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Species Composition, Distribution, and Seasonal Abundance of *Liriomyza* Leafminers (Diptera: Agromyzidae) Under Different Vegetable Production Systems and Agroecological Zones in Kenya

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ABSTRACT A longitudinal study to identify the species of *Liriomyza* leafminer, their distribution, relative abundance, and seasonal variation, including their host range, was conducted in vegetable fields at three altitudes in Kenya from November 2011 to November 2012. Three main species were identified: *Liriomyza huidobrensis* (Blanchard), *Liriomyza sativae* Blanchard, and *Liriomyza trifolii* (Burgess), of which *L. huidobrensis* was the most abundant across all altitudes irrespective of the cropping season and accounting for over 90% of the total *Liriomyza* specimens collected. *Liriomyza* species were collected from all infested incubated leaves of 20 crops surveyed belonging to seven families: Fabaceae, Solanaceae, Cucurbitaceae, Malvaceae, Brassicaceae, Amaranthaceae, and Amaryllidaceae. However, more than 87.5% of the *Liriomyza* species were obtained from only four of these crops: *Pisum sativum* L., *Phaseolus vulgaris* L., *Solanum lycopersicum* L., and *Solanum tuberosum*, thereby demonstrating that Fabaceae and Solonaceae crops are the most important hosts with regard to *Liriomyza* species richness and relative abundance. *L. huidobrensis* had the widest host range (20 crops), followed by *L. sativae* (18 crops) and *L. trifolii* (12 crops). Although *L. trifolii* has been considered the dominant *Liriomyza* leafminer in Kenya, this study suggests that this may not be the case anymore, as *L. huidobrensis* dominates at all altitudes.

KEY WORDS *Liriomyza huidobrensis; Liriomyza sativae*, *Liriomyza trifolii*, Altitude, Host plant

Introduction

Production of vegetables for both domestic and export markets in Kenya is a major source of income, employment, and food for smallholder farmers, especially women (HCDA 2010, 2013). The horticultural sector in Kenya is one of the fastest-growing agricultural sectors, and in 2012, horticultural exports generated above US$1.08 billion in foreign exchange (HCDA 2013). Flowers and vegetables constituted the biggest horticultural export, representing 48.9 and 35.2%, respectively, of export value (HCDA 2013). However, *Liriomyza* leafmining flies (LMF; Diptera: Agromyzidae) are among the most important insect pests of economic importance on vegetables and flowers, limiting the horticultural sector from achieving its full potential (Njuguna et al. 2001, KEPHIS 2007, Chabi-Olaye et al. 2008). LMF pests are the most important cause of interception of Kenya's fresh vegetables and flowers in European market due to their quarantine status (Kedera and Kuria 2003, Chabi-Olaye et al. 2008, EPPO 2013, FVO 2013, EUROPHYT 2014).

Farmers' approach to control LMF in export vegetables and flowers is limited to routine insecticide applications. According to Gitonga et al. (2010), dimethoate, abamectin, imidacloprid, alphacypermethrin, and beta-cyfluthrin are the most common insecticides used against LMF and other pests' complex in vegetable production systems in Kenya. However, while various studies reported that abamectin, alphacypermethrin, and beta-cyfluthrin can effectively control LMF (Kabira 1985, Murphy and La Salle 1999, Weintraub 2001, Kaspi and Parrella 2005), a recent study in Kenya by Guantai (2011) revealed that, at recommended doses, none of the aforementioned insecticides used in Kenya is effective against the larval stage of *Liriomyza huidobrensis*, the most aggressive and abundant of all the invasive LMF species identified in Kenya. Indiscriminate application of synthetic insecticides had led to low levels of parasitism (<5.2%) by the major parasitoid species associated with the pest across all altitudes in Kenya (Chabi-Olaye et al. 2008). Furthermore, high cost, human and animal health hazards, environmental risks, and rejection of export products due to high pesticides residue levels are associated

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with such routine chemical pesticides application (Braun and Shepard 1997, Gitonga et al. 2010, Okoth et al. 2014, PIP 2013, RASFF 2013). There is therefore a need to develop sound, environmental-friendly, and efficient integrated pest management (IPM) techniques to control LMF pests in Kenya and East Africa. However, a prerequisite for a successful IPM approach is to better understand the LMF species composition; abundance; and the effect of seasons, vegetable production systems, and agroecology on the pest (Mwatawala et al. 2006).

It has long been known that *Liriomyza trifolii* (Burgess), introduced from Florida, USA, through chrysanthemum cuttings at Masongaleni, Makueni County, in 1976 is the main *Liriomyza* species infesting ornamentals and vegetables in Kenya (Spencer 1985). Heavy infestation by *L. trifolii* over the years and its subsequent spread throughout the country and to other host plants and abroad resulted in closure of many flower farms, loss of jobs, and loss of overseas markets due to quarantine requirements (Spencer 1985, IPPC 2005). The perception that *L. trifolii* was the most important invasive *Liriomyza* species in Kenya persisted over the years (IPPC 2005). A countrywide survey in Kenya by Chabi-Olaye et al. (2008) revealed the existence of other invasive species: *Liriomyza huidobrensis* (Blanchard) and *Liriomyza sativae* Blanchard, with *L. trifolii* dominating at the low and mid altitudes and *L. huidobrensis* dominating at the high altitude. *L. huidobrensis* is known to adapt and predominantly colonize hosts at colder higher elevations, mostly above 1000 m. a.s.l. (Spencer 1989, Shepard et al. 1998, Sivapragasam and Syed 1999, Rauf et al. 2000, Weintraub 2001, Andersen et al. 2002, Chabi-Olaye et al. 2008, Tantowijoyo and Hoffmann 2010, Mujica and Kroschel 2011), whereas *L. sativae* is the dominant pest in lowland areas (Andersen et al. 2002, Rauf et al. 2000, Spencer 1989). However, neotropical populations of *L. huidobrensis, L. sativae*, and *L. trifolii* have continued to depict high adaptability with complex histories of invasion and establishing in many countries worldwide, exhibiting interspecific interactions causing damage to many crops and growing ever more difficult to control (Chaney 1995, Kang 1996, Costa-Lima et al. 2010, Yıldırım and Ünay 2011, Geo et al. 2011). In Kenya, most agricultural crop production systems have four cropping seasons, including the long rains, the short rains, the cold dry, and the hot dry seasons, which vary with respect to altitude and have been inconsistent especially at the mid and low altitudes since 1980s (Hassan 1998, Jaetzold et al. 2006). Thus, production of vegetable crops as host plants of *Liriomyza* species is not equally important across altitudes. In addition, occurrence and relative abundance of leafminers in relation to seasons and host plants may reflect the impacts of climate and their distinct preference for host plants (Murphy and LaSalle 1999, Johansen et al. 2003, Tran et al. 2005, Tran et al. 2007, Rauf and Shepard 1999). The varying ecosystems may affect the distribution of *Liriomyza* species and functional diversity, thus also affecting activities of associated natural enemies. This suggests that the inventories of LMF pest on host crops may have changed significantly over time. However, none of the previous studies carried out in Kenya covered the seasonal variation of LMF species across the altitudes, vegetable production systems, and host plants.

The aim of the present study was to identify and determine the LMF species composition, their seasonal variation, relative abundance, and their host range in various agroecological zones and vegetable production systems in Kenya.

Materials and Methods

Study Sites. Three sites were selected based on altitudes, namely, highland >1,800 m. a.s.l (Nyeri County, Central Kenya), midland from 1,000 to 1,800 m. a.s.l (Kajiado County, Rift Valley Region), and lowland <1000 m. a.s.l (Makueni County, Eastern Region), in Kenya (Hassan 1998). In each altitude, three locations with high productivity of vegetables and reliable irrigation schemes were selected for the study. This was to allow for continued field monitoring throughout the year. The three altitudes were located at least 65 km apart, and locations within altitudes were approximately 5 km apart. Details on locations' coordinates, altitudes, mean annual temperature and rainfall, LMF host crops grown, and seasons are provided in Table 1. Generally, most agricultural crop production areas in Kenya are characterized by four cropping seasons, namely, the long rains, the short rains, the cold dry, and the hot dry seasons, which vary with respect to altitude and have been inconsistent especially at the mid and low altitudes since 1980s (Hassan 1998, Jaetzold et al. 2006; Table 1). In the different altitude levels, the production of vegetable crops as host plants for *Liriomyza* species was not equally important, hence the sampled crops varied in each altitude level.

Field Surveys and Sampling Methods. Monthly field surveys were carried out from November 2011 to November 2012 to determine the species composition, abundance, and distribution of *Liriomyza* species on crops in three locations across each of the three different altitudes of vegetable production in Kenya.

During each observation date at each altitude, LMF infestation and LMF species composition and abundance were evaluated. To determine the LMF infestation at the field level, the sampling area per field was subdivided into four equal quadrants and from each quadrant, 50 leaves from the middle stratum of different plants were picked at random and examined for leafminer infestation (leaves with punctures and/or mines) and the total number infested was recorded. Leaves from the middle stratum of plants were preferred for sampling to leaves from the upper or lower parts of plants because upper leaves are most often clean or have only punctures and leaves from the lower part have old mines with larvae already dropped into soil for pupation, while the leaves from the middle stratum have pupae, "live mines" (mines containing larva) and punctures.

As for LMF abundance and species composition, a maximum of 25 infested leaves per quadrant, with developing or developed mines containing leafminer

Table 1. Summary of comparable attributes per altitude area

Attributes	Highland	Midland	Lowland
Location and GPS coordinates[a]	Sagana (S0°21'9.972", E37°5'13.632", 1880 m a.s.l) Kabaru (S0°17'48.408", E37°6'28.116", 2061 m a.s.l) Naromoru (S0°11'9.312", E37°6'36.972", 2221 m a.s.l)	Namelok (S2°43'6.096", E37°27'39.06", 1177 m a.s.l) Empiron (S2°50'57.948", E37°32'15.144", 1423 m a.s.l) Inkisanjani (S2°53'56.4", E37°34'51.564", 1466 m a.s.l)	Kwakyai (S2°23'6.612", E38°0'9.504", 835 m a.s.l) Kikoo (S2°23'50.928", E37°59'8.052", 867 m.a.s.l) Mangelete (S2°41'57.552", E38°7'32.268", 792 m a.s.l)
Minimum to maximum temperature[b]	8 to 24°C	16 to 28°C	21 to 31°C
Mean rainfall range[b]	~1500 to 2000 mm	~450 to 1200 mm	~800 to 1200 mm
Common *Liriomyza* host crops grown[a]	Potato (*Solanum tuberosum* L.); kales (*Brassica oleracea acephala* L.); cabbage (*Brassica oleracea* L.); pea varieties (*Pisum sativum* L.); French bean (*Phaseolus vulgaris* L.); kidney bean (*Phaseolus vulgaris* L.)	Kidney bean varieties; tomato (*Solanum lycopersicum* L.); French bean	Tomato; common bean; cowpea (*Vigna unguiculata* (L.) Walp); brinjal (*Solanum melongena* L.); sweet pepper (*Capsicum spp.* L.); green gram (*Vigna radiate* (L.) R. Wilczek); okra (*Abelmoschus esculentus* (L.) Moench); courgette (*Cucurbita pepo* L.); butternut squash (*Cucurbita moschata* Duchesne ex Poir.); bitter gourd (*Momordica charantia* L.); pumpkin (*Cucurbita maxima* Duchesne); watermelon (*Citrullus lanatus* (Thunb) Matsun and Nakai)
Short rainy season[a]	Nov 2011 Oct- Nov 2012	Nov 2011 and 2012	Nov 2011 and 2012
Dry and hot season[a]	Jan-Feb 2012 Sept 2012	Jan-Mar 2012 Sept–Oct 2012	Jan-Mar 2012 Sept-Oct 2012
Long rainy season[a]	Mar-June 2012	April–June 2012	April-June 2012
Cold and dry season[a]	July-Aug 2012	July-Aug 2012	July-Aug 2012

[a] Our field observation.
[b] Hassan 1998, Jaetzold et al. 2006.

larvae ("live mines"), were picked, giving a total of 100 leaves per field for laboratory incubation and observations. The infested leaves per field were immediately stored in perforated plastic paper bags and afterwards transferred onto damp paper towels and then placed in plastic rearing containers (19 by 13 by 8 cm) to prevent drying of leaves. The rearing containers were closed with lids containing muslin windows (16 by 9.5 cm) for ventilation and were parked in large cooler boxes to prevent overheating before transportation to the laboratory. After 5 to 10 d, pupae were collected from the rearing containers per field using soft camel hair brushes as they formed, counted, and incubated in bulk in plastic petri dishes with labels until adults of leafminer flies emerged. Laboratory conditions were maintained at 25 ± 2°C and 80 ± 5% R.H. Adult *Liriomyza* species were preserved in 80% ethanol and identification done using conventional taxonomic keys and identification keys from the *Liriomyza* leafminer flies project at the International Center of Insect Physiology and Ecology (ICIPE), Duduville campus, Nairobi, Kenya. The *Liriomyza* species were further sent to the Royal Museum of Central Africa, Belgium, for confirmation. Voucher specimens of identified adult *Liriomyza* species are stored in the entomological museum at the ICIPE, Duduville campus, Nairobi, Kenya.

Data Analysis. The proportion of leafminer-infested leaves (leafminer incidence) was calculated as the number of infested leaves multiplied by 100 and divided by 200 (i.e., total number of leaves picked at random from the middle stratum of the plants from the four quadrants per field). As the leaves were sampled over time, to avoid pseudo-replication, the proportion of leafminer-infested leaves was averaged and the averages were used as the data for analysis (Hurlbert 1984). Proportions were arcsine-transformed and then subjected to two-way ANOVA to assess the effect of cropping season and altitude. Means were separated using Student Newman–Keuls test. The data were analyzed in R version 3.0.2 statistical software (R Development Core Team 2013).

Results

Leafminer Fly Incidence in Farmer Fields. *Liriomyza* leafminer-infested crops were found in all three surveyed locations at each altitude throughout the study period. There was significant interaction between altitude and season in terms of incidence of leafminer puncture and mines on leaves, $F_{6,\ 24} = 10.8$, $P < 0.0001$, thus the variation in infestation levels between altitudes depended on the season. The leafminer incidence ranged from 35.7 to 71.7% across the different altitudes and seasons (Table 2). Infestation levels varied significantly between seasons at highland ($F_{3,\ 8} = 43.1$, $P < 0.0001$) and midland ($F_{3,\ 8} = 7.0$, $P = 0$), and no significant differences at lowland ($F_{3,\ 8} = 1.3$, $P = 0.331$). At highland, infestation was highest in the dry hot season and lowest in the long rainy season, whereas at midland, infestation was highest in the short rainy season and lowest in the dry cold season (Table 2). The dry hot season recorded relatively higher LMF infestation than the other seasons (Table 2). During the dry hot season, of all the 20 crops sampled, the highest leafminer infestation was recorded on French bean (79.5% of leaves), kidney bean (79.1%), snow pea (70.0%), and potato (69.5%) at the high altitude, with the lowest observed on potato (0.5%), okra (10.0%), and onion (14.0%) at the mid altitude (Table 3).

Leafminer Flies Species Composition, Abundance, and Distribution From Infested Leaves. A total of 46,879 Agromyzidae *Liriomyza* leafminer adult flies composed of *L. huidobrensis, L. sativae L. trifolii*, *Liriomyza bryoniae* (Kaltenbach), and unidentified *Liriomyza* species were recorded on the 20 crops sampled belonging to seven families, namely, Fabaceae, Solanaceae, Cucurbitaceae, Malvaceae, Brassicaceae, Amaranthaceae, and Amaryllidaceae. The most abundant species was *L. huidobrensis,* representing overall 90.5% of all LMF species collected, and with 94.4, 92.4, and 84.4% at high, low, and mid altitudes, respectively (Table 4). The relative abundance of *L. sativae* was much lower than that of *L. huidobrensis*, representing overall only 6.2% of LMF species collected, but relatively more common in the lowland (5.8%) and midland (9.5%) compared to highland (3.7%; Table 4). *L. trifolii* was rarely found during this study, representing overall only 2.7% of LMF, with 1.0, 5.7, and 1.5% of LMF at the highland, midland, and lowland, respectively (Table 4). Overall, *L. huidobrensis, L. sativae*, and *L. trifolii* represented 99.4% of all *Liriomyza* species in the study sites. Seasonal comparisons of these species at each altitude revealed that *L. huidobrensis* was more abundant at all altitudes, accounting for more than 70% of the three *Liriomyza* species throughout the study period (Table 5). *L. sativae* was generally more abundant during the hot dry season at all altitudes and less abundant during the dry cold season at the high and

Table 2. Incidence of leafminer-infested leaves during different cropping seasons at low, mid, and high altitudes of vegetable production systems in Kenya

Altitude	LMF-infested leaves (mean ± se %) per season			
	Short rains	Dry hot	Long rains	Dry cold
Highland	53.0 ± 1.5b	71.7 ± 0.9a	35.7 ± 4.2c	56.6 ± 2.0b
Midland	56.6 ± 3.8a	53.6 ± 2.1a	55.1 ± 5.5a	36.0 ± 4.1b
Lowland	49.6 ± 1.5a	55.7 ± 5.0a	48.0 ± 2.3a	49.2 ± 2.2a

Within row, means followed by the same lowercase letter are not significantly different at $P = 0.05$ (Student–Newman–Keuls test).

Table 3. Leafminer fly percentage infestation (mean ± se %) in farmers' fields on different host plants across low, mid, and high altitudes of vegetable production systems in Kenya

Crop	*n*	Short rains	*n*	Dry hot	*n*	Long rains	*n*	Dry cold
Highland								
Courgette	3	52.7 ± 3.5	1	43.5	4	58.0 ± 12.2	1	68.0
French bean	20	44.6 ± 3.4	13	79.5 ± 4.9	12	32.0 ± 4.0	13	54.8 ± 3.0
Garden pea	1	51.5	5	64.9 ± 11.1	4	28.5 ± 2.6	5	53.7 ± 4.3
Kidney bean	3	60.2 ± 18.5	13	79.1 ± 7.2	8	30.7 ± 6.7	3	65.5 ± 9.4
Potato	16	53.7 ± 3.6	21	69.7 ± 5.0	23	31.1 ± 2.7	6	59.4 ± 4.9
Snow pea	30	57.9 ± 3.0	26	70.0 ± 4.1	39	36.7 ± 2.9	23	56.2 ± 2.2
Spinach	–	–	–	–	–	–	1	80.0
Sugar snap	5	63.8 ± 6.7	8	72.4 ± 6.7	5	53.3 ± 4.9	4	53.5 ± 5.8
Sweet pepper	1	45.0	1	54.5	1	29.5	1	35.5
Tomato	1	15.0	1	35.0	3	40.8 ± 2.3	2	58.3 ± 21.3
Midland								
Courgette	–	–	1	25.0	–	–	–	–
Cowpea	–	–	1	80.5	–	–	–	–
French bean	19	57.6 ± 5.2	39	55.6 ± 4.2	15	46.4 ± 4.0	14	28.7 ± 4.2
Garden pea	–	–	1	–	–	–	–	–
Kidney bean	9	86.9 ± 2.5	30	60.6 ± 4.2	17	61.7 ± 3.8	10	32.5 ± 5.6
Okra	–	–	1	10.0	–	–	–	–
Onion	–	–	1	14.0	–	–	–	–
Potato	1	36.5	1	0.5	1	56.5	1	39.5
Tomato	15	39.2 ± 2.3	53	51.7 ± 3.6	29	54.8 ± 3.3	32	39.6 ± 3.7
Watermelon	–	–	–	–	1	35.0	2	45.8 ± 7.3
Lowland								
Bitter gourd	1	60.5	–	–	–	–	–	–
Brinjal eggplant	–	–	1	82.0	–	–	–	–
Butternut squash	–	–	–	–	–	–	1	39.0
Cowpea	1	23.5	7	39.6 ± 10.8	3	46.5 ± 11.0	–	–
Dolichos bean	–	–	1	79	–	–	–	–
French bean	3	69.5 ± 7.2	–	–	–	–	–	–
Kale	–	–	3	12.8 ± 4.7	1	71.5	–	–
Kidney bean	16	48.6 ± 3.0	38	63.7 ± 3.4	13	53.9 ± 3.8	10	41.3 ± 3.1
Okra	1	35.5	9	49.9 ± 4.0	12	37.9 ± 4.1	2	45.8 ± 2.8
Pumpkin	1	28.0	2	49.0 ± 17.0	1	57.5	–	–
Sweet pepper	–	–	1	18.5	1	41.0	1	18.5
Tomato	17	50.2 ± 3.8	66	55.9 ± 2.6	36	49.3 ± 2.3	42	52.0 ± 1.8
Watermelon	1	40	4	53.0 ± 13.7	6	45.2 ± 8.4	2	50.8 ± 6.8

n = number of sampled fields.

Table 4. Species composition, abundance, and distribution of *Liriomyza* leafminer flies identified from infested leaves at low, mid, and high altitudes of vegetable production systems in Kenya

Liriomyza spp.	Number of LMF specimen per altitude			Total
	Highland ($n = 327$)	Midland ($n = 294$)	Lowland ($n = 304$)	
L. huidobrensis	26,788	7,257	10,134	44,179
L. sativae	583	850	516	1,949
L. trifolli	66	479	89	634
Liriomyza spp. (unidentified)	77	19	6	102
L. bryoniae	10	3	2	15
Total	27,524	8,608	10,747	46,879

n = number of sampled fields.

Table 5. Species composition and abundance of the most frequent and invasive *Liriomyza* species at low, mid, and high altitudes during different cropping seasons of vegetable production systems in Kenya

Number of LMF specimen per altitude and season (% of LMF species)			
Season	*L. huidobrensis*	*L. sativae*	*L. trifolii*
Highland			
Short rains	6,604 (97.4%)	139 (2.1%)	36 (0.5%)
Dry hot	5,435 (94.0%)	334 (5.8%)	15 (0.3%)
Long rains	4,569 (98.6%)	60 (1.3%)	6 (0.1%)
Dry cold	10,180 (99.4%)	50 (0.5%)	9 (0.1%)
Midland			
Short rains	814 (94.1%)	36 (4.2%)	15 (1.7%)
Dry hot	2,355 (71.1%)	580 (17.5%)	379 (11.4%)
Long rains	2,002 (87.7%)	210 (9.2%)	71 (3.1%)
Dry cold	2,086 (98.2)	24 (1.1%)	14 (0.7%)
Lowland			
Short rains	1,249 (99.8%)	3 (0.2%)	0 (0.0%)
Dry hot	4,056 (92.7%)	270 (6.2%)	51 (1.2%)
Long rains	3,103 (93.0%)	204 (6.1%)	28 (0.8%)
Dry cold	1,726 (97.2%)	39 (2.2%)	10 (0.6%)

mid altitudes and during the short rains at the low altitude (Table 5). *L. trifolii* was most abundant in the dry hot season at the mid altitude and remained relatively low at both high and the low altitudes in all cropping seasons (Table 5).

***Liriomyza* Species Host Plants Diversity.** A total of 20 different vegetable crops were sampled from the different altitudes, of which all were identified as host plants of leafminer flies (Tables 6–8). More than 87.5% of the total *Liriomyza* species were reared from six plant species belonging to two families: Fabaceae (snow pea, sugarsnap, common bean, and French bean) and Solonaceae (tomato and potato; Tables 6–8) from all the altitudes. Crops from the family Fabaceae were the most commonly grown at high altitude and consequently were the most common *Liriomyza* host plants at the high altitude, with snow pea being the most affected, whereas kidney bean was the least affected (Table 6). At the mid altitude, the Solonaceae and the Fabaceae were the most affected crop families, with tomato being the most affected and potato the least affected of the Solonaceae, whereas French bean and cowpea were the most and least affected, respectively, of the Fabaceae (Table 7). The Solonaceae and the Fabaceae were also the most affected crop families at the low altitude, with tomato and sweet pepper being the most and the least affected of the Solonaceae, whereas kidney bean and dolichos bean were the most and the least affected of the Fabaceae, respectively (Table 8). The least affected crops were spinach (Amaranthaceae) at high altitude (Table 6), onion (Amariliidaceae) and okra (Malvaceae) at the mid altitude (Table 7), and kale (Brassicaceae), at the low altitude (Table 8). *L. huidobrensis* had the widest host range (20 crops) and had the highest abundance on these crops (Tables 6–8), followed by *L. sativae* (18 crops) and *L. trifolii* (12 crops; Tables 6–8). These three *Liriomyza* species were consistently reared in high abundance on snow pea from the high altitude, whereas tomato was the most affected host at the low and mid altitudes (Tables 6–8). *L. bryonae* and the unidentified *Liriomyza* species were less abundant and were reared from four and nine crops, respectively (Tables 6–8). The number of host plants varied across the altitudes. The lowland had the highest number of crops surveyed, i.e., 13 host plants, whereas 10 host plants each were surveyed in the highland and midland (Tables 6–8).

Discussion

Leafminer incidence and the resulting counts of emerging LMF were recorded in all the survey sites across the three altitudes of vegetable production in Kenya. This suggests a widespread distribution of LMF in Kenya. With regard to altitudes, LMF was more abundant in the highlands relative to mid and lowlands. This may be attributed to the fact that the LMF

Table 6. *Liriomyza* species abundance on different host plants at high altitude

Plant family/scientific name	Common name	*n*	Number of LMF (% of LMF per crop)					
			L. huidobrensis	*L. sativae*	*L. trifolii*	*L. bryoniae*	*Liriomyza* species[a]	Total
Fabaceae								
Pisum sativum L.	Snow pea	118	12,443 (45.2%)	274 (1.0%)	28 (0.1%)	3 (0.0%)	30 (0.1%)	12,778 (46.4%)
Pisum sativum L.	Sugar snap	22	3,076 (11.2%)	43 (0.2%)	9 (0.0%)	–	–	3,128 (11.4%)
Phaseolus vulgaris L.	French bean	58	2,148 (7.8%)	93 (0.3%)	20 (0.1%)	4 (0.0%)	27 (0.1%)	2,292 (8.3%)
Pisum sativum L.	Garden pea	15	2,039 (7.4%)	7 (0.0%)	2 (0.0%)	–	5 (0.0%)	2,053 (7.5%)
Phaseolus vulgaris L.	Kidney bean	27	1,311 (4.8%)	36 (0.1%)	1 (0.0%)	1 (0.0%)	5 (0.0%)	1,354 (4.9%)
Fabaceae total		240	21,017 (76.4%)	453 (1.7%)	60 (0.2%)	8 (0.0%)	67 (0.2%)	21,605 (78.5%)
Solanaceae								
Solanum tuberosum L.	Potato	66	3,383 (12.3%)	98 (0.4%)	3 (0.0%)	–	10 (0.0%)	3,494 (12.7%)
Solanum lycopersicum L.	Tomato	7	508 (1.9%)	14 (0.1%)	3 (0.0%)	2 (0.0%)	–	527 (1.2%)
Capsicum L.	Sweet pepper	4	188 (0.7%)	6 (0.0%)	–	–	–	194 (0.7%)
Solanaceae total		77	4,079 (14.8%)	118 (0.4%)	6 (0.0%)	2 (0.0%)	10 (0.0%)	4,215 (15.3%)
Cucurbitaceae								
Cucurbita pepo L	Courgette	9	1,659 (6.0%)	10 (0.0%)	–	–	–	1,669 (6.1%)
Cucurbitaceae total		9	1,659 (6.0%)	10 (0.0%)	–	–	–	1,669 (6.1%)
Amaranthaceae								
Spinacia oleracea L.	Spinach	1	33 (0.1%)	2 (0.0%)	–	–	–	35 (0.1%)
Amaranthaceae total		1	33 (0.1%)	2 (0.0%)	–	–	–	35 (0.1%)
Total for all crops		327	26,788 (97.3%)	583 (2.1%)	66 (0.2%)	10 (0.0%)	77 (0.3%)	27,524 (100.0%)

[a] *Liriomyza* species: unidentified specimen.
n = number of sampled fields.

Table 7. *Liriomyza* species abundance on different host plants at mid altitude

Plant family/scientific name	Common name	*n*	Number of LMF (% of LMF per crop)					
			L. huidobrensis	*L. sativae*	*L. trifolii*	*L. bryoniae*	*Liriomyza* species[a]	Total per crop
Solanaceae								
Solanum lycopersicum L.	Tomato	129	3,592 (41.7%)	595 (6.9%)	383 (4.5%)	3 (0.0%)	18 (0.2%)	4,591 (53.3%)
Solanum tuberosum L.	Potato	4	153 (1.8%)	5 (0.1%)	1 (0.0%)	–	–	159 (1.9%)
Solanaceae total		133	3,745 (43.5%)	600 (7.0%)	384 (4.5%)	3 (0.0%)	18 (0.2%)	4,750 (55.2%)
Fabaceae								
Phaseolus vulgaris L.	Kidney bean	66	1,456 (16.9%)	132 (1.5%)	58 (0.7%)	–	–	1,646 (19.1%)
Phaseolus vulgaris L.	French bean	87	1,706 (19.8%)	84 (1.0%)	29 (0.3%)	–	1 (0.0%)	1,820 (21.1%)
Pisum sativum L.	Garden pea	1	1 (0.0%)	–	–	–	–	1 (0.0%)
Vigna unguiculata (L.) Walp	Cowpea	1	–	–	1 (0.0%)	–	–	1 (0.0%)
Fabaceae total		155	3,163(36.7%)	216 (2.5%)	88 (1.0%)	0 (0.0%)	1 (0.0%)	3,468 (40.3%)
Cucurbitaceae								
Cucurbita pepo L.	Courgette	1	176 (2.0%)	33 (0.4%)	3 (0.0%)	–	–	212 (2.5%)
Citrullus lanatus (Thunb) Matsun and Nakai	Watermelon	3	153 (1.8%)	–	–	–	–	153 (1.8%)
Cucurbitaceae total		4	329 (3.8%)	33 (0.4%)	3 (0.0%)	–	–	365 (4.2%)
Malvaceae								
Abelmoschus esculentus (L.) Moench	Okra	1	12 (0.1%)	1 (0.0%)	4 (0.1%)	–	–	17 (0.2%)
Malvaceae total		1	12 (0.1%)	1 (0.0%)	4 (0.1%)	–	–	17 (0.2%)
Amarilidaceae								
Allium cepa L.	Onion	1	8 (0.1%)	–	–	–	–	8 (0.1%)
Amarilidaceae total		1	8 (0.1%)	–	–	–	–	8 (0.1%)
Total for all crops		294	7,257 (84.3%)	850 (9.9%)	479 (5.6%)	3 (0.0%)	19 (0.2%)	8,608 (100.0%)

[a] *Liriomyza* species: unidentified specimen.
n = number of sampled fields.

collections were dominated by *L. huidobrensis*, which is known to adapt and predominantly colonize hosts at colder higher elevations, mostly above 1000 m. a.s.l. (Spencer 1989, Shepard et al. 1998, Sivapragasam and Syed 1999, Rauf et al. 2000, Weintraub 2001, Andersen et al. 2002, Chabi-Olaye et al. 2008, Tantowijoyo and Hoffmann 2010, Mujica and Kroschel 2011). However, this species was not only predominant at the high altitude but also at the warmer mid and the low altitudes, a finding that contrasts previous studies in Kenya indicating that *L. sativae* and *L. trifolli* predominate in the two later altitudes (Chabi-Olaye et al. 2008). This finding suggests that *L. huidobrensis* is more aggressive and is adapting to warmer areas and may be displacing *L. trifolli*, which has long history of establishing in Kenya, as well as *L. sativae* at the low and the mid altitudes. Species displacement is a potentially widespread phenomenon, receiving much attention from ecologists

Table 8. *Liriomyza* species abundance on different host plants at low altitude

Plant family/scientific name	Common name	*n*	Number of LMF (% of LMF per crop)					
			L. huidobrensis	*L. sativae*	*L. trifolii*	*L. bryoniae*	*Liriomyza* species[a]	Total
Solanaceae								
Solanum lycopersicum L.	Tomato	161	7,416 (69.0%)	356 (3.3%)	53 (0.5%)	2 (0.0%)	1 (0.0%)	7,828 (72.8%)
Solanum melongena L.	Brinjal eggplant	1	122 (1.1%)	25 (0.2%)	–	–	1 (0.0%)	148 (1.4%)
Capsicum L.	Sweet pepper	3	15 (0.1%)	3 (0.0%)	–	–	–	18 (0.2%)
Solanaceae total		165	7,553 (70.3%)	384 (3.6%)	53 (0.5%)	2 (0.0%)	2 (0.0%)	7,994 (74.4%)
Fabaceae								
Phaseolus vulgaris L.	Kidney bean	77	1,319 (12.3%)	43 (0.4%)	2 (0.0%)	–	1 (0.0%)	1,365 (12.7%)
Vigna unguiculata (L.) Walp	Cowpea	11	159 (1.5%)	18 (0.2%)	12 (0.1%)	–	1 (0.0%)	190 (1.8%)
Phaseolus vulgaris L.	French bean	3	33 (0.3%)	1 (0.0%)	–	–	–	34 (0.3%)
Lablab purpureus (L.) Sweet	Dolichos bean	1	4 (0.0%)	–	–	–	–	4 (0.0%)
Fabaceae total		92	1,515 (14.1%)	62 (0.6%)	14 (0.1%)	–	2 (0.0%)	1,593 (14.8%)
Cucurbitaceae								
Citrullus lanatus (Thunb) Matsun and Nakai	Watermelon	13	358 (3.3%)	20 (0.2%)	4 (0.0%)	–	–	382 (3.6%)
Momordica charantia L	Bitter gourd	1	145 (1.4%)	–	–	–	–	145 (1.4%)
Cucurbita maxima Duchesne	Pumpkin	4	42 (0.4%)	5 (0.1%)	–	–	–	47 (0.4%)
Cucurbita moschata Duchesne ex Poir.	Butternut squash	1	30 (0.3%)	–	–	–	–	30 (0.3%)
Cucurbitaceae total		19	575 (5.4%)	25 (0.2%)	4 (0.0%)	–	–	604 (5.6%)
Malvaceae								
Abelmoschus esculentus (L.) Moench	Okra	24	439 (4.1%)	40 (0.4%)	12 (0.1%)	–	2 (0.0%)	493 (4.6%)
Malvaceae total		24	439 (4.1%)	40 (0.4%)	12 (0.1%)	–	2 (0.0%)	493 (4.6%)
Brassicaceae								
Brassica oleracea acephala L.	Kale	4	52 (0.5%)	5 (0.1%)	6 (0.1%)	–	–	63 (0.6%)
Brassicaceae total		4	52 (0.5%)	5 (0.1%)	6 (0.1%)	–	–	63 (0.6%)
Total for all crops		304	10,134 (94.3%)	516 (4.8%)	89 (0.8%)	2 (0.0%)	6 (0.1%)	10,747 (100.0%)

[a] *Liriomyza* species: unidentified specimen.
n = number of sampled fields.

because it affects the structure of communities (Reitz and Trumble 2002, Reitz 2007, DeBach 1966, Abe and Tokumaru 2008). This phenomenon is common in *L. sativae* and *L. trifolli* under field conditions. However, Chen and Kang (2004, 2005) found that *L. huidobrensis* replaced *L. sativae* as the predominant pest in all areas of varying altitudes in China. Subsequent studies by Gao et al. (2011) in the Chinese province of Hainan revealed that *L. trifolii* displaced *L. sativae*, which was the predominant pest on *Vigna unguiculata* L. Similarly, *L. sativae* was also displaced by *L. trifolii* in the western United States (Trumble and Nakakihara 1983, Palumbo et al. 1994). However, in Japan, the opposite occurred, where *L. trifolii* was displaced by *L. sativae* (Abe and Kawahara 2001, Abe and Tokumaru 2008). Thus, given that *L. huidobrensis* was the most abundant, in addition to its wider distribution as determined in this study, the species constitutes the greatest threat to vegetables and ornamentals production in Kenya. Additionally, the spread of *L. huidobrensis* from higher altitudes to lower altitudes and its high adaptation could serve as an indicator that the same may be obtained in neighboring Uganda, where, according to our unpublished data, LMF are currently not considered to be of high importance, with *L. sativae* dominating countrywide, whereas *L. huidobrensis* is limited to higher altitudes (K.K.M. Fiaboe, personal communication). The three most important LMF species in Kenya are *L. huidobrensis*, *L. sativae*, and *L. trifolii*, representing 99.4% of total LMF species. This implies that *L. bryonae* and the unidentified *Liriomyza* species are currently negligible in vegetable production systems of Kenya. This, in addition to the low population of *L. sativae* and *L. trofolii* during this survey, suggests that special attention should be given to *L. huidobrensis* control. Further field surveys will be required in Kenya as well as neighboring countries to assess the status of LMF species composition and abundance over several years in vegetable productions systems.

Although different host plants present an array of chemical, nutritional, and morphological challenges for larval development, the three most abundant *Liriomyza* species identified in this study are highly polyphagous, attacking plants in several families (Spencer 1990, Murphy and LaSalle 1999, Andersen et al. 2002, Tran et al. 2006). In our survey, we identified *L. huidobrensis, L. sativae*, and *L. trifolii* from 20, 18, and 12 different infested crops, respectively. This may suggest that the current host range for *L. huidobrensis* and *L. sativae* is relatively high compared to that of the long-established *L. trifolii* in Kenya. Unlike *L. trifolii* and *L. sativae* larvae, which are relatively small and feed on the upper mesophyll of the leaves, that of *L. huidobrensis* is larger and more aggressive by feeding in the lower mesophyll, mine into the petioles and pods, and causing more damage to the plant photosynthetic area; thus, severe yield reduction is inevitable (Weintraub and Horowitz 1995). Being the most polyphagous species, in addition to its aggressiveness and high abundance at all altitudes, *L. huidobrensis* constitutes the greatest LMF challenge to vegetables and ornamentals production in Kenya.

Although most *Liriomyza* species are polyphagous with a broad and diverse host range (Spencer 1990, Murphy and LaSalle 1999, Andersen et al. 2002, Tran et al. 2006), they also exhibit host plant preference (Zhao and Kang 2003, Tokumaru and Abe 2005). In the present study, snow pea (Fabaceae) was the most highly attacked *Liriomyza* host plant in the high altitude, whereas tomato (Solonaceae) was the most highly attacked *Liriomyza* host plant at both mid and low altitudes. This finding is consistent with previous studies, indicating that the fabaceaes and solanaceaes are the most suitable host for *Liriomyza* species development (Mujica and Kroschel 2011, Tran et al. 2007, Tokumaru and Abe 2005, Chabi-Olaye et al. 2008). Kale (Brassicaceae), onion (Amarilidaceae), and sweet pepper (Solonaceae) had lower LMF abundance. Chabi-Olaye et al. (2008) also found that field infested onion and kale leaves in Kenya resulted to very few numbers of *Liriomyza* species identified, whereas Martin et al. (2005) found that Asian broccoli (*Brassica alboglabra* L.; Brassicaceae) was the least preferred host for the chrysanthemum leafminer. *L. huidobrensis* was the only *Liriomyza* species identified from onion and butter squash infested leaves. *L. huidobrensis* was also found infesting onion in California (Reitz and Trumble 2002), and a previous study in Kenya also revealed *Liriomyza* species infesting butter squash (Chabi-Olaye et al. 2008). Although host availability varied across altitudes in this study, *Liriomyza* species can potentially exploit new host plants encountered in newly colonized habitats, especially under conditions where their common hosts are rare or absent (Via 1984). While the factors accounting for the differential LMF attraction and infestation are unclear, it is known that the plant hosts volatiles may play a significant role in pest attraction (Mattiacci et al. 2001, Hartmann 2004, Arimura et al. 2005, Takken and Dicke 2006, Wei et al. 2007). Furthermore, differential host plant preference between LMF and their natural enemies, where some of the preferred host plants of the pest might be less suitable to natural enemies' colony development and/or performance against LMF, may also contribute to the observed differences (Fagoonee and Toory 1983, Knodel-Montz et al. 1985, Minkenberg and Ottenheim 1990, Wei et al. 2000). Therefore, an understanding of the semiochemical basis for attraction between most important host plants (e.g., Fabaceae and Solanaceae) and less important plants (e.g., Brassicaceae and Amarilidaceae) as well as the semiochemical and morphological effects of these LMF host plants on the most important and efficient natural enemies could provide a solid foundation for management of LMF. Further studies to elucidate the parameters above will also help in minimizing the over reliance on synthetic insecticides currently used in their control in Kenya.

The occurrence and relative abundance of leafminers in relation to seasons and host plants may reflect the impacts of climate and their distinct preference for host plants (Murphy and LaSalle 1999, Johansen et al. 2003). *Liriomyza* species can be present in the fields throughout the year, as shown in this study. Apart from *L. huidobrensis*, whose abundance remained relatively high throughout all the cropping seasons at all altitudes, *L. trifolii* and *L. sativae* were more abundant during the hot dry season as compared to the other seasons across all altitudes. This finding is consistent with previous studies, indicating that *L. sativae* was very abundant in the dry season compared to the rainy season in Southern Vietnam and in Ho Chi Minh City (Tran et al. 2005, Tran et al. 2007). While Rauf and Shepard (1999) found that infestations by *L. huidobrensis* occurred heavily during the dry season compared to the rainy season, the present study, however, revealed that the species remained relatively abundant throughout the cropping seasons at all altitudes. This may suggest that *L. huidobrensis* is not only adapting at all altitudes, more aggressive, and polyphagous, but is also consistently high at all altitudes throughout the different cropping seasons despite the varied climatic conditions and crops available.

In conclusion, *Liriomyza* species pose a threat to vegetables and ornamentals at different altitudes in Kenya. Of all LMF identified in this study, *L. huidobrensis* constitutes the greatest challenge to vegetable production by being consistently the most abundant and most polyphagous species at all altitude areas and all seasons. Additionally, the species is adapting to warmer climates at the mid and low altitudes, thus displacing *L. trifolii*, which is long-established at these altitudes in Kenya. Whereas a quick action concerning the management of these pests should be put in place, the results of this study should serve as a signal to other countries like Uganda where it is still considered a high-altitude pest. It is also important to determine the molecular background of *L. huidobrensis* identified in Kenya compared to that in countries where the species is still limited to higher altitudes to test for genetic differences between populations for effective future management. Further studies to assess the species composition, abundance, and possible displacement over time as well as to elucidate the semiochemical and morphological effects of host plants on LMF species infestation and their associated natural enemies are warranted.

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