

Leafminer Fly (Diptera: Agromyzidae) Occurrence, Distribution, and Parasitoid Associations in Field and Vegetable Crops Along the Peruvian Coast

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ABSTRACT Leafminer flies (Diptera: Agromyzidae) are important agricultural pests worldwide. The objective of our study was to assess the relative importance of agromyzids and their associated parasitoids in field and vegetable crops along the Peruvian coast. In total, nine leafminer fly species were identified in 27 crops. The most dominant species was *Liriomyza huidobrensis* (Blanchard) (88.0%). *Liriomyza sativae* Blanchard was the second most dominant species (8.59%) but mainly found in the most northern part of Peru. On average, a parasitism of 29.5% was registered by 63 parasitoids belonging to the families Eulophidae (41 spp.), Braconidae (11 spp.), Pteromalidae (8 sp.), Fitigidae (1 sp.), and Mymaridae (2 spp.). The endoparasitoids *Halticoptera arduine* (Walter) (48.2%), *Chrysocharis flacilla* Walker (19.5%), and *C. caribea* Boucek (8.0%) as well as the ectoparasitoid *Diglyphus websteri* (Crawford) (8.7%) were the most abundant parasitoids. *H. arduine* was not only the most abundant and efficient parasitoid but also parasitized all leafminer fly species in 25 crops. The wide adaptation of the parasitoids *H. arduine*, *C. flacilla*, *C. caribea*, *D. websteri*, *D. begini*, and *Ganaspidium* Weld sp. to different host plants and leafminer fly species indicates the potential use of those parasitoids for biological control programs. The high diversity of parasitoids supports the assumption that leafminer flies are of neotropical origin. The heavily pesticide-based pest management practices along the Peruvian coast should take more advantage of the richness of parasitoids by augmenting its efficacy through the adoption of integrated pest management.

KEY WORDS *Liriomyza huidobrensis*, *Liriomyza sativae*, biological control, parasitoids

The genus *Liriomyza* (Diptera: Agromyzidae) contains >300 leafminer fly species, which are worldwide distributed; 35 species occur in the Neotropics and 19 species have been identified in Peru (Korytkowski 1982, Parrella 1987, Spencer 1990). The genus includes 23 species of economic importance because of their damage to a wide range of agricultural and horticultural crops and ornamental plants. Five species are polyphagous, which is an uncommon characteristic among the family Agromyzidae. Over the past three decades, the three highly polyphagous leafminer fly species *L. huidobrensis* (Blanchard), *L. sativae* Blanchard, and *L. trifolii* (Burgess) have invaded many new areas worldwide (Shepard et al. 1998, Rauf et al. 2000). *L. huidobrensis* and *L. sativae* are known as serious pests in agricultural production systems along the Peruvian coast (Raven 1993). Both species have many host plants in the families Cucurbitaceae, Leguminosae, Solanaceae, Brassicaceae, Asteraceae, and Compositae and others (Musgrave et al. 1975, European and Mediterranean Plant Protection Organization [EPPO] 2009). *Liriomyza* spp. cause both direct and indirect damage to plants. Larval mining in pali-

sade parenchyma tissue reduces the photosynthetic capacity of plants up to 62% (Johnson et al. 1983), and severely infested leaves may fall (EPPO 2009). A further damage to leaves is caused by females, which use the ovipositor to make holes, so-called “feeding punctures” in the upper and/or lower surfaces of the leaves promoting the production of leaf exudates on which both females and males feed. Other wounds, called “oviposition punctures,” are made to insert eggs below the leaf surface (Parrella et al. 1984). Egg-laying females may also act as vectors for diseases (Zitter and Tsai 1977, Matteoni and Broadbent 1988) such as *Alternaria alternata* (Fr.) Keissl. (Deadman et al. 2000). Control of leafminer flies is difficult for several reasons. Adults may rapidly develop pesticide resistance (Parrella et al. 1984, MacDonald 1991) and leafminer fly larvae are inaccessible to many pesticides because they develop inside leaves and pupate in soil. Translaminar pesticides, like abamectin and cyromazine, acting on larvae, currently have been shown to provide effective chemical control. Natural enemies may also provide effective control in field crops (Johnson and Hara 1987, Johnson 1993, Liu et al. 2009), but there is evidence that pesticides that kill leafminer fly parasitoids may cause or exacerbate leafminer fly out-

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breaks (Johnson et al. 1980, Murphy and LaSalle 1999).

Liriomyza spp. are known to have many natural enemies, particularly in their region of origin in the New World (Waterhouse and Norris 1987, Murphy and LaSalle 1999). Noyes (2004) listed over 300 species of leafminer fly parasitoids, and over 80 species that are known to attack various *Liriomyza* species. Cisneros and Mujica (1997) observed on the central coast of Peru a rich complex of parasitoids, consisting of the ectoparasitoid *Diglyphus* spp. and the two endoparasitoids *Halticoptera arduine* (Walter) and *Chrysocharis* spp. as the most abundant. Field and vegetable crops as hosts of leafminer flies are cultivated along the Peruvian coast in a distinct temperature gradient from a northern tropical to a southern subtropical climate. The objective of our study was to gain a systematic understanding of the composition, spatial distribution and diversity of leafminer fly species and associated parasitoids as well as on leafminer fly host plant preferences and field infestation as influenced by this temperature gradient in the autumn and winter cropping season. The study should provide new information on potential leafminer fly parasitoid species and their climatic preferences that could be best used for biological control in different crop production systems and agroecologies.

Materials and Methods

Climatic Characteristics of the Peruvian Coast. The Peruvian coast has a total length of 3,080 km and is characterized by a long narrow desert, which is occasionally split by rivers that provide water for intensive agricultural production. Its climate is determined by the Humboldt Current, which is a cold-water current of the southeast Pacific Ocean flowing from the southern tip of Chile to northern Peru. The cold water cools the marine air that is not conducive to generating precipitation during the whole year although clouds and fog are produced. In accordance with the international climate classification of Köppen, the Peruvian coast has two types of climates (Instituto Geofísico del Perú [IGP] 2007). A semiwarm and very dry climate (arid, subtropical) with an average temperature of 19°C is common in almost the whole region of the coast from the departments of Lambayeque to Tacna. A very dry warm climate (arid, tropical) with an average temperature of 24°C occurs in the northern coast of Peru from Piura to Tumbes, with strong rains from December to April, and long dry spells from May to November (Table 1).

Field Survey. Potato (*Solanum tuberosum* L.), bean (*Phaseolus vulgaris* L.), and tomato (*Lycopersicon esculentum* Miller) are usually grown in fields of a size of 1–2 ha; other vegetable crops are cultivated on much smaller plots (0.1–0.25 ha). The potato-growing season lasts from May to October, during the Peruvian winter. Surveys to study the occurrence and distribution of leafminer fly and their associated parasitoids were conducted in the winter, from July to August 2003, and autumn cropping season, from April to May

Table 1. Annual precipitation and max and min. temperatures in the winter and autumn cropping season of the surveyed regions along the Peruvian coast

Regions	Precipitation (mm)	Winter (July 2003)		Autumn (April 2004)	
		Temperature °C			
		Max	Min.	Max	Min.
Tumbes	610	26.8	20.4	32	22.1
Piura	80	27.8	17.2	32.9	21.6
Lambayeque	23	25.6	15.8	31	20.1
La Libertad	10	21.7	14.1	25.2	16.8
Ancash	12	21.8	11.9	24.2	20.1
Lima	11	18.9	13.2	24.1	18.1
Ica	1.5	21.4	12.9	27.8	17.9
Arequipa	5.6	19.3	11.7	26	16.7
Moquegua	15.6	22.6	11.3	25	19.3
Tacna	33.4	19.6	10.2	26.2	15.1

2004, in 10 agricultural production regions along the Peruvian coast from Tumbes (0°01' 11'' S) in the north of Peru to Tacna (18°21' 05'' S) in the south in a total of 29 provinces. In the different regions the production of field and vegetable crops as host plants of leafminer flies are not equally important, hence the sample size varied in each region. The survey did not take into account the different plant-protection measures and pesticide applications by farmers and therefore does not reflect undisturbed herbivore-parasitoid relationships.

Sampling Method. On average, 30 leafminer fly-infested leaves were randomly collected from each field sampled, covering a total of 459 fields, with 243 and 216 fields in the winter and autumn cropping season, respectively. During the daily surveys, the leaf samples collected were immediately stored in paper bags and afterwards transferred onto damp paper towels into plastic containers (15 × 25 × 10 cm) to avoid drying of the leaves. Leaf layers were separated with dry paper towels and all towels were changed at 2-d intervals for the following 6 d. Boxes were closed with a lid containing muslin windows (20 × 12 cm) for ventilation and kept at temperatures of 20°C. After 7–10 d pupae were collected from the boxes and stored in plastic petri dishes until adults of either leafminer flies or endoparasitoids hatched. Leaves were returned to the container to identify the ectoparasitoids. Specimens were identified using conventional taxonomic keys and reference collections. Voucher specimens of collected leafminer flies and parasitoids are stored in CIP's entomological museum at CIP headquarter in Lima, Peru. In each infested field, the infestation intensity was visually assessed on 30 plants randomly selected per field by using a rating scale from low (1–25%), middle (26–50%) to high (>50%) leaf infestation.

Statistical Analysis. *Field Infestation and Parasitism.* Data from the different regions, crop plants, and cropping seasons were pooled ($n = 458$ fields) and differences in infestation analyzed using χ^2 goodness-of-fit contingency table. The likelihood-ratio χ^2 test was used to assess the null hypotheses. For the analysis of the numbers of larvae per leaf and parasitism, we

Table 2. Relative abundance of leafminer fly species identified in two cropping seasons along the Peruvian coast

Agromyzidae species	Cropping seasons				Total	
	Autumn		Winter		No.	%
	No.	%	No.	%		
<i>Amauromyza</i> sp.	3	0.03	27	0.14	30	0.10
<i>Cerodontha dorsalis</i>	—	—	3	0.02	3	0.01
<i>Japanagromyza</i> sp.	2	0.02	4	0.02	6	0.02
<i>Liriomyza graminivora</i>	—	—	37	0.19	37	0.13
<i>Liriomyza huidobrensis</i>	7,396	81.93	17,796	90.79	25,192	88.00
<i>Liriomyza sativae</i>	1,066	11.81	1,393	7.11	2,459	8.59
<i>Liriomyza</i> sp. 1	542	6.00	338	1.72	880	3.07
<i>Liriomyza</i> sp. 2	—	—	3	0.02	3	0.01
<i>Melanagromyza</i> sp.	18	0.20	—	—	18	0.06
Total	9,027	100.00	19,601	100.0	28,628	100.00

included only those fields from which individuals had been reared ($n = 254$ fields). We used generalized linear models, with Poisson error distribution (link = log) corrected for overdispersion (Sileshi 2006, 2007) to test for seasons, regions, and host plant effects. When significant models were found, separation of means was performed using Tukey honestly significant difference test at $P \leq 0.05$. Before the analysis, insect counts were square root ($x + 0.5$) transformed and percentage of parasitism data arcsine-transformed. The program used for these calculations was JMP-version 8.0.2 statistical package (SAS Institute 2009).

Parasitoid Diversity. The alpha diversity was measured using the indices Richness (S), Shannon-Wiener (H'), Evenness (E), and Simpson (1-D). Species richness is the simplest way to describe community and regional diversity (Magurran 1988), and forms the basis for the ecological modeling of the community structure (Gotelli and Colwell 2001). The Shannon-Wiener diversity index is widely used for comparing diversity between various habitats, and it is notoriously sample-size dependent and tends to be weighted slightly toward species richness (Clarke and Warwick 2001). Evenness is a measure of the relative abundance of the different species making up the richness of an area. Equitability takes a value between 0 and 1, with one being complete evenness. Simpson's Diversity Index is a measure of diversity that takes into account both richness and evenness. The value of this index also ranges between 0 and 1; the greater the value, the greater the sample diversity. This index represents the probability that two individuals randomly selected from a sample will belong to different species (Magurran 1988). The beta diversity was measured by Bray-Curtis cluster analysis of parasitoid similarity. Similarity measures the distance (based on species composition) between all pairs of sites (Magurran 2004). Parasitoid diversity indices were calculated using Biodiversity Pro software version two (McAleece et al. 1997). Alfa diversity indices (Shannon-Wiener, Evenness, and Simpson) by season and regions were subjected to analysis of variance (ANOVA) (SAS Institute 2009), followed by pairwise χ^2 tests, at $P \leq 0.05$.

Results

Leafminer Fly Species and Their Distribution Along the Peruvian Coast. In total, 28,628 Agromyzidae leafminer fly adults, representing nine species (*Liriomyza huidobrensis*, *L. sativae*, *L. graminivora* Korytkowski, *Liriomyza* sp. 1, *Liriomyza* sp. 2, *Amauromyza* sp., *Melanagromyza* sp., *Japanagromyza* sp., and *Cerodontha dorsalis* Loew) were collected from all crops surveyed; 19,601 (eight species) and 9,027 (six species) adults were reared from the collections during the winter and autumn cropping season, respectively (Table 2). The most abundant species was *L. huidobrensis* (88.0%) recovered from eight regions in both cropping seasons; it could not be found in the most tropical regions of Tumbes and Piura. In contrast, the relative abundance of the closely related species *L. sativae* was much lower (8.6%); this species was only common in the northern part of Peru, mainly in the region of Tumbes and Piura (Fig. 1).

Host Plants of Leafminer Fly Species. Of a total of 35 horticulture and field crops (32 in the autumn and 29 in the winter seasons), 29 crops were identified as host plants of leafminer flies (Table 3). More than 93% of the leafminer flies were reared from nine plant species: common bean; potato; faba bean, *Vicia faba* L.; alfalfa, *Medicago sativa* L.; pea, *Pisum sativum* L.; tomato; cowpea, *Vigna unguiculata* (L.) Walp.; pumpkin, *Curcubita maxima* Duchesne; and cucumber, *Cucumis sativus* L., while other crops were only slightly infested. In six cultivated species (asparagus, *Asparagus officinalis* L.; broccoli, *Brassica oleracea* L. variety *italica*; cauliflower, *Brassica oleracea* L. variety *botrytis*; eggplant, *Solanum melongena* L.; muskmelon, *Cucumis melo* L. and wild watermelon, *Citrullus lanatus* (Thunberg) Mansfeld) no leafminer fly infestation could be found (Table 3). Crops of the family Fabaceae are the most important leafminer fly host plants considering both species richness (five species) and relative abundance (63.2%). With 23 crops, *L. huidobrensis* had the widest host plant range, followed by *L. sativae* that was found attacking six crops (Table 3).

Leafminer Fly Infestation. Leafminer fly-infested field and vegetable crops were found in all 10 regions and 29 provinces surveyed in autumn and winter season along the Peruvian coast. The number of infested

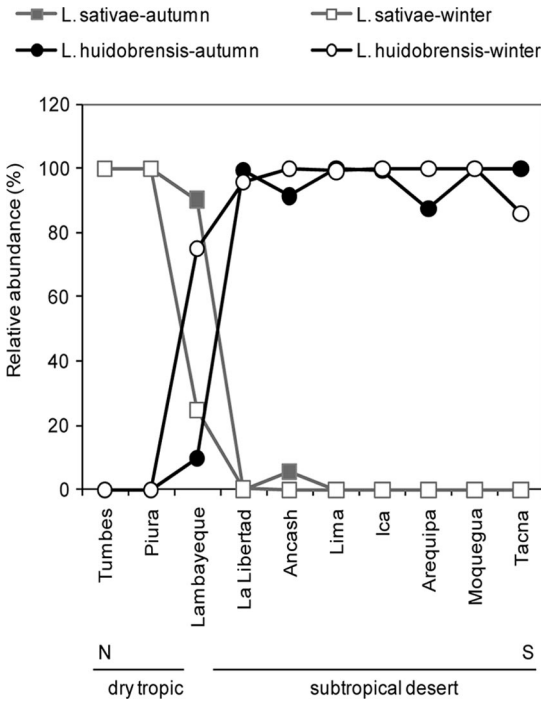


Fig. 1. Distribution and relative abundance of *L. huidobrensis* and *L. sativae* in two cropping seasons along the Peruvian coast.

fields differed significantly between seasons ($G = 138.2$; $df = 3$; $P < 0.0001$). In the winter cropping season, the leafminer fly infestation was more serious; on average 91.8% of the fields were infested compared with only 45.8% in the autumn cropping season (Table 4). Accordingly, the infestation intensity was also highest in the winter cropping season, with 49.4% of the fields showing a leaf infestation of $>26\%$ to $>50\%$. The number of infested fields was affected by region ($G = 46.07$; $df = 27$; $P < 0.0125$). In the central and southern regions (La Libertad, Ancash, Lima, Ica, Arequipa, Moquegua, and Tacna) the number of infested fields increased by over 36% from the autumn to winter season (Table 4). The highest increase of infested fields was found in the Ica region with 69.4% of infested fields from the autumn (9.8%) to winter (79.2%) season. In the northern regions of Tumbes, Piura, and Lambayeque, in which the highest mean temperature prevails in both cropping seasons, compared with all other regions, no differences between cropping seasons were found (Table 4).

Significant differences of infested fields were found between the different leafminer fly host plants ($G = 242.12$; $df = 102$; $P < 0.0001$) (Table 3). In the autumn season, a high number of infested fields with high infestation intensity were registered only in faba bean (*Vicia faba* L.) (40.0% of fields) and common bean (23.3% of fields). In the winter season: faba bean, common bean, green pea (*Phaseolus vulgaris* L. variety *vulgaris*), pea, soybean (*Glycine max* (L.) Merr.), pumpkin, and cabbage (*Brassica oleracea* L. variety

capitata) presented $>30\%$ of fields with high infestation intensity.

Larval infestation was not influenced by season ($\chi^2 = 1.38$; $df = 1$; $P = 0.239$) or region ($\chi^2 = 13.8$, $df = 9$, $P = 0.129$) but varied significantly among host crops ($\chi^2 = 73.3$; $df = 27$; $P < 0.0001$). In general, Cucurbitacea and Fabaceae families had the highest larval infestation with averages of 12.6 ± 3.5 and 10.7 ± 1.3 larvae per leaf, respectively (Table 3). The lowest infestation was observed in Amarilidaceae with an average of 0.18 ± 0.08 larvae per leaf. Main host plants for leafminer larvae were cabbage (51.4), faba bean (20.2 ± 5.7), pumpkin (18.4 ± 6.3), common bean (12.6 ± 2.6), pea (11.7 ± 2.6), and cowpea bean (7.4 ± 2.5).

Parasitism, Parasitoid Diversity, and Regional Distribution. Parasitism showed significant differences between seasons ($\chi^2 = 4.74$; $df = 1$; $P = 0.029$) and crops ($\chi^2 = 6.11$; $df = 9$; $P = 0.009$), but no effect of regions was observed ($\chi^2 = 47.2$; $df = 27$; $P = 0.728$). In the winter and autumn season mean parasitism rates of 48.4 and 42.0% were found. The parasitism rate was nonexistent in yellow Peruvian chili (*Capsicum baccatum* L.) and highest in chard (*Beta vulgaris* L. variety *cicla* L.) (91.7%), Chinese cabbage (*Brassica campestris* L. variety *pekinensis*) (80.0%), and celery (*Apium graveolens* L. variety *dulce*) (78.5%) (Table 3). In general, parasitism rates varied according to the level of leaf infestation, with highest rates at low infestation ($r = -0.3652$; $P < 0.0001$).

In total, 17,768 parasitoids emerged from all leafminer fly samples. Parasitoids consisted of 63 species belonging to three super families and five families: Eulophidae (41 spp.), Braconidae (11 spp.), Pteromalidae (8 sp.), Fitigidae (1 sp.), and Mymaridae (2 spp.) (Table 5). Not all parasitoids, especially those of minor importance, could be identified to the species level. *Halticoptera arduine* (48.2%), *Chrysocharis flacilla* Walker (19.5%), *C. caribea* Boucek (8.0%), *Diglyphus websteri* (Crawford) (8.7%), *D. begini* (Ashmead) (4.5%), and *Ganaspidium* sp. (4.3%) were the most important parasitoids identified in this survey. These species represented 93.2 and 94.1% of all parasitoids reared in the winter and autumn cropping season, respectively. The larval-pupal parasitoids *H. arduine* (52.3%) and *C. flacilla* (38.9%) were the dominant species in both seasons. *H. arduine* was the dominant species in the regions of Tumbes, Piura, Lambayeque, La Libertad, Ancash, Lima, Ica, and Moquegua; *C. flacilla* in Arequipa and Tacna (Fig. 2). The endoparasitoids *H. arduine*, *C. brethesi*, and *Ganaspidium* sp. and the ectoparasitoid *D. websteri* were recovered in all regions.

Alfa Diversity. No significant differences were found in the Shannon-Wiener ($\chi^2 = 0.06$; $df = 1$; $P = 0.79$), Evenness ($\chi^2 = 1.44$; $df = 1$; $P = 0.23$), and Simpson ($\chi^2 = 0.41$; $df = 1$; $P = 0.52$) diversity indices between cropping seasons although species richness (S) varied significantly between seasons (Likelihood ratio $\chi^2 = 19.76$; $df = 1$; $P < 0.0001$), with the highest number of 51 parasitoid species in the winter season compared with 28 species found during the autumn

Table 3. Leafminer fly infestation intensity in two cropping seasons, mean parasitism and no. of Agromyzidae species reared from different field and vegetable crops in farmer's field along the Peruvian coast

Plant families/scientific name	Common name	Infestation intensity (%)										Mean larvae per leaf (SE)	Mean parasitism (%)		
		Autumn		Winter											
		No. ^a	L ^b	M	H	No.	L	M	H						
Amarillidaceae															
<i>Allium cepa</i> L. var. <i>aggregatum</i>	Scallion (1) ^c	2	0.0	0.0	0.0	3	100.0	0.0	0.0				0.2 (0.1)	64.6	
Apiaceae															
<i>Aptium graveolens</i> L. var. <i>dulce</i>	Celery (1)	6	83.3	0.0	0.0	5	40.0	20.0	20.0				3.8 (1.1)	78.5	
Asparagaceae															
<i>Asparagus officinalis</i> L.	Asparagus	2	0.0	0.0	0.0	—	—	—	—				—	—	
Asteraceae															
<i>Lactuca sativa</i> L.	Lettuce (1,6)	9	55.6	11.1	0.0	7	57.1	28.6	14.3				3.1 (0.9)	61.3	
<i>Tagetes erecta</i> L.	Margold (1,5,7)	2	0.0	0.0	0.0	3	33.3	66.7	0.0				0.7 (0.4)	28.3	
Brassicaceae															
<i>Brassica oleracea</i> L. var. <i>capitata</i>	Cabbage (1)	4	0.0	0.0	0.0	1	0.0	0.0	100.0				51.4	23.2	
<i>Brassica oleracea</i> L. var. <i>botrytis</i>	Cauliflower	3	0.0	0.0	0.0	—	—	—	—				—	—	
<i>Brassica oleracea</i> L. var. <i>italica</i>	Broccoli	1	0.0	0.0	0.0	—	—	—	—				—	—	
<i>Brassica campestris</i> L. var. <i>pekinensis</i>	Chinese cabbage (1)	3	33.3	0.0	0.0	—	—	—	—				0.3	80	
<i>Brassica campestris</i> L. var. <i>rapa</i>	Turnip (1)	3	33.3	0.0	0.0	2	100.0	0.0	0.0				1.8 (1.0)	41.2	
<i>Raphanus sativus</i> L.	Radish (1)	4	75.0	0.0	0.0	2	50.0	50.0	0.0				2.2 (0.5)	40	
Chenopodiaceae															
<i>Beta vulgaris</i> L. var. <i>cicla</i>	Chard (1)	3	33.3	0.0	0.0	1	100.0	0.0	0.0				0.3 (0.3)	91.7	
<i>Beta vulgaris</i> L. var. <i>vulgaris</i>	Beetroot (1,4)	7	57.1	0.0	0.0	7	57.1	28.6	0.0				1.3 (0.4)	49.8	
<i>Spinacea oleracea</i> L.	Spinach (1,2,4)	4	75.0	0.0	0.0	3	66.7	33.3	0.0				1.1 (0.9)	48.5	
Cucurbitaceae															
<i>Citrullus lanatus</i> (Thunberg) Mansfield	Wild watermelon	4	0.0	0.0	0.0	1	0.0	0.0	0.0				—	—	
<i>Cucumis sativus</i> L.	Cucumber (1)	6	33.3	16.7	16.7	—	—	—	—				—	—	
<i>Cucumis melo</i> L.	Muskmelon	1	0.0	0.0	0.0	—	—	—	—				—	—	
<i>Cucurbita pepo</i> L.	Zucchini (1)	3	33.3	0.0	0.0	—	—	—	—				5.5	32.9	
<i>Cucurbita maxima</i> Duchesne	Pumpkin (1)	7	0.0	14.3	14.3	4	0.0	25.0	50.0				18.4 (6.3)	25	
Fabaceae															
<i>Medicago sativa</i> L.	Alfalfa (1,2,4,9)	29	34.5	3.5	17.2	—	—	—	—				5.3 (1.3)	57.7	
<i>Cicer arietinum</i> L.	Chickpea (2)	3	0.0	0.0	0.0	—	—	—	—				0.5	25	
<i>Glycine max</i> (L.) Merrill	Soybean (2)	3	33.3	16.7	16.7	3	33.3	0.0	0.0				5.3 (2.8)	25.4	
<i>Phaseolus vulgaris</i> L. var. <i>vulgaris</i>	Green pea (1)	1	100.0	0.0	0.0	2	50.0	0.0	0.0				6.3 (5.9)	56.3	
<i>Phaseolus lunatus</i> L.	Common bean (1,2,8)	30	33.3	6.7	23.3	31	22.6	32.3	45.2				12.6 (2.6)	40.7	
<i>Phaseolus lunatus</i> L.	Lima bean	2	0.0	0.0	0.0	4	25.0	0.0	0.0				—	—	
<i>Vicia faba</i> L.	Faba bean (1)	5	20.0	20.0	40.0	12	16.7	16.7	66.7				20.2 (5.7)	44.5	
<i>Pisum sativum</i> L.	Pea (1)	2	50.0	50.0	0.0	21	28.6	28.6	38.1				11.7 (2.6)	46.6	
<i>Vigna unguiculata</i> (L.) Walpers	Cowpea bean (2)	7	71.4	14.3	14.3	5	0.0	80.0	20.0				7.4 (2.5)	31.8	
Gramineae															
<i>Zea mays</i> L.	Maize (3,7)	—	—	—	—	2	0.0	100.0	0.0				1.5 (1.3)	52.4	
Lamiaceae															
<i>Ocimum basilicum</i> L.	Basil (1)	—	—	—	—	1	100.0	0.0	0.0				0.9	42.9	
Solanaceae															
<i> Capsicum annuum</i> L.	Sweet pepper (1)	21	9.5	4.8	0.0	1	100.0	0.0	0.0				0.1 (0.0)	53.3	
<i>Capsicum baccatum</i> L.	Yellow chili (1)	9	0.0	0.0	0.0	10	60.0	0.0	0.0				0.3 (0.1)	0	
<i>Solanum melongena</i> L.	Eggplant	1	0.0	0.0	0.0	—	—	—	—				—	—	
<i>Solanum tuberosum</i> L.	Potato (1)	15	33.3	0.0	6.7	72	58.3	15.3	20.8				7.3 (1.6)	49.4	
<i>Lycopersicon esculentum</i> Miller	Tomato (1)	17	35.3	0.0	17.7	16	37.5	31.3	18.8				5.9 (2.0)	33.5	

^a Number of surveyed fields; ^b L = low (1–25%), M = middle (26–50%) and H = high (>50%); ^c Agromyzidae species: *Liriomyza huidobrensis* (1), *Liriomyza sativae* (2), *Liriomyza graminicola* (3), *Liriomyza* sp. 1 (4), *Liriomyza* sp. 2 (5), *Anauromyza* sp. (6), *Cerodontha dorsalis* (7), *Japanagromyza* sp. (8), and *Melanagromyza* sp. (9).

Table 4. Leafminer fly infestation intensity in two cropping seasons in farmer's fields in different regions along the Peruvian coast

Regions	Infestation intensity (%)								Differences between seasons (<i>P</i>)
	Autumn				Winter				
	No. ^a	Low ^b	Middle	High	No.	Low	Middle	High	
Tumbes	8	62.5	0.0	0.0	9	22.2	11.1	22.2	0.134
Piura	15	26.7	0.0	20.0	8	12.5	37.5	12.5	0.062
Lambayeque	15	46.7	20.0	20.0	14	42.9	35.7	21.4	0.345
La Libertad	30	36.7	3.3	0.0	35	48.6	31.4	20.0	<0.0001
Ancash	12	50.0	0.0	0.0	15	53.3	26.7	6.7	0.029
Lima	16	31.3	6.3	12.5	45	28.9	24.4	33.3	0.014
Ica	24	20.8	0.0	0.0	41	36.6	26.8	26.8	<0.0001
Arequipa	33	6.1	6.1	27.3	40	67.5	15.0	17.5	<0.0001
Moquegua	27	33.3	0.0	0.0	17	52.9	11.8	29.4	<0.0001
Tacna	36	36.1	11.1	11.1	19	26.3	15.8	57.9	<0.0001
Mean (%)		31.0	5.1	9.7		42.4	23.5	25.9	<0.0001

^a Numbers of surveyed fields; ^b Low (1–25%), middle (26–50%), and high (>50%).

season (Table 6). Regarding regions, significant differences were observed in the Shannon-Wiener index ($\chi^2 = 20.4$; $df = 9$; $P = 0.015$), but not in the Evenness ($\chi^2 = 6.04$; $df = 9$; $P = 0.74$) or Simpson ($\chi^2 = 10.32$; $df = 9$; $P = 0.32$) indices. The highest value of Shannon-Wiener index was registered in the region of Tumbes ($H' = 1.28$) and the lowest in the Lima region ($H' = 0.61$).

Beta Diversity. The Bray-Curtis cluster analysis of similarity of all parasitoid species was influenced by the abundance of endo- and ectoparasitoids sampled in the different regions. The Tumbes region appeared as an isolated group (G1) because of the high abundance of ectoparasitoids (Fig. 3; Table 6). All other regions formed one main group (G2) that is divided in two subgroups (SGs), with SG1 composed by the regions of Ancash, Ica, La Libertad, Lima, Lambayeque, and Piura in the center of Peru, and SG2

composed by the regions of Moquegua, Tacna, and Arequipa in the southern part of Peru. SG1 and SG2 are characterized by the dominance of endoparasitoids whose abundance ranged from 73.1 to 91.1% (Table 6). While *H. arduine* was the dominant endoparasitoid in SG1, the endoparasitoid *C. flacilla* was dominant in SG2 found at almost all sampling sites. The highest similarity in terms of species composition was between Lima and Lambayeque regions (84.9%), while the least similarity was between La Libertad and Tumbes regions (13.0%).

Association of Parasitoids to Leafminer Fly Species. Leafminer fly parasitoids were reared from the different leafminer fly species, but the highest relative parasitoid abundance (90.1%) and richness (42 species) was observed from the leafminer fly *L. huidobrensis* (Table 7). *L. sativae* was the second most important leafminer fly species (6.1%). Although this

Table 5. Parasitoid species associated with leafminer fly species in field and vegetable crops along the Peruvian coast

Parasitoids taxa	Reared adults					
	Winter		Autumn		Total	
	No.	%	No.	%	No.	%
Eulophidae						
<i>Chrysocharis caribea</i> Boucek	1,301	9.15	128	3.61	1,429	8.04
<i>C. brethesi</i> Schauff & Salvo	132	0.93	37	1.04	169	0.95
<i>C. flacilla</i> Walker	2,083	14.64	1,379	38.93	3,462	19.48
<i>Chrysocharis Förster</i> (5 spp.)	5	0.04	6	0.17	11	0.06
<i>Chrysonotomyia thysanoides</i> (De Santis)	39	0.27	53	1.50	92	0.52
<i>Chrysonotomyia Ashmead</i> (5 spp.)	102	0.72	9	0.25	111	0.62
<i>Closterocerus</i> Westwood (2 spp.)	11	0.08	0	0.00	11	0.06
<i>Diaulinopsis callichroma</i> Crawford	143	1.01	66	1.86	209	1.18
<i>Diaulinopsis</i> Crawford (2 spp.)	24	0.17	21	0.59	45	0.25
<i>Diglyphus begini</i> (Ashmead)	556	3.91	271	7.65	827	4.65
<i>Diglyphus websteri</i> (Crawford)	1,297	9.12	242	6.83	1,539	8.66
<i>Zagranmosoma</i> Ashmead (6 spp.)	6	0.04	2	0.06	8	0.05
Eulophidae spp. (14 spp.)	35	0.25	4	0.11	39	0.22
Pteromalidae						
<i>Halticoptera arduine</i> (Walter)	7,439	52.29	1,133	31.99	8,572	48.24
Pteromalidae (7 spp.)	29	0.20	4	0.11	33	0.19
Mymaridae						
Mymaridae (2 spp.)	18	0.13	0	0.00	18	0.10
Braconidae						
Braconidae (11 spp.)	429	3.02	8	0.23	437	2.46
Fitigidae						
<i>Ganaspidium</i> Weld sp.	577	4.06	179	5.05	756	4.25
Total	14,226	100.0	3,542	100.0	17,768	100.0

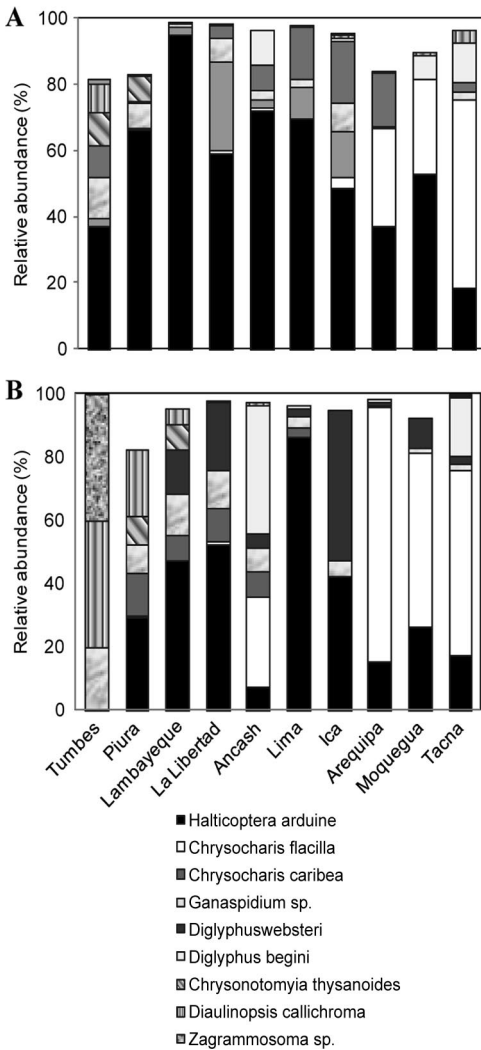


Fig. 2. Distribution and relative abundance of main leafminer fly parasitoids in the (A) winter and (B) autumn cropping season along the Peruvian coast.

species represented a low relative abundance, a considerable high number of 33 parasitoids were associated with this species. *H. arduine* was the only parasitoid identified from all leafminer fly species; it was the dominant parasitoid in *Cerodontha dorsalis* Loew (66.7%), *L. huidobrensis* (49.3%), and *L. sativae* (51.0%) (Table 7). Other important parasitoids were *C. flacilla* (57.0%) on *Liriomyza* sp. 1 and *C. caribea* (77.3%) on *L. graminivora*, respectively. The other parasitoids did not show a clear dominance for certain leafminer fly species. Endoparasitoids were most important for controlling all leafminer flies, with the exception of the leafminer fly *Amauromyza* sp. In this species the ectoparasitoids *Diauliniopsis callichroma* Crawford and *Chrysonotomyia thysanoides* (De Santis) were more abundant than endoparasitoids.

Relationships of Parasitoids to Leafminer Fly Host Plants. Highest parasitoid species richness was found in the family Fabaceae, with the highest number in common bean and cowpea (28 and 25 species, respectively) (Table 8). In potato, a total of 15 parasitoid species, with 14 and 6 species during the winter and autumn cropping season, respectively, were identified. Lowest species richness was found in those crops with a general low relative abundance of leafminer flies. The larval-pupal parasitoid *H. arduine* parasitized different leafminer fly species in 25 crops and showed the widest range of host plants (Table 8). However, this species was not present in chickpea (*Cicer arietinum* L.) and sweet pepper, and had low abundance in chard and maize (*Zea mays* L.). *C. caribea* and *C. flacilla* had the second and third widest range of leafminer fly host plants with 24 and 21 crops, respectively. Parasitoids often showed clear host preferences like *C. caribea* in maize or *D. websteri* in sweet pepper.

Discussion

Leafminer Fly Species and Infestation Along the Peruvian Coast. Rivers originating in the high Andes and flowing to the Pacific Ocean have formed productive valleys along the Peruvian coast, favoring year-round intensive irrigated agricultural production. The Peruvian coast has an extension of 3,000 km in a north to south direction in which the climate changes from dry tropical to desert subtropical with much lower annual mean temperatures in the central and southern part (Table 1). In these valleys, nine leafminer fly species were identified in two successive surveys carried out during the winter and autumn cropping season. The two species *L. huidobrensis* and *L. sativae* showed clearly the largest distribution and greatest abundance and are economically the most important leafminer flies along the Peruvian coast.

In the two northern regions Tumbes and Piura leafminer fly infestation was lowest with a variation of 62–55% between the autumn and winter cropping season. In the region of Lambayeque the leafminer fly infestation was highest in both seasons (87–100%). In all other regions south of Lambayeque a marked higher infestation during the winter cropping season (85–100%) compared with the autumn cropping season (20–58%) could be found (Table 4). These differences in the leafminer fly infestation are associated with the different climatic conditions, which favor the abundance and population dynamics of the two main leafminer species *L. huidobrensis* and *L. sativae* along the Peruvian coast.

According to our surveys, *L. huidobrensis* is clearly more abundant and adapted to the subtropical desert climate of the central and southern coastal region south of Lambayeque, while *L. sativae* prefers the dry tropical climate of the northern region. The region of Lambayeque can be seen as a transition zone in which the climate still favors *L. sativae* but also allows the development of *L. huidobrensis*. Hence, the presence of both leafminer fly species caused the highest in-

Table 6. Diversity indices for leafminer fly parasitoids and strategic groups in different regions and cropping seasons along the Peruvian coast

	Richness (S)	Shannon-Wiener (H')	Evenness (E)	Simpson (1-D)	Parasitoid strategic group (%)	
					Endo	Ecto
By regions						
Tumbes	14	1.278a	0.852	0.732	51.5	48.5
Piura	18	0.963ab	0.749	0.622	73.1	26.9
Lambayeque	21	0.757ab	0.584	0.471	90.8	9.2
La Libertad	18	0.753ab	0.583	0.456	91.1	8.9
Ancash	10	0.642ab	0.517	0.386	75.3	24.7
Lima	17	0.606b	0.514	0.364	89.1	10.9
Ica	31	0.931ab	0.547	0.489	75.8	24.2
Arequipa	11	0.626ab	0.546	0.383	91.0	9.0
Moquegua	13	0.761ab	0.678	0.506	90.9	9.1
Tacna	15	0.624ab	0.514	0.385	79.7	20.3
By season						
autumn	51a	0.693	0.566	0.447	81.1	18.9
winter	28b	0.745	0.573	0.436	84.3	15.7

Means followed by different letters are significantly different according to the Tukey honestly significant difference test for regions and the *t*-test for seasons at $P \leq 0.05$.

festation in both seasons. According to Spencer (1990), *L. sativae* is restricted in South America to warmer, low-elevation areas, whereas *L. huidobrensis* is present at low and high elevations. Raven (1993) pointed out that *L. sativae* is better adapted to hot conditions and could replace *L. huidobrensis* during the summer season in some vegetable crops at the Peruvian coast. For *L. huidobrensis* it is known that highest population and infestation normally occur in the central coastal region of Peru during the winter cropping season from July to October with the lowest population in the hottest months from December to April (Cisneros and Mujica 1999). These field observations are supported by the studies carried out by Haghani et al. (2007), who found out that 25°C was the

optimum temperature for fecundity and intrinsic rate of natural increase of *L. sativae*. According to Peacock et al. (2006), in New Zealand *L. sativae* is established only in those regions that have a maximum summer temperature above 18°C. In contrast, *L. huidobrensis* is adapted to lower temperatures. The highest feeding activity and oviposition capacity of *L. huidobrensis* was obtained at 18°C (own observations). Lowest temperature thresholds have been found for all developmental stages in a range between 6–8°C (Vercrembre and De Crozals 1993, Lanzoni et al. 2002). The adaptation of *L. huidobrensis* to lower temperatures was also demonstrated during the El Niño phenomenon in Peru in the years 1997–1998. An average increase of the minimum temperature of 5°C during the winter season

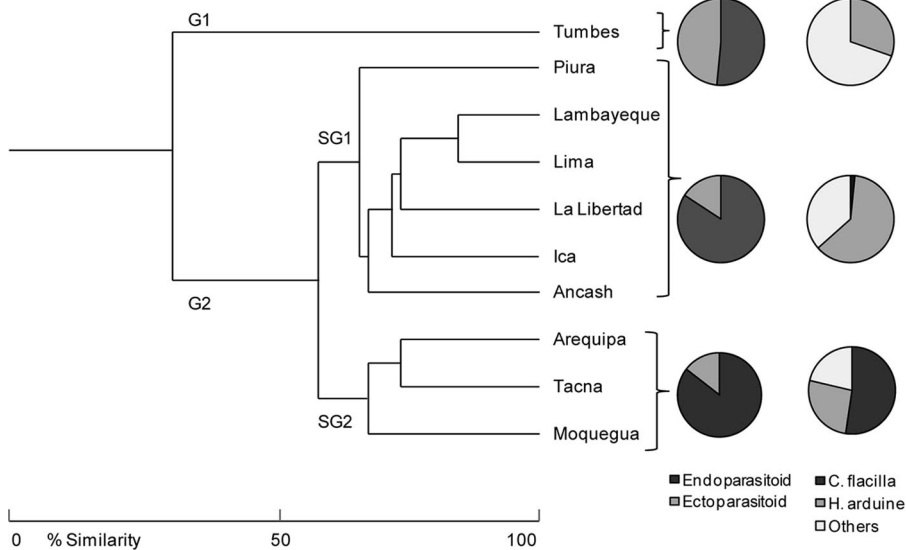


Fig. 3. Bray-Curtis cluster analysis of parasitoid similarity in 10 regions of the Peruvian coast. Differences between the main groups (G1 and G2) and between the subgroups (SG1 and SG2) and G1 are indicated by the relative abundance of endo- and ectoparasitoids and of the dominant parasitoids *C. flacilla* and *H. arduine*.

Table 7. Relative abundance, species richness, and relative importance of ecto- and endoparasitoids per leafminer species in two cropping seasons along the Peruvian coast

Agromyzidae species	Relative abundance		Species richness (no.)			Strategic groups (%)										Other species	Total
	No.	%	Autumn	Winter	Total	Endoparasitoids			Ectoparasitoids				Chrysonotomya thysanotides				
						Chrysocharis flacilla	Chrysocharis caribea	Chrysocharis brethesi	Canaspidium sp.	Diglyphus websteri	Diglyphus beggii	Diglyphus callichroma		Diaulmopsis thysanotides			
<i>Anaeromyza</i> sp.	13	0.07	4	8	7	15.4	0.0	7.7	0.0	0.0	0.0	0.0	23.1	15.4	30.7	100.0	
<i>Cerodontha dorsalis</i>	3	0.02	0	3	2	66.7	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	
<i>Japanagromyza</i> sp.	93	0.52	5	7	7	30.1	2.2	18.3	10.8	36.6	1.1	0.0	0.0	0.0	0.9	100.0	
<i>Liriomyza graminivora</i>	44	0.25	0	7	6	2.3	6.8	77.3	6.8	0.0	2.3	0.0	0.0	0.0	4.5	100.0	
<i>Liriomyza huidobrensis</i>	16,016	90.14	17	39	42	49.3	20.1	7.8	0.8	8.8	5.1	0.9	0.5	6.0	6.0	100.0	
<i>Liriomyza sativae</i>	1,087	6.12	22	25	33	51.0	0.3	7.0	1.6	5.4	0.2	5.7	6.8	15.7	15.7	100.0	
<i>Liriomyza</i> sp.1	328	1.85	8	7	10	18.0	57.0	10.4	1.2	0.3	1.5	0.0	0.3	10.7	10.7	100.0	
<i>Liriomyza</i> sp.2	21	0.12	0	6	6	28.6	4.8	28.6	23.8	0.0	0.0	4.8	0.0	9.4	9.4	100.0	
<i>Melanagromyza</i> sp. without leafminer found	3	0.02	4	0	3	33.3	33.3	0.0	33.3	0.0	0.0	0.0	0.0	0.1	0.1	100.0	
Total	160	0.90	7	18	20	13.8	28.8	8.8	1.3	22.5	5.6	0.6	3.1	11.1	11.1	100.0	
Total	17,768	100.0	51	28	63												

dropped the *L. huidobrensis* population drastically, by >81% (Cisneros and Mujica 1999).

Host Plants of Leafminer Flies. The leafminer fly *L. huidobrensis* is a highly polyphagous species with host plants deriving from at least 14 plant families (Spencer 1990). Korytkowski (1982) registered in Peru host plants of the families Chenopodiaceae, Compositae, Cruciferae, Cucurbitaceae, Fabaceae, Malvaceae, Solanaceae, Umbeliferae, and Liliaceae. In our survey we could identify 23 crops infested with *L. huidobrensis*; sweet pepper, basil (*Ocimum basilicum* L.), and marigold (*Tagetes erecta* L.) are host plants that have been not reported before. *L. sativae* has a wide host range including several important cultivated plants of the families Cucurbitaceae, Fabaceae, and Solanaceae; but which is not as large as that of the related species *L. huidobrensis* (Spencer 1990). Korytkowski (1982) reported six host plants from Peru. In our survey, we also found six host crops, but of these, soybean, chick pea (*Cicer arietinum* L.), and cowpea of the family Fabaceae as well as spinach (*Spinacea oleracea* L.) of the family Chenopodiaceae are new registrations. *L. graminivora* was recovered from leaves of young maize plants in the Lima region. This species might only become economically important at high population densities but this has never been reported (Spencer 1973). *Japanagromyza* sp. emerged only from common bean collected from the Ica region in the autumn and winter cropping season, which is in agreement with Korytkowski (1982). The species occurs in crops at the Peruvian coast only occasionally and has no economic importance (Raven 1993). A few adults of *C. dorsalis* were recovered from maize in the Tacna region in the winter cropping season, which is the first report of maize acting as a host plant for this leafminer fly species in Peru. Previously, Korytkowski (1982) reported its occurrence on an unspecified wild grass in Peru. Commonly, host plants of *C. dorsalis* include many fodder and wild grasses of the family Gramineae (Raven 1993). *A. maculosa* was recovered from lettuce (*Lactuca sativae* L.) and marigold, both of the family Asteraceae, in the La Libertad region. These two host plants are new records for this rare leafminer fly species in Peru.

Parasitism, Parasitoid Diversity, and Regional Distribution. Percentage of parasitism was mainly influenced by crops. The survey was carried out in farmers' fields without taking different plant protection measures or pesticide applications into consideration, thus, it could have contributed to the differences on parasitism observed. Hence, parasitism and parasitism rates of leafminer flies by ecto- and endoparasitoids might have been differently influenced in the wide range of crops surveyed. Application of insecticides, seasons, parasitoid species, and host species has been related to differences on rates of parasitism (Poe and Montz 1981). In Israel, parasitism rates of *L. huidobrensis* by the ectoparasitoid *D. isaea* (Walker) were significantly lower after treatments with either cyromazine or abamectin compared with controls (Weintraub 1999, 2001). Ectoparasitoids are more exposed to insecticide applications and hence are gen-

Table 8. Species richness and relative abundance of main parasitoid species associated to different leafminer fly host plants in two cropping seasons along the Peruvian coast

Plant family/ common name	Species richness			Relative abundance (%)										Other species			
	Winter	Autumn	Total	Halticoptera arduine			Endoparasitoids			Ectoparasitoids							
				<i>Chrysocharis flacilla</i>	<i>Chrysocharis caribea</i>	<i>Ganaspidium sp.</i>	<i>Diglyphus websteri</i>	<i>Diglyphus begni</i>	<i>Diadlinopsis callichroma</i>	<i>Chrysonotomomyia thysanoides</i>							
Amarilidaceae																	
Scallion	3	0	3	71.4	0.0	14.3	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apiaceae																	
Celery	10	8	12	21.5	35.6	8.2	8.5	8.5	2.5	22.2	0.0	0.0	0.0	0.0	0.0	1.5	1.5
Asteraceae																	
Lettuce	8	4	10	91.3	2.8	0.8	3.8	3.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	1.1	1.1
Marigold	9	0	9	24.0	4.0	4.0	12.0	12.0	0.0	0.0	16.0	0.0	0.0	0.0	0.0	40.0	40.0
Brassicaceae																	
Cabbage	8	2	8	70.1	0.8	21.4	5.5	5.5	1.1	0.0	0.5	0.0	0.0	0.0	0.0	0.6	0.6
Cauliflower	0	2	2	62.5	37.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turnip	3	4	6	59.7	22.1	13.0	1.3	1.3	0.0	0.0	1.3	0.0	0.0	0.0	0.0	2.6	2.6
Radish	6	5	6	45.4	11.8	26.9	11.8	11.8	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7
Chenopodiaceae																	
Chard	4	1	5	8.3	8.3	33.3	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	16.8	16.8
Beetroot	10	4	10	73.7	12.2	3.1	0.8	0.8	7.6	1.1	0.4	0.0	0.0	0.0	0.0	1.1	1.1
Spinach	6	5	9	49.3	1.4	1.4	39.4	39.4	1.4	0.0	0.0	0.0	0.0	0.0	1.4	5.7	5.7
Cucurbitaceae																	
Cucumber	4	6	7	80.2	1.6	5.7	3.1	3.1	8.3	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.1
Zucchini	5	4	7	39.0	44.5	2.7	2.7	2.7	7.7	0.0	0.5	0.0	0.0	0.0	0.0	2.9	2.9
Pumpkin	5	3	5	69.9	17.3	2.6	0.0	0.0	5.1	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fabaceae																	
Alfalfa	16	14	19	20.8	43.8	13.3	5.3	5.3	3.4	1.5	1.0	0.4	0.4	0.4	10.5	10.5	10.5
Bean	20	18	28	54.4	5.2	9.6	5.8	5.8	14.2	5.6	0.5	0.1	0.1	0.1	4.6	4.6	4.6
Chickpea	0	4	4	0.0	0.0	25.0	25.0	25.0	25.0	0.0	0.0	0.0	0.0	0.0	25.0	25.0	25.0
Cowpea	21	13	25	57.5	0.0	0.6	12.4	12.4	1.2	0.1	5.3	9.8	9.8	9.8	13.1	13.1	13.1
Faba bean	16	8	18	29.1	31.4	1.3	1.7	1.7	9.2	15.1	3.2	0.2	0.2	0.2	8.8	8.8	8.8
Green bean	4	1	4	56.2	33.5	0.0	0.0	0.0	9.7	0.0	0.5	0.0	0.0	0.0	0.1	0.1	0.1
Pea	13	7	14	50.4	9.5	20.1	0.7	0.7	14.1	1.9	1.5	0.1	0.1	0.1	1.7	1.7	1.7
Soya bean	13	0	13	26.2	0.0	3.3	9.8	9.8	13.1	0.0	13.1	11.5	11.5	11.5	23.0	23.0	23.0
Gramineae																	
Maize	7	0	7	6.3	8.3	70.8	4.2	4.2	0.0	2.1	0.0	0.0	0.0	0.0	8.3	8.3	8.3
Lamiaceae																	
Basil	2	0	2	91.7	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Solanaceae																	
Sweet pepper	0	1	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Potato	14	6	15	47.6	33.2	1.2	4.0	4.0	12.4	0.1	0.1	0.0	0.0	0.0	1.4	1.4	1.4
Tomato	6	4	7	86.3	7.3	3.6	0.2	0.2	2.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	0.6

erally more affected than endoparasitoids. Sotomayor (1998) studied the effect of abamectin on the endoparasitoid *H. arduine* and the ectoparasitoid *D. websteri* and found that only eggs of *H. arduine* were affected but not larvae or pupae. Instead, in *D. websteri* all developmental stages were affected by abamectin. In addition, parasitism rates varied according to the level of leaf infestation, with highest rates at low infestation (negatively density-dependent parasitism).

In our study we found that endoparasitoids are definitely more important in controlling leafminer flies, but that also ectoparasitoids (*Diglyphus* sp., *Diaulinopsis callichroma*, or *Chrysonotomyia thysanoides*) can reach higher parasitism rates in certain leafminer fly species such as *Amauromyza* sp., *Japanagromyza* sp., or *L. sativae* (Table 7). Host feeding by female ectoparasitoid is considered an additional important mortality factor (Honda et al. 2006), but which is difficult to determine in field studies and was not part of this study.

Leafminer flies of the family Agromyzidae are known to have rich natural enemy communities. In the Neotropics, Salvo and Valladares (1998) identified 69 parasitoid species of Agromyzidae leafminer flies in natural, urban and agricultural habitats of Central Argentina. Therefore, it can be stated that the Peruvian coast also hosts a very rich parasitoid community with its 63 parasitoid species identified in our survey. In addition to parasitoid species known from Agromyzidae leafminer flies in Peru, the species *C. caribea*, *C. brethesi*, *C. flacilla*, and *C. thysanoides* identified in this study are new records for Peru. The parasitoids *H. arduine*, *C. flacilla*, *C. caribea*, *D. websteri*, *D. begini*, and *Ganaspidium* sp. were the most common parasitoids found in our survey, of which *H. arduine* was the most dominant (48.2% of reared adults). This is in line with former studies carried out at the central coast of Peru (Redolfi et al. 1985, Sanchez and Redolfi 1985).

H. arduine is of Neotropical origin and is reported from Peru, Chile, and Argentina. It is adapted to a wide range of ecologies from the coastal region of Peru and Chile to high altitudes of 2,950 m in Argentina (Sanchez and Redolfi 1985, Neder de Roman 2000) and 3,400 m in Peru (own observation). *H. arduine* requires 25.5–28.5 d at 21.5°C to complete its life cycle (Arellano and Redolfi 1989, Neder de Roman 2000). Only *L. huidobrensis* has been reported as a host of *H. arduine* in Peru and other countries. In our survey, *H. arduine* was also reared from nine additional leafminer fly species: *Amauromyza maculosa*, *Cerodontha dorsalis*, *Japanagromyza* sp., *Melanagromyza* sp., *L. graminivora*, *L. sativae*, two unidentified *Liriomyza* species and one unspecified Agromyzidae species. A total of 27 plant species of 10 families were suitable for the development of at least one leafminer fly species. *H. arduine* parasitized leafminer flies in all 25 host plants, indicating its high adaptation and potential as an effective biocontrol agent.

C. flacilla is also a Neotropical species (De Santis 1983, Sanchez and Redolfi 1985, Hansson 1987). *C. flacilla* has been reared from different leafminer fly species (*Liriomyza bahamondesi* Blanchard, *L. fla-*

veola Fallen, *L. quadrata* (Malloch), *Melanagromyza virens* Loew and *Phytomyza platensis* Brèthes) in other countries (De Santis 1983, Hansson 1987), but only from *L. huidobrensis* in Peru. Therefore, the survey identified eight new host species for this parasitoid: *Cerodontha dorsalis*, *Japanagromyza* sp., *Melanagromyza* sp., *L. graminivora*, *L. sativae*, two unidentified *Liriomyza* species and one unspecified Agromyzidae species.

C. caribea has been earlier reported from Argentina, Barbados, Bolivia, Brazil, Caribbean, Peru, Trinidad, Tobago, Uruguay, and Venezuela (Boucek 1977, De Santis 1983, Hansson 1987, De Santis and Fidalgo 1994, Salvo and Valladares 1997). Its host range is limited to the family Agromyzidae such as *L. huidobrensis*, *L. munda* Frick, and *L. sativae* (Murphy and Lasalle 1999). For the Peruvian coast its occurrence on *L. huidobrensis* could be reported for the first time within this study. Further, the survey identified six new leafminer fly species as hosts for this parasitoid: *Amauromyza maculosa*, *Japanagromyza* sp., *L. graminivora*, two unidentified *Liriomyza* species and one unspecified Agromyzidae species.

D. begini and *D. websteri* are distributed worldwide as parasitoids of *L. huidobrensis* and *L. sativae* (Johnson and Hara 1987). *D. websteri* has been identified previously from *L. huidobrensis* and *C. dorsalis* and other Agromyzidae species at the Peruvian coast (Raven 1993). *A. maculosa*, *Japanagromyza* sp., *L. graminivora*, two unidentified *Liriomyza* species, and one unspecified Agromyzidae species represent new hosts for this parasitoid.

Parasitoid diversity was affected by the particular climatic conditions along the Peruvian coast and this was supported by alpha and beta diversity analysis. *H. arduine*, *D. websteri*, and *Ganaspidium* sp. showed a wide distribution along the Peruvian coast from north to south, which clearly indicates their adaptation to different climates. *C. flacilla* was more abundant in the southern part of Peru and *C. caribea* in the north and central coast, which indicates that both species have probably more specific climatic requirements. Neder de Roman (1986) described the occurrence of *C. flacilla* in the highlands of Argentina, which is characterized by a warm climate with an average temperature of 18–20°C (max. 30°C and min. 4°C). Further, our results indicate that ectoparasitoids are more abundant at higher temperatures in the tropical region of northern Peru or during warmer vegetation periods. In Tumbes, ectoparasitoids represented 80% of the parasitoid population in autumn but only 41% during the winter season. Likewise, it was the only region where *H. arduine* did not occur in the autumn season (Fig. 2).

Relationships of Parasitoids to Leafminer Fly Host Plants. Host plant and leafminer fly larvae related factors that are important in host finding by parasitoids include visual cues from plants, structure and habitat, and size of leafminer fly larvae (Godfrey 1994, Hawkins 1994, Finidori-Logli et al. 1996); further, volatiles released by feeding larvae or plants damaged by adults and larvae direct many parasitoids to plant habits and

their hosts in the long and short distance range (Dicke and Minkenberg 1991). In northern Peru, cowpea and soybean were the most frequent host plants of *L. sativae*. *H. arduine* was the dominant parasitoid of this leafminer fly, but cowpea (57.5%) was clearly the preferred host plant compared with soybean (26.2%). Zehnder and Trumble (1984) found that population densities of *C. parisi* (parasitoid of *Liriomyza sativae* and *L. trifolii*) were markedly different in adjacent plantings of different crops (tomato and celery, *Apium graveolens* L. variety *dulce*). Host plant characteristics are critical factors affecting direct or indirect herbivore vulnerability to parasitoids (Price et al. 1980). Direct effects occur when plant characteristics such as glandular leaf trichomes impede parasitoids' searching capacity, or when plant odors or nectar attracts parasitoids (Gross and Price 1988). Indirect plant effects on parasitism of herbivores occur when plants influence the growth rate of herbivores or the presence of toxic compounds in the hemolymph (Campbell and Duffy 1979), which, in turn, affects parasitoid development. Parasitoids for example developed differently in *Liriomyza* larvae, when their hosts were fed with tomatine. However, host plant species have been mentioned as the most important source of variation of fitness in generalist herbivorous insects (Parrella et al. 1983, Leddy et al. 1993). From the perspective of the parasitoid, host suitability may be enhanced or reduced by the plant used by the herbivore, which in turn affects parasitoid fecundity, survival, sex ratio, oviposition behavior, success of parasitism and body size (Vinson 1976). Salvo and Valladares (2002) studied the influence of 12 host plants of *L. huidobrensis* on parasitoid body size, showing that faba bean is most suitable for both *L. huidobrensis* and its parasitoids.

Given the polyphagous nature of the main *Liriomyza* species, effective biological control in many different host crops might depend on matching the most effective parasitoid species complex with the given *Liriomyza* species and host crops (Johnson and Hara 1987). The wide host plant and leafminer fly adaptation of the parasitoids *Halticoptera arduine*, *C. flacilla*, *C. caribea*, *D. websteri*, *D. begini*, and *Ganaspidium* sp. shows great potential of those parasitoids for classical biological control programs, allowing its use in a number of different crops and leafminer fly associations.

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