

Research Article

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Phenologies of Canada thistle (*Cirsium arvense*) and *Cirsium* species native to the upper Midwest: implications for the ecological host range of the biocontrol agent *Hadroplontus litura*

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Abstract

Native *Cirsium* species play an important role in landscapes across North America. *Hadroplontus litura* (F.) (formerly *Ceutorhynchus litura*), the stem-mining weevil and biological control agent of Canada thistle [*Cirsium arvense* (L.) Scop.] can complete its life cycle on five *Cirsium* species native to the upper Midwest. Although these five *Cirsium* species are within the fundamental host range of *H. litura*, as determined by host-range tests, we wanted to explore whether phenological differences among *Cirsium* species help define the field ecological host range of *H. litura*. The objective of this study was to determine the phenology of *Cirsium* species native to the upper Midwest in relation to *C. arvense* and *H. litura*. Our goal was to explore whether shoots of native *Cirsium* species could escape *H. litura* shoot oviposition in spring due to delayed shoot emergence relative to *C. arvense*. Soil cumulative growing degree days (GDD) were a superior predictor of shoot emergence for perennial *Cirsium* species or initiation of leaves in biennial *Cirsium* species, with a 2.4 times larger effect on time to emergence relative to air GDD. All native *Cirsium* species initiated new leaves or shoots before *C. arvense* shoot emergence, even when native *Cirsium* species growth was delayed in the spring. In turn, *C. arvense* shoots emerged approximately 1 to 3 wk before female *H. litura* began to lay eggs. As such, all native *Cirsium* plants had shoots available for *H. litura* oviposition. There was no phenological separation between native *Cirsium* and *C. arvense* shoot emergence or initiation that would render native *Cirsium* species safe from *H. litura* attack. Based on the phenology of shoot emergence or initiation in the spring, all tested *Cirsium* species native to the upper Midwest would be within the ecological host range of *H. litura*.

Introduction

Native *Cirsium* species play an important role in landscapes across North America (Eckberg et al. 2017). Of significance, native thistle flowers produce a high-sugar nectar and are a pollen source for more than 200 species of native pollinators, including a variety of butterflies, bees, and other insects (Eckberg et al. 2017; Fussell and Corbet 1992; Hilty 2015; Lye et al. 2010; Robertson 1929). Native *Cirsium* flowers provide a food source for birds, insect defoliators, and seed feeders (Eckberg et al. 2017; Hilty 2015), such as the American goldfinch (*Spinus tristis* L.), which feeds heavily on thistle seed during its breeding season (Stokes 1950). The high moisture content of native *Cirsium* seed in the milky stage of development provides an important source of water (Gluck 1985).

The ubiquitous, invasive perennial Canada thistle [*Cirsium arvense* (L.) Scop.] is native to Europe and the Mediterranean region (Slotta et al. 2010) and has been introduced worldwide. *Cirsium arvense* may have been introduced into North America from multiple continents (Slotta et al. 2006), and populations are genetically diverse (Slotta et al. 2010). It is considered one of the worst weeds of agricultural and natural systems (Cripps et al. 2011). In North America, *C. arvense* is present in 42 states and 12 Canadian provinces and has a noxious weed status in 46 states (USDA-NRCS 2022). *Cirsium arvense* is a herbaceous perennial plant, with above-ground shoots dying back over the winter and underground roots surviving from year to year (Moore 1975). Plants reproduce through seed and vegetative spread via underground lateral roots to form large interconnected clonal patches (Donald 1994; Moore 1975). *Cirsium arvense* plants rapidly colonize new areas and are difficult to control in perennial and annual cropping systems (Tiley 2010).

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Management Implications

In 1998, *Hadroplontus litura*, the stem-mining weevil and biological control agent of *Cirsium arvense* (Canada thistle), was introduced into a limited area in Minnesota, with a resulting decline in *C. arvense* populations. The state of Minnesota is interested in expanding and augmenting its *C. arvense* biological control program. Before recommending *H. litura* for release into additional sites, we wanted to determine the host range of *H. litura* on *Cirsium* species native to the upper Midwest. Previous work documented that *H. litura* could complete its life cycle on *Cirsium discolor* (field thistle), *Cirsium muticum* (swamp thistle), *Cirsium altissimum* (tall thistle), *Cirsium flodmanii* (Flodman's thistle), and *Cirsium undulatum* (wavy-leaved thistle) in no-choice tests in the spring. Based on the phenology of shoot emergence/initiation in the spring presented in this study, all tested *Cirsium* species native to the upper Midwest have the potential to be within the ecological host range of *H. litura*. As such, we recommend further studies on *H. litura* search and acceptance behavior be determined in the field, outside a screen cage, to further define the ecological host range of *H. litura*. Although we are not aware of published accounts of *H. litura* accepting these native *Cirsium* species as hosts in the field, it would be prudent for managers to document any observed attack.

In North America, *Hadroplontus litura* (F.) (formerly *Ceutorhynchus litura*) was first introduced as a biological control agent for *C. arvense* in 1965 (Peschken and Beecher 1973). In the United States, it has since become established in Idaho, Montana, Nebraska, North Dakota, Oregon, Utah, Virginia, Washington, and Wyoming (Winston et al. 2009). Adult *H. litura* overwinter in the soil and leaf litter. In spring, the onset of adult activity is synchronized with the emergence of *C. arvense* shoots from the soil (Gramig et al. 2015; Peschken and Wilkinson 1981; Zwolfer and Harris 1966). Adults initially feed on leaves of emerging shoots (Peschken and Beecher 1973; Rees 1990; Zwolfer and Harris 1966). Females oviposit in the midvein on the underside of leaves, and larvae progress through three instars (Zwolfer and Harris 1966). Larvae successively mine leaf midribs, stems, and crowns of *C. arvense* plants throughout the spring and summer (Zwolfer and 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 and Beecher 1973; Rees 1990; Zwolfer and Harris 1966). *Hadroplontus litura* is univoltine (produces one generation per year).

The fundamental host range of a weed biological insect is defined as the set of plant species on which the insect can complete its life cycle (Schaffner 2001; Van Klinken 2000). The ecological host range is a subset of the fundamental host range and comprises plant species that biocontrol agents exploit as hosts in the field (Schaffner 2001). 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 (Zwolfer and Harris 1966). There are no *Carduus* or *Silybum* species native to North America, but there are at least 62 native species of *Cirsium* (Keil 2006). Initial host-range testing indicated that *H. litura* fed on clustered thistle (*Cirsium brevistylum* Cronquist), wavy-leaved thistle [*Cirsium undulatum* (Nutt.) Spreng.], and Flodman's thistle [*Cirsium flodmanii* (Rydb.) Arthur] (Zwolfer 1965; Zwolfer and Harris 1964, 1966).

Recent work by Katovich et al. (2022) expanded the fundamental host range of *H. litura* to include the native *Cirsium* species swamp thistle (*Cirsium muticum* Michx.), field thistle [*Cirsium discolor* (Muhl. ex Willd.) Spreng.], and tall thistle [*Cirsium altissimum* (L.) Sprengel.]. The federally threatened Pitcher's thistle [*Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray] (U.S. Fish and Wildlife Service 2019), was accepted for oviposition, but no adults were found in development tests, so it is not known whether *H. litura* can complete its life cycle on this species.

Although these native *Cirsium* species are within the fundamental host range of *H. litura*, it is unclear whether *H. litura* adults would accept these native *Cirsium* species as hosts in the field, where weevils would exhibit normal host search and acceptance behavior.

Differences in phenology between a host plant, such as *C. arvense*, and native non-host plants can also narrow a biocontrol agent's host range in the field (Louda 1998). We were unable to find reports in the literature of non-target attack by *H. litura* in the field. As such, the objective of our research was to further characterize the ecological host range of *H. litura* by comparing the phenologies of spring shoot emergence of *Cirsium* species native to the upper Midwest with the phenologies of *C. arvense* and *H. litura*. Our goal was to explore whether shoots of native *Cirsium* species could escape *H. litura* shoot oviposition in spring due to delayed shoot emergence relative to *C. arvense*. This work expands on our previous work on the fundamental host range of *H. litura* (Katovich et al. 2022) by further characterizing the ecological host range of *H. litura* on previously untested *Cirsium* species native to the upper Midwest.

Materials and Methods

Trial Design

A common garden was established at the University of Minnesota St Paul Field Station to compare the relative phenologies of native *Cirsium* species and *C. arvense*. We established a common garden so that all *Cirsium* species could be propagated at the same latitude and longitude and under the same environmental conditions (Berend et al. 2019; Liang 2016). Native *Cirsium* plants often grow at low densities at sites (Eckberg et al. 2017) and do not often co-occur. Establishing a common garden was thought to be the best method to make direct comparisons of shoot emergence among species. When planting the common garden, we tried to provide optimum growing conditions for all species.

Cirsium species included in the common garden, along with seed and plant sources are listed in Table 1. Propagation methods as well as *H. litura* colony establishment were as described in Katovich et al. (2022). *Cirsium* species included: three native biennial species—*C. altissimum*, *C. discolor*, and *C. muticum*; three native perennial species—*C. flodmanii*, *C. undulatum*, and *C. pitcheri*; and the introduced perennial *C. arvense*. We collaborated with the Minnesota Biological Survey to locate sources for each native *Cirsium* species when possible or purchased *Cirsium* seed or plants from local seed sources.

Because *H. litura* adult females actively oviposit in the spring, *Cirsium* plants were established each summer before monitoring and overwintered so initiation of leaf growth from rosettes or emerged perennial shoots would be available in the spring when adults became active.

Cirsium species were transplanted into the common garden in a randomized complete block design with six replications each year

Table 1. *Cirsium* species included in the common garden (St Paul, MN).^a

Scientific name	Common name	Life cycle	Legal Status	Seed/plant source
<i>Cirsium arvense</i>	Canada thistle	Perennial	Prohibited Noxious Weed (MN)	St Paul, MN (44.989920°N, 93.185503°W)
<i>Cirsium altissimum</i>	Tall thistle	Biennial	None	Cumberland, IA (41.274186°N, 94.870336°W)
<i>Cirsium discolor</i>	Field thistle	Biennial	None	Maplewood, MN (44.929148°N, 92.997039°W)
<i>Cirsium flodmanii</i>	Flodman's thistle	Perennial	None	Morning Sky Greenery, Morris, MN (45.607745°N, 95.856771°W)
<i>Cirsium muticum</i>	Swamp thistle	Biennial	None	Prairie Moon Nursery (43.903211°N, 91.637046°W) and Burnham Wildlife Management Area, Polk County, MN (47.630295°N, 96.35160°W)
<i>Cirsium undulatum</i>	Wavy-leaved thistle	Perennial	None	Germplasm Resources Information Network (GRIN), https://npgsweb.ars-grin.gov
<i>Cirsium pitcheri</i>	Pitcher's thistle	Monocarpic Perennial	Threatened species (U.S. Fish and Wildlife Service); native to Ontario, WI, MI, IL, IN	Chicago Botanic Garden (Lake Michigan area, original source not known)

^aAll native species are present in Minnesota, except for *Cirsium pitcheri*, which is native and present east of Minnesota. *Cirsium arvense* is a nonnative invasive species.

starting in 2015, a year before data collection. Each *Cirsium* species was present once in each block. The soil type was a Waukegan silt loam (fine-silty over sandy, mesic Typic Hapludolls) with 6.8% organic matter and pH of 6.7. When the trial was first established in July 2015, each plot consisted of one plant spaced 1.2 m apart and watered as needed. In the fall of 2015, 2016, and 2017, *Cirsium* seeds were also planted in each plot in late summer so that seeds could stratify in situ over the winter to germinate and establish plants the following year. Additional propagated seedlings were transplanted each spring to replace plants that did not survive the winter; however, data were not collected on those plants until the following spring and summer.

In the summers of 2015 and 2016, the area was cultivated with a hand-driven mechanical cultivator and manually weeded for weed control within and between plots. Due to high *Cirsium* mortality over the winter of 2015/2016, two additional replications (eight total) were added in spring of 2016 to compensate for expected loss of plants from season to season. After continued high winter kill in the winter of 2016/2017, low-profile warm- and cool-season turf-grasses were seeded over the area in April 2017 to provide cover for *Cirsium* species, reduce the weed pressure, and catch snow to insulate *Cirsium* species during the winter, all of which reduced plant mortality.

In each spring of 2016 through 2019, dates of new leaf emergence on biennial rosettes and shoot emergence of perennials were recorded beginning as soon as the snow had melted. We rated individual *Cirsium* species in the common garden at 0 for no shoot emergence (perennials) or leaf initiation on rosettes (biennials) and 1 for shoot emergence or leaf initiation.

Determination of Growing Degree Days

We calculated cumulative air and soil growing degree days (GDD) to determine which had a greater influence on *Cirsium* shoot emergence in the spring. Phenological events were recorded by the day of the year, with Day 1 corresponding to January 1. Cumulative air and soil GDD were calculated from the Midwest Regional Climate Center online data portal using data from the on-site, University of Minnesota, St Paul reporting station (44.9902°N, 93.1824°W; elevation: 296 m). Mean percent shoot emergence as a function

of cumulative soil GDD are presented for each species across years (Supplementary Figure 1a–g).

We calculated air GDD with the following equation (Midwest Regional Climate Center):

$$GDD = T_{mean} - T_{base}, \text{ if } T_{mean} \text{ is greater than } T_{base} \quad [1]$$

$$GDD = 0, \text{ if } T_{mean} \text{ is less than } T_{base}$$

where $T_{base} = 0$ C and $T_{mean} = \text{mean temperature: } (T_{max} + T_{min})/2$.

Cumulative GDDs required for first *Cirsium* emergence were estimated using a base temperature of 0 C (Donald 2000) beginning on January 1. Cumulative GDD were also calculated beginning on April 1 for each year to compare with values reported by Donald (2000). Cumulative soil GDD were calculated with the following formula (Martinson et al. 2007):

$$\text{Soil GDD} = \sum[(T_{max} + T_{min})/2 - T_{base}]_n \quad [2]$$

where $T_{base} = 0$ C, T_{max} = maximum daily soil temperature, and T_{min} = minimum daily soil temperature.

A base temperature of 0 C (Donald 2000) beginning on January 1 (Day 1 for all years) was used for calculations of cumulative soil GDD. To reflect the change in cover in the common garden, soil temperatures used to calculate soil GDD were taken at a 10-cm depth under bare soils in 2016 and 2017 and under sod in 2018 and 2019.

Statistical Analysis of *Cirsium* Common Garden Experiment

To assess whether *Cirsium arvense* emergence coincided with emergence of native *Cirsium* species, we conducted a series of survival analyses. Survival analysis, also known as time-to-event analysis, is well suited to our context, as we aim to assess differences in time to shoot emergence among *Cirsium* species (Klein et al. 2013; McNair et al. 2013; Romano and Stevanato 2020). The Kaplan-Meier method (Kaplan and Meier 1958) provides a non-parametric means of visually assessing differences in time to emergence. Using pooled data on date of shoot emergence from 2016 through 2019, we first estimated Kaplan-Meier survival curves for each *Cirsium* species (Stata v. 16.1, StataCorp, 4905 Lakeway

Drive, College Station, TX 77845). We then calculated the Kaplan-Meier estimate of cumulative incidence (Gooley et al. 1999) as follows:

$$1 - \text{Kaplan-Meier estimate} = \text{Kaplan-Meier estimate of cumulative incidence} \quad [3]$$

We plotted the probability of shoot emergence on the y axis (Kaplan-Meier estimate of cumulative incidence) and day of the year (Day 1 = January 1) on the x axis (SigmaPlot v. 14, Inpixon Indoor Intelligence, 2479 E. Bayshore Road, Suite 195, Palo Alto, CA 94303).

To formally test whether there were significant differences in time to emergence between species, we applied the log-rank test for equality of survivor functions (Peto et al. 1977), which compares the observed number of events per species with what would be expected if the survival curve were the same for each (i.e., H_0 = no difference in time to event between species). To assess whether there were significant pairwise differences in time to emergence between species, we conducted Holm-Sidak pairwise comparison tests and created a matrix of each of the seven *Cirsium* species. Each cell of the matrix shows whether the pairwise comparison between the two species was significantly different.

Finally, we extended our time-to-event analysis by estimating Cox proportional hazards models on pooled data from 2016 through 2019. We modeled time to shoot emergence for all perennial species and time to new leaf initiation for all biennial species. When we combined perennial and biennials, we modeled time of emergence, whether from shoot emergence or initiation of shoots. The Cox proportional hazards method allowed us to control for continuous-time covariates (explanatory variables) that may influence *Cirsium* emergence, namely cumulative air GDD and cumulative soil GDD. This method allowed us to simultaneously evaluate the importance of soil and air GDD on shoot emergence/initiation time (Cox 1972; Templ et al. 2016). The global null hypothesis that air GDD and soil GDD do not affect time to emergence or leaf initiation was tested with a likelihood ratio test.

The Cox proportional hazard model creates hazard ratios associated with each model parameter, which may be interpreted as the change in risk of an event (i.e., emergence) if that parameter increases by 1 unit (e.g., 1 GDD). A hazard ratio of 1 indicates no effect of the covariate (air GDD or soil GDD), while a hazard ratio greater than 1 indicates an increased risk of emergence per 1 GDD, and a hazard ratio of less than 1 indicates a decreased risk of emergence.

Phenology of *Hadroplontus litura*

The phenology of *H. litura* was monitored in 2016, 2017, and 2018 at a *C. arvense* nursery on the St Paul Field Station near the common garden. *Hadroplontus litura* adults were added to caged, potted *C. arvense* plants during the preceding summer and overwintered with the pot-in-pot technique (Katovich et al. 2022; Mathers 2003). We used caged plants to increase the probability of collecting F_1 adults, which are cryptic and difficult to find in the field (Gramig et al. 2015). After the first indication of adult activity in the spring, six *C. arvense* plants were sampled at weekly intervals. At each sampling time, two stems from each plant with adult feeding damage were dissected. Presence of eggs or first instar larvae were noted. Once first instar larvae were recorded, weekly sampling was discontinued to allow remaining larvae to continue their development. First generation adult (F_1) activity was detected

by observing new adult leaf feeding or finding adults crawling on screened cages. At this time, all plants were searched for adults. Accumulated air GDD were calculated from January 1 of each year to when eggs, larvae, and F_1 adults were first observed on potted, caged *C. arvense*.

Results and Discussion

Winter and Spring Temperatures and Snow Cover

Air and soil temperatures and the amount and duration of snow cover varied considerably during the winters and springs of 2016 through 2019 (Figure 1). As we could not record shoot emergence or leaf initiation until the snowpack melted, duration of snowpack during March and April dictated when we first collected data. In March and April of 2016 and 2017, there were 0 and 5 d of snow cover, respectively (Table 2; Figure 1). As a result, we were able to begin collecting emergence data on March 14 (Day 74) in 2016 and March 20 (Day 79) in 2017 (Table 2). In 2018, we had a blizzard in St Paul, MN, on April 15 (Day 105) and the snow did not melt from the field until later in April (Figure 1). Consequently, the first observation for 2018 was delayed until April 25 (Day 115), 41 and 36 d later than 2016 and 2017, respectively (Table 2). In 2019, colder than normal winter temperatures led to lower air and soil cumulative GDD for the first data collection date (Table 2). A rapid warm-up in late March of 2019 allowed us to collect emergence data on March 25 (Day 86), but we were unable to collect data for one date in mid-April because of a 19-cm snow event (Figure 1).

Cirsium arvense Emergence in a Common Garden

Cirsium arvense survived all plantings over all 4 yr. From 2016 through 2019, the mean date of *C. arvense* shoot emergence ranged from April 10 (Day 100, 372 air GDD and 64 soil GDD) in 2017, to May 6 (Day 126, 639 air GDD and 169 soil GDD) in 2019 (Figure 2; Table 3). The delay in *C. arvense* emergence in 2019 was most likely the result of cooler air and soil temperatures in March and April (Table 2). Donald (2000) created a model of *C. arvense* emergence using a nonlinear logistic dose-response regression model and predicted that between 1% and 80% of *C. arvense* shoots would emerge between 197 and 587 GDD using a base air temperature of 0 C. When we calculated air GDD, starting on April 1, there were 204, 222, 330, and 566 GDD for the average date of *C. arvense* emergence in 2016, 2017, 2018, and 2019 respectively. Air GDD were within the range described by Donald (2000) for *C. arvense* emergence.

Native *Cirsium* Establishment and Winter Survival

It was difficult to establish and maintain all native *Cirsium* species in the common garden, especially during the winters of 2016 and 2017 with bare soils and subsequent winterkill. *Cirsium muticum* did not readily establish in the well-drained silt loam soil at the common garden. As its common name implies, this plant grows best in moist areas near marshes and wetlands (Eckberg et al. 2017). Rosettes of *C. muticum* suffered high rates of mortality over the course of the experiment. Spring emergence ratings were based on 43% ($n = 13/30$) of established plants over all 4 yr. *Cirsium undulatum* established each year, but only 13% of plants survived the winter over all 4 yr (emergence ratings: $n = 4/30$) most likely due to the St Paul location situated at the northern edge of its natural range. *Cirsium pitcheri* plants that survived the first winter

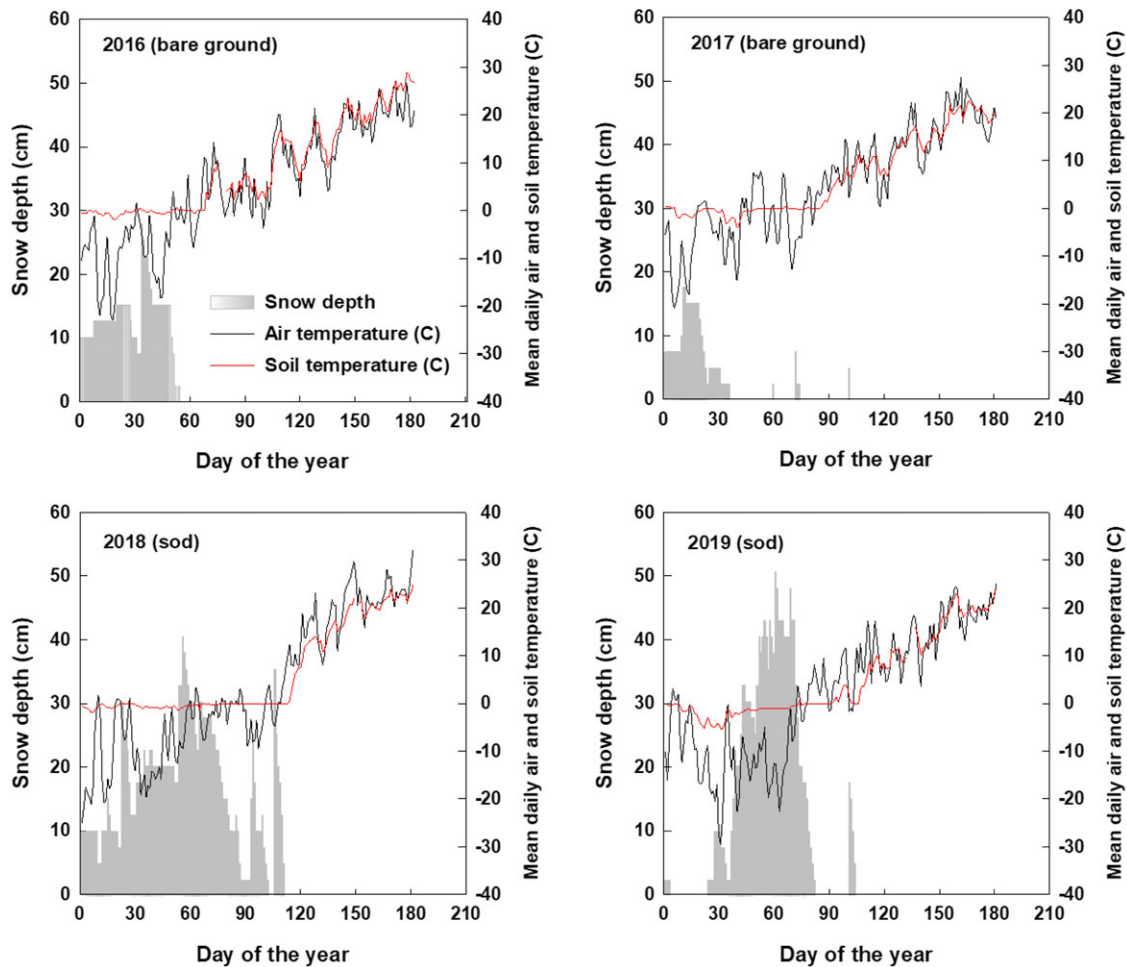


Figure 1. Mean snow depth, and mean air and soil temperatures from January 1 to June 30, 2016 to 2019. Soil temperatures were taken at a 10-cm depth under bare soil in 2016 and 2017 and under sod in 2018 and 2019. St Paul Field Station, St Paul MN (44.990263°N, 93.179938°W).

flowered the following summer, although this plant can take 2 to 8 yr to flower in the sand dunes of its native habitat (Eckberg et al. 2017; Havens et al. 2012). The native *Cirsium* species *C. flodmanii*, *C. altissimum*, and *C. discolor* established and overwintered most successfully at our site but at lower rates than *C. arvense*. The invasive *C. arvense* clearly was the most successful colonizer of the *Cirsium* species tested.

Emergence of Native *Cirsium* Species in a Common Garden

Shoots of the perennials *C. flodmanii*, *C. undulatum*, and *C. pitcheri* emerged before the first observation date in the spring (mid- to late March) in 2016 and 2018, before snowmelt. In 2017, only 25% of *C. flodmanii* shoots had emerged on the first observation date on March 20, but all shoots had emerged (maximum emergence = 1.0) by the end of March. In 2019, no *C. flodmanii* shoots emerged until April 8. This delayed emergence was likely due to cooler soil temperatures. When plants survived the winter, shoots of the other perennial species, *C. undulatum* and *C. pitcheri*, emerged by the first observation dates, before snowmelt during all years. However, only 4 of 30 and 6 of 30 plants (total over 4 yr of the study) survived the winter to emerge the following spring for *C. undulatum* and *C. pitcheri*, respectively.

In 2016, 2017, and 2018 all rosettes of the biennials *C. discolor*, *C. altissimum*, and *C. muticum* initiated growth of new leaves

before snowmelt in the early spring, with two exceptions. In 2016, only 80% of *C. altissimum* rosettes had initiated new leaves before snowmelt. In 2019, only 43% and 83% of rosettes of *C. discolor* and *C. altissimum* had developed new leaves by the first observation date after snowmelt, respectively, most likely due to cool air and soil temperatures (Supplementary Figure 1b–d).

Because not all native *Cirsium* plants in each replication survived until the following spring, emergence data were collected on the surviving plants. Time to emergence (Kaplan-Meier estimate of cumulative incidence curves) were plotted for each species (Figure 3). From Figure 3, it is visually apparent that *C. arvense* emerged later than the native *Cirsium* species. Among native *Cirsium* species, *C. undulatum* emerged earlier than *C. discolor*, *C. altissimum*, or *C. pitcheri* (Figure 3). The log-rank test rejected the null hypothesis of equivalence among species' survival curves at the 1% level of significance ($P \leq 0.001$). From this, we conclude that there were significant differences among survival curves for *Cirsium* species, as the number of observed events (emerging shoots/leaves) are dissimilar to the number of events expected under the null hypothesis (Supplementary Table 1). Results of the Holm-Sidak multiple comparison test showed that shoots of *C. arvense* emerged later than those of native *Cirsium* species. *Cirsium undulatum* emerged earlier than *C. arvense*, *C. discolor*, and *C. altissimum*. There were no differences in emergence time among the remaining native *Cirsium* species (Table 4).

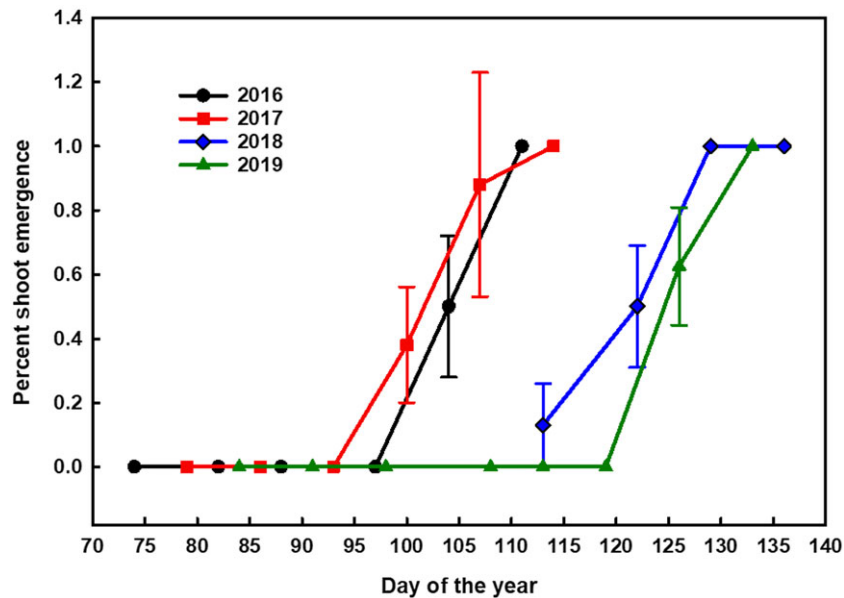
Table 2. *Cirsium* common garden (St Paul, MN) number of days with snow cover in April and May and date of first possible data collection in spring of 2016 through 2019.

Year	No. of days with snow cover March–April	First data collection following spring snowmelt			
		Date	Day of the year ^a	Cumulative air GDD ^b	Cumulative soil GDD ^c
2016	0	March 14, 2016	74	147	36.1
2017	5	March 20, 2017	79	141	18.1
2018	46	April 25, 2018	115	134	3.1
2019	27	March 25, 2019	84	79	0.0

^aNumber of days to first data collection starting at January 1.

^bCumulative growing degree days (GDD_{base 0}) calculated starting on January 1 for each respective year.

^cCumulative soil GDD calculated from January 1. Soil temperatures at a 10-cm depth were used to calculate soil GDD under bare soil in 2016 and 2017 and under sod in 2018 and 2019. Soil temperatures were collected at the University of Minnesota, St Paul Field Station.

**Figure 2.** *Cirsium arvense* vegetative shoot emergence in the spring in the *Cirsium* species common garden (St Paul MN) in 2016, 2017, 2018, and 2019. Percent maximum emergence of 1.0 is equivalent to 100% shoot emergence. Days of the year start with January 1 as Day 1.

We also modeled time to shoot emergence for perennial *Cirsium* species, time to new leaf initiation for all biennial species, and shoot emergence/leaf initiation time for all species combined using the Cox proportional hazards model, using pooled data from 2016 through 2019 and including air and soil GDD as independent covariates. The global null hypothesis that air GDD and soil GDD do not affect time to emergence or leaf initiation was tested with a likelihood ratio test and rejected at the 1% significance level.

Soil GDD hazard ratios for perennial, biennial, and all *Cirsium* species combined, were greater than 1.0 (Table 5). Conversely, hazard ratios for air GDD were less than 1.0. For all *Cirsium* species combined, for every 1-unit increase in cumulative soil GDD, the “risk” or chance of emergence was increased by 1.2%. For every 1-unit increase in cumulative air GDD, the chance of emergence was increased by 0.5%. Thus, cumulative soil GDD has an approximately 2.4 times larger effect on time to emergence relative to air GDD, which is reasonable, as shoots are under the soil or near the soil surface in the early spring. Hazard ratios for soil GDD for biennial and perennial species were 1.011 and 1.016, respectively (Table 5). Thus, with the accumulation of each additional soil GDD in the spring, the risk, or chance of emergence of *Cirsium* plants, was higher than with the accumulation of 1 GDD calculated

from air temperatures. Soil GDD have been used to accurately predict germination of annual species (Harvey and Forcella 1993; Martinson et al. 2007) and may describe perennial or biennial shoot emergence more accurately than air GDD (Wu et al. 2013) (Figure 1; Supplementary Material).

In practice, soil temperature data are not always readily available. For this reason we presented our results on a calendar basis (day of the year) rather than soil GDD. Phenological sequences of events can be reliable across years (Herms 2004), and our objective was to determine the relative spring emergence among *Cirsium* species. We monitored *Cirsium* shoot emergence across 4 yr, in which spring temperatures, snowfall, and snowmelt varied considerably (Figure 1). Our results showed that *C. arvense* shoots emerged consistently later than native *Cirsium* species

Hadroplontus litura Phenology

First adult activity of *H. litura* was observed in the spring from mid-April (2016) to early May (2018) on caged and overwintered *C. arvense* plants, coinciding with the emergence of *C. arvense* vegetative shoots (Table 3). Similar results were reported by Gramig

Table 3. *Hadroplontus litura* and *Cirsium arvense* phenology 2016 through 2019.^a

Year	<i>H. litura</i> eggs		<i>H. litura</i> larvae		<i>H. litura</i> F ₁ adults		<i>C. arvense</i>		
	Date	Air GDD ^b	Date	Air GDD ^b	Date	Air GDD ^b	Mean shoot emergence	Air GDD ^b	Soil GDD ^c
2016	April 26	646	May 19	1,098	June 15	2,041	April 14	319	161
2017	May 8	827	May 8	827	June 19	2,185	April 10	372	64
2018	May 10	521	May 24	930	June 14	1,787	April 23	97	3
2019							May 6	639	169

^a*Hadroplontus litura* monitored in the field on caged *Cirsium arvense* plants at the University of Minnesota, St Paul, MN. Date indicates when life stage was first recorded.

^bCumulative air growing degree days (GDD_{base 0}) beginning on January 1 for each respective year.

^cCumulative soil GDD (GDD_{base 0}) calculated from January 1. Soil temperatures at a 10-cm depth were used to calculate soil GDD under bare soil in 2016 and 2017 and under sod in 2018 and 2019. Soil temperatures were collected at the University of Minnesota, St Paul Field Station.

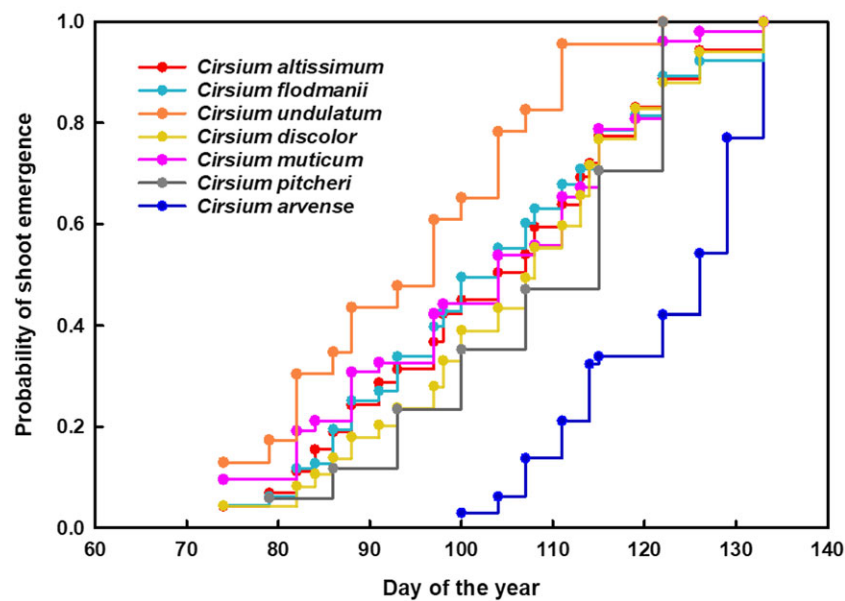


Figure 3. Emergence of *Cirsium arvense* and native *Cirsium* species in 2016, 2017, 2018, and 2019 using Kaplan-Meier cumulative incidence curves. Probability of 1.0 is equivalent to 100% shoot emergence. Days of the year start with January 1 as Day 1. Common garden field trials, St Paul, MN.

et al. (2015), Peschken and Wilkinson (1981), and Zwolfer and Harris (1966).

We first observed *H. litura* eggs on April 26 (646 air GDD), May 8 (827 air GDD), and May 10 (521 air GDD) in 2016, 2017, and 2018, respectively, approximately 1 to 3 wk after first emergence of *C. arvense* shoots each year (Table 3). Larvae were first observed on May 19 (1,098 air GDD), May 8 (827 air GDD), and May 24 (930 air GDD) in 2016, 2017, and 2018, respectively. However, different head capsule measurements indicated that multiple instars were present, so larvae development likely began before sampling.

F₁ adults are cryptic and very difficult to recover in the field (Gramig et al. 2015; Peschken and Beecher 1973). At our St Paul site, we first collected F₁ adults in screen-caged plants on June 15 (2,041 air GDD), June 19 (2,185 air GDD), and June 14 (1,781 air GDD) in 2016, 2017 and 2018, respectively (Table 3). These dates are similar to those reported near Bozeman, MT, near 45.6778°N (Rees 1990) and earlier than the August emergence recorded in the most northern location documented, Regina, SK, Canada, near 50.4547°N (Peschken and Wilkinson 1981).

A logistic regression model created by Gramig et al. (2015) predicted that *H. litura* egg medium development time (when 50% of a cohort were in the egg stage) occurred when greater than 235 air GDD_{base 0 C} had accumulated after soil temperatures warmed to 9

C. Because we recorded date of first egg observation rather than median egg development, it was not possible to determine whether our results align with those of Gramig et al. (2015). At sites in eastern North Dakota (48.7016°N to 46.3628°N), *H. litura* eggs were found from mid-May to the beginning of June (Prischmann-Voldseth et al. 2016), a period of 2 to 3wk later than what we found at St Paul, MN, a more southerly site. *Hadroplontus litura* appear to oviposit later at locations farther north, mirroring the later emergence of F₁ adults at more northerly sites (Peschken and Wilkinson 1981).

In conclusion, for all species, soil cumulative GDD was a superior predictor of emergence of shoots of perennial *Cirsium* species or initiation of leaves in biennial species emergence compared with air GDD. Native *Cirsium* initiated new leaves or shoots before *C. arvense* shoot emergence in the spring, even when the native species' growth was delayed during snow events, blizzards, or cooler temperatures of the springs of 2018 and 2019. In turn, *Cirsium arvense* shoots emerged approximately 1 to 3 wk before female *H. litura* adults began to lay eggs. As such, all native *Cirsium* plants had shoots available for *H. litura* oviposition. In the spring, there was no phenological separation between native *Cirsium* and *C. arvense* shoot emergence or initiation that would render native *Cirsium* species safe from *H. litura* attack. Based on the phenology

Table 4. *Cirsium* shoot emergence in the spring in the *Cirsium* common garden (St Paul, MN), 2016 through 2019.^a

	<i>C. arvense</i>	<i>C. altissimum</i>	<i>C. discolor</i>	<i>C. flodmanii</i>	<i>C. undulatum</i>	<i>C. muticum</i>	<i>C. pitcheri</i>
<i>C. arvense</i>	x						
<i>C. altissimum</i>	+	x					
<i>C. discolor</i>	+		x				
<i>C. flodmanii</i>	+			x			
<i>C. undulatum</i>	+	+	+		x		
<i>C. muticum</i>	+					x	
<i>C. pitcheri</i>	+						x

^aAll pairwise comparisons (Holm-Sidak method). Comparisons should be made across rows. A plus sign (+) indicates that the *Cirsium* species in that row emerged significantly earlier than the *Cirsium* in the column ($P < 0.05$). An "x" indicates no comparison to be made.

Table 5. *Cirsium* species emergence in the common garden (St Paul, MN), 2016 through 2019.^a

Covariate	All <i>Cirsium</i> species ^b			Perennial <i>Cirsium</i> species ^c			Biennial <i>Cirsium</i> species ^d		
	Hazard ratio	Increase in expected hazard ^e	P-value	Hazard ratio	Increase in expected hazard ^e	P-value	Hazard ratio	Increase in expected hazard ^e	P-value
Air GDD (base 0)	0.995	0.5%	<0.001	0.994	0.6%	<0.001	0.996	0.4%	<0.001
Soil GDD (base 0)	1.012	1.2%	<0.001	1.016	1.6%	<0.001	1.011	1.1%	<0.001

^aCox proportional hazards regression of cumulative air and soil growing degree days (GDD) for combined perennial and biennial *Cirsium* species.

^b $n = 621$.

^c $n = 319$, *C. flodmanii*, *C. arvense*, *C. undulatum*, *C. pitcheri*.

^d $n = 302$, *C. discolor*, *C. altissimum*, *C. muticum*.

^ePercent increase per 1.0 GDD.

of shoot emergence/initiation in the spring, all tested *Cirsium* species native to the upper Midwest have the potential to be within the ecological host range of *H. litura*. As such, we recommend further studies on *H. litura* search and acceptance behavior be determined in the field, outside a screen cage, to further define the ecological host range of *H. litura*. Although we are not aware of published accounts of *H. litura* accepting these native *Cirsium* species as hosts in the field, it would be prudent for managers to document any observed attack.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2023.3>

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