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RESEARCH ARTICLE

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Biological control of Canada thistle (*Cirsium arvense*) revisited: host range of *Hadroplontus litura* on *Cirsium* species native to the Upper Midwest, USA

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ABSTRACT

In 1998, *Hadroplontus* (formerly *Ceutorhynchus) litura,* a stem-mining weevil, was introduced into a limited area in Minnesota for the biological control of Canada thistle, *Cirsium arvense*. Although showing a preference for *C. arvense*, initial host range testing in the 1960s indicated *H. litura* attacked other native *Cirsium* species. Before promoting or augmenting biocontrol with *H. litura* in Minnesota, we wanted to further define the host range of *H. litura* on native *Cirsium* species. Our objective was to determine whether *H. litura* could feed, oviposit and complete development on *Cirsium* spp. native to the Upper Midwest of the USA. In no-choice tests, female *H. litura* accepted all native *Cirsium* species for oviposition. In addition, *H. litura* was able to complete development to the adult stage on swamp thistle, *Cirsium muticum*, field thistle, *Cirsium discolour*, and tall thistle, *Cirsium altissimum,* and we confirmed the published host range test results of completed development on Flodman's thistle, *Cirsium flodmanii*. These *Cirsium* species are within the fundamental host range of *H. litura*. No adults were found in development tests with Hill's thistle, *Cirsium pumilum var. hillii*, a threatened or species of concern in the Upper Midwest, or Pitcher's thistle, *Cirsium pitcheri*, a federally listed threatened species. Larval tunnelling was documented in *C. pitcheri*. We recommend that field tests be conducted, where search and host acceptance behaviour can occur under field conditions to further define the ecological host range of *H. litura*.

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Introduction

The ubiquitous invasive perennial, Canada thistle, *Cirsium arvense* (L.) Scop., is native to Europe and the Mediterranean (Slotta et al., 2010) and has been introduced worldwide. It is considered one of the worst weeds of agricultural and natural systems (Cripps et al., 2001). In North America, *C. arvense* is present in 42 states, 12 Canadian provinces and has a noxious weed status in 46 states (USDA, NRCS, 2022).

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Figure 1. *Cirsium* species no-choice oviposition test set-up. *Cirsium* leaves were inserted into florist foam and then placed inside glass jars. Mating pairs of *Hadroplontus litura* were released into the jars. After one day, leaves were dissected and the number of *H. litura* eggs were counted. St. Paul, MN. 2016.

The stem-mining weevil, *Hadroplontus litura* (F.), is native to western Europe (GBIF, 2022). In North America, *H. litura* was first introduced into Canada as a biological control agent for *C. arvense* in 1965 (Peschken & Beecher, 1973). It was subsequently introduced into the USA in 1972, with the first releases in Montana and has since become established in Idaho, Montana, Nebraska, North Dakota, Oregon, Utah, Virginia, Washington and Wyoming (Winston et al., 2007). In 1998, *H. litura* was introduced into a limited area in Minnesota, with a resulting long-term decline in populations of *C. arvense* (Chandler, 2009).

Adult *H. litura* overwinter in the soil and leaf litter. In spring, the onset of adult activity is synchronised with the emergence of *C. arvense* shoots from the soil (Gramig et al., 2015; Peschken & Wilkinson, 1981; Zwolfer & Harris, 1966). Adults initially feed on leaves of emerging shoots (Peschken & Beecher, 1973; Rees, 1990; Zwolfer & Harris, 1966). Females oviposit in the mid-vein on the underside of leaves and larvae progress through three instars (Zwolfer & Harris, 1966). Larvae successively mine leaf midribs, stems, and crowns of *C. arvense* plants throughout the spring and summer (Zwolfer & Harris, 1966). Third-instar larvae emerge from *C. arvense* plants in late summer, pupate in the soil, and emerge as adults from July to October, depending on location (Peschken & Beecher, 1973; Rees, 1990; Zwolfer & Harris, 1966). *Hadroplontus litura* is univoltine (produces one generation per year).

Reports conflict regarding the efficacy of *H. litura* as a biocontrol agent against *C. arvense*. Reed et al. (2006) found that *H. litura* infestations did not reduce thistle stem counts, number of flowers or overwinter survival in *C. arvense* stands in two South Dakota wildlife management areas. In contrast, when measured 15 years after release of *H. litura*, Rees (1990) report a 75–92% reduction in *C. arvense* stem density in plots infested with *H. litura* larvae. Underground roots suffered higher winter

Figure 2. *Cirsium* species no-choice development test set-up. Marked mating pairs of *Hadroplontus litura* adults were released into caged *Cirsium* plants. Plants were monitored for emergence of F1 adults. St. Paul, MN 2016, 2017, 2018.

mortality rates as a consequence of *H. litura* larval mining and adults dispersed 9 km over 15 years (Rees et al., 1990). In the spring, larvae tunnel through stems and disrupt the transport of photoassimilates to roots, resulting in reduced levels of free sugars and fructans. However, carbohydrate levels recover later in the summer (Hein & Wilson, 2004).

Efficacy of *H. litura* may increase when combined with other *C. arvense* management strategies or release of additional biocontrol agents. Peschken and Wilkinson (1981) report that *H. litura* did not control *C. arvense* stands alone but could contribute to a decline in populations when combined with additional plant stressors, such as pathogens or other insects. Markin and Larson (2011) documented significant decline in *C. arvense* abundance after ten years when *H. litura* was released in combination with the Canada thistle gall fly, *Urophora cardui* (L.), and the Canada thistle stem weevil, *Larinus planus* (F.). After attack by *H. litura*, *L. planus*, *U. cardui*, and the leaf defoliator, thistle tortoise beetle, *Cassida rubiginosa* Müller, total non-structural carbohydrates were 67% lower in *C. arvense* roots the following spring, compared with roots of plants without the presence of insect agents (Liu et al., 2000).

Burns et al. (2013) concluded that *H. litura* 'was a relatively weak biological control agent' but could suppress *C. arvense* stands in combination with competitive plant species, such as sunflower, *Helianthus annuus* L. In addition, competition from the native, cool-season needle and thread grass, *Hesperostipa comata* (Trin. & Rupr.) Barkworth, coupled with *H. litura* attack, reduced root biomass, which may compliment restoration efforts over either control method used alone (Ferrero-Serrano et al., 2008). Lastly, the combination of *H. litura* injury and herbicide applications reduced *C. arvense* shoot biomass more than either control strategy alone (Collier et al., 2007).

The University of Minnesota herbarium lists six thistles in the *Cirsium* genus as native to Minnesota (Table 1). These include three biennials; tall thistle, *Cirsium altissimum* (L.) Spreng., field thistle, *Cirsium discolour* (Muhl. ex Willd.) Spreng., and swamp thistle, *Cirsium muticum* Michx., and three perennials; Flodman's thistle, *Cirsium flodmanii* (Rydb.) Arthur, wavy-leaved thistle, *Cirsium undulatum* (Nutt.) Spreng., and Hill's thistle, *Cirsium pumilum* var. *hillii* (Nutt) Spreng. Of note, *C. pumilum* var. *hillii* is a monocarpic perennial (Keil, 1997) and is listed as a species of special concern in Minnesota (Minnesota Department of Natural Resources, n.d.), Michigan (Michigan State University, n.d.), and a threatened species in Wisconsin (Wisconsin Department of Natural Resources, n.d.) and Ontario (Ontario Ministry of the Environment, Conservation and Parks, 2021). *Cirsium pumilum* var. *hillii* is found most often in dry prairies and savanna woodlands. Although not endemic to Minnesota, Pitcher's thistle, *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Grey, is a threatened species and is native to the dune ecosystem of the Great Lakes region (US Fish and Wildlife Service, 2019). Non-target attack of *C. pitcheri* by agents released for biological control of other *Carduus* and *Cirsium* species is a concern (Havens et al., 2012).

In North America, *H. litura's* primary host is *C. arvense*, although its host range includes the *Cirsium-Silybum-Carduus* complex of the Asteraceae subtribe, Carduinae

Table 1. *Cirsium* species included in *Hadroplontus litura* host range testing. All native species are present in Minnesota except for *Cirsium pitcheri*, which is native and present east of Minnesota. *Cirsium arvense* is a non-native invasive species.

Scientific name	Common name	Life cycle	Legal Status – Upper Midwest	Propagation method, seed/plant source
Cirsium arvense	Canada thistle	perennial	Prohibited Noxious Weed-MN	Root segments/St. Paul, MN (44.989920, −93.185503)
Cirsium altissimum	tall thistle	biennial	none	Seeds/Cumberland, Iowa (41.274186, −94.870336)
Cirsium discolour	field thistle	biennial	none	Seeds/Maplewood, MN (44,929148, −92.997039)
Cirsium flodmanii	Flodman's thistle	perennial	none	Plants/Morning Sky Greenery (45.607745, −95.856771)
Cirsium muticum	swamp thistle	biennial	none	Seeds/Prairie Moon Nursery (43.903211, −91 .637046) and Burnham Wildlife Management Area, Polk County, MN (47.630295, −96.35160)
Cirsium pumilum var. *hillii*	Hill's thistle	monocarpic perennial	Special Concern: MN, MI Threatened: WI, Ontario	Plants/Ordway Prairie, MN (45.444663, −95.244426)
Cirsium undulatum	wavy-leaved thistle	perennial	None	Seeds/Germplasm Resources Information Network (GRIN)
Cirsium pitcheri	Pitcher's thistle	monocarpic perennial	Threatened species-USFWS. Native to Ontario, WI, MI, IL, IN	Seeds/Chicago Botanic Garden (Lake Michigan area, original source not known)

(Zwolfer, 1965). There are no *Carduus* or *Silybum* species native to North America, but there are at least 62 native species of *Cirsium* (Keil, 1997). Initial host range testing indicated that *H. litura* fed on native clustered thistle, *Cirsium brevistylum* Cronquist, *C. undulatum* and *C. flodmanii* (Zwolfer, 1965; Zwolfer & Harris, 1964; Zwolfer & Harris, 1966). Oviposition or larval development was not reported in these native thistle species with one exception. Larval development was observed in *C. undulatum* when eggs or newly hatched larvae were placed into a pre-made hole in the stem and then re-checked (Zwolfer & Harris, 1966). Slotta et al. (2012) reported that the host range of *C. arvense* biocontrol insects, *L. planus* and the thistle seed head weevil, *Rhinocyllus conicus* Froel, did not follow phylogenetic lines developed for *Cirsium* species, which were derived from native *Cirsium* DNA sequences. Therefore, they recommend that a more comprehensive list of *Cirsium* species should be included in host range testing of *C. arvense* biological control insects.

Before promoting or augmenting biocontrol with *H. litura* in Minnesota, we wanted to further define the host range of *H. litura* on native *Cirsium* species. If *H. litura* only develops on *C. arvense*, a programme to augment and support biological control with *H. litura* could be implemented to provide a cost-effective, long-term suppressive management tool for *C. arvense*. The objective of our research was to determine whether *H. litura* could feed, oviposit, and complete development on *Cirsium* spp. native to the Upper Midwest, some of which were not included in the original host range testing.

Materials and methods

Cirsium *plant propagation*

We collaborated with the Minnesota Biological Survey to locate sources for each native thistle when possible or purchased *Cirsium* thistle seed or plants from local seed sources (Table 1). Since *H. litura* adults actively oviposit in the spring, *Cirsium* plants were established each summer prior to host range testing and overwintered so initiation of leaf growth from rosettes or emerged perennial shoots would be available in the spring when adults became active. Plants were propagated and experiments conducted at the University of Minnesota, St. Paul Field Station (lat/long: 44.9902/-93.1824; elevation: 296 m). For host range tests, we used excised leaves and outdoor-grown potted plants. As such, tests may not reflect insect herbivore behaviour in the respective environmental niche for each individual *Cirsium* species in its native habitat. This intent was to develop general knowledge on host specificity of *H. litura* on a *Cirsium* relevant to our region. Further research is necessary to determine responses of *H. litura* to native *Cirsium* under field conditions.

In 2014, 2015, and 2016, two years prior to each year of host range testing, seeds of all *Cirsium* species, except the perennials *C. arvense* and *C. flodmanii,* were germinated using two techniques. Field stratification consisted of planting seeds in plug trays filled with a standard commercial potting mix (LC8; 70–80% Canadian sphagnum peat moss, 20–25% perlite, 5–10% vermiculite; Sungro Horticulture, 770 Silver Street, Agawam, MA 01001). Trays were placed outside in November and lightly mulched with straw to overwinter. Mulch was removed in early spring (April in Minnesota) when seedlings emerged. In case field stratification failed, *Cirsium* seeds were also

stratified in the lab by adding moistened sand to a 90-mm diameter x 15-mm deep plastic petri dish, adding a layer of seeds, then covering the seeds with additional moist sand. Petri dishes were sealed and placed in a refrigerator at 4 C°. After six weeks, seeds were removed and planted in a plug tray filled with the standard potting mix described previously.

In the spring of 2015, 2016 and 2017, one year prior to testing, all *Cirsium* seedlings propagated via the described procedures were transplanted outdoors into 11.4-l pots using the same commercial potting mix used previously, with the addition of a 1:1 ratio of a greenhouse soil (silt loam:sand:manure:peat at a 1:1:1:1, v/v/v/v). Instead of seedlings, *C. flodmanii* and *C. arvense* shoot segments were planted the summer prior to testing using this same pot protocol. Few *C. pumilum* var. *hillii* germinated from seed despite various germination strategies. As a result, we collected and transplanted rosettes from Ordway Prairie, MN during the summer of 2016 and 2017 to establish plants for testing the following spring. Considering the difficulty in establishing several of the native *Cirsium*, plants were fertilised once at transplanting with a slow-release fertiliser containing macro- and micro-nutrients (Osmotcote Plus, 15-9-12 plus micronutrients, Scotts Company LLC, 14111 Scottslawn Road, Marysville, OH 43040), at a rate of 112 kg/ha NH3–N, NO3, 37 kg/ha P2O5, and 71 kg/ha K20. The added nutrients were released over a period of four months, so a full dose was not present in the potting soil at any one time. The nutrient levels were consequential for transplanting, but inconsequential after established. Each autumn prior to testing, potted thistle plants were overwintered in the field using a pot-in-pot method (Mathers, 2003) to ensure winter survival during Minnesota winters. This technique consisted of digging a hole in the ground, then placing an empty 11.4 L pot into the hole so that the rim of the pot was level with the soil. Next, a potted plant was inserted into the empty pot. This method facilitated easier removal of potted plants the following spring. Plants were lightly mulched with straw for overwintering. This technique is similar to that used by Peschken and Derby (1992) to overwinter potted *C. arvense* plants in Regina, Saskatchewan. Multiple plants of each species were established so that replicated host-range field trials could be conducted.

In spring 2017, we found that all overwintered native *Cirsium* crowns had been foraged by small rodents, even though they were placed in a fenced enclosure. Of note, all *C. arvense* crowns were left undisturbed. As a result, in the fall of 2017, all plants were individually caged with 0.635-cm square mesh galvanised steel hardware cloth that extended outside of the pot into the ground. In the springs of 2017 and 2018, all overwintered native thistles were present and survived, except for *C. undulatum*. For this reason, *C. undulatum* was not included in in development or single-choice tests.

Hadroplontus litura *colony establishment*

To establish insect colonies, adult *H. litura* were purchased (Biological Control of Weeds Inc., 1418 Maple Drive, Bozeman, MT 59715) and were received in July 2015, 2016, and 2017. Once received, adults were released immediately into caged *C. arvense* plants established in 11.4 L pots and were maintained outside. *Hadroplontus litura* adults were overwintered outside on the caged *C. arvense* plants using the pot-in-pot method. When adults became active in subsequent springs, they were collected from the overwintered plants for use in host range tests.

Hadroplontus litura host range tests

To further delineate the host range of *H. litura*, we conducted no-choice feeding and oviposition tests, no-choice development tests and single-choice oviposition tests. Host plant acceptance by *H. litura* includes both oviposition choice by females and the ability of larvae to complete development. Once *H. litura* females lay their eggs into a plant stem, developing larvae are unable to change host plants. Consequently, successful female oviposition ultimately determines the potential host range of this weevil species. If a *Cirsium* species was not accepted for oviposition, then it was considered not at risk for *H. litura* larval stem-mining and was not included in no-choice larval development testing. All host range development tests were conducted in the field on caged plants in April through June 2016, 2017 and 2018. Details on individual host range tests follow.

No-choice oviposition tests

No-choice and oviposition tests were conducted in the spring and early summer when *H. litura* females were laying eggs. Procedures were similar to those described by Gerber et al. (2009) for *Ceutorhynchus scrobicollis* Nerenscheimer and Wagner host range tests. Adults were collected from overwintered, caged *C. arvense* plants described previously. Prior to inclusion in oviposition experiments, females were offered *C. arvense* to ensure that they were laying eggs using the procedure described by Gerber et al. (2009) and only ovipositing females were used in subsequent experiments. Each replicate of the no-choice and oviposition test was prepared as follows. A hydrated piece of florist foam was placed inside a self-sealing clear plastic bag. A hole was pierced in the top of the bag and an excised *Cirsium* spp. leaf was inserted into the florist foam through the hole. Leaves were a minimum of 5 cm in length as Zwolfer and Harris (1964) found *H. litura* did not oviposit on leaves shorter than 5 cm. A single leaf-foam unit was placed into a 1-L glass canning jar and the jar was covered with nylon mesh secured with a jar ring lid. A mating pair of *H. litura* was placed into each jar (Figure 1). Jars were kept indoors at room temperature near a window and exposed to the same spring/early summer photoperiod as outdoors. After one day, leaves and petioles were dissected and checked for eggs. Feeding and number of eggs per leaf were recorded. Percent feeding on the leaf was visually estimated. If eggs were not found on the *Cirsium* test plant leaf at the end of one day, it was replaced with a fresh *C. arvense* leaf for an additional day and checked for eggs to confirm that the female was still ovipositing. A replication was only counted as valid if eggs were sequentially laid in this *C. arvense* leaf. Additional jars containing *H. litura* on an excised *C. arvense* leaf were always included as controls when testing native *Cirsium* to ensure that conditions conducive for oviposition were present. A minimum of 10 replications were completed for each species with each individual jar a replication. Mean percent feeding, number of eggs, and mean standard error values were calculated.

No-choice development tests

Since all native *Cirsium* were accepted for oviposition in no-choice oviposition tests, no-choice development tests were conducted on all thistle species, except for *C. undulatum*. *Cirsium undulatum* rosettes did not survive the winters of 2016, 2017 or 2018, so plants were not available for testing the following spring. Caged, potted thistle plants were

maintained outdoors in an open area protected by surrounding trees. In spring, active adults were collected from the colonies maintained on caged *C. arvense* plants overwintered in the field. Adults were marked with a paint pen to make them easier to recover from test plants, and to differentiate parents from F1 progeny (Katovich et al., 2019). Prior to inclusion in trials, females were tested on *C. arvense* for egg laying and only ovipositing females were used in experiments. For each trial, two marked *H. litura* mating pairs were placed on each caged, potted thistle plant and then removed after two weeks (Figure 2). Caged plants were monitored for emergence of F1 progeny later in the season by checking for new adult leaf feeding, or for adults climbing on the interior of screen cages. Each plant was checked for F1 progeny a minimum of three times and number of *H. litura* progeny was recorded for each plant. At the final collection time, all plants were dissected and checked for larval mining and tunnelling. Caged *C. arvense* plants were tested separately, but concurrently with native *Cirsium* spp. as controls. A minimum of five replications of each *Cirsium* spp. were tested, with each caged plant a replication.

Single-choice oviposition tests

In 2017 and 2018, single-choice oviposition tests were conducted for all native *Cirsium* species except *C. undulatum,* because rosettes did not survive the winters of 2016 and 2017. Adult females were presented with an oviposition choice between a native *Cirsium* or *C. arvense* leaf. This test is less conservative than no-choice oviposition trials and allows females to choose where they want to deposit eggs. Overwintered *H. litura* were collected from the colony maintained on caged *C. arvense* plants after they became active in the spring. Prior to inclusion in tests, all *H. litura* females were placed in an oviposition test on *C. arvense* as previously described in the no-choice oviposition test protocol. One mating pair of *H. litura* was placed into a glass jar and simultaneously offered an excised leaf of the native *Cirsium* test species, and a *C. arvense* leaf. Leaves were placed in 1 L glass canning jars kept indoors at room temperature. Jars were placed near a window and exposed the same spring/early summer photoperiod as outdoors. After one day, leaves were dissected and the number of *H. litura* eggs recorded, along with presence/absence of feeding. Each exposure period was treated as one replicate. Replicates were only regarded as valid when females laid eggs into *C. arvense* or *Cirsium* spp. leaves.

Results

No-choice oviposition tests

Under no-choice conditions, female *H. litura* accepted all native thistle species tested for oviposition (Table 2). *Cirsium pumilum* var. *hillii* was not included in no-choice oviposition testing because the limited number of available plants were saved for single-choice oviposition tests (discussed later). Most eggs were laid in the leaf midrib or leaf petiole, with fewer than 10% of eggs laid in the leaf blade. Eggs were laid singly or in clusters. From these results, we conclude that *H. litura* females can accept these native *Cirsium* species for oviposition. Visual estimation of adult feeding on all species of *Cirsium* was minimal and ranged from less than 1% to 3% (Data not shown). However,

Table 2. Results of *Hadroplontus litura* no-choice oviposition tests with leaves of *Cirsium* species collected from the field. St. Paul, MN. 2016.

		Number of eggs		
Cirsium species	Number of replications	Total	Mean no. per replication	± Mean SE
C. arvense	74	309	4.2	0.4
C. discolour	10	77	7.7	1.3
C. flodmanii	10	56	5.6	0.9
C. pitcheri	10	41	4.1	1.0
C. muticum	10	89	8.9	1.4
C. altissimum	10	106	10.6	1.9
C. undulatum	10	45	4.5	1.0

oviposition tests do not determine whether these native *Cirsium* species can support *H. litura* development through the third-instar larval stage, our next step was to conduct no-choice development tests.

No-choice development tests

Unmarked F1 adults (offspring) were recovered on caged *C. flodmanii*, *C. altissimum, C. discolour,* and *C. muticum* plants at the same time that unmarked F1 *H. litura* were found in caged *C. arvense* control plants (Table 3). From this we conclude that *H. litura* larvae were able to complete development to the third-instar larval stage in these native *Cirsium* species and the pupae were able to successfully develop to adults in the soil. These *Cirsium* species are within the fundamental host range of *H. litura*. Of the native *Cirsium* species tested, *C. discolour* appeared similar to *C. arvense* in ability to support development of *H. litura*. No *C. undulatum* survived for inclusion in no-choice development tests. In a common garden established at the St. Paul Field Station, St. Paul, MN, USA, *C. undulatum* established each year of the experiment, but only 13% of plants survived the winter over the four years of the study (Katovich et al. unpublished).

Unfortunately, two of five *C. pitcheri* plants died of undetermined causes when the experiment was conducted in 2018 (Table 3). No F1 *H. litura* adults were recovered from the caged dead plants nor from the three remaining caged live plants. However, we noted larval tunnelling in one of the three live *C. pitcheri* plants, but no live or dead *H. litura* larvae were found.

Table 3. Results of *Hadroplontus litura* no-choice development tests on caged *Cirsium* species, St. Paul, MN, 2016–2018.

		Number of replications		Numbers of adults emerged		
Cirsium species	Year	Total	With adult emergence[a]	Total	Mean per replication	Range
C. arvense	2016–2018	10[b]	8	27	2.7	0–7
C. discolour	2016	8	6	112	14.0	0–43
C. flodmanii	2017	5	1	9	1.8	0–9
C. pitcheri	2018	5	0	0	0.0	0
C. pumilum var. *hillii*	2018	5	0	0	0.0	0
C. muticum	2016, 2018	7	5	7	1.0	0–2
C. altissimum	2017	5	2	6	1.2	0–5

[a]Sum of alive and dead adults.
[b]Total number of replications over three years.

Table 4. Results of single-choice oviposition tests. *Hadroplontus litura* adults offered a choice between native *Cirsium* and *Cirsium arvense* leaves. St. Paul, MN. 2017–2018.

			Mean egg number per plant		Percent distribution of eggs	
Cirsium species	Year	Number of replications	Native *Cirsium*	*C. arvense*	Native *Cirsium*	*C. arvense*
C. discolour	2017	6	4.8	2.5	66	34
C. flodmanii	2017	7	2.4	2.9	46	54
C. pumilum var. *hillii*	2018	5	0.6	3.2	16	84
C. pitcheri	2017	7	1.1	4.1	22	78
C. muticum	2018	5	1.0	2.6	28	72
C. altissimum	2017	6	1.5	4.8	24	76

Three of five *C. pumilum* var. *hillii* plants also died of undetermined causes when the experiment was conducted in 2018 (Table 3). Of these three dead plants, no tissue remained at the conclusion of the trial so we could not dissect stem or crown tissue to determine whether larvae contributed to mortality. Upon dissection of the two surviving plants, no larvae or larval tunnelling were found in roots or crowns. Based on these limited results and undetermined nature of death of *C. pitcheri and C. pumilum* var. *hillii* plants, additional tests are needed to determine whether they are within the fundamental host range of *H. litura*.

Since *H. litura* larvae pupate in the soil, it was necessary to conduct development tests with caged potted plants. This allowed us to collect and count F1 offspring. However, the soil mix did not always simulate the soil texture, water holding capacity, innate fertility and nutrient additions during rosette establishment and does not reflect the unique habitats of *Cirsium* species. Such is the case with *C. pitcheri*, common to low nutrient sand dunes and coastal habitat (Havens et al., 2012) where plant quality may have been altered compared to a field setting.

Single-choice oviposition tests

In single-choice oviposition tests, where *H. litura* females were able to choose which host to accept for oviposition, eggs were deposited on all native thistles tested (Table 4). *Cirsium undulatum* was not tested because potted rosettes did not survive the winters of 2016 or 2017. Compared with *C. arvense,* there were more eggs deposited on *C. discolour* leaves and a similar number deposited on *C. flodmanii* leaves. Eggs were present in the remaining species, but when given a choice, *H. litura* preferred *C. arvense* over *C. pumilum* var. *hillii, C. pitcheri, C. muticum, and C. altissimum,* with approximately 70–75% of eggs laid on *C. arvense* plants. From these results, we conclude that *H. litura* females will accept all tested species for oviposition, even in the presence of *C. arvense*. However, *C. arvense* is clearly preferred for oviposition over *C. pumilum var. hillii*, *C. pitcheri*, *C. muticum* and *C. altissimum*.

Discussion

Our results show that *H. litura* was able to complete development on *Cirsium* native to Minnesota and the upper Midwest, including *C. muticum*, *C. flodmanii*, *C. discolour*, and *C. altissimum* in no-choice development tests. These *Cirsium* species are within the fundamental host range of *H. litura*.

In no-choice oviposition tests, female *H. litura* laid eggs on *C. pumilum* var. *hillii,* a species of special concern or of threatened status in Minnesota, Michigan, Wisconsin and Ontario. *Hadroplontus litura* females also laid eggs on the federally threatened *C. pitcheri* thistle. However, no adults emerged from development tests in either species. Larval tunnelling was documented in one of three *C. pitcheri* plants, but no *H. litura* larvae were found. No larvae were present or larval tunnelling found in *C. pumilum var. hillii.* More than half of *C. pumilum var. hillii* and *C. pitcheri* thistle plants died during the course of the experiment conducted in 2018. The dead *C. pumilum var. hillii* plants had decomposed at the conclusion of the trial so we could not dissect stem or crown tissue to determine whether larval tunnelling occurred. It is unclear whether *C. pumilum* var. *hillii* and *C. pitcheri* died as a result of *H. litura* attack, or whether mortality was caused by other factors.

Cirsium undulatum rosettes did not survive in two of three winters during the course of our study. so we were unable to complete larval development or single-choice tests for this species However, previous studies indicated that *H. litura* completed larval development on *C. undulatum* when *H. litura* eggs or larvae were transferred onto plants. (Zwolfer & Harris, 1966).

Cirsium discolour, *C. altissimum*, *C. flodmanii* and *C. muticum* are within the fundamental host range of *H. litura* as they completed development on these native *Cirsium* species under no-choice conditions. Because we were unable to find reports in the literature of non-target attack by *H. litura* in the field, it is not clear whether *H. litura* adults would accept these *Cirsium* species under field conditions, or if they did, could sustain populations over time. In fact, Grevstad et al. (2021) complied a large database of weed biocontrol agents introduced to North America between 1946 and 2015. They conclude that only 35% of native non-target plants, with a pre-release test history of oviposition or larval development, had post-release field use by biocontrol agents.

Our study is the first to examine the development of *H. litura* in these native *Cirsium* species. Since *H. litura* larvae pupae in the soil, it was necessary to conduct development tests in caged potted plants to ensure recovery of F1 adults. The ecological host range of *H. litura* would encompass insect behaviour in a field setting, where the weevils would exhibit normal host search and acceptance behaviour and would typically be a subset of the fundamental host range (Van Klinken & Edwards, 2002; Schaffner, 2001).

Host plant acceptance by an insect herbivore involves a complex hierarchy of stimuli, of which individual components are difficult to quantify (Cripps et al., 2016). However, differences in phenology between a host plant, such as *C. arvense* and native non-host plants can narrow a biocontrol agent's host range in the field (Louda, 1998). Host plant density, relative availability, and field distribution (Cripps et al., 2016; Moffat et al., 2013) can help define the ecological host range of biocontrol insect herbivores. Additionally, host plant quality can affect insect herbivore performance within its ecological host range (Centre et al., 2014; Walker et al., 2008). The native *Cirsium pitcheri* was the only thistle whose ecological niche is depauperate of nutrients (Kayri Havens, personal communication), and as such may have had higher tissue levels of macro- and micronutrients when started in commercial potting mix then transplanted into sand. *Cirsium pumilum* var. *hillii* is found in calcareous loams in Karst topography and sandy soil prairies in Minnesota (Welby Smith, personal communication), and may have had slightly elevated tissue nutrient levels than would occur *in situ*. Both

could have altered *H. litura* performance, but to our knowledge, would not have altered host specificity. All other native *Cirsium* in our study, and *C. arvense,* thrive across broad ranges of habitat, nutrient levels, and soil types, including the Waukegan silt loam present at the field station.

Based on the current concern for development on native non-target species, Cripps et al. (2001) conclude that in the United States, *H. litura* probably would not have been approved in today's regulatory climate. However, we were unable to document non-target attack by *H. litura* in the field. Therefore, we recommend field testing, such as in a *Cirsium* common garden, where search and acceptance behaviour can occur in a more natural setting. Such a study could be similar to the field screening of *Hadroplontus trimaculatus* (F.) on *Carduus* and *Cirsium* species (Dunn & Campobasso, 1993). Additional studies, assessing the impact of non-target acceptance by *H. litura* on native *Cirsium* at the population level (Catton et al., 2016), would further define the ecological host range of *H. litura*.

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