

Research Article

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Development of a growing degree-day model to estimate *Linaria vulgaris* shoot emergence and prospects for improving biological control efforts

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Abstract

Yellow toadflax (*Linaria vulgaris* Mill.; Scrophulariaceae) is an invasive herbaceous perennial weed of agricultural and natural habitats throughout North America. In pastures or native rangelands, use of biological control is an attractive option, particularly if the agent can be established quickly. *Rhinusa pilosa* (Gyllenhal) (Coleoptera: Curculionidae), a stem-galling weevil, was first released in Canada in 2014 to evaluate its potential to control *L. vulgaris*. *Rhinusa pilosa* requires young, vigorously growing shoots to establish. Ability to estimate when adequate shoots will be available could inform release timing, thus improving establishment success. There is currently no growing degree-day (GDD) model for *L. vulgaris*. Our main objective was to develop a GDD model for the emergence of *L. vulgaris* shoots and discuss the utility of such a model in relation to the establishment of *R. pilosa* in Nova Scotia. Four sites containing five randomly placed 1-m² quadrats were monitored for the emergence of *L. vulgaris* shoots twice weekly in spring to summer 2017 and 2018 by recording number of shoots and shoots with flower buds. A GDD ($T_{\text{base}} 2\text{ C}$) model for shoot emergence of *L. vulgaris* was developed and validated using independent shoot emergence data. Shoots emerged in the spring between 124 and 244 GDD with 90% of all shoots emerged between 681 and 1,117 GDD. Model estimation for the initiation of shoot emergence was 74 GDD, with 10%, 50%, and 90% shoot emergence estimated to occur at 179, 409, and 811 GDD, respectively. *Rhinusa pilosa* adults were released in 2016 (three sites) and 2017 (one site), and number of shoots with galls was recorded. Galls were observed in all three sites in 2016 and in three of the four sites in 2017, with none found in 2018. Timing of release and soil moisture are discussed as factors affecting establishment of *R. pilosa* in Nova Scotia.

Introduction

Yellow toadflax (*Linaria vulgaris* Mill.; Scrophulariaceae), is a herbaceous perennial weed of Palearctic origin that has invaded agricultural and natural habitats throughout most of Canada and the continental U.S.A. since its introduction in the 1600s (Saner et al. 1995; Sutton 1988; USDA-NRCS 2021). The weed has recently invaded western North America, including both prairie croplands (Leeson et al. 2005) and natural grasslands grazed by livestock and native ungulates (De Clerck-Floate and McClay 2013; Lehnhoff et al. 2008). Annual crop weed surveys conducted in 2000 to 2004 identified *L. vulgaris* as a significant invader of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), canola/rapeseed (*Brassica napus* L.), mustard (*Brassica juncea* L.), and field peas (*Pisum sativum* L.) in the Peace River area of northern Alberta and the Aspen Parkland ecoregion of Canada's Prairie Provinces (Leeson et al. 2005). Similar surveys in Atlantic Canada have documented the occurrence of *L. vulgaris* in cereal crops in New Brunswick and Prince Edward Island (Thomas and Ivany 1990; Thomas et al. 1994) and corn (*Zea mays* L.) and orchard crops in Nova Scotia (S Olmstead, personal communication).

Linaria vulgaris has a wide tolerance for different environmental conditions and habitat types within the temperate regions where it grows; for example, dry or mesic sites as far north as 65°N and elevations from 0 to above 2,000 m in North America (Lehnhoff et al. 2008; Saner et al. 1995). Spring emergence of vegetative shoots from root buds can begin as early as mid-March in some regions of Colorado and as late as mid-June in other regions of the state (Beck 2014). In Canada, peak flowering can occur anytime from mid-June to late July (Saner et al. 1995). *Linaria vulgaris* shoot emergence in northern Germany begins in early April when soil temperatures reach 5 to 10 C (Kock 1966), indicating that temperature-based variables such

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Management Implications

Linaria vulgaris (yellow toadflax) is an invasive weed of agricultural and natural areas throughout most of Canada and the continental United States (e.g., perennial and annual crops, pastures, native rangelands). The recently introduced stem-galling weevil, *Rhinusa pilosa*, is showing promise as a biological control agent of *L. vulgaris* in western Canada. *Rhinusa pilosa* requires access to young, vegetative shoots of *L. vulgaris* for egg-laying and subsequent gall formation. Hence, a model to estimate the emergence of *L. vulgaris* shoots may serve to facilitate better timing of *R. pilosa* release to match host-plant development. We developed and validated a growing degree-day model to estimate *L. vulgaris* shoot emergence and compared our model with the timing of past *R. pilosa* releases in Nova Scotia, Canada. The initial establishment of *R. pilosa* following these first releases (2016 to 2017) was found to be most successful at sites with 48% to 58% shoot emergence and high soil moisture, suggesting moisture availability may be another limiting factor to successful establishment of this potential biocontrol agent. Gall formation, however, declined at all sites in the second and third years after release, indicating an inability to establish well in Nova Scotia for reasons unknown. A tentative “window of opportunity” for gall formation between shoot emergence and flower bud formation was identified, and the developed model can be used to estimate the initiation of this window to help improve timing of future *R. pilosa* releases.

as growing degree days (GDD) may be useful for estimating spring shoot emergence. Emergence and development phenology of this weed species has not been studied in detail in Atlantic Canada.

Linaria vulgaris can be managed with traditional methods such as herbicides and tillage in some situations. Available herbicides are currently limited to preharvest glyphosate applications in several annual crops (Baig et al. 1999) and picloram, aminocyclopyrachlor, and chlorsulfuron in rangeland and pasture (Almquist et al. 2015; Johnson et al. 2014; Lym 2014). Intraspecific genetic variation in North American populations of *L. vulgaris* is wide and may reduce efficacy of some herbicides (Ward et al. 2008). Intensive tillage and summer fallow can control *L. vulgaris* (Morishita 1991), but increased adoption of zero- or minimum-till management regimes have reduced availability of this strategy, and *L. vulgaris* therefore remains a persistent perennial weed of agricultural crops (Baig et al. 1999). Tillage and herbicide applications are also not practical in pastures or natural lands (e.g., native rangelands), necessitating the need for alternative management strategies in these areas.

Given the limited availability of effective control strategies for *L. vulgaris*, there has been persistent interest in the use of biological control agents as part of an overall management program. This is especially the case for control in pastures or native rangelands where an effective biological control agent could be a feasible alternative to herbicide use. When evaluating a particular biological control agent it is important to understand how the host (plant species) responds to climate shifts (Davis et al. 2010) and interacts with insect herbivores in time and space (Croy et al. 2021). The interaction between biological control agent and host is critical for the successful establishment and control of the target weed (Harms et al. 2020). Such knowledge will inform when and where to release biocontrol insects using plant growth models that predict



Figure 1. A stem of *Linaria vulgaris* with a gall induced by egg deposition of *Rhinusa pilosa*. Taken at the Antigonish site (Nova Scotia, Canada) in May 2017. Photo credit: Lienna Hoeg.

optimal times of availability and quality of their host resource (Kriticos et al. 2021).

Rhinusa pilosa (Gyllenhal) (Coleoptera: Curculionidae) is a host-specific stem-galling weevil released for biocontrol of *L. vulgaris* in Canada in 2014. Details on *R. pilosa* host interactions during oviposition, gall induction, and gall development are described in Barnewall (2011), Barnewall and De Clerck-Floate (2012), and Gassmann et al. (2014). Briefly, *R. pilosa* overwinters as an adult and emerges in early spring to mate and feed on the host plant before females deposit eggs into the meristematic apical area of newly emerging, vegetative *L. vulgaris* shoots (Barnewall and De Clerck-Floate 2012). There is only one generation per year, but females are seasonally long-lived and can be available throughout the emergence period of *L. vulgaris* shoots. However, peak oviposition occurs early in the growing season depending on local environmental conditions (Gassmann et al. 2014). For such insects, the period of oviposition must be synchronized with the emergence and quality of the specific plant part needed for optimum gall (Figure 1) and offspring development (Aoyama et al. 2012; Yukawa et al. 2013). Hence, an accurate GDD model to predict the timing of *L. vulgaris* shoot emergence could inform the release timing for *R. pilosa* and potentially increase the probability for successful establishment at new release sites. The main objective of this research was to develop a GDD model to estimate *L. vulgaris* shoot emergence.

Materials and Methods

Site Selection

Four sites (two pastures and two non-managed areas) in Nova Scotia were identified as having established populations of

Table 1. Location, description, and *Linaria vulgaris* patch size at sites used for release of *Rhinusa pilosa* and development of growing degree-day models to estimate *L. vulgaris* shoot emergence in Nova Scotia, Canada.

Site	Geo-coordinates	Size of study area	Description
Bible Hill	45.37069°N, 63.25756°W	—m ² — 229.1	South-facing slope next to barn on Dalhousie Agricultural Campus
Scotsburn	45.60109°N, 62.81801°W	2271.2	Actively managed hayfield
Antigonish	45.53599°N, 62.08891°W	105.6	Actively managed hayfield
MacElmon	45.39118°N, 63.42830°W	527.9	Wild area near entrance to Provincial Park

L. vulgaris (Table 1). *Linaria vulgaris* was observed at these sites for 2 to 3 yr before this study, and populations were composed of patches measuring 2 to 4 m² within each site.

Emergence and Development Data

Linaria vulgaris shoot emergence was monitored in five permanent 1-m² quadrats that were randomly placed throughout each site. Quadrats were spaced at least 2 m apart (Scotsburn, Bible Hill, and Antigonish) and up to 4 m apart (MacElmon Pond) to represent all patches of *L. vulgaris* at the site. Newly emerged *L. vulgaris* shoots were counted and marked with colored elastic bands once or twice weekly from late April until August. Emergence data were collected in 2017 and 2018 from three sites: Bible Hill, Antigonish, and MacElmon; and from Scotsburn in 2017 only. This provided a total of 7 site-years of emergence data for calibration and validation of the emergence model. Emergence data were expressed on a percent cumulative scale for modeling purposes. Percent cumulative emergence was determined by (1) converting the number of new shoots emerged on each counting date into cumulative emergence (running sum) for each quadrat and (2) expressing cumulative emergence as percent cumulative emergence using the following formula:

$$\sum_{i=1}^n \text{Percent cumulative emergence } Q_n = \left(\frac{\text{Cumulative emergence } Q_n}{\text{Total cumulative emergence } Q_n} \right) \times 100 \quad [1]$$

where *i* is the first counting date, *n* is the last counting date, *Q_n* is a given quadrat on a given counting date, cumulative emergence is the running emergence sum on a given counting date in *Q_n*, and total cumulative emergence is the total sum of new shoots emerged in *Q_n* by the end of the emergence period. Galls within these plots and shoots with flower buds were recorded in all quadrats in all sites.

Weather Data

Hourly air temperature at each site was recorded using temperature loggers (Watchdog 1400 series data loggers, Spectrum Technologies, Aurora, IL, USA, 60504). Data loggers were protected by a solar radiation shield and were attached to wooden stakes approximately 0.5 m above the soil surface. Cumulative GDD were calculated using the formula:

$$GDD = \sum_{i=1}^n (T_{\text{mean}} - T_{\text{base}}) \quad [2]$$

where *T_{mean}* is the mean daily air temperature, *T_{base}* is the lowest air temperature at which we assumed *L. vulgaris* shoot emergence would not occur, and *n* is the number of days over which GDD are calculated and summed. An upper temperature threshold for *L. vulgaris* emergence is not known and was not considered in model development. The data loggers, in addition to air temperature, also recorded soil moisture (% v/v) at 5 to 8 cm below the soil surface at 30-min intervals using a SM 100 sensor from Spectrum Technologies.

Development of GDD Models

Cumulative *L. vulgaris* shoot emergence was plotted as a function of cumulative GDD using nonlinear regression. Fitting of nonlinear equations, as well as parameter estimates for these equations, was conducted using the Gauss-Newton algorithm in PROC NLIN of SAS for Windows (v. 9.4, SAS Institute, Cary, NC, USA). Percent cumulative shoot emergence was related to cumulative GDD with a three-parameter logistic equation of the form:

$$Y = \frac{a}{1 + \left(\frac{x}{x_0} \right)^b} \quad [3]$$

where *Y* is cumulative shoot emergence, *x* is cumulative GDD, *a* is the theoretical maximum emergence, *x₀* is the cumulative GDD at 50% emergence, and *b* is the slope of the inflection point of the curve (Donald 2000). The base air temperature for *L. vulgaris* shoot emergence was determined by iterating a series of base temperatures (0 to 5 C in 1 C intervals) in Equation 3 using the complete data set until the best fit was obtained between percent cumulative shoot emergence and cumulative GDD (Izquierdo et al. 2009). The best fit was obtained for *T_{base}* = 2 C. Given no current biological justification for using an alternative *T_{base}*, 2 C was chosen based on the fit obtained using this value. The model was calibrated using data from four randomly chosen site-years (out of the total 7 site-years) and then validated using emergence data from the remaining 3 site-years.

Assessing Fit of the GDD Model

Goodness of fit for the emergence model was determined by calculating the coefficient of determination (*R*²), adjusted coefficient of determination *R*²_{Adj}, and root mean-square error (RMSE) using formulas available in Bowley (2008). Values were calculated manually using observed emergence and estimated emergence from the model output in SAS. Goodness of model fit was based on low RMSE and *R*²_{Adj} values close to 1.

Validation of the GDD Model

The emergence model was validated with shoot emergence data from 3 site-years (Bible Hill-2017, Antigonish-2017, and Antigonish-2018) not used for model calibration. *Linaria vulgaris* shoot emergence data from these sites were expressed as cumulative percent emergence and plotted against cumulative GDD at each site. Estimated emergence for each site was determined using the calibrated model. Model estimations were plotted against observed emergence at each site, and the RMSE and *R*²_{Adj}

Table 2. Parameter estimates for the three-parameter logistic model used to describe the relationship between cumulative *Linaria vulgaris* shoot emergence and cumulative growing degree days (GDD) calculated from air temperature ($T_{\text{base}} = 2\text{ C}$) in Nova Scotia, Canada.

Model parameters ^a		
a	x_0	b
104.2 ± 3.1	409.4 ± 14	-2.7102 ± 0.2
[97.9, 110.4]	[381.5, 437.2]	[-3.1121, -2.3079]

^aThe model was a three-parameter logistic equation of the form $Y = \frac{a}{1 + (\frac{x}{x_0})^b}$, where Y is

cumulative shoot emergence, x is cumulative GDD, a is the theoretical maximum emergence, x_0 is the cumulative GDD at 50% emergence, and b is the slope of the inflection point of the curve. Values represent the mean parameter estimate ± 1 SE. Values in brackets are the lower and upper 95% confidence limits of the parameter estimates.

described above were used to assess agreement between observed data and model estimates.

Biological Control Agent Release and Monitoring

Rhinusa pilosa were obtained from a laboratory colony maintained at the Agriculture and Agri-Food Canada, Lethbridge Research and Development Centre in May 2016. At the Antigonish, Scotsburn, and Bible Hill sites, 100 weevils (ca. 50:50 ratio females:males) were released on May 27, 2016, and at the MacElmon site on May 31, 2017, in the middle of a patch within each site. Establishment success was determined by visually surveying the entire patch of *L. vulgaris* at each site on August 24, 2016 (but not MacElmon), October 30, 2017, and August 29, 2018, and counting all galls observed (Figure 1). Galls were located by walking slowly through each site and carefully moving aside the *L. vulgaris* (approximately 50 to 60 cm in height).

Results and Discussion

Development of the GDD Model

Bud sprouting on perennial weed creeping roots in temperate climates commonly occurs at temperatures between 0 and 5 C (McAllister and Haderlie 1985; White et al. 2015), facilitating shoot emergence early in the growing season. *Linaria vulgaris* shoots emerged between 124 and 244 GDD (April 18 and May 11) and reached 90% emergence between 681 and 1,117 GDD (June 16 and July 20). *Linaria vulgaris* shoots also emerged in mid- to late April in northern Germany (Kock 1966), and Willden and Evans (2018) reported rapid spring emergence of the related species Dalmatian toadflax [*Linaria dalmatica* (L.) Mill.] in Utah, USA. The *L. vulgaris* emergence timing in our study is also similar to shoots of other perennial weeds emerging from creeping roots in Nova Scotia (White et al. 2015; Wu et al. 2013) and elsewhere in North America (Donald 2000; Webster and Cardina 1999) and is likely indicative of the typical emergence timing of this weed species in Nova Scotia.

Plotting shoot emergence as a function of GDD improved model fit relative to day of year (data not shown). The proposed emergence model (Table 2) provided good fit to the observed emergence data and accurately estimated cumulative emergence as a function of cumulative GDD (Figure 2). Model estimation for the initiation of emergence was 74 GDD and 10%, 50%, and 90% emergence were estimated to occur at 179, 409, and 811 GDD, respectively. Model estimation for *L. vulgaris* shoot emergence also generally agreed closely with the observed emergence

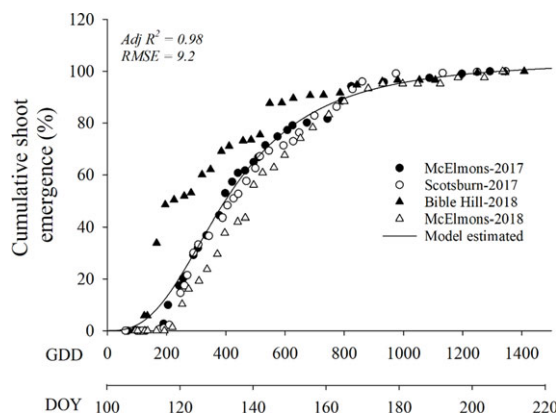


Figure 2. Percent cumulative *Linaria vulgaris* shoot emergence as a function of cumulative growing degree days (GDD) calculated from air temperature ($T_{\text{base}} = 2\text{ C}$) at sites used for model calibration in Nova Scotia, Canada. Symbols represent the mean of five observations. The line is a fitted nonlinear three-parameter logistic equation of the form $Y = \frac{a}{1 + (\frac{x}{x_0})^b}$, where Y is cumulative shoot emergence, x is cumu-

lative GDD, a is the theoretical maximum emergence, x_0 is the cumulative GDD at 50% emergence, and b is the slope of the inflection point of the curve. Parameter estimates are provided in Table 2. Day of year (DOY) is provided for general reference to calendar date. RMSE, root mean-square error.

at each validation site (Figure 3). Each site had a high R^2_{Adj} and low RMSE, though emergence was estimated to occur earlier than observed values at Antigonish-2018 (Figure 3C). Observed emergence between 200 and 300 GDD at Bible Hill-2017 was also more rapid than estimated by the model at this site (Figure 3A).

Good fit of the developed model indicates that the model can likely estimate emergence accurately enough to facilitate efficient release of biological control agents based upon where and when there would be optimal availability of high-quality host resources for the agent. Gall-producing biocontrol agents such as *R. pilosa* are sensitive to the spring phenology of their host plants because they require young, actively growing plants for optimal gall formation and as a source of freshly mobilized carbohydrates to support reproductive success (Harris and Shorthouse 1996; Sedlarević Zorić et al. 2019; Weis 2014). *Rhinusa pilosa* avoids oviposition in shoots that have initiated flower bud formation (Barnewall and DeClerck-Floate 2012), and galls will therefore not develop on these shoots. The time between shoot emergence and flower bud formation therefore represents the window of opportunity for *R. pilosa* to oviposit and develop the gall. Observations from this study at the two sites (Bible Hill and Antigonish) where a moderate number of galls were formed in 2016 found this window to range between 95 and 108 d (1,280 to 1,412 GDD) in 2017 and to be narrower in 2018 (52 to 71 d, 540 to 804 GDD) (Table 3). This difference in the available time to capitalize upon the emerging shoots in conjunction with low soil moisture levels in 2017 (Supplementary Table 1) may have negatively impacted the ability of *R. pilosa* to successfully establish at these sites.

Utility of a GDD Model to Improve *Rhinusa pilosa* Release in Nova Scotia

Release of *R. pilosa* in 2016 occurred at 445, 399, and 387 GDD, when, according to the shoot emergence model, approximately 58%, 50%, and 48% of the shoots had emerged for Bible Hill, Scotsburn, and Antigonish, respectively. In 2017, the release occurred at 441 GDD, when approximately 61% of the shoots

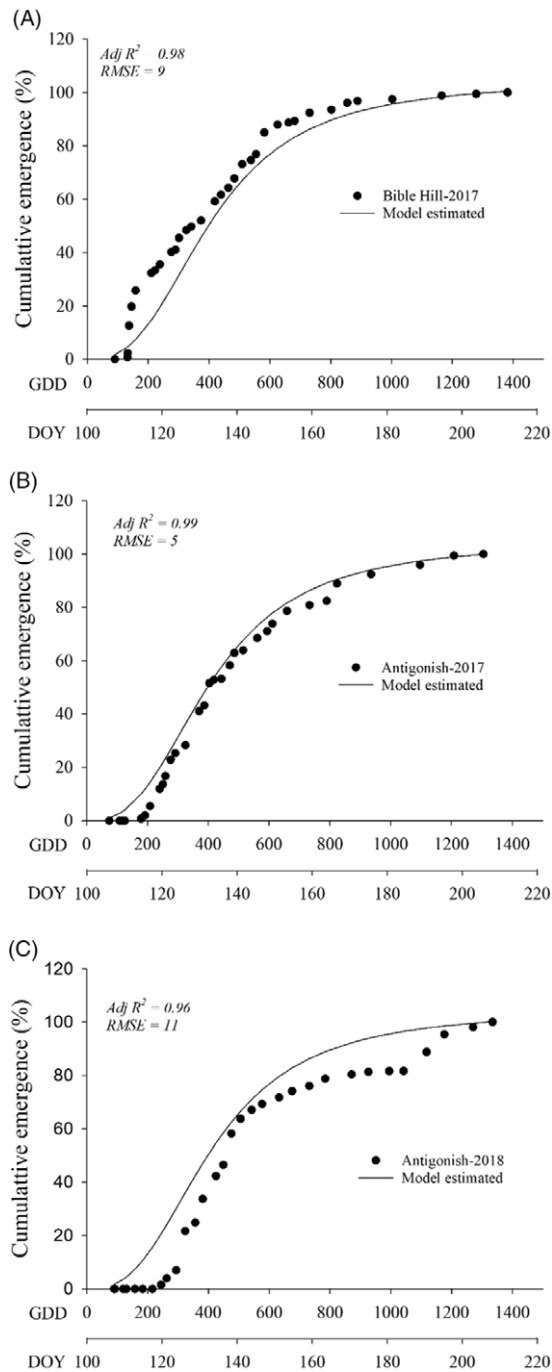


Figure 3. Observed and calibrated model estimated *Linaria vulgaris* shoot emergence as a function of cumulative growing degree days (GDD) calculated from air temperature ($T_{base} = 2\text{ C}$) at sites used for model validation in Nova Scotia, Canada: (A) Bible Hill-2017, (B) Antigonish-2017, and (C) Antigonish-2018. Symbols represent the mean of five observations. Lines are a fitted nonlinear three-parameter logistic equation of the form $Y = \frac{a}{1 + (\frac{x}{x_0})^b}$, where Y is cumulative shoot emergence, x is cumulative GDD, a is the theoretical maximum emergence, x_0 is the cumulative GDD at 50% emergence, and b is the slope of the inflection point of the curve. Parameter estimates are provided in Table 2. Day of year (DOY) is provided for general reference to calendar date. RMSE, root mean-square error.

had emerged at MacElmon Pond. It is likely that these releases occurred well ahead of flower bud formation (in July of 2016), allowing adequate time for oviposition and gall formation. Post-release in 2016, there was evidence of high *R. pilosa*

establishment at the Antigonish site (211 galls), moderate establishment at the Bible Hill site (24 galls), and poor establishment at the Scotsburn site (2 galls). The release at the MacElmon site in May of 2017 showed poor establishment in August of the same year, with only 1 gall found, despite having an estimated 60% of the shoots emerged and available as hosts. Furthermore, the number of galls found in the first year after release was 11, 3, 0, and 0 for the Antigonish, Bible Hill, Scotsburn, and MacElmon sites, respectively. Galls were found in the quadrats between May 29 and June 28, 2017 (404 to 888 GDD) at all sites. Surveys in 2018 found no galls at any of the sites. Our shoot emergence model could benefit from a similar flower bud formation model and, used together with current and forecast weather data, could estimate the potential duration of the window of opportunity for any given site in any given year. Such information could serve to move release timings either earlier or later than they are currently occurring (by calendar date).

Linaria vulgaris is reported to grow better and produce more shoots under wetter conditions (Nadeau et al. 1991), which could contribute to the production of a higher-quality resource for *R. pilosa* and impact its ultimate success as a biological control agent. Such a relationship between water availability and insect performance has also been reported for other gall-forming weed biological control agents and their host plants (Harris and Shorthouse 1996; Hinz and Müller-Schärer 2000). Average monthly soil moisture and cumulative monthly rainfall showed differences across sites and years in our study, which may explain the poor gall formation at most sites by the end of the study (Supplementary Table 1). For example, in 2016, Antigonish had high soil moisture levels (>30% in April and May, >20% in June, and >10% in July) and the best initial *R. pilosa* establishment. Bible Hill had soil moisture levels of 10% to 20% over these same months and a lower rate of establishment. Scotsburn had soil moisture levels <10% and the lowest number of galls. Soil moisture levels in April and May 2017 were 20% to 30% in Antigonish, Bible Hill, and MacElmon in April and May but dropped to 10% to 20% during June and July. Similarly, Scotsburn had soil moisture levels just above 10% for April to July. The number of galls observed in 2017 at these sites was lower than in 2016, suggesting that reduced moisture availability in 2017 may have affected *R. pilosa*. By 2018, despite soil moisture levels being >20% in April and May and 10% to 20% in June and July in Antigonish, Bible Hill, and MacElmon, no galls were found at any site. Results from our study therefore suggest an important role for moisture availability in the quality of shoots of *L. vulgaris* emerging each year and the subsequent success of *R. pilosa*. We must also add that we did not evaluate overwinter survival, predation, or competition in this study. Over time, any of these factors, alone or in combination with one another and environmental factors (e.g., moisture availability), may impact *R. pilosa* establishment and persistence in Nova Scotia. This emphasizes the importance for a high level of establishment during the year of release to ensure population numbers sufficient to withstand these factors in subsequent years.

In conclusion, a GDD model has been developed to estimate the emergence timing for *L. vulgaris*. Synchronizing release of a biocontrol agent such as *R. pilosa* to coincide with peak abundance of quality *L. vulgaris* shoots could very well aid in establishment of sustained field colonies of the weevil. Establishment success has been shown to be positively related to the starting population size of the released insect (e.g., Grevstad 1999). When the supply of insects for release is small, as is the case with *R. pilosa*, production

Table 3. Julian days and growing degree days (GDD, in parentheses) for initiation and conclusion of shoot emergence and gall formation and initiation of flower bud formation for *Linaria vulgaris* from two sites in Nova Scotia, Canada, in 2017 and 2018.^a

Year	Site	Shoot emergence		Gall formation		Flower bud formation	
		Initiation	Conclusion	Initiation	Conclusion	Initiation	Window of opportunity ^b
2017	Bible Hill	107 ^a (132) ^b	206 (1,382)	154 (520)	180 (919)	215 (1,544)	108 (1,412)
	Antigonish	120 (179)	206 (1,305)	150 (418)	180 (839)	215 (1,459)	95 (1280)
2018	Bible Hill	115 (124)	207 (1,343)	—	—	186 (928)	71 (804)
	Antigonish	130 (244)	210 (1,334)	—	—	182 (784)	52 (540)

^aValues reported are Julian days with GDD in parentheses. GDD ($T_{base} = 2\text{ C}$).

^b“Window of opportunity” is defined as the time (number of days, GDD in parentheses) between initiation of shoot emergence and initiation of flower bud formation.

of numerous galls during the year of release could help increase the probability of survival into subsequent years. Future studies are now needed to: (1) test the ability of the GDD shoot emergence model to estimate the optimal timing for release of *R. pilosa*, (2) develop a GDD flower bud phenology model to identify the window of opportunity for successful *R. pilosa* release, (3) investigate the impact of soil moisture on *L. vulgaris* shoot quality for gall formation by *R. pilosa*, and (4) evaluate other factors, that is, overwintering mortality and predation/parasitism for impact on *R. pilosa* persistence post-establishment.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2022.6>

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