A Single Swede Midge (Diptera: Cecidomyiidae) Larva Can Render Cauliflower Unmarketable

Chase A. Stratton,1 Elisabeth A. Hodgdon,1 Samuel G. Zuckerman,2 Anthony M. Shelton,3 and Yolanda H. Chen1,4

1Department of Plant and Soil Sciences, University of Vermont, 63 Carrigan Drive, Burlington, VT 05405, 2Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, 3Department of Entomology, Cornell University, New York State Agricultural Experiment Station, 630 West North Street, Geneva, NY 14456, and 4Corresponding author, e-mail: yolanda.chen@uvm.edu

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Abstract

Swede midge, Contarinia nasturtii Kieffer (Diptera: Cecidomyiidae), is an invasive pest causing significant damage on Brassica crops in the Northeastern United States and Eastern Canada. Heading brassicas, like cauliflower, appear to be particularly susceptible. Swede midge is difficult to control because larvae feed concealed inside meristematic tissues of the plant. In order to develop damage and marketability thresholds necessary for integrated pest management, it is important to determine how many larvae render plants unmarketable and whether the timing of infestation affects the severity of damage. We manipulated larval density (0, 1, 3, 5, 10, or 20) per plant and the timing of infestation (30, 55, and 80 d after seeding) on cauliflower in the lab and field to answer the following questions: 1) What is the swede midge damage threshold? 2) How many swede midge larvae can render cauliflower crowns unmarketable? and 3) Does the age of cauliflower at infestation influence the severity of damage and marketability? We found that even a single larva can cause mild twisting and scarring in the crown rendering cauliflower unmarketable 52% of the time, with more larvae causing more severe damage and additional losses, regardless of cauliflower age at infestation.

Key words: damage threshold, marketability threshold, invasive pest, Brassica production, Cecidomyiidae

Swede midge (Diptera: Cecidomyiidae) is an invasive pest threatening Brassica production in the Northeastern United States and Eastern Canada (Hallett and Heal 2001; Olfert et al. 2006; Chen et al. 2011). Feeding by swede midge larvae results in a range of damage, from slight swelling of plant tissue to scarring, twisting, branching, and most severely, the complete loss of the apical bud (Chen and Shelton 2007; Chen et al. 2009). Once established in an area, swede midge is extremely difficult to remove (Chen et al. 2011). A decade after the midge invaded Ontario, Canada, losses to broccoli and cauliflower (Brassica oleracea Gp. Botrytis and Gp. Italica, respectively) can exceed 85% annually (Hallett and Heal 2001). Swede midge outbreaks have reversed previous integrated pest management (IPM) gains in cole crops because growers often resort to calendar-based spraying (Hallett and Sears 2013). There is a critical need for better insecticide treatment thresholds (Hallett and Sears 2013) and alternative management tactics for swede midge (Chen and Shelton 2007; Chen et al. 2009), both of which depend on a comprehensive understanding of pest biology and susceptibility to treatments (Kogan 1998).

Cecidomyiids are challenging insect pests because of their ability to manipulate plant growth, resulting in galls and tumorous formations (Maia et al. 2005; Vitou et al. 2008; Vijaykumar et al. 2009; Hall et al. 2012; Stuart et al. 2012; Uechi et al. 2017). Specifically, swede midge is difficult to control due to: 1) the short adult life span and concealed feeding of larvae (Readshaw 1966; Hallett et al. 2009a, Chen et al. 2011); 2) multiple overlapping generations with irregular emergence phenotypes that are difficult to predict (Hallett et al. 2009b); and 3) all developmental stages of susceptible Brassica hosts seem impacted by herbivory (Hallett 2007).

Although swede midge clearly manipulates plant growth, no studies have examined the relationship between timing of larval feeding and the emergence of market-relevant damage symptoms in Brassica vegetables. Visible damage within an infested cauliflower field could be due to separate infestations from different calendar days. It is unclear whether the ultimate loss of a marketable plant is due to the final infestation, or a compounded effect from multiple infestations. Effective IPM programs depend on accurate damage (the level of infestation that causes damage; Walker 1983; Hallett and Sears 2013) and marketability thresholds (the level of infestation that renders a plant unmarketable; Hallett and Sears 2013). Unfortunately, typical scout and spray IPM practices are impractical for swede midge because market-relevant damage is difficult to confirm until after
labeled larvae have left the plant (Wu et al. 2006; Chen et al. 2011). Testing the relationship between feeding and damage relative to crop phenology could allow more precision in the timing of pesticide applications rather than calendar-based sprays (Hallett et al. 2009a, Hallett and Sears 2013).

Current conventional management recommendations for swede midge are to use systemic neonicotinoids at transplant, followed by regular sprays of foliar insecticides for the remainder of the growing season (Chen et al. 2011; Hodgdon et al. 2017), disrupting decades of effective IPM in Brassica systems (Rodríguez Salamanca 2014). An alternative approach is to use an action threshold based on the capture of five males per pheromone trap per day with a minimum 7-d pesticide retreatment interval (Hallett and Sears 2013). This strategy reduces damage to acceptable levels in cabbage, but not cauliflower, possibly because cabbage heartleaves protect the developing meristem from feeding larvae (Andaloro et al. 1983). Also, organic growers are limited to using large-scale crop rotations (Chen et al. 2009) and/or covering crops with specialty insect netting (Hodgdon et al. 2017), both expensive strategies.

Swede midge damage differs across and within groups of B. oleracea vegetables (e.g., cabbages, cauliflower, broccoli, etc.) (Chen et al. 2011). Infestations result in the lack, reduced size, or distorted growth of the marketable portion of cauliflower composed usually of white inflorescence meristem. Here, we studied the relationship between swede midge infestation and plant damage on cauliflower to test how the timing and severity of swede midge infestation influences market-relevant damage. We applied first-instar larvae to cauliflower to ask: 1) How many swede midge larvae does it take to cause visible damage to cauliflower? 2) How many larvae render cauliflower crowns unmarketable? and 3) Does the age of cauliflower at infestation influence the likelihood that it will be unmarketable?

Materials and Methods

Plant Production and Colony Rearing

A laboratory-reared colony of swede midge was used for both laboratory and field trials (origin: Swiss Federal Research Station for Horticulture, Wädenswil, Switzerland). Midge were reared on cauliflower plants, Brassica oleracea group Botrytis ‘Snow Crown’ (Harris Seeds, Rochester, NY), due to midge preference (Hallett et al. 2009b) and large bud size. Seeds were planted in 128-cell trays (Harris Seeds, Rochester, NY) and transplanted into 15 cm circular planting pots, rather than 7 cm pots. To test the relationship between larval density and damage severity, 0, 1, 3, 5, 10, or 20 larvae were applied to uninfested cauliflower with 8–10 true leaves, using 20 replicate plants for each larval density. Infested plants were grown in mesh cages (1 m × 0.7 m × 0.7 m, BioQuip, Rancho Dominguez, CA) for 10 d under rearing conditions (described above). After 10 d of development, young leaves were removed using a scalpel and larvae were gently rinsed from the leaves using deionized water. A dissecting microscope was used to count the number of larvae that physically responded to a gentle touch with a probe. Summary statistics from these trials were used to estimate the proportion of larvae that survived the artificial infestations. We found that half the larvae survive the procedure, with 0.4 ± 0.11, 1.5 ± 0.25, 2.25 ± 0.34, 5.7 ± 0.63, and 10.4 ± 0.77 (mean ± SE) moving larvae for 1, 3, 5, 10, and 20 larvae, respectively.

Artificial Infestation Procedure—Method Validation

To validate that larvae remained intact after applications to treated plants, additional trials testing larval survival were performed. Larvae (0, 1, 3, 5, 10, or 20) were applied to plants with 8–10 true leaves, using 20 replicate plants for each larval density. Infested plants were grown in mesh cages (1 m × 0.7 m × 0.7 m, BioQuip, Rancho Dominguez, CA) for 10 d under rearing conditions (described above). After 10 d of development, young leaves were removed using a scalpel and larvae were gently rinsed from the leaves using deionized water. A dissecting microscope was used to count the number of larvae that physically responded to a gentle touch with a probe. Summary statistics from these trials were used to estimate the proportion of larvae that survived the artificial infestations. We found that half the larvae survive the procedure, with 0.4 ± 0.11, 1.5 ± 0.25, 2.25 ± 0.34, 5.7 ± 0.63, and 10.4 ± 0.77 (mean ± SE) moving larvae for 1, 3, 5, 10, and 20 larvae, respectively.

What Is the Damage/Marketability Threshold for Swede Midge?

To test the relationship between larval density and damage severity, 0, 1, 3, 5, 10, or 20 larvae were applied to uninfested cauliflower with 8–10 true leaves, replicated over 25 plants for each treatment density. The cauliflower plants tested were grown for 8 wk using the conditions described above, with the exception that they were transplanted into 15 cm circular planting pots, rather than 7 cm pots. Following the artificial larval infestation, treated plants were returned to the greenhouse in large pop-up cages and grown for ~21 d. To prevent larvae from completing their life cycle and reinfecting treated plants prior to data collections, circular, flat, acetate sheets were fastened around plant stems with cotton filling the extra space between the sheets and the stem. This design successfully restricted larvae from reaching the soil where they pupate.

Cauliflower were evaluated using a scale adapted from Hallett (2007), described in Table 1. Cauliflower plants with a score ≥1 were unmarketable using this scale (C.A.S., personal observations). To determine how many swede midge larvae cause damage to cauliflower (damage threshold), the frequencies of plant damage ratings across larval treatment densities were tested using a log-linear regression. The relationship between larval density and marketability (marketability threshold) was tested using a binary-logistic regression. Using the models fitted from our data, the lowest numbers of larvae that cause damage and render cauliflower unmarketable were estimated.

Does the Age of Cauliflower at Infestation Influence the Likelihood That It Will Be Marketable?

We tested if plant age and the number of larvae influenced market-relevant plant damage using a potted plant experiment from
July 1, 2015 to August 30, 2015 at the Bio-Research Complex at the University of Vermont. We chose the site because it was at least 5 km away from any commercial Brassica plantings, minimizing background midge populations that could influence the study. The study site was situated between outdoor hoop-house structures. Due to the low background population of midges in this area, our study design allowed all plants, regardless of infestation date, to be grown outside for the entire experimental period. In order to minimize disturbance to the study and control weeds, we covered the study area (3 × 15 m) with black landscape fabric. We raised cauliflower in 15 cm circular planting pots between Jackson traps with a swede midge pheromone lure (Solida Distributions, Saint-Ferréol-les-Neiges, Québec) to verify that midges remained absent from the field.

To test whether plant age has an effect on plant damage and the likelihood of marketability, 0, 1, 5, 10, or 20 larvae were applied to plants of three age groups (30 [2 true leaves], 55 [4–6 true leaves], and 80 [6–8 true leaves] d after seeding [DAS]), replicated across 30 cauliflower plants in a randomized complete block design. After hardening off 4 wk old seedlings for 2 d, we placed randomly assigned plants to the different treatments at the start of the study, so each plant remained in the same location for the entire experiment. Each block consisted of two trays (0.3 × 0.5 m) that hold six pots each in a 2 × 3 grid. We placed six plants randomized by treatment date and larval density in a zig-zag pattern in the trays. We were concerned that the circular acetate sheets may constrict cauliflower stems through the course of this trial, so instead we loosely fastened fine mesh around the base of the stem to restrict larvae from reaching the soil.

We inoculated midge larvae on the treatment plants at 30, 55, and 80 DAS. On each inoculation date, we brought the subset of pre-assigned plants into an onsite hoop-house. Under a dissecting microscope, we infested cauliflower using the same micropipette method, but the outermost layer of the waxy cuticle was also gently abraded using Kimwipes (Uline, Pleasant Prairie, WI), so the water droplets could adhere to the small meristems of the youngest plants. In order to control for any damage this may have caused, we also abraded older plants.

After the larval inoculations, we assessed the treatment plants for damage every 4 wk. Plants infested at 30 DAS were assessed 4, 8, and 12 WAT, plants infested at 55 DAS were assessed at 8 and 12 WAT, and plants infested at 80 DAS were evaluated 12 WAT. We were able to visually differentiate swede midge damage from other herbivores including diamondback moth (Plutella xylostella L.) (Lepidoptera: Plutellidae) and imported cabbageworm (Pieris rapae L.) (Lepidoptera: Pieridae) that feed on foliage rather than the developing meristem (see Table 1 for swede midge damage descriptions). We recorded plant marketability at the end of these trials using standards developed from discussions with a local vegetable grower (A.J., personal communication). Cauliflowers with scarring or twisting within the inner petioles of the crown were unmarketable.

We used a log-linear and binary-logistic regression to test how larval density, plant age, and their interaction influenced damage and marketability, respectively. We used the model output to predict the larval density and plant age that had the highest impact on damage and marketability. All statistics were performed using R version

| Damage value | Cauliflower symptoms |
|--------------|----------------------|
| 0            | No damage            |
| 1            | Mild twisting to 1 leaf or florets |
| 2            | Mild twisting of stem, 2–3 leaves, or florets and/or mild swelling of petioles |
| 3            | Severe twisting of 2–3 leaves or florets and/or severe swelling of petioles |
| 4            | Severe twisting and/or crumpling of stem, 3+ leaves, or florets; severe swelling and/or scarring of petioles and/or florets |
| 5            | Severe twisting of stem, leaves, and florets; severe scarring of stem, leaves, petioles, and florets |
| 6            | Death of apical meristem and/or multiple compensatory shoots |

Fig. 1. (a) Counts for cauliflower damage scores of different larval densities applied to plants in the laboratory. Twenty plants per treatment were assessed for damage at 10 d postlarval infestation using a modified scale from Hallett (2007) (described in Table 1). Larval density was positively correlated with plant damage ($z = 4.16; P < 0.001$). (b) Binomial logistic regression testing the effect of larval density on the likelihood that infested cauliflower will be marketable. Histograms indicating the number ($n$) of marketable ($P = 1$) and unmarketable ($P = 0$) cauliflower are also reported for each treatment density. Larval density was negatively correlated with marketability ($z = -3.40; P < 0.001$).
Fig. 2. (a) Counts for cauliflower damage scores of different larval densities applied to plants at 30 DAS. Thirty plants per treatment were assessed for damage at 4, 8, and 12 wk postlarval infestation using a categorical damage scale described in Table 1. Damage at 12 wk is shown. Larval density was positively correlated with plant damage ($z = 3.418; P < 0.001$). (b) Binomial logistic regression testing the effect of larval density on the likelihood that cauliflower infested 30 DAS will be marketable. Histograms indicating the number of marketable ($P = 1$) and unmarketable ($P = 0$) cauliflower are reported for each treatment density. Larval density was negatively correlated with marketability ($z = -3.364; P < 0.001$). (c) Counts for cauliflower damage scores of different larval densities applied to plants at 55 DAS. Thirty plants per larval density were assessed for damage at 4 and 8 wk postlarval infestation. Damage at 8 wk is shown. Larval density was positively correlated with plant damage ($z = 5.455; P < 0.001$). (d) Binomial logistic regression testing the effect of larval density on the likelihood that cauliflower infested 55 DAS will be marketable. Histograms reporting marketable and unmarketable cauliflower are reported for each treatment density. Larval density was negatively correlated with marketability ($z = -3.364; P < 0.001$). (e) Counts for cauliflower damage scores of different larval densities applied to plants at 80 DAS. Thirty plants per larval treatment were assessed for damage at 4 wk postlarval infestation. Larval density was positively correlated with plant damage ($z = 5.907; P < 0.001$). (f) Binomial logistic regression testing the effect of larval density on the likelihood that cauliflower infested 80 DAS will be marketable. Histograms indicating the number of marketable ($P = 1$) and unmarketable ($P = 0$) cauliflower are reported for each treatment density. Larval density was negatively correlated with marketability ($z = -5.852; P < 0.001$).
Results

Plants treated with more larvae experienced more severe damage (Fig. 1a; log-linear regression, $z = 4.158$, $P < 0.001$) and a reduced likelihood that the plant would be marketable (Fig. 1b; binary-logistic regression, $z = −3.400$, $P < 0.001$). We found that the single larva treatment most often caused minor twisting to leaf stems and florets, rendering cauliflower unmarketable 52% of the time. Ten larvae resulted in a range of damage from mild twisting of leaves to severe swelling and scarring of florets, rendering 68% of the plants unmarketable. Damage from the 20 larvae treatment also varied, but most often resulted in severe swelling and scarring in the developing crown, rendering 82% of the plants unmarketable.

The same trend held in the field potted plant trials, with more larvae causing more cauliflower damage (Fig. 2a, c, and e; log-linear regression, $z = 3.689$, $P < 0.001$) and a lower likelihood of marketability (Fig. 2b, d, and f; binary-logistic regression, $z = −2.894$, $P < 0.001$). Larval density and plant age at infestation did not have a significant interaction for damage ($z = −0.540$, NS) or marketability ($z = −0.213$, NS), meaning that similar patterns of damage and marketable losses were present across larval treatments for the different cauliflower age groups. Cauliflower age alone also did not directly influence damage or marketability ($z = 1.464$, $−0.572$; NS, NS). Altogether, our data suggest that midge larvae cause significant damage and marketable losses regardless of cauliflower age.

Discussion

Our results contribute important findings about swede midge: 1) half of the larvae perish following our inoculation procedure (see Materials and Methods); 2) any quantity of larval feeding can cause noticeable damage on cauliflower (Fig. 1a); 3) a single larva can render cauliflower unmarketable 52% of the time (Fig. 1b); and 4) damage and marketable losses occur regardless of cauliflower age at infestation (Fig. 2).

Given that there is essentially no larval threshold for swede midge on cauliflower, we suggest plants be protected for the entire season. Our trials tested larval densities that are much lower than would be experienced in an infested field where females oviposit clusters of 5–20 eggs on host plants (Readshaw 1966). Traditional scout and spray IPM approaches remain inappropriate for managing swede midge in cauliflower because market-relevant damage can result from any larval feeding and adults can emerge throughout the growing season (Hallett et al. 2009a, Chen et al. 2011; Samietz et al. 2012; Hallett and Sears 2013; Des Marteaux et al. 2015).

Other Cecidomyiidae species have been shown to excrete digestive enzymes that disrupt growth and development on their host (Tooker and De Moraes 2007, 2010; Tooker 2012). The same has been presumed but not tested in swede midge. The fact that our single larva treatment rendered half of the cauliflower unmarketable yet half of the larvae die following our procedure is troubling. However, it would be interesting to specifically test if damage is caused from salivary excretions or physical injury caused by larvae. If larval excretions distort cauliflower growth independent of physical damage, then a more accurate damage or marketability threshold could be determined by applying known volumes of extracted saliva to plants. These additional trials could also lead toward a more complete understanding of how, so few larvae are able to cause such significant losses in cauliflower.

In addition, we tested how cauliflower damage varies following a single oviposition event. Swede midge has a short life cycle and multiple generations occur in infested fields (Hallett et al. 2009b). How damage and marketability vary in response to multiple infestations remains untested. Our results suggest that multiple infestations would further reduce the likelihood that plants are marketable, but swede midge damage varies across and within different Brassica cultivars (Chen et al. 2011). Further work testing how multiple infestations influence cauliflower damage and how single infestations influence damage to other Brassica crops are warranted.

Heading brassicas, like cauliflower, may also be more susceptible to swede midge herbivory than those with multiple meristems. As mentioned, we still do not know whether larval excretions impact development throughout the plant or only within the infested meristem. If swede midge damage is localized to the developing meristem, plants with multiple growing points, like canola and brussels sprouts, may only lose a portion of marketable growth. That said, whether the number or severity of infested meristems on crops with multiple growing points influences ultimate damage or marketability has not been tested.

Swede midge poses a major threat to Brassica production in its introduced range (Hallett and Heal 2001; Chen et al. 2011; Hallett and Sears 2013). While systemic insecticides and calendar-based foliar sprays effectively manage swede midge conventionally (Hallett et al. 2009a), regular spraying reverses previous gains in IPM programs developed for other Brassica pests (Hallett and Sears 2013; Rodriguez Salamanca 2014), like diamondback moth and imported white cabbage worm (Furlong et al. 2013). Furthermore, large-scale crop rotations can provide control for organic producers (Chen and Shelton 2009) but only temporarily on farms with limited acreage because a portion of pupae remain dormant in the soil (Readshaw 1966; Hallett 2007; Naert et al. 2012). To avoid dormant populations, growers are recommended to rotate at least 2 km away from previous Brassica plantings for at least 3 yr. Tactics that prevent mated females from finding and ovipositing on host plants (e.g., repellents), males from finding and mating with females (e.g., pheromone mating disruption), and/or physically block midges from contacting Brassica crops (e.g., exclusion netting) will be more effective long-term solutions to manage swede midge organically.

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