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Larval Performance and Adult Attraction of *Delia platura* (Diptera: Anthomyiidae) in a Native and an Introduced Crop

Patricia C. Guerra,[1] Clifford B. Keil,[2,3] Philip C. Stevenson,[1,4] Diego Mina,[5] Servio Samaniego,[5] Eduardo Peralta,[5] Nelson Mazon,[5] and Timothy C. B. Chancellor[1]

[1]Natural Resources Institute, University of Greenwich, Greenwich, ME4 4TB, Kew TW9 3AB, United Kingdom (pguerra123@gmail.com; p.c.stevenson@greenwich.ac.uk; t.c.b.chancellor@greenwich.ac.uk), [2]Pontifical Catholic University of Ecuador, School of Biological Sciences, Museum of Invertebrates, Quito, Ecuador (Keil617@yahoo.com), [3]Corresponding author, e-mail: Keil617@yahoo.com, [4]Royal Botanic Gardens, Kew, Surrey, United Kingdom, and [5]Instituto Nacional de Investigaciones Agropecuarias, Programa Nacional de Leguminosas y Granos Andinos, Santa Catalina Station, Quito, Ecuador (dfmch777@gmail.com; serviosama_26@hotmail.com; peraltaedu55@gmail.com; nelsonmazon@yahoo.es)

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Abstract

Delia platura Meigen is an important pest in crops around the world. Its host range includes almost 50 species, and it can develop in soil organic matter. In Ecuador, *D. platura* is a serious problem for the crop, *Lupinus mutabilis* Sweet (Chocho), and it also attacks broccoli (*Brassica oleracea* L.). After broccoli is harvested, crop residue is mixed with soil or collected and stored close to Chocho fields. The objectives of this study were to determine the adaptive responses of larvae reared on different hosts and whether *D. platura* females are preferentially attracted to germinating *L. mutabilis* seeds or broccoli residue. Accordingly, larval performance and attraction of female *D. platura* reared on broccoli residue and *L. mutabilis* seeds were evaluated. The number of larvae, pupae, and adults were higher when reared on broccoli. Conversely, pupal weight was higher and time from larva to pupa, pupa to adult, and total life cycle were longer in flies reared on *L. mutabilis.* Although *D. platura* developed more quickly on broccoli, *L. mutabilis* was also a good host since pupae were heavier compared with flies reared on broccoli. *Delia platura* females reared on broccoli preferred broccoli residue to *L. mutabilis* in an olfactometer. Volatiles from broccoli residue in soil may attract *D. platura* females and stimulate oviposition on *L. mutabilis* seeds. Environmentally benign production of *L. mutabilis* crops with minimal insecticide applications may require the elimination of fresh broccoli residue as fertilizer in soils where *L. mutabilis* is cultivated.

Key words: *Lupinus mutabilis*, *Delia platura*, olfactometry, host adaptation, broccoli

The bean seed fly, *Delia platura* (Meigen) (Diptera: Anthomyiidae), is a polyphagous insect and an important global pest in cropping systems. The larvae mine and destroy germinating seeds of many legumes, cereals, tubers, and tobacco (Bessin 2004, Gill et al. 2013). The host range of *D. platura* includes nearly 50 species of plants. However, it can also develop in organic matter in humid soils. This organic matter may be the main larval food source when no germinating seeds are available (Finch 1989). Oviposition sites can be located by *D. platura* females by olfaction alone (McLeod 1964; Hough-Goldstein and Bassler 1988; Gouinguené and Städler 2005, 2006a, 2006b). Therefore, orientation to volatiles is a likely mechanism for host location by adult females.

Lupinus mutabilis (Fabaceae) is a traditional Andean crop grown for high protein seeds known as chocho. These seeds are blanched and served in a variety of salads and sauces. Chocho is particularly important in the diet of indigenous groups whose diet has been high in carbohydrates and low in protein. Cultivation and consumption of chocho has been increasing recently. *Delia platura* causes serious damage to *L. mutabilis* crops throughout the Andes. Larvae mainly attack seedlings by feeding on emerged roots and cotyledons. Losses of >60% of seedlings 2 wk after sowing have been reported in Ecuador. Plants that survive are weak and less resilient to subsequent attacks by other pests and plant pathogens (Lomas et al. 2012).

Although *D. platura* has been recognized as a secondary pest of *L. mutabilis* in the Andean region of Ecuador, its pest status on Chocho crops has increased recently (Lomas et al. 2012). This change may be related to the production of *Brassica oleracea* var *Italica* (broccoli) in the same area and frequently in the same fields in rotation. Broccoli residue is collected from broccoli fields after harvest and used as soil fertilizer. Broccoli production was on a small scale until an export market was developed in the 1990s. Broccoli is intensively and widely produced throughout the year in the Ecuadorian Andes (three harvests per month from different plantings) and is dominated by large-scale enterprises, with ~65% of output from areas >100 ha in large properties ("haciendas") for export and domestic consumption (Gall 2009, Manosalvas-Arias 2012). In contrast, *L. mutabilis* cultivation is limited to land areas called "Unidades de producción agricola" or "minifundios", small pieces of land of up to 0.5 ha. These parcels have been typically worked as family farms (Censo Nacional Agropecuario 2003) and account for most of the production of *L. mutabilis* in Ecuador. More than 56% of *L. mutabilis* cultivation has been in the provinces of Cotopaxi and Chimborazo (Caicedo and Peralta 2000), where broccoli is also cultivated due to favorable climatic and economic conditions (Gall 2009).

Due to the heavy use of chemical insecticides, *D. platura* has not been a serious threat to broccoli production. *Delia platura* can be found in all phenological stages when broccoli is growing in fields (stems), and in broccoli residues (stems and leaves) remaining in fields before and after harvest. Broccoli residues are commonly collected by small farmers and put in large piles close to family plots to feed farm animals or mixed into soil as an organic fertilizer. It is not known if *D. platura* females are preferentially attracted to germinating seeds of *L. mutabilis* or *B. oleracea* residues, or how *D. platura* larvae adapt to these two different hosts.

Brassica oleracea is a known host of various *Delia* species. The detoxification mechanisms for sulfur-containing compounds in broccoli, such as glucosinolates, could be similar to those used by other insect pests (Burow et al. 2008, Hopkins et al. 2009). These detoxification mechanisms may enable *D. platura* to successfully infest a variety of hosts including *L. mutabilis*.

Quinolizidine alkaloids are plant defensive compounds against herbivores (Wink 1984, 1992a; Wink and Römer 1986). There are high concentrations of these alkaloids in seeds of lupines (1–4% of dried weight; Wink 1992a, Carey and Wink 1994). Apparently, these compounds do not prevent *D. platura* larvae from feeding on *L. mutabilis* seeds. These secondary metabolites might be responsible for the bitter taste and low palatability of raw *L. mutabilis* seeds. For human consumption, *L. mutabilis* seeds have to be debittered before eating through washing with water. Tolerance or detoxification of the alkaloids found in *L. mutabilis* seeds could enable *D. platura* to exploit this host plant (Gross et al. 1988, Wink 1992b, Villacrés et al. 2010, Villacreces 2011).

Oviposition preference by insects can be influenced by previous experience on a determinate host. For example, ovipositing females will prefer a host on which they developed for at least part of their life cycle, developing host fidelity (Jaenike 1978). On the other hand, female insects may choose to oviposit on a host where offspring survival and performance will be maximized; a principle known as "mother knows best" or the preference–performance hypothesis (Valladares and Lawton 1991). There is conflicting evidence among studies in which the host fidelity or the preference–performance hypotheses have been tested. Both positive and negative correlations have been found between adult preference for a host and larval performance (Gripenberg et al. 2010).

This study had two objectives designed to determine the suitability and preference for the two host plants for *D. platura*. First, the performance of *D. platura* larvae on both hosts was evaluated and second, attraction of *D. platura* gravid females to *B. oleracea* residues and germinating *L. mutabilis* seeds was evaluated under laboratory conditions in an olfactometer. This attraction to potential hosts was evaluated with females reared on broccoli, *L. mutabilis*, and diet. The results of these experiments will assist our understanding whether broccoli has influenced the increase in prevalence of *D. platura* as a pest on *L. mutabilis* and provide insight for the formulation of management strategies for this pest.

Materials and Methods

Insects

Delia platura was reared at the Santa Catalina Experimental Station, Instituto Nacional de Investigaciones Agropecuarias (INIAP) in Quito, Ecuador, under ambient laboratory conditions (10–24°C and a photoperiod of 12:12 [L:D] h). Mass rearing began with 200 pupae that were collected from a plot of *L. mutabilis* located in the village of Canchagua, Cotopaxi Province, in April 2013. Mass rearing was done with an artificial diet (Harris et al. 1966). Once the appropriate quantity of adult flies was obtained (F3 generation), performance tests of larvae on *L. mutabilis* seeds and *B. oleracea* residue were conducted. Subsequently, 200 adult flies were taken from the mass rearing, separated in two groups and allowed to oviposit on germinated seeds of *L. mutabilis* or *B. oleracea* residues. Larvae were reared on these two different hosts until adult emergence. Adult female flies obtained after one generation on the different hosts were used for the olfactometer oviposition attraction experiment. Female flies reared on the artificial diet were also evaluated in the olfactometer for attraction to *L. mutabilis* or *B. oleracea*.

Plants

Seeds of *L. mutabilis* var. 450 *Andino*, a widely used, fast growing, and high-yielding variety (Caicedo et al. 2010), were obtained from the seed bank of the Programa Nacional de Leguminosas y Granos Andinos (PRONALEG-GA) in Ecuador. The 450 *Andino* variety is characterized by a high content of alkaloids (lupanine 3.92% dry weight; Caicedo et al. 2010). Seeds were placed in seed beds (24 by 30 cm) with sterilized soil for germination in a greenhouse. The seed bed was lightly watered every day until roots emerged. Soil was obtained from the fields of Santa Catalina Experimental Station. Conventionally grown broccoli was obtained from a local market. Only stems were used for experiments.

Larval Performance of *D. platura* on *L. mutabilis* and *B. oleracea* Residue

The performance of *D. platura* larvae was evaluated on *L. mutabilis* seeds and *B. oleracea* residue in 100-ml jars with different larval rearing substrates. Each jar contained 40 g of sterilized soil, 4 g of broccoli residue or four seeds of *L. mutabilis* var. *Andino* 450 (seed weight ranged from 1 to 1.3 g) at the point of germination. Twenty eggs from the mass rearing were placed in each container. Eggs were checked daily until larvae emerged. To avoid disturbing larvae developing inside the host, larvae were counted about 2 wk before they were predicted to finish pupation. By this time, they were large enough to be easily found in the soil inside the jars. After they were counted, larvae were replaced in the jars, covered with soil, and lightly sprayed with several ml of water. After the first larva had pupated, the jars were checked every two days. Number, weight, and area of each pupa, and the time to reach the pupal and adult stages in each host were recorded. To measure pupal area, a digital photograph was taken and the area defined by the oval border of the pupa was calculated with ImageJ analysis software (W. Rasband, Maryland, MD). Photographs of pupae were taken next to a scaled piece of paper to standardize magnification of the images. Pupae were weighed individually with an analytical balance (Ohaus, Adventurer

AR3130, Parsippany, NJ). Pupae were placed in plastic petri dishes (7 cm diameter) and covered with mesh. Moist filter paper was placed in the bottom to maintain humidity. Each petri dish was labeled with the date, name of the host, and number of the plastic rearing jar. Petri dishes were checked every day for adult emergence and the dates recorded. The experiment was replicated 10 times for each host. The data from the 10 replicates were pooled prior to analysis. Differences in pupal weight, pupal area, time to reach pupation and adult stages were tested for significance using a Student's *t*-test for independent samples (Zar 2010). When necessary, data were log-transformed (base n) before analysis to meet *t*-test assumptions.

Attraction of *D. platura* to *L. mutabilis* and *B. oleracea* Residue

A four-port olfactometer was used to assess the preference of *D. platura* females for *L. mutabilis* or *B. oleracea*. The olfactometer was modified from the design of Vet et al. (1983). Three glass jars were connected to each of the four ports, water (to provide humidity to the system), the stimulus, and an empty catch jar. The stimuli consisted of 1) germinated seeds of *L. mutabilis*, 2) *B. oleracea* residue, 3) sterilized soil (control A), and 4) an empty glass jar (control B). Flies were not allowed to contact the stimuli inside the olfactometer but were able to orient toward the odors. Twelve mated female flies reared on broccoli residue, *L. mutabilis*, or diet were introduced to the olfactometer chamber. After 20 min, the time in which adult flies settled or began to move slowly inside the olfactometer based on previous observations, the experiment began by starting a pump to draw air through a hole in the base of the olfactometer chamber. Flow rates were regulated with adjustable flow meters to avoid air turbulence inside the system and to promote laminar flow from the four ports. The overall flow rate was regulated to 2.5 liter/min. Flies were exposed to the stimuli for 1 h, and the number in each capture jar and at each olfactometer port was counted. Flies that did not orient to one of the ports or enter a capture jar were not counted. Six repetitions per fly host were performed. Different sets of female flies were tested in each repetition. Glass jars and hoses connected to the olfactometer were not used in two tests consecutively and were washed with neutral detergent and alcohol to avoid residual odors. The arrangement of the stimuli was also changed for each repetition. Air flow was directed through activated charcoal filters to remove contaminants prior to entry in the olfactometer. Data were analyzed with a multitrial, heterogeneity Chi-square analysis, using as the null hypothesis, a 1: 1: 1: 1 expected ratio of flies at each one of the four ports. Each experiment was analyzed separately, and then the aggregate data were analyzed against the null hypothesis with a heterogeneity G test based on the Chi-square distribution (Sokal and Rohlf 1969).

Results

Larval Performance of *D. platura* on *L. mutabilis* and *B. oleracea* Residue

Life Cycle on *L. mutabilis* and Broccoli Residue

The life cycle of *D. platura* developing on *L. mutabilis* was significantly longer than *D. platura* reared on broccoli ($t_{15} = 3.78$; $P < 0.05$; Table 1). The mean number of days for *D. platura* to complete its life cycle from the egg to adult stage when reared on *L. mutabilis* was 47.2 ± 3.2 d. In contrast, *D. platura* developing on *B. oleracea* completed their life cycle >9 d before flies in *L. mutabilis* (Table 1). Development time from larva to pupa ($t_{15} = 3.98$; $P < 0.05$) and pupa to adult ($t_{15} = 2.32$; $P < 0.05$) for flies reared on *B. oleracea* was shorter than for flies that were reared on *L. mutabilis* (Table 1).

Table 1. Performance of *D.platura* reared on *B.oleracea* residue and emerging *L.mutabilis* seedlings under laboratory conditions

Variable	*B. oleracea* residue	N_b	*L. mutabilis* seeds	N_l
Total life cycle duration (d)	37.3 ± 6.8a	47	47.2 ± 3.2b	18
Duration larva–pupa (d)	25.9 ± 0.9a*	83	31.4 ± 0.9b*	38
Duration pupa–adult (d)	6.8 ± 1.6a*	47	11.9 ± 1.5b*	18
No. of larvae surviving	11.0 ± 4.6a	110	6.1 ± 2.0b	61
No. of pupae	8.3 ± 6.0a	83	3.8 ± 2.5b	38
No. of adults	4.7 ± 3.9a	47	1.8 ± 1.6b	18
Pupa weight (mg)	4.0 ± 0.6a	110	6.5 ± 0.8b	61
Pupa area (cm2)	0.05 ± 0.01a	110	0.06 ± 0.005a	61

Data are reported as mean ± SE for each group. Different letters in the same row indicate a significant difference ($P < 0.05$, Student's *t*-test). Initial $N = 200$ eggs for each host (*B. oleracea* and *L. mutabilis*). There were 10 rearing containers for each host with 20 eggs per container at the beginning of the experiment. N declined with larval mortality as the experiment progressed (N_b—sample size on broccoli and N_1—sample size on *Lupinus*). Data denoted with an * were n-log transformed prior to analysis.

Survival of Different Life Stages of *D. platura*

The number of *D. platura* larvae ($t_{18} = 3.09$; $P < 0.05$; Table 1), pupae ($t_{18} = 2.17$; $P < 0.05$; Table 1), and adults ($t_{18} = 2.18$; $P < 0.05$; Table 1) surviving from larvae reared on *L. mutabilis* were significantly lower than in *B. oleracea* (Table 1). In contrast, pupae that developed from larvae reared on *L. mutabilis* were heavier than pupae from larvae reared on *B. oleracea* ($t_{17} = -7.37$; $P < 0.05$; Table 1). There was no difference in the size (surface area) of pupae between individuals reared on *B. oleracea* or *L. mutabilis* (Table 1). Only 9% of flies reared on *L. mutabilis* survived to the adult stage. The survivorship for flies reared on *B. oleracea* was 23.5%. The difference in total survivorship between the two rearing substrates was significantly different ($t_{18} = 2.18$; $P < 0.05$).

Attraction of *D. platura* to *L. mutabilis* and *B. oleracea* Residue

In all three sets of experiments with three different types of females, reared on *L. mutabilis*, *B. oleracea*, and artificial diet, the six replications were homogeneous by the heterogeneity Chi-square test. The respective heterogeneity Chi-square values were as follows: broccoli-reared females $\chi^2 = 18.22$, *L. mutabilis*-reared females $\chi^2 = 19.70$, diet-reared females $\chi^2 = 13.32$; in all cases, there were 15 degrees of freedom. Therefore, the data for all six replications were pooled for the final analysis. Gravid females of *D. platura* reared on broccoli oriented to the port of the olfactometer with broccoli odors in a proportion significantly greater (58.5%) than predicted by random choice (χ^2 [df = 3, $N = 72$] = 31.75; $P < 0.05$; Fig. 1a). For flies reared on germinated *L. mutabilis* seeds and artificial diet, there was no preference for any stimuli (Fig. 1b and c), *L. mutabilis*-reared females, χ^2 (df = 3, $N = 72$) = 5.03 ns; diet-reared females, χ^2 (df = 3, $N = 72$) = 1.55 ns. It should be noted that in the experiments with *L. mutabilis*-reared females, broccoli was the least preferred odor source (13.6%) as compared with the other three odor sources, *L mutabilis* seeds (31.8%), sterile soil (28.8%), and the empty control (25.8%; Fig. 1b). The responses of the females reared on artificial diet were uniform across all four odor sources, 30.4%—broccoli, sterile soil—26.1%, *L. mutabilis*—23.2%, and empty control—20.3% (Fig. 1c).

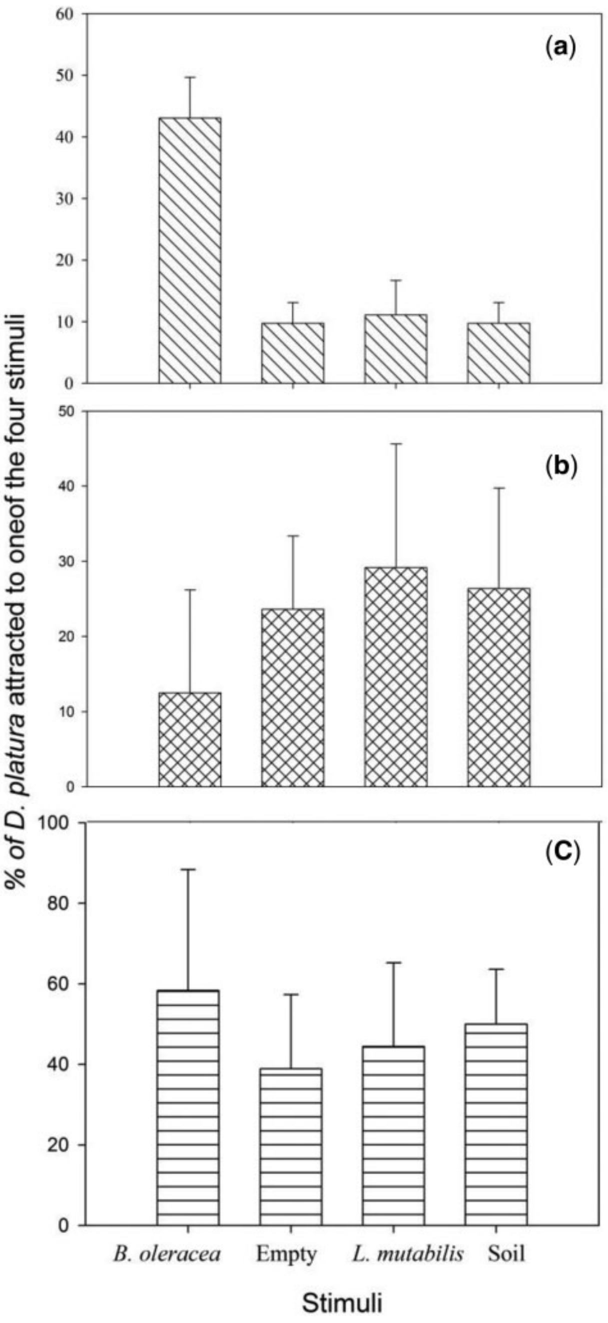

Fig. 1. Percentage of *D. platura* gravid females reared on *B. oleracea* residue (**a**), *L. mutabilis* seeds (**b**), and artificial diet (**c**) and attracted by *B. oleracea* residue, *L. mutabilis* seeds, and controls (empty odorless jar and sterilized soil) in a four-port olfactometer. Bars denote standard errors ($n = 72$). Data were analyzed with a multitrial, heterogeneity Chi-square test. Treatments were significantly different in (a) $\chi^2_{(3)} = 28.86$, $P < 0.05$ and were not significant in (b) and (c) ($P > 0.05$).

Discussion

Larval Performance of *D. platura* on *L. mutabilis* and *B. oleracea* Residue

Delia platura had a shorter life cycle and shorter larval and pupal development times when reared on *B. oleracea* residues in comparison to flies reared on emerging *L. mutabilis* seedlings. Quinolizidine alkaloids in lupines are feeding deterrents for nonspecialist insects and are generally avoided by polyphagous insects (Wink 1992a, 1998). High levels of lupanine and sparteine, the primary alkaloids in *Lupinus*, extended developmental time and survival of the generalist insect, *Spodoptera eridiana* (Lepidoptera: Noctuidae) (Johnson and Bentley 1988). However, the concentrations of alkaloids in *L. mutabilis* seeds (1–4% of dry weight) decrease between 20% to 100% during germination in different species of lupines (Wink and Witte 1984). These changes in alkaloid concentration may be due to the use of nitrogen from these alkaloids to synthesize primary metabolites (e.g., proteins), necessary for growth (Wink and Witte 1984). This decrease in alkaloid concentration may explain higher weights of *D. platura* pupae reared on *L. mutabilis* germinating seeds in comparison to broccoli residues.

The low numbers of surviving larvae and pupae that developed in *L. mutabilis* may be explained by deterrent properties of quinolizidine alkaloids. Cinnamoyl and tigloyl derivatives of lupines were deterrent to sixth-instar larvae of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) (Bentley et al. 1984). These derivatives both occur in the seeds of *L. mutabilis* (Hatzold et al. 1983), where they may also prevent first-instar *D. platura* larvae from penetrating seeds.

Attraction of *D. platura* to *L. mutabilis* and *B. oleracea* Residue

Newly emerged and mated females reared on *B. oleracea* residues chose *B. oleracea* residues in preference to germinated seeds of *L. mutabilis* when exposed simultaneously to these two stimuli and the controls. This suggests that previous larval experience in broccoli residue is an important determinant of host choice for *D. platura* females. However, Finch (1989) considered that *D. platura* prefers to oviposit on decaying plant material. For example, decaying plants and seedlings of onion were preferred for oviposition by *D. platura* and the onion fly, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae) over healthy seeds and onion bulbs (Dindonis and Miller 1980). Everts et al. (1985) recovered more *D. platura* adults from onion plants with *Fusarium* basal root infection as compared with healthy onion plants. When preference was tested, *D. platura* preferred to oviposit in *Fusarium*-infested onion bulbs in comparison with healthy bulbs. Similar results were found by Hough-Goldstein and Bassler (1988). Containers inoculated with the soil bacteria, *Xanthomonas campestris*, *Erwinia herbicola*, and *Flavobacterium* sp. stimulated oviposition of seedcorn maggot females in comparison with noninoculated containers. Chemical compounds from the seed coats and germinated seeds from *Phaseolus vulgaris* were extracted, identified, and related with oviposition preference of *D. platura* by Gouinguené and Städler (2006a,b). In this experiment, *D. platura* females responded principally to octanol and octanone. These compounds are characteristic odors of fungi and other microorganisms and are not compounds produced by the seeds.

Soil microbiology may play an important role in the selection of an oviposition site by *D. platura* by degrading *B. oleracea* residues and producing chemical cues that attract *D. platura* females. Hough et al. (1981, 1982) concluded that decomposition of sulfur compounds in onion bulbs by bacteria produced volatile sulfides; compounds that could be used as chemical cues for host finding by the onion fly, *D. antiqua*. Similar processes could be occurring when volatiles released during decomposition of *B. oleracea* residues by microorganisms are used by *D. platura* females for host finding. To fully understand the interactions reported here, further studies are needed to identify compounds released during broccoli decomposition and the soil biota (bacteria and fungi) that enable this process.

Our results suggest that the use of *B. oleracea* residue to fertilize *L. mutabilis* fields may have contributed to the increased pest status of *D. platura* in the Andean region of Ecuador. *Delia platura* preferred and performed better in broccoli residue in comparison with *L. mutabilis* seedlings. *Delia platura* has probably been systematically transported in broccoli residues by smallholder farmers to fields where *L. mutabilis* is commonly sown in soil with residues from broccoli crops. This residue is mixed with soil or stored close to these family plots. There are two possible sources of infestation: First, *L. mutabilis* crops may be contaminated by *D. platura* larvae developing in *B. oleracea* residue when these residues are mixed in soils to be planted with *L. mutabilis*. Second, adult females can develop in piles of broccoli residue close to *L. mutabilis* fields. These females can locate *B. oleracea* residues in fields by olfaction and oviposit in soils with germinated *L. mutabilis* seeds.

Delia platura is considered one of the most important insect pests of *L. mutabilis* during the first stages of growing in comparison with other insect pests (Guerra et al. 2014). Successful production of *L. mutabilis* crops with minimal insecticide applications may depend on the elimination of broccoli residue as fertilizer in soils where *L. mutabilis* is going to be cultivated or the extermination of *D. platura* inside the residues. This last approach could be achieved by thoroughly composting broccoli residues before adding them to the soil. Another alternative could be to study soil microbiota since this is an important component in the *L. mutabilis*–broccoli–*D. platura* system. Managing and manipulating the soil microbiota to control or deter *D. platura* may be an interesting alternative to explore.

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