insect used against an invasive weed in the European Union (Grevstad et al., 2013). In late 2014, the Canadian Food Inspection Agency (CFIA) granted a release letter for both biotypes in Canada. The insect has been recommended for release in the United States by USDA-AHPIS Technical Advisory Group (TAG) and has been progressing through the subsequent steps in the release review process. All stages of the knotweed psyllid are sap feeders, using sucking mouthparts to remove sap from the phloem cells of leaves and stems. Adult females of *A. itadori* lay approximately 600–700 eggs on plant surfaces over their lifetime (Shaw et al., 2009). Time from egg to adult is 33 days at 23°C with the insects passing through five nymphal instars following hatch (Grevstad et al., 2013; Laznik & Trdan, 2012). The psyllids overwinter as adults in the bark crevices of neighbouring trees. In Japan, they are known to use *Pinus densiflora* Zieb. & Zucc. and *Cryptomeria japonica* D. Don (Miyatake, 2001). In the introduced range, however, they are expected to use other coniferous trees, as has been observed for other *Aphalara* species (Hodkinson, 2009). The species is not expected to be limited by winter hosts, as it has been observed to overwinter in other conifer species in the UK, as well as non-conifers and dead tree trunks (Clewley & Wright, 2014). *A. itadori* is multivoltine and is predicted to go through two to three generations in the majority of sites in North America, based on climate data and observed emergence dates in Japan (Myint, Nakahira, Takagi, Furuya, & Shaw, 2012; Bourchier, unpublished data).

In Canada, releases of *A. itadori* have been conducted at sites in British Columbia, Alberta and Ontario (Bourchier, unpublished data). Although the adults have been observed to overwinter successfully when released as diapausing adults in the fall and to lay large numbers of eggs in spring or following a summer release, the resulting nymphs have appeared scarce, and the persistence of multiple generations across years at a site has not been observed (Robert Bourchier, personal communication). While the small size of *A. itadori* nymphs, and the dispersal capabilities of the adults, make field monitoring difficult, it appears that nymphal survival in the introduced range in Canada is proving an obstacle for agent establishment. We sought to examine some of the factors that might be contributing to the comparatively poor performance of *A. itadori* at Canadian release sites, compared to their performance in laboratory tests. We conducted a field experiment using potted *F. japonica* plants to explore the effects of native predators on nymphal survival in *A. itadori*. Additionally, we conducted a second

field experiment to compare adult oviposition and nymphal survival on young (recent regrowth after a mid-summer cutting treatment) versus old (late season mature growth) *F. japonica* foliage. Our objectives were to determine (a) the effects of native antagonists on nymphal survival of *A. itadori* in Canadian release sites and (b) how foliage age of *F. japonica* affects *A. itadori* establishment. We discuss our results in the context of integrated weed management, exploring the possibility that *A. itadori* establishment in Canadian release sites could be improved through integration of releases with *F. japonica* cutting treatments.

2 | METHODS

2.1 | Plant production

F. japonica roots were collected from a site in Hamilton, ON, Canada, (43.270144, -79.895753), on 10 May 2019. Roots of a similar thickness (1–1.5 cm diameter) were selected and cut into sections of around 3–4 cm in length. Care was taken to ensure that each section contained at least one node. Root sections ($N = 190$) were washed and weighed ($6.45 \text{ g} \pm 0.257$ (mean \pm SE)) before being planted in 0.5 L pots filled with Fafard Agro-Mix G2 (Sun Gro Horticulture). On 19 July 2019, 60 plants of similar size were selected and transplanted to 3-L pots filled with potting soil as above.

2.2 | Insect production

All *A. itadori* used in the experiments were reared at Agriculture and Agri-Food Canada, Lethbridge Research and Development Centre, Alberta, Canada. Psyllids from the Kyushu (southern) biotype were used for experiment one, as these have been shown to perform better on *F. japonica* (Grevstad et al., 2013). Experiment two utilized a new line of psyllids, generated by crossing Kyushu (southern) biotype females with Hokkaido (northern) biotype males.

2.3 | Experiment 1: The effects of predation on *A. itadori* nymphal survival

We sought to quantify the effects of exposure to native predators on nymphal survival in *A. itadori*. On 8 August 2019, 60 experimental plants were transferred to a large growth chamber (BioChambers). Chamber conditions were kept at 25°C and 75% RH, with a 16:8 hr (light/dark) diel period. A mesh bag made from mosquito netting (Fabricland) was placed over each plant, secured using a stick of bamboo and a wooden clothes pin.

Forty *A. itadori* adults were collected into 50-ml plastic centrifuge tubes (FroggaBio) using a manual aspirator (Ward's Science). One tube of 40 psyllids was placed at the base of each plant, inside the mesh bag. Tubes were then opened to allow psyllids access to the plants. On 18 August 2019, after a period of 10 days, the mesh

bags were removed from the experimental plants, and psyllids were removed by repeatedly disturbing the plants. The mean (SE) number of eggs on each plant was then estimated (285.68 ± 16.88) by scanning the upper surface of each leaf using a magnifying glass.

Potted *F. japonica* plants ($N = 60$) were divided equally among three treatments. Plants were allocated non-randomly, ensuring that mean numbers of *A. itadori* eggs were similar among treatments. Treatments were as follows: (a) plants were left open to allow access to all predators, (b) a band of sticky resin (Tanglefoot™) was painted around the plant pots to exclude crawling predators, (c) plants were enclosed within mesh bags, and a band of sticky resin (Tanglefoot™) was painted around the plant pots to exclude both flying and crawling predators.

On 19 August 2019, experimental plants bearing *A. itadori* eggs were transported to a field site in Uxbridge ON, Canada (44.088, -79.1093). The site consisted of a clearing (approximately 5 m by 10 m) within a mixed hardwood forest interspersed with planted red pine trees, *Pinus resinosa* (Pinales: Pinaceae). The site was characterized by exposed sandy soils with little ground vegetation. Because we suspected that ants might represent the greatest predation threat to *A. itadori* nymphs, we conducted a site-wide ant survey prior to experimental set-up. This survey suggested the presence of only one species, *Formica subsericea* (Say; Hymenoptera: Formicidae). Plants were positioned systematically to ensure even distribution of treatments across the site, and neighbouring plants were a minimum of 1 m apart. Plants were watered as needed, and predator surveys were conducted every three days during the experiment. A single observer would scan each plant for a period of one minute, and any predators observed were recorded.

On 4 September 2019, after an exposure of 17 days (a period long enough that any viable *A. itadori* eggs would have hatched), experimental plants were transported back to the laboratory at the University of Toronto. Leaves and stems of all plants were examined under a dissecting microscope, and the numbers of *A. itadori* nymphs were recorded.

2.4 | Experiment 2: The effects of *F. japonica* foliage age on *A. itadori* establishment

We compared *A. itadori* adult oviposition and nymphal survival on young and old *F. japonica* foliage. Two large patches of *F. japonica* were identified at a site in the Toronto ravines system (43.679103, -79.377532 and 43.679261, -79.377848). On 26 July 2019, half of each *F. japonica* patch was cut to just above soil level using a pair of pruning shears. Five weeks after the cutting treatments, a total of 40 *F. japonica* branches (20 from each patch) were enclosed in fine mesh bags made from mosquito netting (Fabricland). Mesh bags were secured to the plant stems using wooden clothes pins. Bagged branches all measured between 60 and 80 cm in length and were divided equally between two treatments: (a) lateral branches of mature, uncut *F. japonica* stems; and (b) new-growth *F. japonica* sprouted from cut stems. All bagged branches were inoculated with 40 *A. itadori* adults by introducing 50 ml plastic centrifuge tubes containing aspirated individuals.

On 12 September 2019, two weeks after the introduction of *A. itadori*, five bags from each treatment (two bags from patch one and three from patch two) were removed by cutting the stem below the bag using scissors and returned to the laboratory at the University of Toronto. All leaves and stems were examined closely under a dissecting microscope, and the total number of *A. itadori* eggs and nymphs on each branch was recorded. On 20 September 2019, three weeks after the introduction of adult psyllids, a further 10 bags from each treatment (five bags from patch one and five from patch two) were returned to the laboratory and egg and nymph numbers were recorded as above. Finally, on 11 October 2019, six weeks after the introduction of psyllids, the final five bags (three bags from patch one and two from patch two) were collected from each treatment and the numbers of eggs and surviving nymphs were recorded as above. A HOBO wireless pendant data logger (Onset, Bourne, MA, 02532) was placed in one of the mesh bags to take temperature readings every 5 min throughout the experiment.

2.5 | Statistical analyses

All statistical analyses were conducted using SPSS version 25 (IBM), and an alpha value of 0.05 was used across all analyses. For experiment one, the numbers of eggs on plants prior to field exposure were compared among treatments using a one-way ANOVA. The numbers of *A. itadori* nymphs recovered from potted plants after field exposure were compared among treatments using a one-way ANOVA. Tukey HSD tests were used for pairwise comparisons. The numbers of predatory insects observed on *F. japonica* plants during insect surveys were compared among treatments using a Kruskal–Wallis test, as data were not normally distributed even after transformation. Pairwise comparisons between treatments were made using non-parametric Tukey HSD (Dunn's multiple comparison) tests.

For experiment two, data from the two *F. japonica* patches were pooled for analysis. The numbers of *A. itadori* eggs and nymphs were compared between old (uncut) and new (cut) *F. japonica* branches using non-parametric Mann–Whitney *U* tests, as data were not normally distributed. Separate Mann–Whitney *U* tests were performed at each time point after the introduction of adult *A. itadori*. Branches that collapsed or died during the experimental period ($N = 1$) were not included in the analyses.

3 | RESULTS

3.1 | Experiment 1: The effects of predation on *A. itadori* nymphal survival

Exposure to crawling predators, that were able to access plants not protected by Tanglefoot™, significantly reduced *A. itadori* survival on *F. japonica* potted plants. Estimates of egg numbers on plants, before

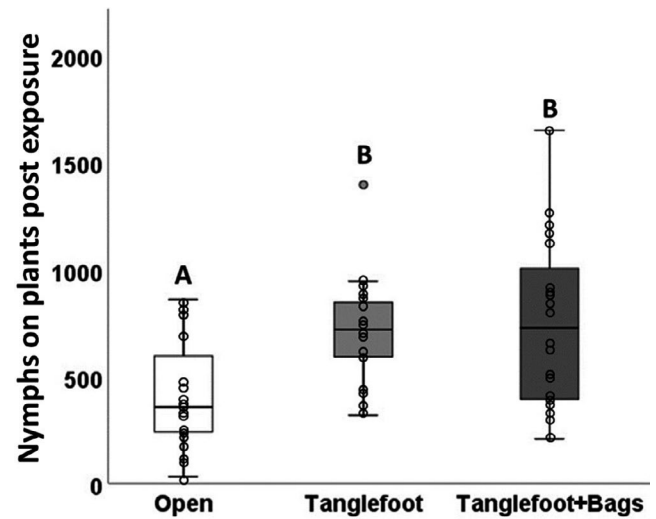


FIGURE 1 Mean numbers of *Aphalara itadori* nymphs recovered from potted *Fallopia japonica* plants placed in the field for 17 days. Treatments were as follows: (1) plants left open to allow access to all predators; (2) Tanglefoot™ used to exclude crawling predators; (3) Tanglefoot™ and mesh bags used to exclude both flying and crawling predators. Box plots represent a summary of the data (minimum, first quartile, median, third quartile, and maximum). Open circles represent outliers (1.5× interquartile range [IQR]). Letters indicate significant differences ($\alpha = 0.05$)

field exposure, did not differ among open plants (285.60 ± 31.439), Tanglefoot™ treated plants (285.95 ± 28.894) and Tanglefoot™+bag treated plants (285.50 ± 28.831 ; $N = 60$, $df = 2$, $F = 0.00$, $p = 1.00$). After 17 days of field exposure, predator exclusion treatments significantly affected survival of *A. itadori* on potted Japanese knotweed plants ($N = 60$, $df = 2$, $F = 7.170$, $p = .002$). Significantly fewer nymphs were recovered from open plants (416.5 ± 57.27) than from Tanglefoot™ treated plants (710.85 ± 54.75 ; $N = 40$, $df = 1$, $F = 294.35$, $p = .009$) or Tanglefoot™+bag treated plants (747.80 ± 86.67 ; $N = 40$, $df = 1$, $F = 331.30$, $p = .003$). No difference in nymph recovery was observed between Tanglefoot™ and Tanglefoot™+bag treated plants ($N = 40$, $df = 1$, $F = 36.95$, $p = .992$; Figure 1).

The number of predatory insects observed on potted *F. japonica* plants during insect surveys varied significantly among treatments ($N = 60$, $df = 2$, $U = 24.57$, $p < .001$). Significantly more insects were observed on open plants ($N = 40$, $df = 1$, $U = 24.0$, $p < .001$), and Tanglefoot™ treated plants ($N = 40$, $df = 1$, $U = 15.17$, $p < .001$), compared to Tanglefoot™+bag treated plants. No significant difference was observed between the numbers of predators on open plants and Tanglefoot™ treated plants ($N = 40$, $df = 1$, $U = 0.78$, $p < .376$). A total of 34 individual potential predators/parasitoids were observed on experimental plants across all arthropod surveys. The majority of these observations consisted of one tiny wasp species ($n = 18$) and a variety of immature spiders ($n = 8$). The remaining observations consisted of several larger wasp species ($n = 5$) and flies ($n = 3$). During egg/nymph counts, conducted under a dissecting microscope, a number of smaller predators were

observed. One such predator, a lacewing nymph, was observed actively feeding on *A. itadori* nymphs.

3.2 | Experiment 2: The effects of *F. japonica* foliage age on *A. itadori* establishment

A. itadori performed better on recently cut Japanese knotweed compared with more mature foliage. Two weeks after the introduction of psyllids, higher numbers of eggs were observed on new regrowth (476.5 ± 154.24) compared to mature (135 ± 56.82) Japanese knotweed; however, the difference was not significant ($N = 9$, $df = 1$, $U = 2.723$, $p = .099$; Figure 2a). No *A. itadori* nymphs were observed on either treatment at this stage. (Figure 2b). The absence of *A. itadori* nymphs at this stage was likely because none or few of the eggs had hatched, as no hatched eggs were observed.

Three weeks after the introduction of psyllids, higher numbers of eggs were again observed on new regrowth (139.25 ± 48.48) compared to mature (52.7 ± 28.88) Japanese knotweed; however,

the difference was not significant ($N = 20$, $df = 1$, $U = 3.2$, $p = .074$; Figure 2a). Significantly more nymphs were recovered from recent regrowth (138.4 ± 46.51) compared with mature Japanese knotweed (14.3 ± 3.83 ; $N = 20$, $df = 1$, $F = 42.417$, $p = .016$; Figure 2b). Although the difference in nymphal survival between treatments was significant, there was a lot of variation in the number of surviving nymphs between replicates in both the regrowth (4–406 nymphs) and mature control (0–40 nymphs) branches.

Six weeks after the introduction of psyllids, *F. japonica* plants had begun to senesce. No significant difference was observed in the number of eggs ($N = 10$, $df = 1$, $U = 0.4$, $p = .527$; Figure 2a), or nymphs ($N = 10$, $df = 1$, $U = 0.4$, $p = .527$; Figure 2b) between younger and older *F. japonica* foliage. No new or surviving adult *A. itadori* were observed on either treatment at this stage. Nymphs observed on both treatments were at a range of developmental stages, suggesting that released adults continued to lay eggs several weeks into the experiment. A HOBO data logger recorded the average temperature over the duration of the experiment as $16.776 \pm 0.103^\circ\text{C}$ (Mean \pm SE).

4 | DISCUSSION

The factors that contribute to non-native species becoming invasive are increasingly being used to predict and understand the success of newly introduced biological control agents (Schulz et al., 2019). We set out to identify key factors limiting the establishment of *A. itadori*, a psyllid recently introduced to Canada as a classical biological control agent for invasive knotweed species. Here, we describe two field experiments conducted to determine the effects of native predators and the age of *F. japonica* foliage on the survival of the psyllid. Survival of *A. itadori* nymphs was significantly reduced when plants were exposed to predators in the field, and the number of surviving nymphs was significantly reduced on older versus younger *F. japonica* foliage. Below, we discuss these results in the context of biological invasion theory and recommend modifications to the agent release programme with a view to maximizing the efficacy of *A. itadori* as a tool for controlling invasive knotweed.

In experiment one, the exclusion of predators from potted *F. japonica* plants significantly increased the survival of *A. itadori* nymphs. One of the most intuitive explanations for the success of invasive species is the enemy release hypothesis (ERH), which suggests that non-native species are released from regulation by antagonists (i.e. predators, parasitoids, pathogens) from their native range, and this results in a rapid increase in distribution and abundance in the introduced range (Keane & Crawley, 2002). Although widely studied (Enders, Havemann, & Jeschke, 2019), the assumptions of ERH have not been consistently supported, particularly by experiments at the community level, where newly introduced species are studied alongside co-occurring native species (Colautti, Ricciardi, Grigorovich, & Maclsaac, 2004). One potential explanation for this is that newly introduced species may suffer from "invasion bottlenecks," whereby a lack of genetic diversity resulting from founder effects leads to a reduction in polymorphic defences (Carr & Eubanks, 2002). A second

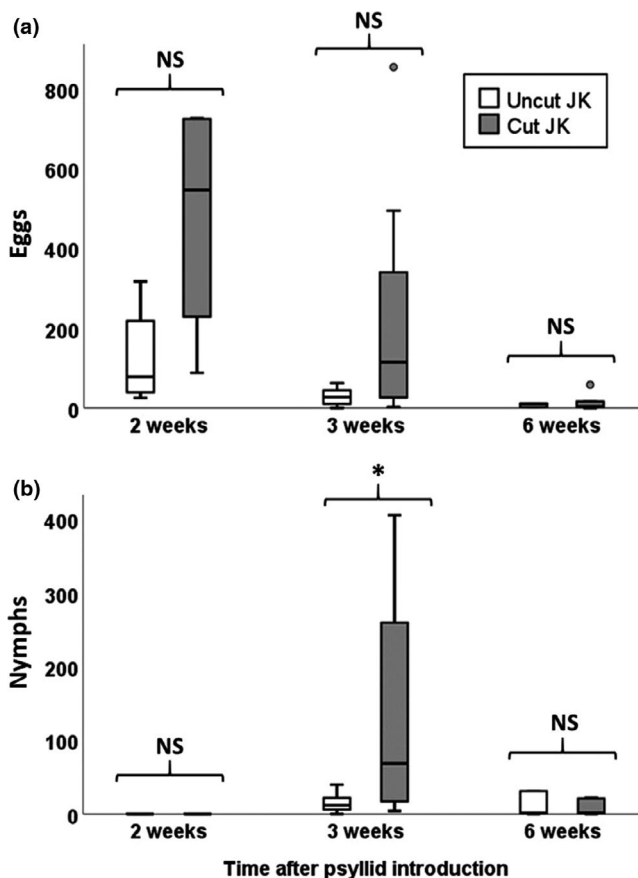


FIGURE 2 Mean numbers of eggs (a) and nymphs (b) recorded on bagged branches of *Fallopia japonica* at three time intervals (2, 3 and 6 weeks) after the introduction of *Aphis itadori* adults. Box plots represent a summary of the data (minimum, first quartile, median, third quartile and maximum). Open circles represent outliers (1.5 \times interquartile range [IQR]). Asterisks indicate significant differences (Mann-Whitney U tests) between old and new foliage at individual time points ($\alpha = 0.05$)

explanation may lie in the “new-associations principle” (Hokkanen & Pimentel, 1989), whereby the naiveté of the introduced species makes them more susceptible to generalist predators. Indeed, these two factors may act concurrently, such that newly introduced species may suffer greater losses, despite exposure to a narrower suite of antagonists. This idea is termed the “increased susceptibility hypothesis” (Barrett & Shore, 1989). Based on ERH, it is logical that any newly released biological control agent would likely need to experience a similar release from their antagonists in order to reach the densities required for effective control of the invasive target. However, for the reasons we have outlined, such a release may not occur even if the agent encounters relatively few antagonists in its introduced range. This is the basis for biotic interference hypothesis, which posits that invasive species benefit from the impact of native antagonists on biological control agents (Goeden & Louda, 1976). There are several examples of biological control agents failing due to predation or parasitism by native species. For example, the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Erebidiae), was released to control tansy ragwort, *Senecio jacobaea* L., but experienced high levels of predation in its introduced range (Crider, 2011; Heimpel & Mills, 2017). Thirteen biological control agents have been released to control spotted knapweed, *Centaurea stoebe*, in eastern Montana. These agents have experienced rates of parasitism reaching as high as 100% from a group of nine native parasitoids (Herron-Sweet, Littlefield, Lehnhoff, Burkle, & Mangold, 2015). In a survey of biological control failures, Stilling (1993) demonstrated that native predators and parasitoids accounted for approximately 20% of all failed biological control introductions. While our results far from condemn *A. itadori* to failure, we highlight the fact that native antagonists could limit its density, distribution and impact.

We observed a marked increase in *A. itadori* mortality on plants to which crawling predators were allowed access, compared with other treatments. These results suggest that crawling predators were more important than flying predators for predation levels in *A. itadori*. Indeed, the number of *A. itadori* nymphs recovered from open plants (open to crawling and flying predators) was significantly lower than the number recovered from Tanglefoot™ treated plants (open to flying predators only). Although it was not possible to identify the specific predators most responsible for mortality in *A. itadori*, it is likely that spiders were the main antagonists, as they were the most common crawling predators observed during insect surveys. It is also possible that other predators, too small to be detected during the field surveys, may have been responsible for much of the predation. Several lacewing nymphs were observed on leaves under the microscope during egg/nymphs counts. Indeed, in one case a lacewing nymph was observed actively feeding on *A. itadori* nymphs under the microscope. Future work could employ molecular gut content techniques to unequivocally identify insects consuming *A. itadori* (see Jacobsen et al., 2019). Sentinel plants should also be observed throughout the growing season to identify potential predators and address seasonal variation in predator activity.

One factor that did not appear to influence *A. itadori* mortality in our study was the activity of native or invasive ants. Invasions

by plants that produce extrafloral nectar can be facilitated by interactions with ants (Junker, Daeler, Dotterl, Keller, & Bluthgen, 2011). *F. japonica* possesses extrafloral nectaries (Ness et al., 2013); however, nectar production appeared extremely low, and no ants were observed on experimental plants in this case. Interactions between *F. japonica* and the invasive European red ant, *Myrmica rubra* (Hymenoptera, Formicidae), have been observed in the northeastern United States, and these interactions appeared to protect *F. japonica* from herbivory by the invasive Japanese beetle, *Popillia japonica* (Coleoptera: Scarabaeidae; Ness et al., 2013). While invasive ants may contribute to the invasive status of *F. japonica* in this way, we found no evidence at our release site that they are negatively influencing the establishment of *A. itadori*. It should be noted, however, that *M. rubra* appeared absent at our study site, and future work should continue to explore the impact of this, and other invasive ants, on the biological control agent.

In experiment two, no significant difference was observed in the numbers of eggs laid by *A. itadori* adults on newer versus older *F. japonica* foliage; however, the number of surviving nymphs was higher on younger regrowth. These results are not necessarily surprising from a plant physiology perspective, as many insects show a preference for younger foliage based on its high nutrient content and relative lack of mechanical defences (Steinbauer, Clarke, & Madden, 1998). It is noteworthy, however, that many fast growing plants concentrate defensive chemicals in young leaves (McKey, 1974; van Dam, Verpoorte, & van der Meijden, 1994). While our results suggest this is not the case in *F. japonica*, future work should examine the effects of foliage age on leaf chemistry. As *F. japonica* foliage ages, there is a noticeable increase in leaf toughness (Ian Jones, personal observation), and this enhanced mechanical defence may restrict feeding in *A. itadori* (Bohinc, Damir, & Stanislav, 2014). Indeed, preliminary data suggest that increased leaf toughness in *F. japonica* (manipulated through growth in varied light environments) significantly reduces *A. itadori* (southern biotype) survival (Jones et al., unpublished data). The improved survival of *A. itadori* on young foliage suggests that the faster growing young stems of *F. japonica* are relatively poorly defended, as would be supported by the growth differentiation balance hypothesis (Herms & Mattson, 1992). Although these results must be treated with caution, as they are based on only one study site, there is a clear difference demonstrated that suggests the agent may perform best when released in early spring, or shortly after herbicide or cutting treatments as part of an integrated pest management programme.

The low nymphal survival on mature foliage serves as a reminder that biological control agents are controlled by bottom-up forces as well as top-down. The resource concentration hypothesis (Root, 1973) would suggest that *F. japonica* is an ideal candidate for biological control, based on its abundance in the introduced range as well as its growth habit, forming dense stands. However, the evolution of increased competitive ability hypothesis suggests that release from antagonists allows invasive plants to allocate more resources to growth, reproduction and defence (Blossey & Nötzold, 1995). Indeed, several non-native species have been observed to possess

enhanced defences, or even develop novel defences, in their introduced range (Cappuccino & Arnason, 2006; Macel, Vos, Jansen, Putten, & Dam, 2014). *F. japonica* is known to grow approximately 1 m taller in its introduced range (Barney, 2006). Establishing dominance in the community earlier in the growth season may allow *F. japonica* to invest more heavily in chemical and mechanical defences. Future work should explore the effects of plant competition on the defensive traits of *F. japonica* (e.g. open vs. closed canopy) with a view to concentrating *A. itadori* releases in areas with a higher probability of success.

In summary, our results suggest that native predators may be negatively affecting the establishment of *A. itadori* in its introduced range. While accurately predicting the effects of antagonists on biological control agents requires a multitrophic framework (including pathogens, parasitoids and hyperparasitoids; Gagic et al., 2011; Harvey, Bukovinszky, & van der Putten, 2010), it is clear that native antagonists have the potential to limit the success of *A. itadori* in North America. The increased performance of *A. itadori* on younger *F. japonica* foliage provides important guidance for the biological control programme. Because damage by *A. itadori*, alone, appears unlikely to halt the spread of invasive knotweeds (Gourley, Li, & Zou, 2016), we recommend that future releases be conducted in the aftermath of cutting or herbicide treatments. Specifically, we suggest early pre-release cutting treatments of knotweed in small refugia areas, separated from the main treatment zones, that would allow suitable foliage regrowth for psyllids to establish in combination with other management tools. Where biological control is used in isolation, releases should be conducted in early spring to target the youngest foliage possible. If releases are later in the field season, the knotweed patch should be trimmed a few weeks prior to the release to create a flush of new foliage to maximize the chances of *A. itadori* establishment. Finally, our results highlight the need for interdisciplinary research between the fields of invasion ecology and biological control. Classical biological control programmes provide an opportunity to carry out planned invasions, allowing researchers to test various invasion hypotheses. Invasion theory, however, can be equally useful for biological control practitioners, particularly for understanding the obstacles for the success of a given agent in a given location.

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

AUTHOR CONTRIBUTION

IMJ, SMS and RSB conceived research. IMJ conducted experiments. IMJ, SMS and RSB contributed material. IMJ analysed data and conducted statistical analyses. IMJ wrote the manuscript. SMS and RSB secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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REFERENCES

- Aguilera, A. G., Alpert, P., Dukes, J. S., & Harrington, R. (2010). Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biological Invasions*, 12, 1243–1252. <https://doi.org/10.1007/s10530-009-9543-z>
- Bailey, J. P., Bímová, K., & Mandák, B. (2009). Asexual spread versus sexual reproduction and evolution in Japanese Knotweed sets the stage for the “battle of the clones”. *Biological Invasions*, 11, 1189–1203. <https://doi.org/10.1007/s10530-008-9381-4>
- Bailey, J., & Wisskirchen, R. (2006). The distribution and origins of *Fallopia bohemica* (Polygonaceae) in Europe. *Nordic Journal of Botany*, 24, 173–199. <https://doi.org/10.1111/j.1756-1051.2004.tb00832.x>
- Barney, J. N. (2006). North American history of two invasive plant species: Phytogeographic distribution, dispersal vectors, and multiple introductions. *Biological Invasions*, 8, 703–717. <https://doi.org/10.1007/s10530-005-3174-9>
- Barrett, S. C. H., & Shore, J. S. (1989). Isozyme variation in colonizing plants. In D. E. Soltis & P. E. Soltis (Eds.), *Isozymes in plant biology* (pp. 106–126). Portland: Dioscorides Press.
- Beerling, D. J., & Dawah, H. A. (1993). Abundance and diversity of invertebrates associated with *Fallopia japonica* (Houtt. Ronse Decraene) and *Impatiens glandulifera* (Royle): Two alien plant species in the British Isles. *Entomologist*, 112, 127–139.
- Blossey, B., & Nötzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology*, 83, 887–889. <https://doi.org/10.2307/2261425>
- Bohinc, T., Damir, M., & Stanislav, T. (2014). Leaf epicuticular wax as a factor of antixenotic resistance of cabbage-to-cabbage flea beetles and cabbage stinkbugs. *Acta Agricultura Scandinavica. Section B Soil and Plant Science*, 64, 493–500. <https://doi.org/10.1080/09064710.2014.926978>
- Bourchier, R. S., Grevstad, F., & Shaw, R. (2013). *Fallopia japonica* (Houtt.) Ronse Decraene, Japanese Knotweed, *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, Giant Knotweed, *Fallopia bohemica* (Chrtek & Chrtková) JP Bailey, Bohemian Knotweed. *Biological Control Programs in Canada, 2001–2012*, 321–328. <https://doi.org/10.1079/9781780642574.0321>
- Bourchier, R. S., & Van Hezewijk, B. H. (2010). Distribution and potential spread of Japanese knotweed (*Polygonum cuspidatum*) in Canada relative to climatic thresholds. *Invasive Plant Science and Management*, 3, 32–39. <https://doi.org/10.1614/IPSM-09-007.1>
- Burckhardt, D., & Lauterer, P. (1997). Systematics and biology of the *Aphalara exilis* (Weber & Mohr) species assemblage (Hemiptera: Psyllidae). *Insect Systematics and Evolution*, 28, 271–305. <https://doi.org/10.1163/187631297X00088>
- Burdon, J. J., & Marshall, D. R. (1981). Biological control and the reproductive mode of weeds. *Journal of Applied Ecology*, 18(2), 649–658. <https://doi.org/10.2307/2402423>

- Cappuccino, N., & Arnason, J. T. (2006). Novel chemistry of invasive exotic plants. *Biology Letters*, 2, 189–193. <https://doi.org/10.1098/rsbl.2005.0433>
- Carr, D. E., & Eubanks, M. D. (2002). Inbreeding alters resistance to insect herbivory and host plant quality in *Mimulus guttatus* (Scrophulariaceae). *Evolution*, 56, 22–30. <https://doi.org/10.1111/j.0014-3820.2002.tb00846.x>
- Chalcoff, V. R., Lescano, N. M., & Devegili, A. M. (2019). Do novel interactions with local fauna have reproductive consequences for exotic plants? A case study with thistles, ants, aphids, and pollinators. *Plant Ecology*, 220(1), 125–134. <https://doi.org/10.1007/s11258-019-00907-2>
- Clewley, G. D., & Wright, D. J. (2014). Winter hosts of *Aphalara itadori* (Hemiptera: Psyllidae), a classical biological control agent of *Fallopia japonica* (Polygonaceae), in the UK. *Biocontrol Science and Technology*, 24, 1197–1201. <https://doi.org/10.1080/09583157.2014.923378>
- Colautti, R. I., Ricciardi, A., Grigorovich, I. A., & MacIsaac, H. J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, 7, 721–733. <https://doi.org/10.1111/j.1461-0248.2004.00616.x>
- Crawley, M. J. (1990). Plant life-history and the success of weed biological control projects. In E. S. Delfosse (Ed.), *Proceedings of the VII international symposium on biological control of weeds* (pp. 17–26). Victoria, Australia: CSIRO Publications.
- Crider, K. K. (2011). Predator interference with the cinnabar moth (*Tyria jacobaeae*) for the biological control of tansy ragwort (*Senecio jacobaea*). *Invasive Plant Science and Management*, 4, 332–340. <https://doi.org/10.1614/IPSM-D-10-00082.1>
- Dommanget, F., Evette, A., Bretona, V., Daumerguea, N., Forestierc, O., Poupard, P., ... Navas, M. (2019). Fast-growing willows significantly reduce invasive knotweed spread. *Journal of Environmental Management*, 231, 1–9. <https://doi.org/10.1016/j.jenvman.2018.10.004>
- Dommanget, F., Evette, A., Spiegelberger, T., Gallet, C., Pace, M., Imbert, M., & Navas, M. L. (2014). Differential allelopathic effects of Japanese knotweed on willow and cottonwood cuttings used in riverbank restoration techniques. *Journal of Environmental Management*, 132, 71–78. <https://doi.org/10.1016/j.jenvman.2013.10.024>
- Enders, M., Havemann, F., & Jeschke, J. M. (2019). A citation-based map of concepts in invasion biology. *NeoBiota*, 47, 23–42. <https://doi.org/10.3897/neobiota.47.32608>
- Gagic, V., Tscharnatke, T., Dormann, C. F., Gruber, B., Wilstermann, A., & Thies, C. (2011). Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proceedings of the Royal Society B*, 278, 2946–2953. <https://doi.org/10.1098/rspb.2010.2645>
- Gammon, M. A., Baack, E., Orth, J. F., & Kesseli, R. (2010). Viability, growth, and fertility of knotweed cytotypes in North America. *Invasive Plant Science and Management*, 3, 208–218. <https://doi.org/10.1614/IPSM-D-10-00018.1>
- Gaskin, J. F., Schwarzländer, M., Grevstad, F. S., Haverhals, M. A., Bouchier, R. S., & Miller, T. W. (2014). Extreme differences in population structure and genetic diversity for three invasive congeners: Knotweeds in western North America. *Biological Invasions*, 16, 2127–2136. <https://doi.org/10.1007/s10530-014-0652-y>
- Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., & Schaffner, U. (2008). Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation*, 141, 646–654. <https://doi.org/10.1016/j.biocon.2007.12.009>
- Goeden, R. D., & Louda, S. M. (1976). Biotic interference with insects imported for weed control. *Annual Review of Entomology*, 21, 325–342. <https://doi.org/10.1146/annurev.en.21.010176.001545>
- Gourley, S. A., Li, J., & Zou, X. A. (2016). Mathematical model for biocontrol of the invasive weed *Fallopia japonica*. *Bulletin of Mathematical Biology*, 78, 1678–1702. <https://doi.org/10.1007/s11538-016-0195-8>
- Grevstad, F., Shaw, R., Bouchier, R., Sanguankeeo, P., Cortat, G., & Reardon, R. (2013). Efficacy and host specificity compared between two populations of the psyllid *Aphalara itadori*, candidates for biological control of invasive knotweeds in North America. *Biological Control*, 65, 53–62. <https://doi.org/10.1016/j.biocontrol.2013.01.001>
- Harvey, J. A., Bukovinsky, T., & van der Putten, W. H. (2010). Interactions between invasive plants and insect herbivores: A plea for a multi-trophic perspective. *Biological Conservation*, 143, 2251–2259. <https://doi.org/10.1016/j.biocon.2010.03.004>
- Havens, K., Jolls, C. L., Knight, T. M., & Vitt, P. (2019). Risks and rewards: Assessing the effectiveness and safety of classical invasive plant biocontrol by arthropods. *BioScience*, 69, 247–258. <https://doi.org/10.1093/biosci/biz015>
- Heimpel, G. E., & Mills, N. (2017). *Biological control: Ecology and applications*. Cambridge, UK: Cambridge University Press.
- Hermis, D. A., & Mattson, W. J. (1992). The dilemma of plants: To grow or defend. *The Quarterly Review of Biology*, 67(3), 283–335.
- Herron-Sweet, C. R., Littlefield, J. L., Lehnhoff, E. A., Burkle, L. A., & Mangold, J. M. (2015). Native parasitoids associated with the biological control agents of *Centaurea stoebe* L. in Montana, USA. *Biological Control*, 86, 20–27. <https://doi.org/10.1016/j.biocontrol.2015.04.001>
- Hodkinson, I. D. (2009). Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): A global synthesis. *Journal of Natural History*, 43, 65–179. <https://doi.org/10.1080/00222930802354167>
- Hokkanen, H. M. T., & Pimentel, D. (1989). New associations in biological control: Theory and practice. *Canadian Entomologist*, 121, 829–840. <https://doi.org/10.4039/Ent121829-10>
- Hollingsworth, M. L., & Bailey, P. (2000). Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese Knotweed). *Botanical Journal of the Linnean Society*, 133, 463–472. <https://doi.org/10.1006/bojl.2000.0359>
- Jacobsen, S. K., Sigsgaard, L., Hansen, K., Harwood, J. D., Chapman, E. G., Hurtado, M. A., & Jensen, A. B. (2019). Generalist predator contributions to the control of *Tetranychus urticae* in strawberry crops documented by PCR-based gut content analysis. *Experimental and Applied Acarology*, 77(2), 133–143. <https://doi.org/10.1007/s10493-019-00351-x>
- Junker, R. R., Daehler, C. C., Dotterl, S., Keller, A., & Bluthgen, N. (2011). Hawaiian ant-flower networks: Nectar-thieving ants prefer undefended native over introduced plants with floral defenses. *Ecological Monographs*, 81, 295–311. <https://doi.org/10.1890/10-1367.1>
- Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17, 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Laznik, T., & Trdan, S. (2012). Damage potential of Japanese knotweed (*Fallopia japonica*) and its biological control with psyllid *Aphalara itadori* Shinji. *Acta Agriculturae Slovenica*, 99, 93–98.
- Macel, M., Vos, R. C., Jansen, J. J., Putten, W. H., & Dam, N. M. (2014). Novel chemistry of invasive plants: Exotic species have more unique metabolic profiles than native congeners. *Ecology and Evolution*, 4, 2777–2786. <https://doi.org/10.1002/ece3.1132>
- Maerz, J. C., Blossey, B., & Nuzzo, V. (2005). Green frogs show reduced foraging success in habitats invaded by Japanese knotweed. *Biodiversity and Conservation*, 14, 2901–2911. <https://doi.org/10.1007/s10531-004-0223-0>
- Maurel, N., Salmon, S., Ponge, J. F., Machon, N., Moret, J., & Muratet, A. (2010). Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions*, 12, 1709–1719. <https://doi.org/10.1007/s10530-009-9583-4>

- McIver, J., & Grevstad, F. (2010). *Natural enemies of invasive knotweeds in the pacific northwest*. Morgantown, West Virginia: Forest Health Technology Enterprise Team.
- McKey, D. (1974). Adaptive patterns in alkaloid physiology. *The American Naturalist*, 108, 305–320. <https://doi.org/10.1086/282909>
- Miyatake, Y. (2001). Psyllids in the southern Osaka. *Minami-Osaka*, 3, 6–10.
- Myint, Y. Y., Nakahira, K., Takagi, M., Furuya, N., & Shaw, R. H. (2012). Using life-history parameters and a degree-day model to predict climate suitability in England for the Japanese knotweed psyllid *Aphalara itadori* Shinji (Hemiptera: Psyllidae). *Biological Control*, 6, 129–134. <https://doi.org/10.1016/j.biocontrol.2012.07.004>
- Ness, J. H., Morales, M. A., Kenison, E., Leduc, E., Leipzig-Scott, P., Rollinson, E., ... von Allmen, D. R. (2013). Reciprocally beneficial interactions between introduced plants and ants are induced by the presence of a third introduced species. *Oikos*, 122, 695–704. <https://doi.org/10.1111/j.1600-0706.2012.20212.x>
- Price, E. A. C., Gamble, R., Williams, G. G., & Marshall, C. (2002). Seasonal patterns of partitioning and remobilization of 14C in the invasive rhizomatous perennial Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decraene). *Evolutionary Ecology*, 15, 347–362. <https://doi.org/10.1023/A:1016036916017>
- Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs*, 43, 95–124. <https://doi.org/10.2307/1942161>
- Schulz, A. N., Lucardi, R. D., & Marsico, T. D. (2019). Successful invasions and failed biocontrol: The role of antagonistic species interactions. *BioScience*, 69(9), 711–724. <https://doi.org/10.1093/biosci/biz075>
- Shaw, R. H., Bryner, S., & Tanner, R. (2009). The life history and host range of the Japanese knotweed psyllid, *Aphalara itadori* Shinji: Potentially the first classical biological weed control agent for the European Union. *Biological Control*, 49, 105–113. <https://doi.org/10.1016/j.biocontrol.2009.01.016>
- Sorokan, A. V., Rumyantsev, S. D., Benkoversuskaya, G. V., & Maksimov, I. V. (2017). The ecological role of microsymbionts in the interaction of plants and herbivorous insects. *Biology Bulletin Reviews*, 7, 506–518. <https://doi.org/10.1134/S207908641706007X>
- Steinbauer, M. J., Clarke, A. R., & Madden, J. L. (1998). Oviposition preference of a Eucalyptus herbivore and the importance of leaf age on interspecific host choice. *Ecological Entomology*, 23, 201–206. <https://doi.org/10.1046/j.1365-2311.1998.00122.x>
- Stiling, P. (1993). Why do natural enemies fail in classical biological control programs? *American Entomologist*, 39, 31–37. <https://doi.org/10.1093/ae/39.1.31>
- Urgenson, L. S., Reichard, S. H., & Halpern, C. B. (2009). Community and ecosystem consequences of giant knotweed (*Polygonum sachalinense*) invasion into riparian forests of western Washington. USA. *Biological Conservation*, 142, 1536–1541. <https://doi.org/10.1016/j.biocon.2009.02.023>
- USDA NRCS. (2011). The PLANTS database. Retrieved from <http://plants.usda.gov>. 455National Plant Data Center, Baton Rouge, LA, 70874-4490, USA.
- Van Dam, N. M., Verpoorte, R., & van der Meijden, E. (1994). Extreme differences in pyrrolizidine alkaloid levels between leaves of *Cynoglossum officinale*. *Phytochemistry*, 37, 1013–1016. [https://doi.org/10.1016/S0031-9422\(00\)89519-9](https://doi.org/10.1016/S0031-9422(00)89519-9)
- Weston, L. A., Barney, J. N., & DiTommaso, A. (2005). A review of the biology and ecology of three invasive perennials in New York State: Japanese knotweed (*Polygonum cuspidatum*), mugwort (*Artemisia vulgaris*) and pale swallow-wort (*Vincetoxicum rossicum*). *Plant and Soil*, 277, 53–69. <https://doi.org/10.1007/s11104-005-3102-x>
- White, S. D. (2007). The efficacy of *Aphalara itadori* as a biological control agent of Japanese knotweed (*Fallopia japonica*). Unpublished Masters Thesis. Imperial College, University of London.
- Wilde, M. (2019). Japanese knotweed and economic loss in nuisance: Framing environmental harm in tort. *Journal of Environmental Law*, 31, 343–349. <https://doi.org/10.1093/jel/eqz016>
- Winston, R. L., Schwarzländer, M., Hinz, H. L., Day, M. D., Cock, M. J. W., & Julien, M. H. (2014). *Biological control of weeds: A world catalogue of agents and their target weeds* (5th ed.). Morgantown, West Virginia: Forest Health Technology Enterprise Team, USDA Forest Service.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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