Research Article

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The development of the asparagus miner (*Ophiomyia simplex* Loew; Diptera: Agromyzidae) in temperate zones: a degree-day model

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Abstract

BACKGROUND: The asparagus miner is a putative vector of *Fusarium* spp., which have been implicated in globally declining asparagus production. Growers currently apply broad-spectrum insecticides for the asparagus miner, but lack management guidelines for adequately controlling the pest. Our aims were (1) to determine the lower developmental threshold of the asparagus miner, (2) develop and validate a degree-day model describing its phenology, and (3) create a developmental time budget for the asparagus miner to help guide growers' management decisions.

RESULTS: We found that the lower developmental threshold for the asparagus miner was 12.1 °C, and that the phenology of the asparagus miner could be reliably predicted over the course of a two-year study. Predictions from the model match well with previously published information on the bionomics of the asparagus miner, but fit better for sampling data collected from the midwestern and eastern United States than for the United Kingdom. The life cycle of the asparagus miner likely requires between 1500 and 2000 degree-days to complete; the longest developmental time requirement was for the pupal stagen

CONCLUSION: This study provides tools for the targeted management of the asparagus miner by offering a degree-day model that may be used to predict its life stages in the north-eastern United States.

Supporting information may be found in the online version of this article.

Keywords: integrated pest management; lower developmental threshold; weather station; Baskerville–Emin; vector; monitoring; trapping

1 INTRODUCTION

A key to successful insect pest management is to be able to adequately time control measures to suppress populations before crop damage occurs. While there are many methods of deducing when to make management actions, one widespread and accurate tool is to employ a degree-day model.[1–5] Degree-day models help time management actions such as pesticide applications in integrated pest management programs,[6] and their use can successfully reduce the number of applications necessary while improving pest control.[5,7–10] Degree-day modeling takes advantage of the fact that the development of insects is dependent on ambient environmental temperatures, and is typically limited by upper and lower temperature boundaries. In the calculation of a degree-day model, the upper and lower developmental thresholds – the temperature below or above which development occurs, respectively[11] – for a species must be determined. Insect species living in temperate climates seldom encounter the upper limit (WR Morrison, unpublished data, 2010, 2011, 2012), which averages about 20 °C above their lower developmental threshold but can range up to 28 °C;[12] therefore, determining the lower developmental threshold may be more important in these cases. The accumulation of daily average temperatures above the lower developmental threshold from the biofix date (a calendar day that marks the beginning of the recording of temperature accumulation) can then be correlated to when particular biological events take place over the course of an insect's lifecycle. Predictions for the accumulated growing degree-days (GDDs) at which life stages occur must be formulated independently from the dataset used for model validation.[13,14] Growers can then use the degree-day model to tailor their management actions to the pest in the geographic area where the model was developed.

Asparagus is produced globally in 62 countries, representing about 196 000 ha of production,[15] and accounting for $83.4 million

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in market value in the United States alone.[16] However, asparagus has been in global decline due to a variety of factors, including the prevalence of insect[17–19] and fungal pests.[20] The asparagus miner (*Ophiomyia simplex* Loew; Diptera: Agromyzidae) is one such pest, and is a putative vector for pathogenic *Fusarium* spp fungi.[21] It is a specialist on asparagus, where it deposits its eggs under the epidermis of the stem near soil level.[22,23] Larvae bore into the stem after hatching, and feed on cortical tissue.[24] The asparagus miner is usually bivoltine in temperate climates, and overwinters as a pupa.[25] Adults emerge in Michigan in mid- to late-May, with the first generation flight peaking around mid-June.[18] Adults begin mating upon emergence, and soon thereafter start laying eggs into asparagus stems where the larvae feed.[26] The second generation adult peak occurs in late July to mid-August (for an illustrated life cycle see reference 27), which produce the overwintering pupae.

In addition to vectoring pathogens, the asparagus miner can impair the ability of the plant to fix carbon by damaging photosynthetic tissue, which may in part result in harvest losses in subsequent years. While there has been ample research into controlling the pathogenic fungi *Fusarium* spp.,[28–34] little work has been devoted to controlling the asparagus miner.[27,35,36] There are currently no management recommendations or programs for the asparagus miner; however, control is imperative, since it preferentially attacks younger fields,[18] which are especially susceptible to *Fusarium* spp. infection. As a result of infection with *Fusarium* spp., the life span of a commercial asparagus field may be reduced by five to eight years.[36]

Degree-day models have been successfully used in the management of related agromyzid species. For example, in the case of the vegetable leafminer (*Liriomyza sativae* Blanchard), a degree-day model was able to adequately predict the species' population dynamics in glasshouses.[2] Schuster and Patel[37] developed a degree-day model for another agromyzid, a serious pest of tomatoes (*L. trifolii* Burgess), in order to accurately predict larval development. More specifically for the asparagus miner, Tuell[18] provided charts with degree-day accumulations and adult abundance data, but did not actually relate the degree-days to phenological events or develop predictions for specific life stages. In addition, the degree-day model in that study was not validated, nor was the lower developmental threshold investigated.

The aims of our study were three-fold: (1) determine the lower developmental threshold of the asparagus miner; (2) develop and validate a degree-day model; (3) create a developmental time budget for the asparagus miner so that asparagus growers can appropriately plan management actions as part of an integrated pest management approach to control the asparagus miner.

2 MATERIALS AND METHODS

2.1 Study site

This study was conducted in five commercial asparagus fields in 2010 and three each in 2011 and 2012, which were located 1.21–16.14 km apart in Oceana County, Michigan (Table 1). Sampling in 2010 started later and was shorter than usual, beginning on June 21 and continuing until September 17 according to the sampling protocol described below for 2011 and 2012. As a result, the 2010 data was used only for verification of the overall 2011 predictions for specific phenological events. All asparagus fields were of var. Millennium, an all-male hybrid of asparagus.

2.2 Phenological events

Accumulated degree-days for predicted asparagus miner phenological events were calculated from weather and insect data collected in 2011 and 2012. The degree-days for critical adult asparagus miner life cycle events were determined for the beginning of flight, first generation peak, beginning of the second generation, second generation peak, and the end of flight. For the immature stages, critical events included first appearance of larvae and pupae in the field, first population peak, and second population peak.

The phenological events for adults were evaluated by monitoring asparagus miner abundance with yellow sticky traps (7.5 cm × 12.3 cm, Great Lakes IPM, Vestaburg, Michigan). Thirty-two sticky traps were set up per field ($N = 96–160$ for all fields combined, depending on year), and these were checked and changed every six to ten days. Sampling occurred from the beginning of asparagus emergence on May 11 to end of adult flight on October 3, 2011 and from March 22 to October 7, 2012. The traps were arranged in transects, with sampling points at 0, 10, 20 and 30 m into the asparagus field from the field edge. Three sets of transects were placed 10 m apart in each field. At each sampling point, there was a canopy trap (placed at 1 m from the ground on a steel conduit) paired with a ground-level trap (10 cm above ground), except during the asparagus harvest when only ground traps were used due to the low height of spear-picking machines. The traps were located in the same place for the duration of the season, and were placed in roughly the same spot in subsequent sampling seasons. Asparagus miners were counted on traps and their numbers were recorded weekly.

Immature asparagus miner stages were sampled by collecting 8–53 stems from each field (mean ± standard error of mean [SEM]: 33.8 ± 11 stems) every six to ten days throughout the growing season from one to five fields per sampling date. The dates of collection ranged from May 31 to October 3, 2011 and from June 14 to October 7, 2012. Stems were collected 30 m into the field from a randomly selected point along the field margin. These were cut 5 cm below the surface of the soil, and cut again at the height of the longest mine. Stems were sealed in plastic bags and placed in a cooler with ice packs until they were transported to the laboratory. Samples were immediately stored at 5 °C in the laboratory, and the stems were processed within 1–14 days. A razor blade was used to carefully peel the epidermis from the asparagus stem to reveal the immature stages. For each stem, the number of larvae and pupae were recorded.

2.3 Weather data collection and degree-day model development

Daily temperature data were obtained from Michigan State University's Enviro-weather station[38] located in Hart at the Michigan Asparagus Research Farm (43°44′11.33″N, 86°21′31.48″W) for 2010 to 2012. The weather station was centrally located among the sampled fields with all the fields located within 10 km, and temperature information was automatically recorded in an electronic database at five-minute intervals.

Summarized monthly and seasonal climatic statistics[39] for Hart, Michigan are given in Table S1 (Supporting Information). All three of the individual March–October growing seasons were on average warmer and wetter than the 30-year normals, which is consistent with regional climatic trends during the past few decades.[40] Mean seasonal temperatures during the three seasons ranged from 1.4 °C above normal in 2011 to 2.9 °C above normal in 2012, while total seasonal precipitation ranged from 52.5 mm

Table 1. Summary of information about the five commercial fields from Oceana County, Michigan that were used in sampling between 2010 and 2012

ID	Area (ha)	Year planted	Nearest Enviro-weather station (km)	End of harvest		Number of insecticide sprays	
				2011	2012	2011	2012
Field 1	3.54	2009	5.7	May 31	June 12	6	5
Field 2	1.82	2008	9.9	June 6	June 19	5	4
Field 3	3.77	2008	7.3	July 6	June 7	7	4
Field 4	6.06	2009	9.8	June 30	na	5	na
Field 5	3.66	2010	10.85	June 30	na	5	na

Note: na, not applicable.

above normal in 2011 to 72.2 mm above normal in 2012. Early season GDD accumulation was exceptionally high during the 2012 season due to a much warmer than normal March (the monthly mean temperature was 8.8 °C above normal). A biofix date of March 1 was used, because this has historically resulted in the best fit for degree-day models in the Great Lakes region (Andresen J, unpublished data). Accumulated GDD were calculated using the Baskerville–Emin method, which approximates the temperature diurnal course using a sine wave and the maximum and minimum temperature for a 24-hour period.[41] The minimum and maximum daily temperatures from the Enviro-weather station were used in the calculation of accumulated degree-days, and the lower developmental threshold reported in this study was used as the base temperature in the model. The Enviro-weather-based accumulated GDD corresponding to important phenological events in the life cycle of the asparagus miner in 2011 were used as the 'predicted GDD' for each event and this was also used in comparisons with other years' asparagus miner abundance data from Michigan and other regions.

2.4 Lower developmental threshold

The lower developmental threshold of the asparagus miner was investigated using environmental growth chambers. Pupae were the focus of the lower developmental threshold experiment. Asparagus miner pupae were collected from the field on September 18, 2010 as well as October 3, 2011 from fields 1 and 4. The exact age of the asparagus miner pupae were not known. In the laboratory, pupae were dissected from the asparagus stems, placed individually into plastic cups (84.8 cm^3, 6 cm × 3 cm *D:H*, Solo Co., Chicago, Illinois), and stored at 3 °C until used in experiments (range 3–196 days; duration of storage did not effect viability of the pupae, Morrison, unpublished data). Pupae were placed into 10 environmental chambers (I-41VL or I-36VL, Percival Scientific, Inc., Perry, Iowa) with a 16 h light:8 h dark photoperiod and 75% humidity, by assigning batches of 20 to 60 pupae randomly to one of 10 constant temperatures with 3–7 replications per temperature: 8 °C, 9 °C, 10 °C, 10.5 °C, 11 °C, 11.5 °C, 12 °C, 14 °C, 16 °C, and 26 °C. For determining the lower developmental threshold, we focused on temperatures around 10 °C, because the asparagus miner emerges in spring so we expected the threshold to be relatively low. About halfway through the experiment, temperatures were randomly reassigned to different environmental chambers to account for any effects due to the chambers. Digital thermometers were placed into each environmental chamber and checked daily to ensure proper temperature conditions, which never varied more than the given temperature ± 0.06 °C (SEM). The pupae were also checked daily for emergence of adults, and pupal duration was noted at time of emergence.

2.5 Comparison to previous years' asparagus miner abundance

In order to evaluate the accuracy of the degree-day model and its universality, the phenological events' predicted GDD from 2011 were regressed against the observed accumulated GDD at which phenological events occurred in previous years from this and previously published studies (see regression for validation [RV], Supporting Information, Table S2). This was done for data ranging from 1912 to the present collected from Michigan, Massachusetts, and the United Kingdom.[17,21,22,24,40] This included validation of the model against observed phenological events for 2012, and the deviation from expectations was calculated for each event between 2011 and 2012. The predicted accumulated GDD for phenological events used in comparisons for this section are derived from the 2011 Enviro-weather station temperature data from Hart, Michigan. The calculated degree-days for previously observed phenological events in the literature were based on weather data collected in the vicinity of insect sampling, in the same year (Supporting Information, Table S2), using the lower developmental threshold elucidated in this study and the Baskerville–Emin method with a March 1 biofix date.

2.6 Developmental time budget

In order to characterize the life cycle of the asparagus miner, a time budget in days and equivalent degree-days was created that included estimates for the egg, larval, pupal and adult stages. Egg duration was estimated from previously published literature, specifically from Fink[23] and Barnes[26] (see developmental time budget [DTB], Supporting Information, Table S2). Larval duration was estimated in three ways. First, it was approximated by determining how many degree-days had elapsed since the first appearance of larvae compared with pupae in the field. Second, the period between the peak larval abundance and the peak pupal abundance was compared. Finally, estimates were made by consulting previously published literature.[22,25,26] In developing degree-day estimates from previous literature for larvae and other stages, we used data from the nearest weather station to where the research was conducted (Supporting Information, Table S2). We applied the Baskerville–Emin[41] method of calculation for the duration of a specific life stage and, combined it with the base temperature from our current work. The pupal duration was estimated by comparing the length of time that it took pupae to develop into adults at the beginning of the season in the field. Additional estimates were obtained by noting the pupal duration from pupae raised in environmental chambers (as described earlier), and by consulting previously published information in a similar manner as to that described earlier.[18,22,23] Lastly, adult lifespan was calculated by placing adults into 26 ± 0.06 °C (16 h light:8 h dark photoperiod and 75% humidity) environmental chambers right after eclosion and feeding them a 10% sugar solution or honey water *ad libitum* on cotton balls. The adults' lifespans were recorded in days and converted into degree-days using the Baskerville–Emin method and 12.1 °C was used as the lower developmental threshold. The different estimates for a given event in the life cycle were averaged, and the mean, range and source of information were listed for each stage.

2.7 Statistics

A repeated measures analysis with first-order autoregressive correlation among the time points was used to evaluate the fit of the degree-day model. Asparagus miner adult abundance was used as the dependent variable and trap height, GDDs, year of data collection and field were used as independent variables in the linear mixed model with a generalized least squares function (R Project for Statistical Computing, http://www.r-project.org/). A Kenward–Roger correction was applied to the degrees of freedom. The residuals were analyzed to evaluate assumptions of normality and the data were log-transformed to meet assumptions of homogeneity of variances and normal distribution around a mean of zero.

While there has been much debate on the proper calculation of the lower developmental threshold,[42] we evaluated both non-linear[43] and linear methods.[4] The model yielding the lowest combined Akaike information criterion (AIC), Bayesian information criterion (BIC) and R^2 (or Efron's pseudo-R in the case of non-linear models)[44] was selected. The linear approximation had the best fit to our data and this model was then used to calculate the lower developmental threshold. As a result, the effect of temperature on pupal duration (d) and developmental rate ($1/d$) against temperature was analyzed with a linear regression.

Two linear regressions were performed to assess the accuracy of the degree-day model for the asparagus miner. First, the predicted phenological event accumulated GDD from 2011 was compared to the observed phenological event accumulated GDD in all other years with linear regression. Second, just a subset of this data, from 2012, was used to validate the degree-day model's predictions from the previous year. To assess the sensitivity of the model to location of data collection, the deviation between each predicted and observed phenological event was calculated, and a one-way analysis of variance (ANOVA) was performed (see locality sensitivity analysis [LSA], Supporting Information, Table S2). Before the analysis, the residuals were inspected to ensure that the assumptions of normality were fulfilled; no transformation of the data was necessary.

3 RESULTS

3.1 Degree-day model development

Overall, the GDD totals were associated with a significant amount of variability in asparagus miner abundance (repeated measures ANOVA: $F_{47,4422} = 47.30$, $P < 0.01$). Beginning of adult flight occurred around 100 GDD, with the first adult population peak at 490 GDD and second population peak at 1530 GDD. Asparagus miner adult flight ended at 1850 accumulated GDD (Table 2). The first pupae and larvae appeared about 280–390 GDD after the beginning of adult flight (Table 2). It then took another 360–450 GDDs before the immature stages reached peak abundance in the field. As a reference, asparagus harvesting took place between 222 and 666 accumulated GDDs, depending on the field and grower.

Table 2. Summary of the predicted accumulated growing degree-days (GDDs) from the 2011 field season in Oceana County, Michigan for different adult and immature phenological events and the deviation from expected in 2012 using the Baskerville–Emin method

Predicted GDD	Phenological event	Deviation from predicted in 2012 (GDD)
Adults		
100	Beginning of flight	57.2
490	First peak	83.1
940	Beginning of second generation	48.3
1530	Second peak	43.9
1850	End of flight	350.2
Immatures		
380	First appearance of larvae	na[a]
490	First appearance of pupae	na[a]
670	First larval peak	96.9
940	First pupa peak	216.7
1530	Second larval peak	104.7
1600	Second pupal peak	274.8

Note: We used a biofix date of March 1, and a base of 12.1 °C in combination with weather data from the Michigan State University Enviro-Weather Hart Station.
[a] Estimates for these two events were considered too biased to include in the analysis because longer harvesting of older fields delayed data collection.

3.2 Lower developmental threshold

The lower developmental threshold was 12.1 °C (Figure 1). It took pupae a mean of 207 ± 15 days to develop at 12 °C, while it only took 14 ± 0.5 days to develop at 26 °C. However, no asparagus miners emerged at 8, 9, 10, 11 or 11.5 °C, even after running the experiment for over 545 days. The asparagus miner developed at significantly different rates between the various temperatures, and the rate increased in a roughly linear manner as temperature increased (Figure 1; Adj. $R^2 = 0.84$, $P < 0.01$). As temperature increased, pupal duration also linearly decreased (Figure 1; Adj. $R^2 = 0.93$, $P < 0.01$).

3.3 Farm-level variation in voltinism

There was significant variability in adult population dynamics between different fields (repeated measures ANOVA: $F_{4,5.5} = 21.99$, $P < 0.01$). While we consistently recorded two immature peaks in both 2011 and 2012 (Figure 2A, B), the results were more variable for the adults. In 2011, we observed one adult generation with a minimal or non-existent second generation in some fields (Figure 3C), while in others, there were two pronounced generations of asparagus miner adults in a season (Figure 3A, B). In 2012, with a more rapid overall accumulation of GDDs, we observed two generations in most fields (Figure 3E, G), though some again had a reduced second generation (Figure 3F).

3.4 Comparison to previous years' asparagus miner abundance

There is a strong and significant correlation between the predicted accumulated GDDs for the 2011 phenological events in the life

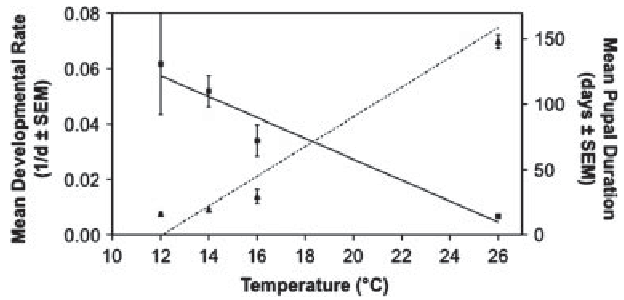

Figure 1. The mean developmental rate (open triangles, dashed line, left axis) and pupal duration (closed squares, solid line, right axis) of the asparagus miner in environmental chambers at various constant temperatures with a 16 h light:8 h dark cycle and 75% humidity. There was no miner emergence at 8 °C, 9 °C, 10 °C, 10.5 °C, 11 °C, and 11.5 °C, despite running the experiment about 545 days. The linear model fit the data best and was significant for the developmental rate ($y = 0.0054x - 0.065$, Adj. $R^2 = 0.84$, $P < 0.01$) and pupal duration ($y = -11.53x + 307.4$, Adj. $R^2 = 0.93$, $P < 0.01$).

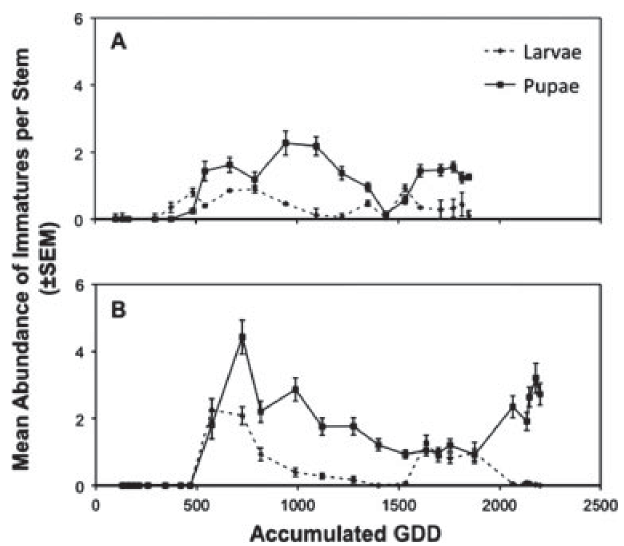

Figure 2. Mean (±SEM) asparagus miner abundance from commercial fields in Oceana County, Michigan for immature stages (pupae – solid line; larvae – dashed line) for (A) 2011 and (B) 2012. Accumulated degree-days are calculated based on data from the Michigan State University Enviro-weather station located in Hart, Michigan with a biofix date of March 1, a base temperature of 12.1 °C, and the Baskerville–Emin calculation method.

cycle of the asparagus miner and the observed accumulated GDDs for previous years (Adj. $R^2 = 0.93$, $P < 0.01$; Figure 4). Moreover, 2011 had 2.5 times more asparagus miners overall on the traps than in 2012. Location of data collection also affected the accuracy of the degree-day model. The average GDD deviation from predicted phenological events is 111.2 ± 13 for miner populations in Michigan, 266.9 ± 66 for those in Massachusetts, and 510.5 ± 131 for those in the United Kingdom. Thus, the most accurate predictions are for observations in Michigan, while observations in Massachusetts are 2.5 times less accurate, and those in Europe are about 4.5 times less accurate than in Michigan (ANOVA, deviation from expectations by location: $F_{2,41} = 11.44$, $P < 0.01$).

3.5 Validation of the degree-day model

There was a strong correlation between the predictions from 2011 for observed events in 2012 (Adj. $R^2 = 0.94$, $P < 0.01$). The mean (±SEM) deviation from the expected GDD for the phenological events in 2012 was 142 ± 37 GDDs, with the most accurate prediction for the second generation adult peak and the least accurate prediction for the end of adult flight (Table 2). Predictions for the adult stage's events were about 1.5 times more accurate than predictions for immature stages in 2012.

3.6 Developmental time budget

According to estimates derived from this study and previously published literature (Supporting Information, Table S3), a generation should last on 731.1 ± 30 GDDs from deposition of egg to the death of the asparagus miner adult (Figure 5). Because the asparagus miner is usually bivoltine, the total life cycle should take on average 1462 GDDs (95% confidence interval [CI]: 1000–1925 GDDs). The egg is the most ephemeral stage, while the larval and adult stages are similar in length, each composing about a quarter of the life cycle for the asparagus miner. When considering Julian days, the pupal stage accounts for a little less than two-thirds of the total life cycle (Supporting Information, Table S4).

4 DISCUSSION

This is the first study to develop and validate a degree-day model for management of the asparagus miner in Michigan. The key phenological events for timing the currently available management methods against the asparagus miner are the first and the second peak adult flights that are the points at which the asparagus miner is most vulnerable to currently available pesticides. Reduced-risk foliar pesticides could be most efficiently timed shortly before both adult population peaks to minimize oviposition into stems and subsequently reduce crop damage (e.g. 350 GDDs for first population and 1350 GDDs for the second peak). In future research, the degree-day model's predictions will be employed in a commercial field setting to evaluate whether its use results in decreased asparagus miner abundance.

Our predicted accumulated GDDs for various phenological events in the life cycle of the asparagus miner deviated from Tuell's[18] study by a mean of 86 ± 21 GDDs for all phenological events. However, there was a mean deviation of 109 ± 26 GDDs and 267 ± 66 GDDs for the bionomic data collected by Lampert *et al.*[25] and Ferro and Gilbertson,[22] respectively. The GDD observed by Ferro and Gilbertson[22] may have deviated more because that data was recorded in Hadley, Massachusetts. Taken together with the fact that there was far more deviation from expected events in the United Kingdom than either Massachusetts or Michigan, this indicates that the degree-day model should be validated in other regions before it is recommended for grower adoption outside the midwestern and eastern United States.

Although lower developmental thresholds for two closely related species of the asparagus miner are already known, these values can vary greatly among species, and therefore, they cannot be used as a starting point for the asparagus miner. For example the lower developmental threshold for pupae of *Liriomyza huidobrensis* is 7.3 °C, while for *L. trifolii* it is 10.7 °C.[45] Both species are cosmopolitan and occur at the same latitudes as the asparagus miner, but *L. huidobrensis* is also found at higher elevations. Our study is the first investigation of the lower developmental threshold for asparagus miner pupae, which our data shows is 12.1 °C. In some cases, there may be varying developmental thresholds for different life stages of the same species,[46] although some related miner species have an isomorphic

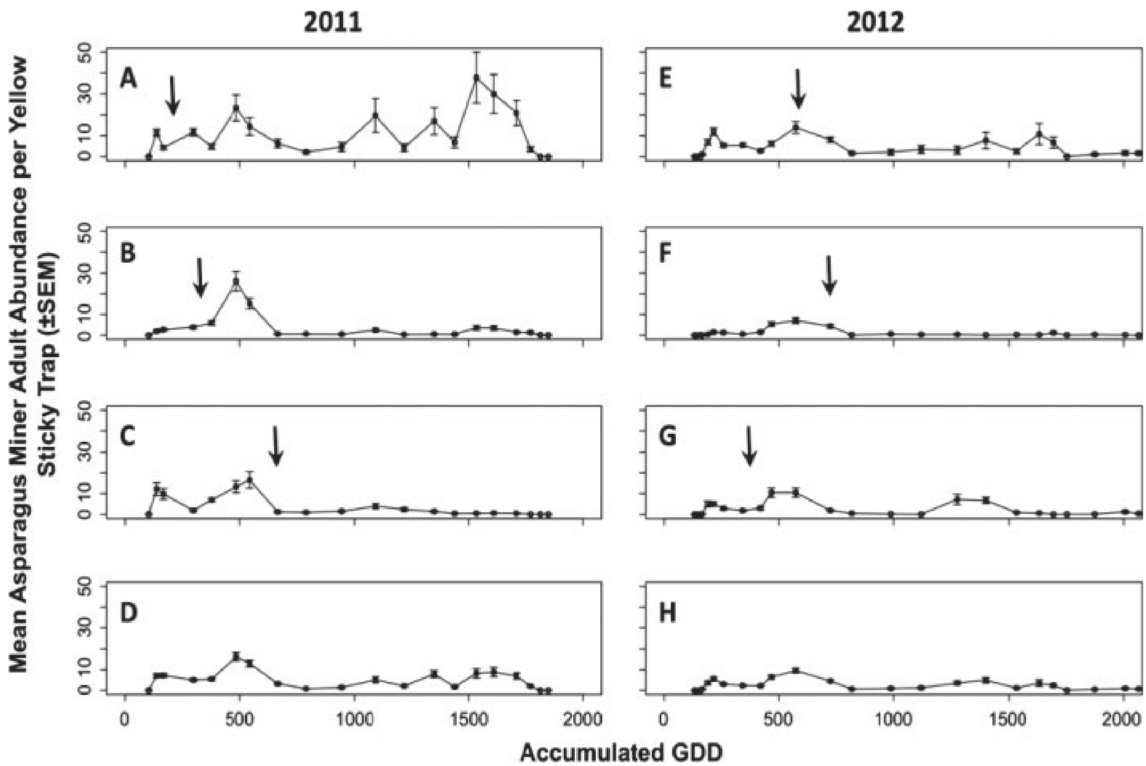

Figure 3. Mean (±SEM) asparagus miner adult population dynamics abundance from Oceana County, Michigan in 2011 (left column) and 2012 (right column) in field 1 (A, E), field 2 (B, F), field 3 (C, G), and overall (D, H). Degree-days were calculated from the Michigan State University Enviro-weather station located in Hart, Michigan with a biofix date of March 1, a base temperature of 12.1 °C, and the Baskerville–Emin calculation method. Arrows indicate when spear harvesting stopped.

developmental rate (i.e.: *L. trifolii* and *L. huidobrensis*).[45] However, isomorphy must be evaluated on a species-by-species basis because stage-specific lower developmental thresholds affect the overall rate of insect development. This will be the focus of future work.

In our study, the average age of the sampled fields was 1–2 years at the beginning of our study, and since miners prefer recently planted fields, these were representative of young, vulnerable fields. In some fields we detected two population peaks, while in others the second peak was lacking or reduced, which could be due to local biotic and abiotic conditions, management actions by the growers, or the age of the asparagus field. In addition, the duration of asparagus harvest is different for young and mature fields: harvest may take 550 GDDs in mature fields after the plants begin developing at *c.* 100 GDDs, and this overlaps with the first adult peak. Previous reports[21] have suggested that the normal six-week harvest for mature fields acts as an impediment to asparagus miner oviposition. In our study, fields with longer harvest times (e.g. field 3 in 2011 and field 2 in 2012) had a reduced second generation of asparagus miners, whereas those with shorter harvests (e.g. field 1 and 2 in 2011; field 1 and 3 in 2012) had a more pronounced second generation of adults. However, this may just be the case for the particular fields that we sampled in the current study, because when a greater number of fields were included in another study,[47] this trend was contradicted. Moreover, extending the harvest season longer than necessary has been shown to deplete the carbohydrate stores of young asparagus plants and reduce yields in subsequent years,[48] so this strategy should not be recommended to growers as a way to manage miners. While there is a clear and consistent first population peak regardless of field, our data highlights the need to pair the degree-day model with scouting in the field during the second asparagus miner adult peak to verify the presence of insects in order to appropriately target management strategies.

The appearance of the first adult asparagus miners ranged between 102–136 GDDs in 2011 and 157–163 GDD in 2012, depending on the field. This variability in emergence may be due to the distance of the field from the weather station that was used to calculate the degree-days. Fields 1 and 2 were located close to the weather station while field 3 was farther away, so it is possible that the reference weather station was less representative, and as a result, the difference between the actual GDD was relatively larger. Regardless, such spatial effects are likely minor compared to the overall accuracy of the degree-day model, and may not significantly affect management decisions, at least in this bioregion.

It takes about 280 GDDs between the emergence of the first adults (at 100 GDDs) to the appearance of the first larvae (at 380 GDDs) in the field, and 390 GDDs between the first adults and pupae. The former is important to know since younger larvae may sometimes be easier to kill with pesticides than older larvae. For example, other agromyzid larvae have been shown to be more susceptible to insecticides at earlier instars than later ones.[49] Moreover, if larvae are killed soon after eclosion, they will not be able to inflict significant damage on the photosynthetic ability of the asparagus plant, and will not render the plant vulnerable to species of *Fusarium*. Up to this point, asparagus growers have not been able to kill asparagus miner larvae, as they remain protected within the stem. However, research is currently ongoing to test systemic insecticides that may be able to target

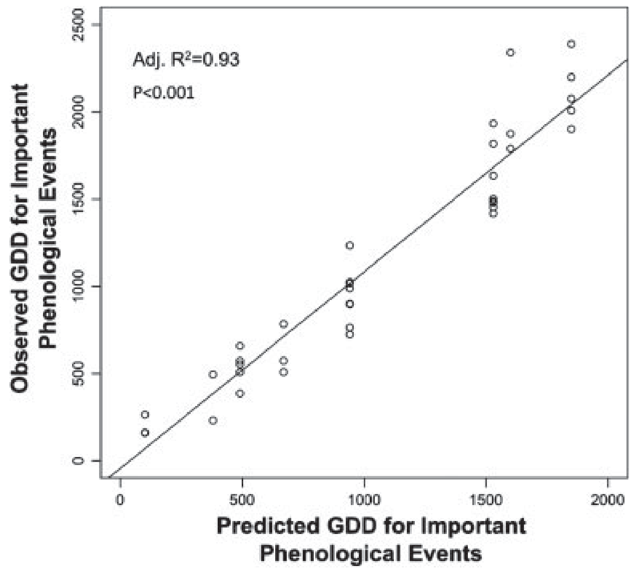

Figure 4. Linear regression for the predicted accumulated growing degree day (GDD) from 2011 for important phenological events against the observed accumulated GDD for the same events in the asparagus miner life cycle from 1974, 1980, 2001, 2010, and 2012. Across years, calculated degree-days are fit with a model containing 12.1 °C as a base, March 1 as a biofix date, and using the Baskerville–Emin algorithm. The model has a significant slope ($y = 1.13x - 44.35$, $P < 0.01$, with an adjusted $R^2 = 0.94$).

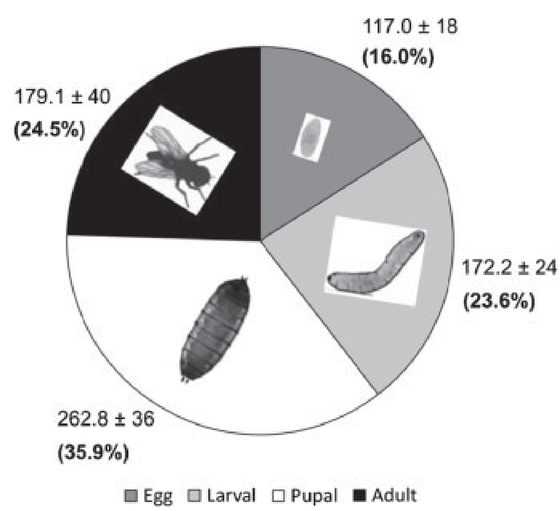

Figure 5. A developmental time budget based on mean ± SEM degree-days to complete each life stage of the asparagus miner from previous estimates in the literature and the current study. The mean developmental time in degree-days is indicated outside each slice for the respective stages, and the percent of the total is in parentheses. Egg duration is shortest, while the pupa is the longest-lasting stage. Illustrations by Marlene Cameron, Michigan State University.

larvae (Szendrei Z, unpublished data). If effective chemistries are found, growers will then be able to use the time between the appearance of first adults and first larvae to guide decisions about when to apply reduced-risk systemic or translaminar insecticides.

According to the developmental time budget described in this study, the total life cycle of the asparagus miner lasts a mean of 1462 degree-days, with an upper limit of about 1925 degree-days. According to our degree-day model, which was calculated separately from the compilation of information from the literature about the length of different stages of the asparagus miner, the end of flight in a season for the asparagus miner should occur around 1850 degree-days. There are two putative explanations for the disjunction in our finding. It may be possible that the degree-day budget systematically underestimates the duration of the life stages for the asparagus miner. This could happen, for example, if the food we used to rear the asparagus miner adults was not as ideal as the food they have access to under natural conditions. Second, it may be possible that because the estimates for the degree-day budget were derived from various geographic locations around the world, there is an amount of inherent uncertainty.[50] However, the degree-day model estimate was uniformly developed from Michigan data, which provides greater certainty and consistency in comparing similar circumstances to each other. Regardless of the exact cause, it is likely that the full life cycle of the asparagus miner requires upwards of 2000 degree-days to complete.

We found that the egg stage was the shortest-lasting stage, while the pupa was the longest-lasting stage. Previous studies with closely related organisms have also found that the egg stage is usually the shortest, and the pupal stage is often the longest, for example in *Liriomyza bryoniae* (Kaltenbach) (Diptera: Agromyzidae)[51] and in *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae).[52]

Overall, the information presented here can be used as part of an integrated pest management program for minimizing economic damage by the asparagus miner and the non-target effects associated with pesticides. The results from this study will be incorporated into the Michigan State University Enviro-weather website for use by asparagus growers. Our results are expected to contribute to the long-term sustainability of asparagus miner management, minimize costs for growers, as well as fill in knowledge gaps about the biology of the asparagus miner.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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