Host Selection of *Liriomyza* Species (Diptera: Agromyzidae) and Associated Parasites in Adjacent Plantings of Tomato and Celery

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ABSTRACT Host preferences of *Liriomyza* species leafminers and their associated parasites were determined from adjacent plantings of celery and tomatoes during 1981 and 1982 in Orange County, Calif. *Liriomyza sativae* Blanchard was the predominant leafminer species reared from tomatoes in 1981 and 1982. Moderate densities of *L. sativae* were found in celery on two sampling dates in 1981, but *L. sativae* did not migrate to celery in 1982, even after tomato plants senesced. *Liriomyza trifolii* (Burgess) demonstrated a significant preference for celery in 1981 and 1982, although density increased in tomatoes in 1982. *Chrysocharis parksi* Crawford and *Diglyphus begini* (Ashmead) were the most numerous parasites reared from *Liriomyza* species infesting tomatoes: *D. begini* predominated initially, but *C. parksi* was prevalent from midseason to late season. *D. begini* and *D. intermedius* (Girault) were the most common parasites reared from celery, with *D. intermedius* demonstrating the greatest host-habitat specificity. Niche selection of the key parasite species is discussed.

THE SERPENTINE leafminers *Liriomyza sativae* Blanchard and *Liriomyza trifolii* (Burgess) have become serious pests of some vegetable crops in California (Johnson et al. 1980a, Spencer 1981, Trumble 1981). The existence of *L. sativae* in California was reported over 30 years ago (Lange 1949), whereas *L. trifolii* was first introduced into the state in the mid- to late-1970s (Parrella et al. 1981). The subsequent spread of *L. trifolii* to all major celery-producing areas in California has resulted in substantial economic losses (Trumble and Nakakihara 1983).

L. sativae and *L. trifolii* are both polyphagous species, with overlapping host ranges. Host summaries compiled by Stegmaier (1968) list tomatoes and celery as hosts for *L. trifolii*, but celery is not reported as a host for *L. sativae*. A survey of California Agromyzidae (Spencer 1981) does not list celery as a host for *L. sativae* nor tomato as a host for *L. trifolii*. However, recent samples taken from commercial growing areas in southern and central California have yielded *L. sativae* and *L. trifolii* from both tomatoes and celery.

In southern California, commercial vegetable plantings are frequently small (8 to 20 ha), and several vegetable crops are commonly grown adjacent to each other within a single field. This situation facilitates insect movement between crops and, upon termination of a crop, insect pests often move to adjacent plantings. Previous studies investigated *Liriomyza*-parasite interactions within one crop (Jensen and Koehler 1970, Johnson et al. 1980b), but parasite complexes have not been compared between crops where *Liriomyza* host ranges overlap. The objective of our study was to examine host preference and population trends of *L. sativae*, *L. trifolii*, and associated parasites in adjacent tomato and celery plantings and to determine the importance of migration of these species between crops.

Materials and Methods

Experiments were conducted at the University of California's South Coast Field Station in Orange County during the summers of 1981 and 1982. Commercial varieties of tomatoes and celery were planted in adjacent plots separated by a 3-m buffer. Tomato plantings consisted of nine rows of plants with 1.5-m centers and 0.46-cm spacing between plants. Tomatoes were transplanted on 13 July 1981 and 14 July 1982. The celery plantings contained 12 double-row beds with 101-cm centers and 17-cm spacing. Celery was transplanted on 5 August and 6 August in both 1981 and 1982. Delaying celery planting by 1 month allowed tomatoes to reach a suitable physiological stage for leafminer acceptance and development. No pesticides were applied, and cultural operations for both crops were consistent with local commercial practices.

Each plot measured 11.6 by 85.3 m and was divided into grids (tomato = 104, celery = 108). One plant was randomly sampled from each grid weekly. One tomato leaf or celery trifoliate with at least one large active mine characteristic of 3rd-instar development was collected from each randomly sampled plant. This was necessary because

Table 1. Host preference of *L. sativae* in tomatoes and celery, 1981 and 1982

Date	Tomatoes	Celery
1981		
20 Aug.	0.11a	0.07a
27 Aug.	1.02a	0.11b
3 Sept.	0.51a	0.08b
10 Sept.	0.75a	0.02b
17 Sept.	0.24a	0.18a
24 Sept.	1.20a	0.67b
1 Oct.	0.73a	0.04b
1982		
31 Aug.	2.43a	0.00b
7 Sept.	1.67a	0.00b
14 Sept.	1.84a	0.00b
21 Sept.	1.64a	0.00b
28 Sept.	—	0.01
5 Oct.	—	0.00

Values represent mean numbers of *L. sativae* per leaf. Means in the same row within each year, followed by the same letter, do not differ significantly ($P < 0.01$), by Student's *t* test.

Table 2. Host preference of *L. trifolii* in tomatoes and celery, 1981 and 1982

Date	Tomatoes	Celery
1981		
20 Aug.	0.02a	1.48b
27 Aug.	0.06a	0.95b
3 Sept.	0.00a	1.90b
10 Sept.	0.00a	0.46b
17 Sept.	0.00a	1.33b
24 Sept.	0.00a	0.65b
1 Oct.	0.00a	1.12b
1982		
31 Aug.	0.35a	4.14b
7 Sept.	0.09a	3.57b
14 Sept.	0.12a	0.48b
21 Sept.	0.12a	1.60b
28 Sept.	—	2.49
5 Oct.	—	0.28

Values represent mean numbers of *L. trifolii* per leaf. Means in the same row within each year, followed by the same letter, do not differ significantly ($P < 0.01$), by Student's *t* test.

several parasite species prefer mature host larvae (Lema and Poe 1979). Leaf samples were placed in 40-dram (ca. 71-g) vials containing paper towel strips which absorbed excess leaf moisture and helped prevent fungal growth. Vials were stored at room temperature (22 to 26°C) for at least 4 weeks to allow development of larvae and emergence of adults. After adult emergence, leafminers were sexed, and these along with their associated parasites were identified to species.

In 1982, only four weekly samples were taken in tomatoes, because the plants declined after a severe storm (no samples were collected after the storm) and few active mines were visible after week 4. Because leafminers and parasites continued to develop in celery, celery samples were taken 2 weeks after tomato termination to monitor any change in species composition.

Densities of naturally occurring *Liriomyza* and associated parasites occurring in each crop were analyzed by using Student's *t* test. Mean numbers of all parasite species within each crop were compared by analysis of variance (ANOVA) and Duncan's multiple range test to determine dominant species in tomatoes and celery.

Results and Discussion

***Liriomyza* Host Preferences.** Tomato was the primary host for *L. sativae* in both 1981 and 1982 (Table 1). In 1981, more *L. sativae* emerged from tomato than from celery on all sampling dates, with significantly higher numbers on five of the seven sampling dates. Density of *L. sativae* reared from celery samples increased on 17 and 24 September 1981. This increase coincided with the termination of irrigation in a nearby tomato planting. However, in spite of this influx, *L. sativae* populations did not continue to expand in celery; very few were found in celery on 1 October.

In 1982, there were significantly more *L. sativae* in tomatoes than in celery during the 4 weeks both crops were sampled. Only one *L. sativae* specimen was reared from celery during the 1982 season, and this occurred on 28 September, 1 week after tomato termination. In 1982, *L. sativae* did not migrate to celery, even after decline of the preferred host. Average *L. sativae* sex ratios were 53 ± 6% males, 46 ± 6% females in 1981 (n = 483), and 47 ± 2% males, 53 ± 2% females in 1982 (n = 831).

Our results indicate that *L. sativae* is capable of completing its life cycle on celery and populations can be sustained at low levels. However, celery is not a preferred host, and will not sustain high population densities if preferred hosts are available in the immediate vicinity.

L. trifolii demonstrated a preference for celery in both 1981 and 1982 (Table 2). This concurs with earlier reports (Trumble and Nakakihara 1983) stating that *L. trifolii* is the dominant leafminer species in the major celery producing counties in California. Whereas there were significantly more *L. trifolii* in celery than in tomatoes on all sampling dates in both years, *L. trifolii* density in tomatoes increased in 1982. Average *L. trifolii* sex ratios included 44 ± 6% females in 1981 (n = 990), 48 ± 4% females in 1982 (n = 1,358).

Fowler and Lawton (1982) documented that agromyzid species abundance is highly correlated with the number of habitats occupied by British umbelliferae. These authors further suggested that the ability of an insect to exploit a host would then increase with degree of exposure of the host to the insect. The recently introduced species, *L. trifolii*, has expanded its host range into all of the major tomato-producing counties in California. Our data, both from this experiment and from trellised tomato plantings (Zehnder and Trumble, unpublished data), suggest that tomatoes are becoming a

Table 3. Percent total *Liriomyza* parasite species reared from tomato and celery foliage during 1981

Sampling date	Crop	*D. begini*	*D. intermedius*	*C. parksi*	*C. ainslei*	*H. circulus*
20 Aug.	T	40a	0b	60a	0b	0b
	C	50a	22b	5b	13b	8b
27 Aug.	T	43a	0d	24b	9cd	20bc
	C	54a	27b	3c	3c	14bc
3 Sept.	T	67a	2b	19b	7b	3b
	C	50a	16b	5bc	3bc	14bc
10 Sept.	T	6b	0b	94a	0b	0b
	C	41a	22ab	3b	0b	16ab
17 Sept.	T	7b	0b	78a	0b	11b
	C	41a	9a	13a	0a	13a
24 Sept.	T	0b	0b	94a	0b	0b
	C	20ab	31a	9b	0b	34a
1 Oct.	T	0b	0b	95a	5b	0b
	C	5b	36a	36a	0b	23ab

Means within a row, followed by the same letter, do not differ significantly ($P \leq 0.05$), by Duncan's multiple range test. Analysis performed on mean values before conversion to percentages. Parasite species comprising less than 5% of the total are not included. T, Tomatoes; C, celery.

more widely accepted host. An analogous situation has occurred in Florida, where *L. trifolii* recently displaced *L. sativae* on tomatoes (D. Schuster, personal communication). Although *L. trifolii* has been an economic pest in Florida since the 1940s, differential susceptibility to pesticides between *L. trifolii* and *L. sativae* may be partially responsible for the species shift.

Parasite Host Preferences. The most numerous parasites associated with *Liriomyza* species in tomatoes were *Chrysocharis parksi* Crawford and *Diglyphus begini* (Ashmead) (Tables 3 and 4). In both years, *D. begini* was the most common species emerging from early season samples and *C. parksi* became dominant in mid- to late season. Johnson et al. (1980b) reported similar results for trellised, fresh-market tomatoes: *Chrysonotomyia punctiventris* (Crawford) and *D. begini* were the most numerous parasites reared from tomato foliage, whereas *C. parksi* was the dominant parasite taken from pupal tray samples. Few *C. punctiventris* were recorded in our foliage samples.

The most common parasites reared from celery foliage were *D. begini*, *D. intermedius* (Girault), *Halticoptera circulus* (Walker), and *C. parksi* (Tables 3 and 4). *H. circulus* reached densities equivalent to *D. begini* and *D. intermedius* in mid- to late-season 1981, but was not as important in 1982. In both years, *D. begini* and *D. intermedius* were documented in early-season samples when overall parasitization was high. As the total number of parasites emerging from foliage samples late in the season decreased, *D. begini* and *D. intermedius* became less dominant. Trumble and Toscano (1983) also have reported *D. begini* and *D. intermedius* as the primary parasites of *L. trifolii* occurring in celery plantings in California.

To more accurately delineate parasite host preferences, a between-crop comparison was performed for the three most numerous parasite species, *C. parksi*, *D. begini*, and *D. intermedius*. *C. parksi* density was significantly higher in tomatoes on 10 of the 11 sampling dates (Fig. 1 and 2). Because very few *L. trifolii* were reared from

Table 4. Percent total *Liriomyza* parasite species reared from tomato and celery foliage during 1982

Sampling date	Crop	*D. begini*	*D. intermedius*	*C. parksi*	*C. ainslei*	*H. circulus*
31 Aug.	T	43a	11c	21b	4c	21b
	C	44a	50a	1b	0b	1b
7 Sept.	T	39a	2b	49a	6b	4b
	C	25b	66a	2c	1c	1c
14 Sept.	T	12b	1b	72a	2b	5b
	C	29b	57a	5c	0c	1c
21 Sept.	T	23b	5b	55a	9b	9b
	C	33a	29a	14a	5b	0b
28 Sept.	T	—	—	—	—	—
	C	29a	34a	10b	10b	2b
5 Oct.	T	—	—	—	—	—
	C	37a	42a	16a	5ab	0b

Means within a row, followed by the same letter, do not differ significantly ($P \leq 0.05$), by Duncan's multiple range test. Analysis performed on mean values before conversion to percentages. Parasite species comprising less than 5% of the total are not included. T, Tomatoes; C, celery.

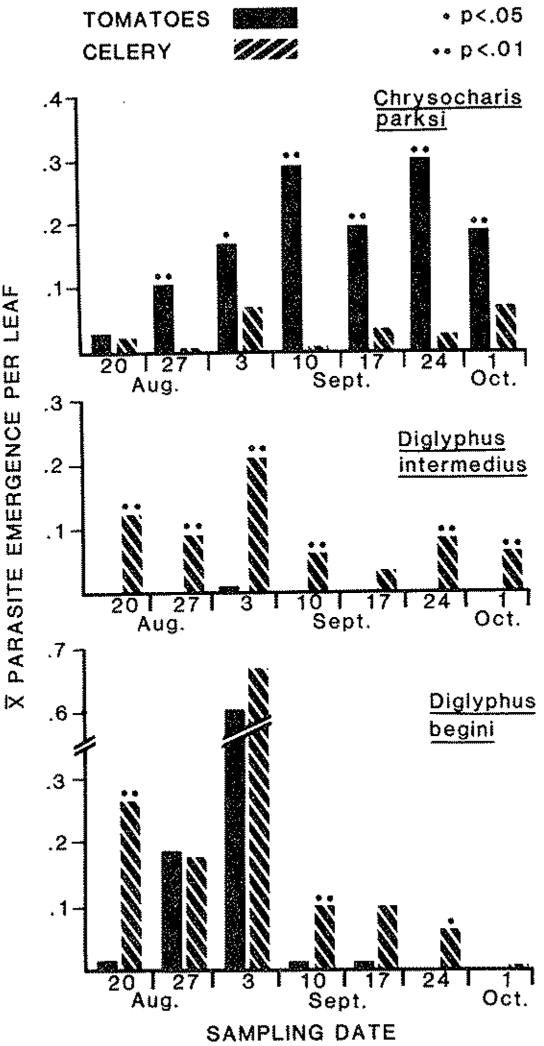

Fig. 1. Segregation of key parasite species of *Liriomyza* in tomatoes and celery, Orange County, Calif., 1981.

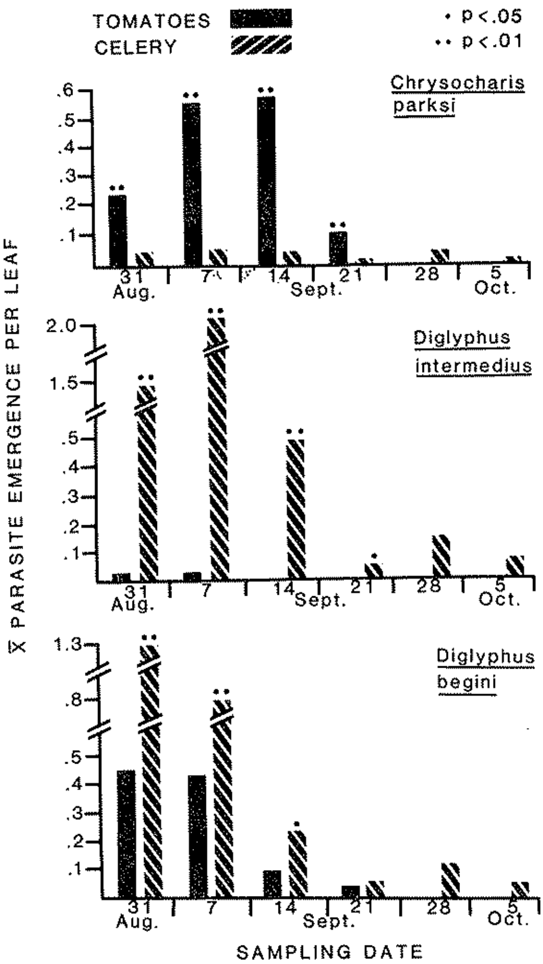

Fig. 2. Segregation of key parasite species of *Liriomyza* in tomatoes and celery, Orange County, Calif., 1982.

tomato samples (Table 2), it is evident that *C. parksi* preferred either *L. sativae* as a host or the tomato plant as a habitat. In contrast, *D. intermedius* was more active in celery where *L. trifolii* was the predominant leafminer species, because less than 2% of the *D. intermedius* specimens were reared from tomatoes (Fig. 1 and 2). Significantly more *D. begini* were collected from celery than from tomato samples on six of 11 sampling dates (Fig. 1 and 2), but *D. begini* was less host or habitat specific than the other two parasite species, both of which showed significant preferences on 10 of the 11 dates when both crops were present.

Our results indicate that *L. sativae*, *L. trifolii*, and some of their natural enemies are clearly differentiating between potential niches. Because immature stages of the two *Liriomyza* species are obligatory internal plant feeders, and the parasite larvae are not migratory, detection of suitable hosts by female leafminers and parasites is critical for survival. The increased energy expenditure required in searching for a specific host or habitat would be advantageous only if development or survival were enhanced. Parrella et al. (1983) demonstrated that *L. trifolii* had significantly greater fecundity and larval survival on celery, the preferred host, than when reared on tomatoes.

Although the relationship between leaf structure, host suitability and quality, and parasitization efficiency of natural enemies has been partially documented for other plant-pest-parasite systems (Hulspas-Jordaan and van Lenteren 1978, van de Merendonk and van Lenteren 1978, Obrycki et al. 1983), little information is available for *Liriomyza*-parasite complexes. Additional studies on the chemical and physiological ecology of host selection are needed in order to delineate the behavioral or physical adaptations occurring in response to leaf structure, and to document the importance of host quality (of both the plant and herbivore) on the fitness of the leafminers and their associated parasites.

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