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BIOLOGY OF LIRIOMYZA

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PERSPECTIVES AND OVERVIEW

The genus *Liriomyza*, erected in 1894 (52), contains more than 300 species. They are distributed widely but are most commonly found in temperate areas; there are relatively few species in the tropics. Within this genus 23 species are economically important, causing damage to agricultural and ornamental plants by their leafmining activity (94). Many of these damaging species are polyphagous, which is uncommon among the Agromyzidae; of 2450 described species in this family only 11 are considered to be truly polyphagous, and 5 of these are in the genus *Liriomyza* (93).

"Serpentine leafminer" was proposed as a common name for any member of this genus because of the wide distribution, polyphagous nature, and morphological similarity of many of the species (98). The Entomological Society of America has adopted this naming policy, with a few exceptions (112). Indeed, many larvae of *Liriomyza* create serpentine mines, which are initially very narrow and gradually enlarge (57), often twisting through the leaf. However, the type of mine produced by *Liriomyza* may be influenced by the developmental stage of the leaf as well as by the host itself (99). Thus, the mines are not always serpentine in all host plants. In addition, mine location in leaves may vary considerably, and either the upper or lower leaf mesophyll may be mined (5, 71). Some species have larval stages that feed in potato tubers (50), bore through stems (34), and feed within seed heads (86).

Most of our knowledge concerning the biology of this genus comes from studies on economically important species. These data have been developed largely since 1900, with an explosion of information since 1975 (76). This reflects the dramatic rise of *Liriomyza* spp. as major pests of numerous ornamental and agricultural crops over the past ten years (72). As a result of

this rise in economic importance, the proceedings from three formal conferences (80, 81, 87) and one informal conference (35) have been published. These, together with published reviews and bibliographies (38, 64, 76, 95, 95a), provide a good starting point for those interested in this genus. A comprehensive review of all economically important Agromyzidae (94) is an outstanding contribution to the biology, ecology, taxonomy, and control of these leafminers.

Out of necessity, this article contains general overviews of various biological parameters within this genus. Where specific studies have been done, these are cited. It is intended that this article not be an exhaustive review of the literature, but rather a selective one covering those studies that best address specific biological aspects of the genus.

ADULTS

Emergence

Adults emerge through the dorsal anterior end of the puparium (the retained last larval integument within which pupation occurs) with the aid of the ptilinum (a temporary bladderlike inflatable structure). This process may take from 5 min to more than 1 hr. Some mortality may occur during this process (61). Newly emerged adults exhibit a positive phototactic response and climb up the sides of a cage or up the stalk of a plant, where they remain quiescent for a period of approximately 20 min while expanding their wings and body. The body is fully sclerotized and colored within 20 min-2 hr (16, 61). Adult females are usually larger than males and emerge from larger puparia (61, 65). Puparium size is positively correlated with adult vigor (65). Males appear to emerge prior to females (J. Yost & M. P. Parrella, unpublished); both sexes generally emerge during early morning hours (61). The time of day of peak emergence varies for different species (5). Studies of sex ratios of adults emerging from pupae indicate a 1:1 sex ratio (61, 96) or a slight bias in favor of females (2, 5). Intensive laboratory rearing of L. trifolii over the past five years has produced approximately a 1:1 sex ratio of emerging adults (M. P. Parrella, unpublished).

Premating and Preoviposition

The majority of adults mate soon after emergence, and almost all females have mated within 24 hr (61, 69, 78). The period of time between adult emergence and mating, i.e. the premating interval, appears to be inversely related to temperature (16) and may differ for the sexes (96). The sexes may remain coupled for as little as 10 min (96), but the norm is 30 min-1 hr. Maximum mating time is about 3 hr. Males and females mate more than once, and multiple matings by the female are needed for maximum egg production

(61). Mating can usually be observed at any time of the day, but it generally occurs during early morning hours (16, 61).

It has been suggested that food, temperature, and relative humidity influence the preoviposition period (16), which may extend up to 5 days after adult emergence. Under greenhouse and laboratory conditions, most females begin oviposition within 24–48 hr after emergence (61, 78).

Mating

During copulation, the male assumes a position behind and alongside the female at about a 45° angle above her body. Occasionally, mounting from the front occurs. In the more typical position, the male's forelegs clasp the mesothorax of the female, his middle legs clasp the female's abdomen, and his hind legs spread the female's wings. The wings of the male are held normally over the body. The male brings his abdomen forward and downward to connect to the female genitalia as the male's hind legs move to rest on the substrate. This position is maintained throughout copulation (61; J. A. Bethke & M. P. Parrella, unpublished). No sex pheromone has been reported by researchers working with *Liriomyza*; however, it is possible that a stridulatory organ present in some males of *Liriomyza* spp. may be used in short-distance vocalizations to attract mates (95). Indeed, the rapid bobbing of males of *L. trifolii* when in close association with females may be a physical manifestation of this auditory signal (J. A. Bethke & M. P. Parrella, unpublished).

Aggressive behavior by male L. trifolii during mating has been observed in the laboratory under severely crowded conditions (J. A. Bethke & M. P. Parrella, unpublished). Upon the approach of a rival male, the coupled male will continually flex his wings until the intruder leaves.

Feeding and Oviposition Behavior

Excellent descriptions of leaf puncturing, feeding, and oviposition are available (7, 16, 61, 96, 111). The following description is from observations with L. trifolii (7), but similar behavior has been noted for L. sativae and L. huidobrensis (J. A. Bethke & M. P. Parrella, unpublished). When a female initiates a leaf-puncturing sequence, the first event observed, regardless of host plant, is a bending of the abdomen to position the ovipositor perpendicular to the leaf. The ovipositor contacts the leaf through a series of rapid thrusts. Once the ovipositor has penetrated the leaf surface, the thrusts becomes slower and more deliberate. At this point the female damages mesophyll cells in a specific manner, creating one of two different types of leaf punctures. If the abdomen is twisted from side to side, a large fan-shaped leaf puncture is created. A tubular leaf puncture is produced when no abdominal twisting follows the puncture. Eggs are deposited in tubular leaf punctures. The difference between oviposition behavior and the creation of a

tubular leaf puncture without an egg is subtle; oviposition entails a pause in slow thrusting followed by a final thrust to deposit an egg. After every leaf puncture the female backs over the wound and feeds from it. The female feeds from all punctures, regardless of whether or not they are used for oviposition. Hence, all leaf punctures can be considered feeding punctures (7); this should clarify considerable confusion in the literature. Males are unable to create their own punctures, but, as many authors indicate (56, 61), they feed from punctures created by females. Leaf puncturing can reduce photosynthesis (71) and may kill young plants (17). Leaf puncture size varies with the size of the adult female (61).

Feeding and oviposition by adults appear to occur primarily during the morning, and the frequency of these activities is positively correlated with temperature (20, 66). Little adult activity is observed after 1800 hr (20, 61, 66, 78). Leaf puncturing may occur with equal frequency on the abaxial and adaxial leaf surfaces (69), but this may depend on the species.

Leaf puncturing and feeding by adult *Liriomyza* undoubtedly serves an important role in host plant assessment. It has been suggested (7) that host feeding is more important in this regard than leaf puncturing. Several researchers have examined the ratio of total punctures to oviposition punctures in an attempt to determine host plant suitability or a general biological characteristic of *Liriomyza* spp. (20, 61, 115). These ratios have ranged from 1:1 to 40:1 and vary with temperature (66), leaf quality, and host plant. Unless the leaf area exposed to flies (126) and the number of flies released onto the plant can be held constant, these ratios are of little value.

Egg-laying capacity varies considerably within the genus *Liriomyza*. Mean egg production per female ranges from less than 100 (25) to greater than 600 (61). Females generally lay the majority of eggs between days 4 and 10 of adult life, depending on temperature (48, 66, 69, 78). Fecundity is strongly related to food source and temperature (16, 61, 66, 78); maximum oviposition occurs between 20–27°C (16, 66) when a constant food source such as honey is provided. Unfertilized females oviposit hundreds of eggs that fail to develop, although ovarian development, egg laying, and other responses appear to be normal (61). Some fertilized females oviposit infertile eggs. Many studies report that individuals of certain *Liriomyza* spp. do not create feeding punctures or lay eggs (5, 61, 78).

Longevity

Most longevity studies have been conducted using caged flies in close association with a host plant or carbohydrate food source (16, 61, 66, 69, 78). Under these conditions, females live 15–20 days and males 10–15 days. Longevity generally decreases at higher temperatures; the presence of honey

dramatically increases longevity. Although no studies have examined the longevity of these flies in the field because of the difficulty associated with studies on individual flies in nature, most laboratory studies have probably overestimated the normal longevity (as well as fecundity) of adults. In laboratory rearing studies (K. Heinz and M. P. Parrella, unpublished) we observed that increasing the size of the rearing container tended to shorten the longevity of *L. trifolii*. In addition, most longevity studies have not considered the importance of the times of adult emergence. For example, the deposition of eggs in leaf material during a 3-hr interval (e.g. during laboratory production) resulted in pupation over a 24-hr period and subsequent adult emergence over a 6-day span. When survivorship of adults emerging from these pupae was examined as cohorts based on the day of adult emergence, different survivorship profiles were produced (K. Heinz & M. P. Parrella, unpublished) (Figure 1). It is possible that a short larval development time may be correlated with adult vigor.

Adults are able to withstand freezing temperatures for short periods (62), so adults that emerge during warmer periods of winter in nearctic and palearctic regions may survive. *Liriomyza trifolii*, which is native to the southern part of the Nearctic, was considered incapable of overwintering in more northern areas. However, the survival of adults and pupae at low temperatures suggests that this species may be able to survive in these areas (53, 99). This factor and others may contribute to their colonization in these habitats.



Figure 1 Percent emergence and survivorship of adult L. trifolii from 500 pupae. All emerged and pupated within a 24-hr period. Adults emerged over a 6-day period.

EGGS

The whitish, transluscent egg is deposited through the adaxial or abaxial leaf surface. The egg varies in size based on the size of the species: e.g. 0.25 mm \times 0.10 mm for L. congesta (16) and 0.28 mm \times 0.15 for L. huidobrensis (2). *Liriomyza* eggs may be confused with thrips eggs oviposited in leaf tissue (54). An egg-staining technique has been developed for detecting eggs of L. trifolii in celery, chrysanthemum, and tomato leaves (75). Eggs are laid singly, but often in close proximity to each other. No epideictic (ovipositiondeterring) pheromone [present in other Agromizidae (49)] has been discovered in Liriomyza (7). Egg nonviability has been estimated to be as high as 20% (5) and is dependent on temperature (16). The eggs increase in size after oviposition, possibly through the imbibition of fluids from plant tissue (16, 102). The period of egg development varies with temperature and ranges from 2-8 days. There appears to be considerable variation in the relationship between temperature and development and in developmental threshold (6.2-13.4°C; Table 1), probably because of differences in species, host plants, and experimental methodology. Sixteen days at 1.1°C is required to cause 100% mortality of L. trifolii eggs in celery (42).

As the eggs develop they become opaque, and gradually the brownish cephalopharyngeal skeleton can be differentiated (5). When about to hatch, the larva is oriented with its anterior extremity, which contains the mouthhook, at the terminus of the egg furthest from the original oviposition puncture made by the female (96). This position results from a 180° rotation of the egg (5). In some species, the larva may eat the eggshell before moving into the leaf mesophyll (5). Pressure exerted by the larva causes the eggshell to become distended longitudinally and eventually to split at its anterior end.

LARVAE

The larva begins feeding immediately after eclosion and feeds incessantly until it is ready to emerge from the leaf (111). Different species of *Liriomyza* feed in different sections of the leaf mesophyll [e.g. *L. trifolii* in the palisade mesophyll, *L. huidobrensis* in the spongy mesophyll (71), and *L. brassicae* in the palisade and spongy mesophyll (94)]. Nonetheless, when larvae are forced to compete for resources because of crowding, they may tunnel into leaf stalks and into the main stem of the plant (96).

The larva is somewhat cylindrical and maggotlike. The anterior end tapers and the posterior end is truncate. Larvae move via peristaltic action of their hydrostatic skeleton. There are four molts and four larval instars. The fourth Annu. Rev. Entomol. 1987.32:201-224. Downloaded from arjournals.annualreviews.org by Department of Primary Industries - Victoria on 02/25/07. For personal use only.

Reference (10) (16) (2) (13) Estimated threshold development (°C) temperature for 12.8 6.2 7.0 14.9 0.0 13.4 $= 0.0262x - 0.352^{d}$ $0.0214x + 0.133^{d}$ 0.0166x - 0.116y = 0.0266x - 0.2660.0355x + 0.529y = 0.0343x - 0.441Development rate regressed on temperature^a ۲ ا y = II 2 2 Apium graveolens Chrysanthemum Phaseolus sp. Phaseolus sp. Phaseolus sp. morifolium Host Vicia faba L. congesta^t L. sativae^c Species of Liriomyza L. sativae L. trifolü L. trifolü L. trifolü

Table 1 Temperature-development studies with the egg stage of *Liriomyza* spp.

*Simple linear regression with temperature $(x)^{\circ}(x) =$ independent variable and development rate (y) (1/day) = dependent variable. The x-intercept method was used to calculate development thresholds

PReported as L. trifolii, but probably L. congesta (78).

^cReported as L. pictella, but probably L. sativae (94).

^aUpper temperatures not used in calculating the regression.

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Species of Liriomyza ^a	Host	Development rate regressed on temperature ^a	Estimated threshold temperature for development (°C)	Reference
L. congesta L. sativae	Vicia faba Phaseolus sp.	$y = 0.0131x - 0.165$ $y = 0.00657x - 0.0305^{b}$	12.6 4.6	(16) (109)
L. sativae	Phaseolus sp.	y = 0.0133x - 0.105	7.9	(62)
L. trifolii	Apium graveolens	y = 0.007x - 0.0587	8.4	(41)
L. trifolü	Phaseolus sp.	y = 0.0130x - 0.111	8.5	(13)
L. trifolii	Chrysanthemum	0.00 5 00 0.0213		ę
L. trifolii	morijotum Lycopersicon	$c_{1c_{0.0}} - xc_{0c_{0.0}} = v$	0.1	(6)
	esculentum	y = 0.0118x - 0.0926	7.8	(16)

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"See footnotes on taxonomy and methodology, Table 1. ^bAll development stages combined for regression analysis. Annu. Rev. Entomol. 1987.32:201-224. Downloaded from arjournals.annualreviews.org by Department of Primary Industries - Victoria on 02/25/07. For personal use only.

Reference (104) (13) (16) (62) 6 (53) Estimated threshold development (°C) temperature for 8.0 9.0 9.7 10.3 10.3 10.4 8.1 0.00662x - 0.0529y = 0.00600x - 0.0539= 0.00662x - 0.05390.00760x - 0.07790.00691x - 0.0771= 0.00651x - 0.0631y = 0.00749x - 0.0771Development rate temperature^a regressed on || || y = (11 > 2 2 Apium graveolens Apium graveolens Dendranthema sp. Chrysanthemum Phaseolus sp. Phaseolus sp. morifolium Host Vicia faba L. congesta Liriomyza^a Species of L. trifolii^b L. sativae L. trifolii L. trifolii L. trifolii L. trifolii

Table 3 Temperature-development studies with the pupal stage of *Liriomyza* spp.

"See footnotes on taxonomy and methodology, Table 1. PReported as L. sativae, but probably L. trifolii.

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Lable 4	I emperature-develo	ipment studies with vari	Development rate	Estimated threshold	
species o Liriomyza	¹ Life stages	Host	temperature ^a	development (°C)	Ref.
L. sativat	e Egg-adult	Phaseolus sp.	y = 0.00381x - 0.0352	9.2	(62)
L. sativat	e Egg-pupa	Phaseolus sp.	y = 0.00310x - 0.0195	6.1	(109)
L. trifolii	Egg-adult	Phaseolus sp.	y = 0.00369x - 0.0311	8.4	(13)
L. trifolii	Egg-adult	Chrysanthemum			
		morifolium	$y = 0.00310x - 0.0195^{b}$	6.3	(13)
L. trifolii	Egg-adult	Apium graveolens	y = 0.00281x - 0.0229	8.1	(41)
L. trifolii	Egg-pupa	Dendranthema sp.	$\mathbf{y} = 0.00728x - 0.0786$	10.1	(53)
*See foo	thotes on taxonomy and emperatures not used in	d methodology, Table 1. n calculating the regression			

instar occurs between puparium formation and pupation and is rarely discussed by most authors. Black sclerotized mouthhooks are left within the mine after the molt and can be used to distinguish the duration of the instars (100), because there are distinct mouthhook sizes for each larval instar. Other researchers have used mine width as an indication of instar duration (109). Because interpretation may vary, the method used to determine larval instar duration must be known; unfortunately, many reports do not explain precisely how this was done. Because of the difficulty in separating larval instars, many authors combine all instars and simply refer to larval duration (Table 2). Authors commonly combine egg and larval development to examine the total time of the immature stages spent within the leaf (see Table 4).

Larval development varies with temperature and host plant (Table 2). In addition, larval development time on a single host varies considerably with leaf position and age, but few authors take this into consideration. Many studies can also be criticized for lack of detail in explaining how development times were calculated (e.g. starting and stopping points, time of egg laying, sampling frequency). These points are especially critical for consistent calculations of the total larval duration of many *Liriomyza* spp., considering that it can be as short as 4–6 days at field/greenhouse temperatures (20, 41). Only one attempt to correlate laboratory development with the development of field populations has been reported (53); the development period for eggs and larvae in the laboratory, 147.5 day-degrees above 10.1°C, corresponded well to the observed development in the field.

As the larvae develop, both the diameter of the mine and the rate of mine formation increase (20, 61). For *L. trifolii*, the volume of leaf material consumed by the third stage larva is 643 times greater than that consumed by the first stage larva, and the feeding rate is 50 times greater (20). Mining causes a reduction in leaf photosynthesis, with the amount of reduction varying according to mine location (71). Metabolic rates of larvae double for every 10° C increase in temperature, but the total amount of leaf tissue consumed by larvae apparently remains the same regardless of temperature (9).

Interspecific competition with mites and aphids may inhibit population increases of *Liriomyza* (59) by affecting larval development. Intraspecific competition in both the field and laboratory may reduce survivorship as well as size of larvae and pupae, and may thus reduce adult vigor (59, 65).

When the larva is ready to pupate it cuts a semicircular slit in the leaf surface, usually at or near the end of the mine. This slit may be located on the upper or lower leaf surface, but depends on the mining location of the larva within the mesophyll. The larva emerges with characteristic peristaltic locomotion. When it is three-fourths out of its mine, the anterior portion waves about high above the leaf surface and the larva literally falls out (61).

Movement outside the mine is the same as within and is accompanied by a rolling motion, which usually forces the larva to fall from the leaf to the ground. Larvae occasionally pupate on leaves or at the base of leaves, stems, or stalks, but this is more common on plants with large curled leaves (squash, gerbera, etc). Larvae emerge from leaves during early daylight hours (61), with the majority of emergence occurring before 0800 hr.

PREPUPAE AND PUPAE

The period between larval emergence and puparium formation is generally referred to as the prepupa. The prepupal period is about 2–4 hr (41, 61), but varies considerably with temperature. The prepupa is negatively phototactic and positively thigmotactic. This stage is extended when the prepupa is exposed to constant light in bare containers (62).

The duration of the pupal stage varies inversely with temperature (Table 3), but at least 50% of the total development time of a *Liriomyza* individual is spent in this stage. Total development time of the pupa at greenhouse/field temperatures is about 8–11 days. Estimated temperature thresholds for development are generally consistent for pupae (Table 3), unlike those for eggs and larvae. This is probably due to more standard estimation methods, because the pupae are exposed and easier to observe. Relative humidity between 30 and 70% is optimum for pupation. It has been suggested that the substrate in which pupation occurs influences successful development to the adult stage (62, 63). Pupal weight and development time and percent emergence of adults from pupae appear constant regardless of host plant (62, 128).

Pupae of *L. trifolii* have exhibited a diapause at 16°C in Italy (99). While this diapause has not been observed in Britain, pupae can remain viable outdoors for several months and are able to withstand freezing temperatures (53). Thus, outdoor populations of *Liriomyza* may survive long enough to reinfest subsequent glasshouse crops.

HOST-PLANT INTERACTIONS, MOVEMENT, AND DISPERSION

Adults

Because the larvae of *Liriomyza* are unable to leave one leaf and enter another, the ultimate choice of host selection rests with the ovipositing adult female. This fact has led to numerous studies of adult preference. Unfortunately, only those studies in which an effort was made to standardize the type, age, and size of the leaves offered to adult flies (126) are of value.

Adult females exhibit distinct preferences for host plants, although their feeding and oviposition behavior remains stereotypic regardless of host (7).

The distribution and density of plant trichomes, the phenolic content, and the nutritional value of hosts were found to influence host selection (19, 26, 36). Little quantitative data are available on within-plant preferences of egg-laying adults (3, 30, 88).

The basis for host-plant preference may be genetic. A comparison of laboratory-selected and wild populations of L. brassicae suggests an increased tendency to oviposit in the host that this species develops on (101).

Few studies on seasonal abundance and distribution of *Liriomyza* spp. have been performed in wild or agricultural systems where more than one species of plant or one species of *Liriomyza* may be present. Research in this area has involved *L. trifolii* and *L. sativae*, which preferred celery and tomato, respectively (121, 122). There is evidence that *L. trifolii* may be replacing *L. sativae* in tomato (89) and gypsophila (83).

Liriomyza adults have long been known to be attracted to yellow cards, and with the application of adhesive these may be very effective monitoring tools (55) and may be useful in studies on movement and dispersal (31). Studies have confirmed that yellow is more attractive to adults than other colors (105), and that high reflectance through the yellow part of the spectrum increases catch (1, 11). Trap location with respect to the crop influences the number and species of flies captured (12, 123). The variance/mean relationship of *L. trifolii* and *L. sativae* trapped on yellow cards has been shown to be very consistent over time in chrysanthemum and tomato (70, 124).

An understanding of the movement and dispersal of economically important Liriomyza has been the objective of numerous studies over the past 35 years. In agricultural fields the within-field spread of leafminers begins slowly at first, generally originating in weed hosts in borders adjacent to field crops (22). Prevailing winds influence the rate and direction of dispersal from the center of origin. Densities are greatest at the point of origin and generally decrease with distance from the source (105, 116). In the greenhouse, where wind was not a factor, the mean distance flown by female flies (21.5 m) was greater than that flown by males (18.0 m) over a 7-day period (31). In addition, it was shown using a generalized distance dispersal model that density decreases more rapidly with distance for males than for females, and that males have slightly more aggregated distributions than females. Data on the sex ratio of adult *Liriomyza* caught on sticky yellow cards vary (12, 31), but most studies show capture of more males than females (11, 123). Based on the fact that females tend to live longer than males, one would expect that more females than males would be caught on yellow traps over a given period of time. Thus the data collected to date suggests differential attraction between the sexes.

The movement and dispersal of adults may be affected by aluminum-foil mulch around tomato and squash plants. This has been shown to reduce

infestations of *Liriomyza* (119), presumably by repelling adult flies. Insecticides have also been shown to repel adults, although effectiveness varies with the chemical and method of application (85).

Larvae

In most cases, experimentally transplanted agromyzid larvae develop on plants phylogenetically related to their natural host and die on plants not related to the normal hosts (10). Some *Liriomyza* species, however, were successfully transferred among Compositae (*Eupatorium* sp.), Urticaceae (*Cannabis* sp.), and Labiatae (*Galeopsis* spp.). Larvae may be far less sensitive to repellent or deterrent chemicals than adults. This stage has evolved a completely parasitic mode of life within the plant; thus larvae have poorly developed sense organs, and hence little ability to discriminate among various host species (92). Consequently, if a female oviposits in plants outside its normal range, there is a possibility that the larva could complete development. This may offer one avenue of host-range expansion in *Liriomyza*.

The possibility of sympatric genetic divergence in L. brassicae was investigated when genetic variation in survival and development time was demonstrated for three strains collected from different host-plant species (101). Formal quantitative genetic studies of L. sativae have been undertaken to determine the amount of genetic variation and to correlate this variation with parameters of host-plant utilization (107, 108). These techniques may be useful in the examination of host races in *Liriomyza* and other genera. A host race is defined as a group of individuals that genetically differs in host plant-related characters from individuals on other hosts. Individuals of the host race do not interbreed with individuals from other hosts because of divergent host preferences (107, 108). Genotype-environment interactions may be examined through correlations of various fitness components (e.g. development time) with environmental variables. These correlations provide estimates of local differentiation and the potential for future evolutionary change (108). Examination of L. sativae over a variety of adjacent crops revealed a significant genotype-environment interaction for development time within populations, which suggests that selection on individuals residing on a crop could lead to host-plant specialization at the species level. The absence of host races in L. sativae has been attributed to frequent migration among closely spaced crops and to crop rotation (107). This promotes interbreeding and prevents groups from becoming isolated, which is necessary for the formation of races. Thus in the absence of agricultural manipulations or in large agricultural monocultures, host races may develop in *Liriomyza* (93). Monoculture may already have been responsible for the development of a host race in L. sativae isolated on melons (misidentified as L. pictella) (61, 94).

Most members of the Agromyzidae are homogametic (8). They generally have obscure polytene chromosomes, which may be why so few species have been studied cytologically (8). Only *Liriomyza urophorina* has been investigated (46, 47); it showed chromosomal polymorphism for six paracentric inversions.

In chrysanthemum, celery, and tomato the distribution of larvae and pupae from field samples is generally clumped (3, 30, 88, 124). When the variance/ mean relationship is examined for larvae using Taylor's power law, the *a* (a sampling factor) and *b* (a species-specific aggregation constant) values calculated for celery (3) and chrysanthemum (30) are very similar. This suggests that further work on celery may lead to sampling plans similar to those developed on chrysanthemum (30).

Leafminers respond favorably to high nitrogen content in leaves (23, 82, 120). Most of the data stem from studies in which nitrogen content is varied by manipulation of general fertilizer regimes. In many cases it is difficult to tell whether mines were fewer with lower fertilizer concentrations because of poor larval survival or reduced egg-laying by adults. A similar problem is encountered when one reviews the large body of information in which cultivars of one plant species are ranked as to sensitivity or resistance to leafminer damage (33, 90, 110).

ECONOMIC IMPORTANCE

The economic impact of *Liriomyza* leafminers in the United States and throughout the world has been considerable; in California alone it was estimated that the chrysanthemum industry lost approximately 93 million dollars to *L. trifolii* from 1981 through 1985 (57a).

Liriomyza leafminers can impact crops in at least six ways: (a) by vectoring disease (127), (b) by destroying young seedlings (17), (c) by causing reductions in crop yields (39, 117), (d) by accelerating leaf drop above developing tomatoes, thus causing "sunburning" of the fruit (26a), (e) by reducing the aesthetic value of ornamental plants (67), and (f) by causing some plant species to be quarantined (42, 54, 69, 72). While the results of most of these six types of damage are obvious [e.g. heavy mining and stippling in young seedlings or transplants can kill a plant and/or dramatically slow growth (17, 103)], it has been difficult to accurately associate specific levels of mining activity with reductions in crop yield. Reductions in photosynthesis and other physiological parameters have been measured in vegetable crops (29, 103) but have not been correlated to yield loss. Studies have shown that greenhouse-raised tomatoes can tolerate high levels of damage by L. sativae without

suffering appreciable losses in yield (43). However, in a recent study (39), L. *bryoniae* on tomato caused yield loss, which was greatest when mining occurred in the leaves close to a young, developing fruit. Predetermined damage thresholds have been incorporated into sequential sampling plans for tomato (28, 114), but these plans have not received wide acceptance. An experimental threshold on L. *sativae* in southern coastal pole-tomato fields in California calls for treatment when an average of 10 pupae per sampling tray per day accumulate over a 3-4 day period (26a).

RESPONSE TO INSECTICIDES

Numerous articles have focused on chemical control of *Liriomyza* leafminers (76) because of their potential for causing damage. Control with insecticides is usually complicated by the insect's biology, i.e. fast development time; smallness and high mobility of adults; a relatively long pupal stage occurring in the soil; high reproductive capability; and egg and larval stages within and protected by leaf tissue. In addition, a mine created by the larva remains in the leaf as long as the leaf survives; thus insecticide application may have little use in preserving the aesthetic value of ornamentals or for preventing yield reduction of vegetables. Insecticide applications have commonly been responsible for outbreaks of *Liriomyza* because the insecticides used are often more toxic to the large parasite complex holding these leafminers in check than to the leafminers themselves (60). Thus it is very important to base spray application on accurate damage thresholds. Much more research is needed in this area. Another possible reason for these outbreaks is that leafminers that receive a sublethal insecticide dose may be physiologically stimulated and thus may cause more damage (60). This theory has remained untested, and not all sublethal effects of insecticides are stimulatory (84).

An important part of the biology of *Liriomyza* is the ability to develop resistance to insecticides. Insecticide resistance has been responsible for failure to control these leafminers for many years (21, 72, 118). However, definitive studies documenting insecticide resistance have only been done with *Liriomyza trifolii* (32, 74), and more work with this and other species is needed. Research must be conducted on resistance, cross resistance, genetics of resistance in the absence of insecticide selection pressure. The insecticide-resistance capability of *L. trifolii* has been speculated as a mechanism in its gradual replacement of *L. sativae* as the primary leafminer in several crops (83, 89, 122). It has been demonstrated that *L. trifolii* is more tolerant of insecticides than several other Agromyzid species (45, 73), but much more comparison of different species of *Liriomyza* is needed. Haynes et al (23a)

have developed a bioassay with insecticide-laced yellow sticky cards that allows rapid assessment of resistance levels in field populations of *L. trifolii*.

RESPONSE TO PARASITES AND PREDATORS

Forty parasite species have been found to use members of the genus *Liriomyza* as hosts (27, 58, 76; M. W. Johnson, unpublished). Only larval and pupal parasites have been found, and under natural conditions parasitism is usually low early in crop development and gradually increases as the crop matures. Under greenhouse conditions, inoculation and augmentation of parasites are needed for effective control. In such situations both larval and pupal parasites have been used (15). Many studies involving these leafminers and their parasites have been concentrated on identifying the parasite complex, estimating its ability to effect control, and determining the impact of insecticides on the parasites. Much more research is needed on the detailed biology (instar preference, fecundity, searching ability, etc) of these parasites, as they use different members of the genus *Liriomyza* as hosts. Few studies are available in this regard (24, 40, 129). For example, it was only recently discovered that L. trifolii is capable of encapsulating the eggs of Dacnusa sibirica (113). To maximize the potential of parasites in biological control of Liriomyza spp., research should focus on biology and proper selection of parasites most likely to succeed in the different cropping systems where these leafminers are a problem. Only limited studies have been done with predators of these leafminers (68).

POSTSCRIPT

The movement of *Liriomyza* spp. within infested plant material has caused a worldwide problem, the magnitude of which is difficult to comprehend. This involves primarily two species, *L. trifolii* (44, 54) and *L. huidobrensis* (69). *Liriomyza trifolii*, which until recently had a relatively limited distribution, can now be considered cosmopolitan and is a major pest on numerous ornamental and vegetable crops almost everywhere it occurs. This polyphagous leafminer has dramatically increased its host range as it has spread into new areas. In 1965 (97), 59 plant hosts were listed for *L. trifolii*. By 1984 this number had increased to 122 (18). In 1986, the number of hosts for *L. trifolii* exceeds 400 (K. A. Spencer, personal communication). This increased host range, coupled with a phenomenal increase in insecticide resistance, has created difficulty in control of *L. trifolii* in a number of crops.

Liriomyza huidobrensis is primarily a problem for importers of cut chrysanthemum flowers into the United States and other areas from South America, where this species is common. It is of concern to the United States Department of Agriculture, Plant Protection and Quarantine, that *L. huidobrensis* is found in the United States, but only in California. Because most cut-flower shipments originating in South America are destined for the eastern United States, the pest has potential for establishment there.

Movement of both species should diminish in the future; those responsible for shipping plant material are fully aware of the potential problem, and considerable research has focused on how to assure that plant material is kept free of *Liriomyza* (41, 54). In addition, several outstanding quarantine guidelines are now available (14, 79).

During the past ten years there has been a dramatic increase in the economic importance of *Liriomyza* leafminers. Researchers have not responded commensurately to this increase. Two factors that have complicated researcher response have been misidentification of species and lack of basic biological information. Regarding the former point, most researchers are aware of potential problems with taxonomy of *Liriomyza* spp. and therefore keep voucher specimens and have experts make the identifications. In addition, more emphasis has been placed on electrophoresis and ovipositor morphology as taxonomic tools (37, 51, 125). Electrophoresis can now be used to separate heretofore indistinguishable immatures of closely related species (51). Other methods of separating larval stages (e.g. larval morphology, mouthhook structure) appear promising (4, 6). With greater emphasis on taxonomy and increased researcher awareness of taxonomic problems, fewer misidentifications should occur in the future (94).

Our knowledge concerning the biology of these leafminers is still undeveloped. Most of the information presented in this review is very general and has come from studies on relatively few species completed over the past 25 years. The next 25 years should yield considerable data on the basic biology of this fascinating group of flies. This data will contribute to the overall understanding of host plant utilization by insects and to the development of more comprehensive and accurate pest management strategies.

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