

Alternative plants for development of picture-winged fly pests of maize

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Accepted: 9 February 2012

Key words: *Euxesta eluta*, *Euxesta stigmatias*, *Chaetopsis massyla*, Poaceae, alternate hosts, sugarcane, corn, capsicum, Diptera, Ulidiidae, *Zea mays*

Abstract

Eleven species of picture-winged flies (Diptera: Ulidiidae: Lipsanini) have been reported attacking maize [*Zea mays* L. (Poaceae)] ears in the Americas. Four of these species are sweet corn pests in America north of Mexico: *Chaetopsis massyla* (Walker), *Euxesta annonae* (Fabricius), *E. eluta* Loew, and *E. stigmatias* Loew. Adults of these four species appear at the beginning of each season following maize-free periods, suggesting other plants act as food sources for maintenance and development of these flies. Studies were conducted in Florida, USA, to evaluate the suitability of several crop and non-crop plants commonly occurring near maize plantings as developmental hosts for these flies. Laboratory trials were conducted using laboratory colonies of *C. massyla*, *E. eluta*, and *E. stigmatias* to determine their developmental rates and pupal survivorship on roots, stems, leaves, or fruits of 14 crop and weed species. All three fly species completed development on all tested crops (*Brassica oleracea* L., *Capsicum chinense* Jacquin, *Capsicum annum* L., *Carica papaya* L., *Persea americana* Mill., *Raphanus sativus* L., *Saccharum officinarum* L., and *Solanum lycopersicum* L.) and weed species [*Amaranthus spinosus* L., *Portulaca oleracea* L., *Sorghum halepense* (L.), and *Typha* spp.], except for *Daucus carota* L. roots and *Solanum tuberosum* L. tubers. Findings of the current study suggest that the presence of multiple host crops in areas surrounding maize fields may help explain the occurrence of these maize-infesting ulidiids immediately after prolonged absences of maize.

Introduction

The picture-winged fly *Euxesta stigmatias* Loew (Diptera: Ulidiidae: Lipsanini) is recognized as a serious pest of sweet corn (*Zea mays* L.) due to larval feeding on silks, kernels, and cobs (Seal & Jansson, 1989). Feeding damage to the silks also results in reduced pollination leading to asymmetric development of kernels (App, 1938). Adults do not cause damage to plants. Females cannot insert their eggs into healthy plant tissue, but rather deposit eggs within natural cracks and crevices or in plant parts previously damaged by weather, disease, vertebrate and inverte-

brate feeding, or mechanical forces. In maize, eggs are deposited into the open end of the ears among the silk or between the husk and silk. The adults feed on plant exudates and pollen on the surface of plants, so they are found on many hosts and surfaces that do not necessarily provide suitable larval food sources (e.g., windows, automotive and farm vehicles). Ten other picture-winged flies attack maize in predominantly tropical and subtropical regions in the Americas: *Chaetopsis massyla* (Walker), *Eumecosomyia nubila* (Wiedemann), *Euxesta annonae* (Fabricius), *Euxesta eluta* Loew, *Euxesta major* (Wulp), *Euxesta mazorca* Steyskal, *Euxesta obliquestriata* Hendel, *Euxesta nitidiventris* Loew, *Euxesta sororcula* (Wiedemann), and *Euxesta thomae* Loew (Chittenden, 1911; Painter, 1955; Díaz, 1982; Arce de Hamity, 1986; Barbosa et al., 1986; Evans & Zambrano, 1991; Wyckhuys & O'Neil, 2007;

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Goyal et al., 2010; Cruz et al., 2011). Larvae of four of these species, *C. massyla*, *E. annonae*, *E. eluta*, and *E. stigmatias*, attack sweet corn in Florida, USA (Goyal et al., 2011).

Maize is not available throughout the year for picture-winged fly development, yet the four species routinely appear in sweet corn fields in southern Florida at the beginning of each season following maize-free periods (July to September). This suggests that other plants are likely acting as food sources for maintenance and development of these flies in the absence of commercial maize. Some known alternative food sources of all four species occur in southern Florida. *Chaetopsis massyla* is known to develop in stems of cattail, *Typha latifolia* L. (Typhaceae) (Allen & Foote, 1992) that are found throughout marshy habitats and on canal banks throughout the state of Florida (Wunderlin & Hansen, 2008). *Euxesta annonae* was found developing in sugarcane stems (*Saccharum officinarum* L.) in Hawaii (Perkins, 1903). Seal et al. (1996) found *E. stigmatias* larvae in grass stems, fruits of decomposing fruiting vegetable and tree crops, and injured tubers and stems of solanaceous crops at Homestead, Florida. Many of these plants can be found in American countries that grow maize. Therefore, many monocot and dicot crops, weeds, and native plants are available that may provide resources for development and survival of these species in the absence of maize. This study was conducted to evaluate alternative plants for the development of *C. massyla*, *E. eluta*, and *E. stigmatias*, the three ulidiids most commonly infesting Florida maize fields.

Materials and methods

The most common commodities (fruits and vegetables) and weeds that grow in close proximity to commercial

maize were evaluated as alternative developmental hosts for each fly species (Table 1). Roots of carrots (taproots), radishes, and potatoes (tubers), fruits of Hass avocado, bell pepper, habañero pepper, tomato, and papaya, leaves of cabbage, and stems of sugarcane were used for experiments. Fully ripe vegetables and fruits to be tested as hosts for larval development were purchased from local markets. Because *C. massyla* has been reared from sugarcane stalks collected in southern Florida that were naturally infested with larvae of the sugarcane borer, *Diatraea saccharalis* (Fabricius) (Lepidoptera: Crambidae) (Goyal, 2010), sugarcane was also evaluated as a host for these flies. Sugarcane stalks were obtained from commercial fields produced in Belle Glade, FL, USA. Our preliminary surveys found ulidiid larvae feeding on damaged weeds around maize fields; therefore, cut stems of selected weed species also were evaluated as hosts for these flies. Weeds used in the experiment were collected from fields at the Everglades Research and Education Center (EREC), Belle Glade.

Our purpose was to present potential food hosts to the flies as they would be found in the agricultural environment. It was not possible to standardize by size, weight, surface, or total volume across all the various plant parts tested without compromising the integrity (and thereby improving the chances of oviposition) of the external surfaces of these hosts. Therefore, the individual fruits, leaves, stems, tubers, and taproots were selected for the tests that appeared to be of equal size within each host type. Plant stems used in the trial (sugarcane and the weed species) were standardized at 7-cm sections. Although most of the tested plant parts were not altered before exposure to flies, a few were manipulated to increase surface area available for oviposition or to maintain moisture levels. Preliminary

Table 1 Commodities and weed species evaluated under laboratory conditions

Order	Family	Common name	Scientific name	Plant part
Apiales	Apiaceae	Carrot	<i>Daucus carota</i> L.	Root
Capparales	Brassicaceae	Cabbage	<i>Brassica oleracea</i> L.	Leaf
		Radish	<i>Raphanus sativus</i> L.	Root
Caryophyllales	Amaranthaceae	Spiny amaranth	<i>Amaranthus spinosus</i> L.	Stem
	Portulacaceae	Little hogweed	<i>Portulaca oleracea</i> L.	Stem
Cyperales	Poaceae	Johnsongrass	<i>Sorghum halepense</i> (L.) Pers.	Stem, root
		Sugarcane	<i>Saccharum officinarum</i> L.	Stem
Laurales	Lauraceae	Hass avocado	<i>Persea americana</i> Mill.	Fruit
Solanales	Solanaceae	Habañero pepper	<i>Capsicum chinense</i> Jacquin	Fruit
		Bell pepper	<i>Capsicum annum</i> L.	Fruit
		Tomato	<i>Solanum lycopersicum</i> L.	Fruit
		Potato	<i>Solanum tuberosum</i> L.	Stem tuber
Typhales	Typhaceae	Southern cattail	<i>Typha</i> spp.	Stem
Violales	Caricaceae	Papaya	<i>Carica papaya</i> L.	Fruit

laboratory trials determined that undamaged sugarcane stalks with fly eggs did not support the development of eggs to adults. Therefore, 0.5 cm diameter holes were drilled 0.5 cm into the internodes of 7-cm long sugarcane billets to mimic the damage of lepidopteran larvae before exposing them to flies. The cut ends of billets were covered with Parafilm® (Pechiney Plastic Packaging, Chicago, IL, USA) to reduce moisture loss, because sugarcane stalks in the field would generally be intact, not cut or broken. The main stems of weeds (spiny amaranth, Johnsongrass, little hogweed, and southern cattail) used in the experiments were also cut into 7 cm lengths and placed in cages. The stems of the weeds were not capped with Parafilm, because our field observations indicated that larvae were found only in the tissue of plants that had been damaged by field equipment. Potential development hosts were exposed to flies within Plexiglas cages (15 × 15 × 15 cm). Most tested plant parts were placed directly on the floor of the cages. To achieve larger surface areas for fly oviposition, stems of weeds, southern cattail, and sugarcane were placed upright inside the cages with one end touching the floor several centimeters away from a wall and the other touching one cage wall. Individual leaves of cabbage were separated from heads and placed on the cage floor for evaluation.

Potential food hosts (Table 1) were exposed to adults of each of the three fly species to acquire plant material naturally infested by direct oviposition, rather than by artificial infestation using eggs from colonies. Flies used for the experiment were from laboratory colonies maintained on artificial *H. zea* diet (product no. F9393B; Bioserv, Frenchtown, NJ, USA) using the method of Hentz & Nuessly (2004) with 10 male:female pairs of a single fly species. Colonies of the three fly species were initiated from adults collected using sweep nets in maize fields in and around Belle Glade, Florida. Wild flies of all the three species were added to the colonies every 2–3 months to reduce potential inbreeding depression. Flies used in the experiment had completed 3–6 generations before beginning the studies. Adults without visible deformities or damaged antennae, legs, or wings were selected for the tests from colony cages containing 5- to 15-day-old flies. Concurrent studies by Goyal et al. (2010) found oviposition rates for these flies to vary from 1 to 23 eggs per day on artificial diet within 5–15 days of adult emergence from puparia. Greatest oviposition for all three species was observed on day 11. The pre-oviposition period for the three species was 10, 3, and 8 days for *C. massyla*, *E. eluta*, and *E. stigmatias*, respectively. Therefore, 10 pairs of flies were placed in each cage with plant parts rather than a single pair to compensate for variation in the pre-oviposition periods and daily oviposition patterns. Flies in the cages were provided with supplementary honey and water. Following a 24-h expo-

sure to the flies that began at 09:00 hours, plant material was removed from the cages and placed in plastic containers (15 cm high × 11 cm diameter) with a screen top (9 cm² area) lined with paper towels to allow development to the pupal stage of any resulting eggs. Larvae of these species normally pupate outside of their food hosts. Plant parts and paper towels were checked for pupae daily after 7 days. Pupae were placed on moistened filter paper (Whatman® 3; Whatman International, Maidstone, UK) in Petri plates and held for adult emergence. Plates were sealed with Parafilm to reduce moisture loss. Adult emergence was recorded daily. Flies were preserved in 70% ethyl alcohol for later identification. Successful emergence of adults of a particular species from these plants was considered to be evidence of a developmental host for that species.

Studies were replicated three times over a 10-month period (December 2008 to January 2009, April to May 2009, and August to September 2009). Each commodity and weed was tested 8–12 times in each of the three seasons (total n = 26–36 for each plant species). All phases of this experiment were conducted in insectary rooms maintained at 26.5 ± 1.0 °C, L14:D10 photoperiod, and 55–70% r.h.

Observations were recorded on the length of the combined egg and larval stages, the number of pupae produced, the length of the pupal stage, and the number of adults emerged for each fly species on each tested plant species. Quantification of oviposition was initially attempted, but it was discontinued after it was determined that more adults emerged from hosts than the number of eggs originally observed. This likely resulted from unobserved eggs deposited in cracks or between structures of the tested plant parts. Percentage pupal survival was calculated by multiplying the quotient of the number of adults that emerged over the total number of pupae collected from each host by 100.

Data analysis

The generalized linear model (Proc GLM; SAS Institute, 2008) was used to conduct an analysis of variance (ANOVA) on the results due to unequal replicate sizes. The experiment was organized in a randomized block design where all the treatments were completely randomized over plots with season as blocks. Fly species (three) and plant species (12) were used as independent variables. None of the fly species developed on two of the tested plants; therefore, results from only 12 plants were included in the analysis. The lengths of the egg plus larval and pupal stages, and percentage pupal survival were used as dependent variables in the model. Due to size differences among the types of tested plant hosts, comparison among these hosts

was not valid for numbers of pupae. Therefore, results for the number of pupae were compared among fly species separately for each tested plant host. Least squared means were used for post-hoc analysis where the interactions of independent variables were significant sources of variation in the ANOVA models. The Tukey's honestly significant difference (HSD) test (SAS Institute, 2008) was used for post-hoc means separation with $\alpha = 0.05$.

Results

All three species deposited their eggs on all the plant species tested. All three species successfully completed development on all tested plant parts except on potato tubers and carrot taproots. The length of the egg plus larval stages was significantly affected by plant host ($F_{11,954} = 1\ 007.16$, $P < 0.0001$), fly species ($F_{2,954} = 884.80$, $P < 0.0001$), and plant host*species interaction ($F_{22,954} = 18.44$, $P < 0.0001$). Season ($F_{2,954} = 0.05$, $P = 0.95$) and the interactions of plant host*season ($F_{22,954} = 0.39$, $P = 0.99$) and fly species*season ($F_{4,954} = 0.24$, $P = 0.91$) did not significantly affect the length of egg plus larval developmental times. Therefore, the data were pooled across seasons for comparisons of mean development times.

The mean egg plus larval developmental time pooled across seasons was shortest for *E. eluta* and longest for *C. massyla* (Table 2). The development times varied from 13–27 days for *C. massyla*, 10–20 days for *E. eluta*, and

12–25 days for *E. stigmatias*. The egg plus larval developmental times for both *C. massyla* and *E. stigmatias* were shortest on bell pepper fruit and longest on spiny amaranth stems. The mean egg plus larval developmental time for *E. eluta* was significantly shorter on bell pepper and tomato fruit and cabbage leaves and longer on spiny amaranth and southern cattail stems than on the other tested plants.

Pupal developmental times were significantly affected by plant host ($F_{11,953} = 1\ 040.92$, $P < 0.0001$), fly species ($F_{2,953} = 117.61$, $P < 0.0001$), and plant host*fly species interaction ($F_{22,953} = 200.70$, $P < 0.0001$). Season ($F_{2,953} = 0.94$, $P = 0.39$) and the interactions of plant host*season ($F_{22,953} = 0.46$, $P = 0.98$) and fly species*season ($F_{4,953} = 0.85$, $P = 0.49$) did not significantly affect pupal developmental times. Therefore, the data were pooled across seasons for comparisons of pupal development times.

The mean pupal developmental time of *C. massyla* varied from 6 (tomato fruit) to ca. 10 days (little hogweed stems) (Table 3). The length of pupal development for *E. eluta* ranged from ca. 5 (tomato and papaya fruit) to 12 days (cabbage leaves and avocado fruit). The pupal development time of *E. stigmatias* varied from ca. 6 (tomato, bell pepper, and papaya fruit) to 12 days (avocado fruit and spiny amaranth stems). No overall pattern of pupal development rate was observed with respect to the fly or plant species. The pupal development times of

Table 2 Egg plus larval developmental times (days) for three Ulidiidae species reared on 12 commodities and weeds

Common plant name	Least squared mean \pm SEM (n; range) ¹			F	d.f.	P
	<i>Chaetopsis massyla</i>	<i>Euxesta eluta</i>	<i>Euxesta stigmatias</i>			
Spiny amaranth	27.0 \pm 0.2Aa (26; 23–31)	19.9 \pm 0.2Ca (26; 17–22)	25.0 \pm 0.2Ba (26; 23–27)	154.54	2,75	<0.0001
Cabbage	14.9 \pm 0.2Ag (27; 13–17)	10.9 \pm 0.2Cf (27; 9–13)	14.0 \pm 0.2Bf (27; 12–16)	146.83	2,78	<0.0001
Radish	17.5 \pm 0.2Aef (31; 16–19)	15.4 \pm 0.2Cc (30; 13–17)	16.2 \pm 0.2Bd (31; 14–18)	51.67	2,89	<0.0001
Papaya	15.5 \pm 0.2Ag (27; 13–17)	12.0 \pm 0.2Ce (27; 10–14)	12.7 \pm 0.2Bg (27; 11–15)	81.49	2,78	<0.0001
Avocado	16.7 \pm 0.2Af (26; 15–18)	14.3 \pm 0.2Cd (26; 12–16)	15.2 \pm 0.2Be (26; 12–19)	31.33	2,75	<0.0001
Johnsongrass	21.4 \pm 0.2Ac (32; 18–24)	18.0 \pm 0.2Cb (32; 16–20)	19.0 \pm 0.2Bc (32; 17–21)	59.15	2,93	<0.0001
Sugarcane	17.9 \pm 0.2Ae (25; 16–20)	15.7 \pm 0.2Cc (25; 14–18)	17.1 \pm 0.2Bd (25; 15–19)	34.68	2,72	<0.0001
Southern cattail	25.3 \pm 0.2Ab (28; 23–27)	19.1 \pm 0.2Ca (28; 17–21)	23.2 \pm 0.2Bb (28; 22–26)	236.90	2,81	<0.0001
Little hogweed	21.0 \pm 0.2Ac (36; 19–23)	17.4 \pm 0.2Cb (36; 15–20)	18.9 \pm 0.2Bc (36; 16–22)	70.84	2,105	<0.0001
Bell pepper	12.7 \pm 0.2Ah (26; 12–15)	10.1 \pm 0.2Cf (26; 8–12)	11.5 \pm 0.2Bh (26; 10–13)	48.50	2,75	<0.0001
Habañero pepper	19.4 \pm 0.2Ad (28; 17–21)	17.2 \pm 0.2Cb (27; 16–18)	18.7 \pm 0.2Bc (28; 17–21)	32.78	2,80	<0.0001
Tomato	15.1 \pm 0.2Ag (28; 13–18)	11.0 \pm 0.2Cf (28; 10–14)	13.3 \pm 0.2Bfg (28; 11–16)	114.15	2,81	<0.0001
F	388.71	291.35	741.26			
d.f.	11,328	11,326	11,328			
P	<0.0001	<0.0001	<0.0001			

Means within a row followed by the same capital letter – and within a column followed by the same small letter – are not significantly different (Tukey's HSD: $P > 0.05$, following ANOVA).

¹n = number of fruits/leaves/stems.

Table 3 Comparison of pupal developmental times (days) of three Ulidiidae species on 12 commodities and weeds

Common plant name	Least squared mean \pm SEM (n; range) ¹			F	d.f.	P
	<i>Chaetopsis massyla</i>	<i>Euxesta eluta</i>	<i>Euxesta stigmatias</i>			
Spiny amaranth	9.3 \pm 0.1Bb (25; 7–11)	7.7 \pm 0.1Cd (26; 6–9)	11.5 \pm 0.1Aa (26; 10–13)	168.07	2,74	<0.0001
Cabbage	8.6 \pm 0.1Ccd (27; 8–9)	11.7 \pm 0.1Aa (27; 11–12)	9.2 \pm 0.1Bc (27; 8.9–9.4)	1810.67	2,78	<0.0001
Radish	6.5 \pm 0.1Cfg (31; 5–7)	6.6 \pm 0.1Be (30; 6–7)	7.4 \pm 0.1Ae (31; 7–8)	57.49	2,89	<0.0001
Papaya	8.1 \pm 0.1Ad (27; 7.8–8.2)	5.1 \pm 0.1Cg (27; 5.0–5.3)	6.0 \pm 0.1Bg (27; 5.7–6.3)	5811.48	2,78	<0.0001
Avocado	9.2 \pm 0.1Ab (26; 8–10)	12.0 \pm 0.1Ca (26; 11–13)	11.5 \pm 0.1Ba (26; 11–12)	324.78	2,75	<0.0001
Johnsongrass	8.8 \pm 0.1Abc (32; 8–11)	5.7 \pm 0.1Bf (32; 4–7)	8.5 \pm 0.1Ad (32; 7–9)	184.11	2,93	<0.0001
Sugarcane	7.4 \pm 0.1Ae (25; 6–8)	6.0 \pm 0.1Cf (25; 5–7)	6.8 \pm 0.1Bf (25; 6–7)	94.62	2,72	<0.0001
Southern cattail	7.3 \pm 0.1Ce (28; 5–9)	10.5 \pm 0.1Ab (28; 9–12)	9.8 \pm 0.1Bb (28; 9–10)	169.24	2,81	<0.0001
Little hogweed	10.4 \pm 0.1Aa (36; 8–12)	10.0 \pm 0.1Ac (36; 9–12)	10.1 \pm 0.1Ab (36; 9–12)	3.09	2,105	0.0497
Bell pepper	6.6 \pm 0.1Bf (26; 6–7)	8.0 \pm 0.1Ad (26; 7.9–8.2)	6.0 \pm 0.1Cg (26; 5.8–6.2)	1333.36	2,75	<0.0001
Habañero pepper	6.8 \pm 0.1Cf (28; 5.7–7.4)	7.8 \pm 0.1Bd (27; 7–9)	8.8 \pm 0.1Ad (28; 8–9)	154.97	2,80	<0.0001
Tomato	6.0 \pm 0.1Ag (28; 5.7–6.4)	5.1 \pm 0.1Cg (28; 5.0–5.3)	5.8 \pm 0.1Bg (28; 5.5–6.2)	448.59	2,81	<0.0001
F	175.80	739.76	741.26			
d.f.	11,327	11,326	11,328			
P	<0.0001	<0.0001	<0.0001			

Means within a row followed by the same capital letter – and within a column followed by the same small letter – are not significantly different (Tukey's HSD: $P > 0.05$, following ANOVA).

¹n = number of fruits/leaves/stems.

E. eluta were faster than the other fly species on spiny amaranth, little hogweed, Johnsongrass and sugarcane stems, and papaya and tomato fruit. The pupae of *C. massyla* developed faster than the two *Euxesta* spp. on habañero pepper and avocado fruit, cabbage leaves, southern cattail stems, and radish bulbs. The pupae of *E. stigmatias* developed faster than other fly species only on bell pepper fruit.

The number of pupae obtained per plant species was significantly affected by fly species ($F_{2,954} = 142.55$, $P < 0.0001$), plant host ($F_{11,954} = 655.36$, $P < 0.0001$), and fly species*plant host interaction ($F_{22,954} = 12.98$, $P < 0.0001$). Season ($F_{2,954} = 0.74$, $P = 0.48$) and the interactions of fly species*season ($F_{4,954} = 0.83$, $P = 0.51$) and plant host*season ($F_{22,954} = 0.65$, $P = 0.89$) did not significantly affect the number of pupae. Therefore, data were pooled across seasons to compare the mean number of pupae of each species obtained in different plant species.

There were significant differences among fly species in the number of pupae that emerged from all tested plant species, except for habañero pepper fruit and little hogweed stems (Table 4). The mean number of pupae that resulted from initial oviposition on the weeds spiny amaranth, Johnsongrass, and little hogweed was generally < 10 per stem. Mean pupae emerging from radish and habañero ranged from 12 to 25 per host. Sugarcane stem pieces produced an average of 22–29 pupae. Most of the remaining tested host plants produced mean pupae counts of > 50 per fruit or leaf. *Euxesta eluta* produced more pupae than the

other fly species on papaya, bell pepper and tomato fruit, cabbage leaves, radish bulbs, Johnsongrass, and southern cattail stems.

Pupal survival was significantly affected by plant host ($F_{11,954} = 18.64$, $P < 0.0001$), but not by fly species ($F_{2,954} = 1.33$, $P = 0.27$), season ($F_{2,954} = 2.21$, $P = 0.11$), or the interactions of fly species*plant host ($F_{22,954} = 1.21$, $P = 0.23$), fly species*season ($F_{4,954} = 0.39$, $P = 0.81$), and plant host*season ($F_{22,954} = 1.41$, $P = 0.10$). Therefore, the data were pooled across seasons and fly species to compare the pupal survival among the hosts. Pupal survival was significantly greater on avocado, papaya, bell pepper, and tomato fruit, and on cabbage leaves than on all but one of the other plants tested (Table 5).

Discussion

Most of the plant species tested in the current study were found to support the development of three species of maize-infesting ulidiid flies (Table 2). No laboratory studies have been conducted in the past to study the successful larval or pupal development or survival of these flies on alternate hosts. However, adult ulidiids have previously been reared by others from field samples of several of these plant species. Huepe et al. (1986) and Koch & Waterhouse (2000) determined that *E. eluta* used bell peppers as a developmental host in Chile. *Chaetopsis massyla* adults were reared from sugarcane stems infested with *D. saccharalis*

Table 4 Number of pupae of three Ulidiidae species that emerged from 12 commodities and weeds

Common plant name	Mean \pm SEM (n; range) ¹			F	d.f.	P
	<i>Chaetopsis massyla</i>	<i>Euxesta eluta</i>	<i>Euxesta stigmatias</i>			
Spiny amaranth	2.9 \pm 2.0B (26; 1–6)	5.2 \pm 2.0A (26; 3–7)	4.3 \pm 2.0A (26; 1–9)	14.88	2,75	<0.0001
Cabbage	60.7 \pm 2.0B (27; 41–75)	87.6 \pm 2.0A (27; 50–136)	64.4 \pm 2.0B (27; 49–84)	33.04	2,78	<0.0001
Radish	14.0 \pm 1.9B (31; 3–31)	25.3 \pm 1.9A (30; 16–39)	16.0 \pm 1.9B (31; 7–24)	30.26	2,89	<0.0001
Papaya	41.9 \pm 2.0C (27; 18–61)	73.4 \pm 2.0A (27; 49–101)	51.4 \pm 2.0B (28; 24–81)	45.62	2,78	<0.0001
Avocado	35.6 \pm 2.0B (26; 14–89)	54.3 \pm 2.0A (26; 32–82)	46.8 \pm 2.0A (26; 27–70)	9.30	2,75	0.0002
Johnsongrass	6.1 \pm 1.8B (32; 1–16)	10.4 \pm 1.8A (32; 1–20)	8.5 \pm 1.8AB (32; 1–14)	8.04	2,93	0.0006
Sugarcane	28.6 \pm 2.0A (25; 15–47)	25.4 \pm 2.0A (25; 17–34)	22.4 \pm 0.9B (25; 12–30)	7.75	2,72	0.0009
Southern cattail	7.1 \pm 2.0B (28; 3–12)	10.0 \pm 2.0A (28; 4–14)	7.8 \pm 2.0B (28; 3–14)	9.94	2,81	0.0001
Little hogweed	7.2 \pm 1.7A (36; 1–12)	7.8 \pm 1.7A (36; 1–18)	7.6 \pm 1.7A (36; 1–17)	0.25	2,105	0.78
Bell pepper	71.0 \pm 2.0B (26; 45–96)	107.3 \pm 2.0A (26; 66–179)	81.7 \pm 2.0B (26; 49–105)	23.79	2,75	<0.0001
Habañero pepper	12.7 \pm 2.0A (28; 5–25)	15.2 \pm 2.0A (27; 8–26)	14.1 \pm 2.0A (28; 7–20)	2.01	2,80	0.14
Tomato	54.7 \pm 2.0B (28; 26–78)	77.1 \pm 2.0A (28; 34–121)	59.5 \pm 2.0B (28; 43–84)	15.44	2,81	<0.0001

Means within a row followed by the same letter are not significantly different (Tukey's HSD: $P > 0.05$, following ANOVA).

¹n = number of fruits/leaves/stems.

Table 5 Pupal survival (%) of ulidiids (pooled across three species) reared from 12 commodities and weeds

Common plant name	Mean \pm SEM (n; range) ¹
Spiny amaranth	86.7 \pm 1.3d (78; 0–100)
Cabbage	99.9 \pm 1.3a (81; 95–100)
Radish	97.7 \pm 1.2ab (92; 68–100)
Papaya	99.9 \pm 1.3a (81; 96–100)
Avocado	99.9 \pm 1.3a (78; 98–100)
Johnsongrass	88.5 \pm 1.2cd (96; 11–100)
Sugarcane	93.7 \pm 1.3bc (75; 61–100)
Southern cattail	98.2 \pm 1.2ab (84; 80–100)
Little hogweed	89.8 \pm 1.1cd (108; 40–100)
Bell pepper	99.9 \pm 1.3a (78; 98–100)
Habañero pepper	89.1 \pm 1.2cd (83; 52–100)
Tomato	99.9 \pm 1.2a (84; 97–100)
F _{11,954}	19.01
P	<0.0001

Means followed by the same small letter are not significantly different (Tukey's HSD: $P > 0.05$, following ANOVA).

¹n = number of fruits/leaves/stems.

collected from Clewiston (Hendry County) and Sebring (Highlands County, both FL, USA), in November 2009 (Goyal, 2010). Seal et al. (1996) collected larvae of *E. stigmatias* from decayed sugarcane stems. Sugarcane is produced on over 161 000 ha in southern Florida and the majority of the sweet corn acreage is surrounded by sugarcane. Keiper et al. (2000) found *C. massyla* larvae and puparia in cattail plants in California, USA. Allen & Foote (1992) also collected *C. massyla* larvae from decomposing cattail stems previously damaged by noctuid caterpillars,

as well as from *Carex lacustris* Willd. stems previously damaged by *Epichlorops exilis* (Coquillett) larvae in Ohio, USA. The large acreage of sugarcane, and the abundance of cattail likely provide suitable hosts for sustaining populations of these maize-infesting flies throughout the year.

Goyal (2010) conducted field surveys to determine the presence of picture-winged flies in major crops around maize fields in Miami-Dade and Palm Beach Counties. Adults of *C. massyla*, *E. eluta*, and *E. stigmatias* were found in sweep net collections and visual observations from spiny amaranth, Johnsongrass, sugarcane, southern cattail, little hogweed, and cabbage. Plant material infested with picture-winged fly larvae also were collected from the field from which the following species emerged: *C. massyla*, *E. eluta*, and *E. stigmatias* from Johnsongrass stems, *E. eluta* and *C. massyla* from bell pepper fruit (collected from culled fruit on the ground in a commercial field), *C. massyla* from southern cattail stems, and *E. eluta* from spiny amaranth stems.

Several other commodities have been found to be developmental hosts of these flies that were not evaluated in our study. *Chaetopsis massyla* has been reared in the USA from onions (*Allium cepa* L.) in Michigan (Merrill, 1951), and from decaying *Narcissus* spp. bulbs in New York (Blanton, 1938). In Hawaii, *E. annonae* has been recorded as a minor pest of pineapple, *Ananas comosus* (L.) Merr. (Illingworth, 1929), reared from the decaying tissue around the flower scars of bananas, *Musa* spp. (Severin & Hartung, 1912), and from sugarcane injured by sugarcane leaf hopper, *Perkinsiella saccharicida* Kirkaldy (Perkins, 1903). *Euxesta eluta* has been reported as a pest of loquat, *Eriobotrya japonica* (Thumb.) Lindl., in Alachua County, Florida

(Anonymous, 2008). Conversely, fresh carrots and potatoes did not support the development of picture-winged flies in the current study, but *E. eluta* and *E. stigmatias* were reared from decaying carrot taproots collected in Brazil (Franca & Vecchia, 1986), and *E. stigmatias* was reared from decaying potato tubers collected in southern Florida (Seal et al., 1996).

Larval and pupal developmental rates in the current study were similar to those reared on sweet corn ears in recent studies (Goyal, 2010). Egg plus larval developmental times on sweet corn ears were 10–15, 9–16, and 10–14 days compared with 12–31, 8–22, and 10–27 days in the current study for *C. massyla*, *E. eluta*, and *E. stigmatias*, respectively. Pupal developmental times were 3–8, 3–8, and 3–7 days when reared on sweet corn ears compared with 5–12, 4–13, and 5–13 days in the current study for *C. massyla*, *E. eluta*, and *E. stigmatias*, respectively. Pupal survival was 100% for all the three species when reared on sweet corn ears, but was much more variable for all three species on alternative hosts (range of 0–100% for *C. massyla*, 50–100% for *E. eluta*, and 11–100% for *E. stigmatias*). The development times for these species on harvested solanaceous fruiting vegetable crops was as fast or faster than those on sweet corn. In southern Florida where small fields of tomatoes and sweet peppers are frequently sequentially planted weekly on large farms, it is common for farm workers to discard imperfect or damaged fruit between the rows of plants or in cull piles at the end of the fields during harvest. Likewise, large piles of culled radishes are frequently deposited along field margins near sweet corn fields. The rapid and successful development of these three fly species in such discarded produce in the vicinity of sweet corn fields during their R1 through R3 maize reproductive stages likely provides an additional important reservoir for these flies during sweet corn season.

In conclusion, all three species (*C. massyla*, *E. eluta*, and *E. stigmatias*) were able to complete development on alternative commercial crop and weed species under laboratory conditions. The plant species tested in the present study are commonly produced commercially in Hendry, Miami-Dade, and Palm Beach Counties, where most of Florida's sweet corn and sugarcane is grown. The presence of multiple host crops throughout the sweet corn production areas may help explain the occurrence of these flies immediately after prolonged absences of maize and provide additional reservoirs from which to move back into treated maize during its growing season. Surveys on different plant commodities and studies of fly movement between host plant commodities are needed to begin to comprehend the relative importance of such reservoirs in the seasonal ecology of these fly pests in the southeastern USA and other affected areas in the western hemisphere.

Acknowledgements

We thank F. Sosa, H.K. Gill, M. Gonzalez, and N. Larsen for assistance with rearing flies. We appreciate the valuable editorial comments provided by Drs. R. McSorley and S. Tiwari at the Department of Entomology and Nematology, University of Florida. This research was made possible by a Hand Fellowship awarded by the Dolly and Homer Hand Group and a Warren Wood Scholarship from the Miami-Dade County Agri-Council.

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