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Review Article

Balancing biological control strategies in the IPM of New World invasive *Liriomyza* leafminers in field vegetable crops

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Abstract

Horticultural field crops worldwide are under threat from three New World *Liriomyza* spp. of leafminers: *Liriomyza sativae, Liriomyza trifolii* and *Liriomyza huidobrensis*. These particular species are characterized by their high degree of polyphagy and the extent to which they have invaded new geographical areas including large parts of the Old World; yield losses can be considerable. The management of agromyzid leafminers has been extensively researched over the last 30 years or so. Most prominently, the effectiveness of insecticides has been dogged by the effects of indiscriminate use. Indigenous natural enemy communities of *Liriomyza* spp., particularly parasitoids, are diverse within their native ranges and there is evidence that in pesticide free areas these can regulate leafminers. They can also be diverse in their adventive ranges in continental areas, as invading *Liriomyza* spp. quickly attract local parasitoids and other polyphagous arthropod predators. An analysis of the literature indicates that agromyzid parasitoids are polyphagous but some may be habitat specific, which explains why they can readily exploit the alien invasive leafminers. The impact of parasitoids and other natural enemies on *Liriomyza* spp. within their adventive ranges has not been studied but circumstantial evidence suggests that they can have a significant impact a few years after the initial invasion of the leafminer.

In the past most attention has been paid to augmentative and classical biological control of *Liriomyza* spp. The results of classical biological control have been mixed. We argue that, based on the ecology of natural enemy communities, more attention needs to be paid in IPM to the enhancement of local natural enemies, particularly in continental areas. Classical biological control needs to take local parasitoid biodiversity into account, otherwise untoward non-target effects may arise. However, this technique may be appropriate where gaps in local parasitoid guilds are identified or in areas where the local natural enemy diversity is depauperate.

Polyphagous New World *Liriomyza* spp.

Field vegetable growing worldwide is under siege from three New World *Liriomyza* spp. (Dipt., Agromyzidae) leafmining flies: *Liriomyza sativae* (Blanchard), *Liriomyza trifolii* (Burgess) and *Liriomyza huidobrensis* (Blanchard). The damage caused to their host plants is very similar for all the species: the larval stages feed within the leaves of the host plants, and at high fly densities this feeding can severely reduce yields and/or kill the plants (Spencer, 1989). Unlike the other two species, however, *L. huidobrensis* makes mines in the chloroplast-containing mesophyll layers, and is potentially more damaging (Weintraub & Horowitz, 1995). Although the Agromyzidae contains many serious (and potentially serious) species (Spencer, 1973, 1989), including other *Liriomyza* spp., the three New World leafminers are characterized by their high degree of polyphagy and the extent to which they have invaded new geographical areas. *Liriomyza trifolii* and *L. huidobrensis* are both widely distributed in the New and Old Worlds and oceanic islands; for *L. trifolii* the invasion and expansion in the Old World has been occurring since about the mid-1970s. *Liriomyza huidobrensis* has yet to get a foothold in continental Africa although recent report suggests the species has invaded Zimbabwe (P. Wilkinson, pers. comm.). *Liriomyza sativae* also has a wide distribution in the New World but is a more recent invader of the Old World where a rapid range expansion is currently occurring in eastern Asia.

Within these regions, all types of producers are affected by one or more of these polyphagous leafminers: smallholder farmers who grow vegetables, horticultural industries (including those under glass) and ornamental flower producers. Besides the damage caused by the larvae, feeding punctures cause loss of vigour and reduce the photosynthetic capacity and mesophyll conductance of plants (Johnson *et al*., 1983). Yield losses in general can be considerable. For example, in Vanuatu in the 1980s, *L. sativae* caused losses of up to 70% in tomato crops (Waterhouse & Norris, 1987). More recently, *L. huidobrensis* has been reported to have caused 100% yield loss in potato crops and up to 70% losses in other crops in some areas of Indonesia (Shepard *et al*., 1998). The literature on economic losses to vegetables and cut flowers is vast, but a useful review, with a particular emphasis on vegetable crop losses, has been produced by Waterhouse & Norris (1987).

The management of agromyzid leafminers has been a topic of extensive research and scientific debate for the last 30 years or so. Synthetic chemical and natural insecticides for leafminer control have been extensively researched and are commonly used worldwide by smallholder farmers and large-scale producers alike. The effectiveness of these insecticides has been dogged by their indiscriminate use, impact on natural enemies and the development of resistance within fly populations. Other control techniques (e.g. yellow board traps, host plant resistance) have also been developed in western Europe and in the Americas and are now used on a very local basis within some countries. However, agromyzid leafminers are known to have rich natural enemy communities, particularly in their areas of origin, and much attention has been paid to augmentative biological control in glasshouses and classical biological control in the field with insect parasitoids (Minkenberg & van Lenteren, 1986; Waterhouse & Norris, 1987). The results of these programmes have been mixed, with most successes being achieved in glasshouses (Minkenberg & van Lenteren, 1986).

As for many damaging insects, the optimum method for leafminer management is to integrate several techniques. Integrated pest management (IPM) also seeks to minimize the disturbance of the control effect on the natural components of the agro-ecosystems (Altieri *et al*., 1983) and thus biological control is an important keystone of IPM. Although IPM does not seem to have been researched extensively for the management of *Liriomyza* spp. on field vegetables, there is now much interest in this, particularly in South-East Asia where the IPM paradigm has been successfully developed for other pests.

Here, we review the origin and spread of the three leafminers and the factors that effect population outbreaks, particularly the impact of pesticides on natural enemies. Next, we consider previous biological control programmes. We then use the information from these reviews to assess the prospects for the development of specific biological control strategies as components of IPM for the leafminers in vegetable crops in the open field. In particular, we highlight the polyphagous nature of leafminer parasitoids and the importance and implications of this for conservation or enhancement of local natural enemies, particularly parasitoids, versus introduction strategies in the biological control of *Liriomyza* spp. in the open field.

Range Expansion in the New World and Centres of Origin

The genus *Liriomyza* contains more than 300 species which are widely distributed in the New and Old Worlds but, nonetheless, most occur naturally in the temperate regions (Parrella, 1987). Spencer (1973) discussed the evolution and distribution of the Agromyzidae in general. Approximately 23 species of *Liriomyza* have been reported as being economically important and five of these are truly polyphagous: the three New World species considered here and the Old World species *Liriomyza bryoniae* (Kaltenbach) and *Liriomyza strigata* (Meigen) (Spencer, 1973). In fact, true polyphagy is uncommon in the Agromyzidae (Spencer, 1973; Parrella, 1987).

The geographical distribution of the three species in the New World is given in Table 1. *Liriomyza trifolii* is present from Ontario (Canada) through most of the eastern and southern United States and from California through to Peru. It is also present in the Caribbean. Spencer (1989) considered that the natural range may extend from the northeastern states of the USA down to the Gulf of Mexico; Spencer (1973) stated that Florida represents the centre of this range. The first ‘outbreaks’ in the USA were reported from Iowa in 1932 (Harris & Tate, 1933). Since then, fly and/or population outbreaks have been reported from Venezuela in 1960/61 (Spencer, 1989), Colombia in 1974/75 (Minkenberg & van Lenteren, 1986), California, 1975/76 (Parrella, 1982) and Canada in the early 1980s (McClanahan, 1983). These dates probably approximate the time of the range expansion throughout the Americas. *Liriomyza sativae* has an equally extensive distribution and is now widespread in the southern states of the USA from Florida to California. It is also present in the Caribbean and throughout much of South America. As with *L. trifolii*, Spencer (1965) considered the endemic focus to be Florida. Serious outbreaks of this leafminer occurred in Florida in about 1948 (Spencer, 1973) and since this time other outbreaks have been reported from an increasing geographical area. However, over recent years, its range in the southern USA has contracted.

Liriomyza huidobrensis is present mostly throughout the western side of the Americas, from California through to Chile. There are records from Brazil from Campinas and Brasilia. Spencer (1973) considered that *L. huidobrensis* has used the Andes as a migration route and that the Amazon Basin has apparently acted as an effective barrier to the east of the continent. The endemic focus of this leafminer may be California and it may have been introduced to South America by early man when dispersing southwards (Waterhouse & Norris, 1987) but this needs to be examined in more detail.

Spencer (1989) considered that some dispersal of leafminers between North and South America (and *vice versa*) is natural. However, several factors have contributed to the broad-scale range expansion of these three leafminers (Parrella & Keil, 1984): for example, the development of extensive horticulture and ornamental flower production throughout the Americas and the increase in trade (and lack of quarantine) within the horticultural business, particularly in chrysanthemum cuttings. In the adventive ranges of the leafminers, further range expansion is sometimes limited by climate. Spencer (1973) stated that *L. trifolii* “can survive in areas where winters are invariably severe with sub-zero temperatures for extended periods, but it only thrives in subtropical and tropical conditions”. In South America, *L. sativae* is restricted to warmer, low-elevation areas, whereas in this region *L. huidobrensis* is present at the higher elevations (Spencer 1989). This is also true in South-East Asia (Rauf & Shepard, 1999; Sivapragasam & Syed, 1999).

Table 1. Geographical records of polyphagous *Liriomyza* spp. in the New World[1].

L. sativae		*L. trifolii*		*L. huidobrensis*	
USA	Alabama	Canada	Ontario	USA	California
	California				
	Florida	USA	most eastern states		
	Georgia		most southern states		
	Maryland		California		
	Ohio				
	South Carolina				
	Tennessee				
	Texas				
Central America	Costa Rica	Central America	Costa Rica	Central America	most countries
	Cuba		Guatemala		
	Jamaica		Mexico		
South America	Argentina	South America	Brazil	South America	Argentina
	Brazil		Colombia		Brazil
	Chile		Guyana		Chile
	Colombia		Peru		Colombia
	Peru		Venezuela		Ecuador
	Venezuela				Peru
					Venezuela
Caribbean	Bahamas	Caribbean	Bahamas	Caribbean	Dominican Republic
	Barbados		Barbados		
	Puerto Rico		Dominican Republic		
	Trinidad		Trinidad		

[1] Records from: Spencer (1973); Spencer (1989), IIE (1992).

In some regions, one species of invasive leafminer is being replaced by another. Spencer (1989) reported that in Florida and California over the last 30 years, *L. sativae* has been replaced by *L. trifolii*. The same interaction between these species has taken place in Hawaii (Waterhouse & Norris, 1987). This displacement might have been chemically induced (Matayoshi *et al*., 1981).

The factors leading to the initial population outbreaks within the leafminers' native ranges are discussed below.

Leafminer Population Outbreaks

Agromyzid leafminers have an egg stage, three larval stages, a pupal stage and an adult stage. Adults of *Liriomyza* spp. are small (no more than about 2 mm long) with yellow and black markings. Spencer (1973) provided a simple key to distinguish the major economically important *Liriomyza* spp. but accurate identification needs to be based on the structure of the male genitalia. The life histories of the three species are very similar, particularly those of *L. sativae* and *L. trifolii*. The following account is summarized from Waterhouse & Norris (1987) and Spencer (1989).

Mating can occur at any time but is more common in daylight hours and within one day of emergence. The females possess ovipositors, which are specially adapted to puncture plants, and they use them to pierce leaf surfaces, making holes through which exuding sap can be obtained. The adults start feeding and ovipositing at sunrise. Males cannot puncture leaves but they have been observed feeding at female-produced puncture sites. The more frequent puncture-feeding by the females reflects their greater nutrient requirement during egg production.

Egg laying begins within a day or so of female emergence and peaks strongly after a week, decreasing thereafter for several weeks. A single mating ensures all the eggs are fertilized and hundreds of eggs can be laid by each female, although numbers can vary considerably (Minkenberg & van Lenteren, 1986). The feeding punctures can also serve as oviposition sites. *Liriomyza sativae* and *L. trifolii* females deposit their eggs (often many per leaf) at random on the upper leaf surface whereas *L. huidobrensis* females normally lay theirs towards the base of the leaf, on or near the midrib (Spencer, 1989). The mines of the former two species are linear or serpentine and broad in shape; the mine of the latter species largely follows the midrib and branches along lateral veins. The shape and form of the mines are variable and depend on the host plant species and cultivar. The third-instar larva leaves the mine by cutting an opening at its end. Emergence occurs primarily in the morning (Charlton & Allen, 1981) and the larvae fall to the ground or onto lower leaves and pupate.

The entire life cycle from egg to adult takes from less than three weeks to more than nine weeks depending on temperature and host plant. Males live only for a few days whereas females survive for up to a week (Charlton & Allen, 1981) and sex ratios for *L. trifolii* vary between 7:4 and 1:1 (Malais & Ravensberg, 1992). Although highly polyphagous, *L. trifolii* has preferred hosts (Compositae and Leguminosae) and populations of flies tend to remain in these crops unless forced to move by either harvesting or crop destruction. (Stegmaier, 1966; Minkenberg & van Lenteren, 1986).

Liriomyza sativae is also a highly polyphagous species, attacking crops mainly in the families Cucurbitaceae, Leguminosae, and Solanaceae. *Liriomyza huidobrensis* has been recorded on 11 families: Caryophyllaceae, Chenopodiaceae, Compositae, Cucurbitaceae, Leguminosae, Liliaceae, Linaceae, Solanaceae, Tropaeolae, Umbelliferae, and Violaceae (Spencer, 1989).

The three leafminers clearly have a number of life history traits that provide them with a comparative advantage (compared with other members of the genus) to disperse to, colonize and breed at new sites. In most of the areas studied, the species are multivoltine and have a high reproductive rate, and dispersal of adults is facilitated by wind. Even so, there are important differences between the three species. For example, Parrella *et al.* (1981) found that the reproductive potential of female *L. trifolii* is about three times higher than that of *L. sativae* or *L. huidobrensis*.

Despite these life history characters, the leafminers were, until about the 1940s, restricted to their endemic ranges in the New World; the first outbreaks occurred within these ranges. The most widely reported reason for the first outbreaks, and their maintenance in the adventive ranges, is the indiscriminate use of insecticides and the negative effects of this on natural enemies. In the USA this was reported as early as the 1950s (Hills & Taylor, 1951). (See Spencer (1973) for further examples.) Therefore, we next examine these natural enemy communities in more detail and the evidence that natural enemies are important in regulating *Liriomyza* spp. in their native and adventive ranges.

Natural enemy communities

Several studies have been made on the natural enemies of *Liriomyza* spp. in North America (e.g. Jensen & Koehler, 1970). Also, as part of previous classical biological control programmes against *L. sativae* and *L. trifolii*, extensive surveys for natural enemies have been made within the native ranges of these leafminers (i.e. eastern and southern USA) (e.g. Murphy, 1984; R. Burkhart, pers. comm.). Inventories of natural enemies have also been made in many of the countries in the adventive ranges of the leafminers. Most of the studies have been based on the traditional paradigm of characters for biological control agents (see Huffaker (1971) for a discussion of these) and have focused on insect parasitoids because of their apparent potential as agents. However, a few predators have been recorded, e.g. empidid and muscid flies have been observed attacking adult *L. trifolii* in Israel (Freidberg & Gijswijt, 1983) and empidid and dolichopodids have been noted attacking *Liriomyza* spp. in Indonesia (Rauf & Shepard, 1999). Parrella *et al.* (1982) have recorded a predatory nematode in California. Arthropod and other predators are likely to be important and warrant further study.

Table 2. Genera of parasitic Hymenoptera which attack leafmining Agromyzidae.

CHALCIDOIDEA			**ICHNEUMONOIDEA**	**CYNIPOIDEA**
EULOPHIDAE	PTEROMALIDAE	TETRACAMPIDAE	BRACONIDAE	EUCOILIDAE
Entedoninae	**Ceinae**	**Platynochellinae**	**Alysiinae: Alysiini**	*Agrostocynips*
Apleurotropis	*Cea*	*Platynocheilus*	*Dapsilarthra*	*Disorygma*
Asecodes			*Epimicta*	*Ganaspidium*
Chrysocharis	**Herbertiinae**	**Tetracampinae**	*Oenonogastra*	*Gronotoma*
Closterocerus	*Herbertia*	*Epiclerus*	*Pseudopezomachus*	*Kleidotoma*
Neochrysocharis		*Tetracampe*	*Symphanes*	*Microstilba*
Pediobius	**Miscogasterinae**			*Nordlanderia*
Pleurotroppopsis	*Ceratetra*		**Alysiinae: Dacnusini**	*Nordlandiella*
Proacrias	*Glyphognathus*		*Chorebus*	*Tobiasiana*
	Halticoptera		*Coloneura*	*Zaeucoila*
Eulophinae	*Heteroschema*		*Dacnusa*	
Cirrospilus	*Lamprotatus*		*Exotela*	
Danuviella	*Mauleus*		*Grandia*	
Diaulinopsis	*Merismus*		*Laotris*	
Diglyphus	*Miscogaster*		*Protodacnusa*	
Hemiptarsenus	*Schimitschekia*		*Symphya*	
Meruana	*Seladerma*			
Pnigalio	*Sphaeripalpus*		**Hormiinae: Exothecini**	
Sympiesis	*Stictomischus*		*Colastes*	
Zagrammosoma	*Thinodytes*			
			Opiinae	
Tetrastichinae	**Pteromalinae**		*Bitomus*	
Aprostocetus	*Callitula*		*Eurytenes*	
Baryscapus	*Cyrtogaster*		*Opius*	
Minotetrastichus	*Oxyharma*			
Pronotalia	*Sphegigaster*			
Quadrastichus	*Stenomalina*			
	Syntomopus			
	Toxeumorpha			
	Trichomalopsis			
	Trichomalus			
	Trigonogastrella			

Table 3. World parasitoids (Chalcidoidea only) of *Liriomyza huidobrensis, L. sativae* and *L. trifolii* (from Noyes, 1998)[1].

Parasitoids	*Liriomyza* spp.		
	L. huidobrensis	*L. sativae*	*L. trifolii*
EULOPHIDAE			
Chrysocharis ainsliei Crawford	+		
Chrysocharis brethesi Schauff & Salvo	+		
Chrysocharis caribea Bouček	+	+	
Chrysocharis flacilla (Walker)	+		
Chrysocharis liriomyzae Delucchi			+
Chrysocharis orbicularis (Nees)			+
Chrysocharis oscinidis Ashmead	+	+	+
Chrysocharis pentheus(Walker)			+
Chrysocharis pubicornis (Zetterstedt)			+
Cirrospilus ambiguus Hansson & LaSalle			+
Cirrospilus vittatus Walker			+
Closterocerus purpureus (Howard)		+	
Closterocerus trifasciatus Westwood		+	
Closterocerus utahensis Crawford		+	+
Diglyphus begini (Ashmead)	+	+	+
Diglyphus intermedius (Girault)	+	+	+
Diglyphus isaea (Walker)	+	+	+
Hemiptarsenus ornatus (Nees)			+
Hemiptarsenus varicornis (Girault)		+	+
Meruana liriomyzae Bouček		+	+
Neochrysocharis diastatae (Howard)		+	+
Neochrysocharis formosa (Westwood)		+	+
Neochrysocharis okazakii Kamijo			+
Quadrastichus liriomyzae Hansson & LaSalle			+
PTEROMALIDAE			
Halticoptera aenea (Walker)	+	+	+
Halticoptera arduine (Walker)	+		
Halticoptera circulus (Walker)	+	+	+
Halticoptera patellana (Dalman)	+		
Lamprotatus tubero Walker	+		
TETRACAMPIDAE			
Epiclerus nomocerus (Masi)			+

[1] The database is not exhaustive.

Genera of parasitic Hymenoptera that attack leafmining Agromyzidae are shown in Table 2. World parasitoids recorded from the three leafminers are diverse and Waterhouse & Norris (1987) listed more than 40 species of parasitoids from the three *Liriomyza* leafminers. To illustrate the diversity we show the Chalcidoidea for *L. sativae*, *L. trifolii* and *L. huidobrensis* in Table 3, which is taken from the database compiled by Noyes (1998). Clearly, there is a rich parasitoid fauna; the better studied a region is, the larger the number of parasitoids known from it. Generalizing from the studies, *L. sativae* and *L. trifolii* are attacked within their native ranges by a community of parasitoids; interestingly, no specific studies seem to have been conducted on *L. huidobrensis* in the northern part of its range. The parasitoids attack the larval stage of these leafminers and are either ectoparasitic or endoparasitic in habit. When fully developed, some species emerge from within the remains of the leafmine (for example, *Diglyphus* spp.; Eulophidae) and other species from the puparium of the fly after it has fallen to the ground (for example, *Chrysocharis* spp.; Eulophidae) (Minkenberg & van Lenteren (1986). The biologies of some of the more important parasitoids recorded in the eastern and southern USA are summarized in Table 4.

Whilst the temporal distribution of species within these communities within North America has been studied in particular vegetable crops (e.g. Jensen & Koehler, 1970; Johnson *et al.*, 1980; Palumbo *et al.*, 1994), the spatial distribution of species and the factors limiting these are less well understood, particularly biotypes and climatic preferences. However, several important facts are known.

Table 4. Summary of biological characters of some common parasitoids of *Liriomyza sativae* and *L. trifolii.*

FAMILY/Species	Life history characteristics	Age of host attacked	Development time (egg to adult)	References
EULOPHIDAE				
Diglyphus begini (Ashmead)	larval ectoparasitoid; solitary	all instars, but late ones preferred	12 days at 22±2°C	Doutt 1957 Allen & Charlton 1981
Diglyphus intermedius (Girault)	larval ectoparasitoid; solitary	all instars, but late ones preferred	13 days at 22±2°C	Hendrickson & Bath 1978 Gordh & Hendrickson 1979
Chrysocharis oscinidis Ashmead	larval-pupal endoparasitoid; solitary	larvae approx. 12 h old (at 27°C); emerges from fly puparium	13 days at 27±2°C	Christie & Parrella 1987
Neochrysocharis diastatae (Howard)	larval endoparasitoid; solitary	young larvae	11 days at 27±2°C	Murphy 1984
BRACONIDAE				
Opius dissitus Muesebeck	larval-pupal endoparasitoid; solitary	all instars; emerges from fly puparium	11 days at 27±2°C	Murphy 1984
EUCOILIDAE				
Ganaspidium utilis Beardsley	larval-pupal endoparasitoid; solitary	all instars; emerges from fly puparium	29 days at 26±2°C	Petcherat & Johnson 1988

Table 5. Apparent "specialists" from parasitoids of *Liriomyza huidobrensis, L. sativae* and *L. trifolii* (from Table 3).

Parasitoids	*Liriomyza* spp.		
	L. huidobrensis	*L. sativae*	*L.trifolii*
EULOPHIDAE			
Chrysocharis ainsliei Crawford	+		
Chrysocharis brethesi Schauff & Salvo	+		
Chrysocharis flacilla (Walker)	+		
Chrysocharis liriomyzae Delucchi			+
Chrysocharis orbicularis (Nees)			+
Chrysocharis pentheus (Walker)			+
Chrysocharis pubicornis (Zetterstedt)			+
Cirrospilus ambiguus Hansson & LaSalle			+
Cirrospilus vittatus Walker			+
Closterocerus purpureus (Howard)		+	
Closterocerus trifasciatus Westwood		+	
Hemiptarsenus ornatus (Nees)			+
Neochrysocharis okazakii Kamijo			+
Quadrastichus liriomyzae Hansson & LaSalle			+
PTEROMALIDAE			
Halticoptera arduine (Walker)	+		
Halticoptera patellana (Dalman)	+		
Lamprotatus tubero Walker	+		
TETRACAMPIDAE			
Epiclerus nomocerus (Masi)			+

Table 6. Actual status of "specific" parasitoids from Table 5.

Known from many other hosts (5-50+), mainly Agromyzidae.	*Chrysocharis ainsliei* *Chrysocharis brethesi* *Chrysocharis liriomyzae* *Chrysocharis orbicularis* *Chrysocharis pubicornis* *Halticoptera patellana*
Known from many other hosts (5-50+), Agromyzidae and others.	*Chrysocharis pentheus* *Cirrospilus vittatus* *Closterocerus trifasciatus*
Known from a few other hosts (less than 5). These species, while not having the wide host ranges of the species above, are at least known from some other hosts.	*Cirrospilus ambiguus* *Epiclerus nomocerus* *Hemiptarsenus ornatus* *Neochrysocharis okazakii*
From poorly known region (e.g. Neotropics). As more is known about the fauna of this region, it is probable that the host range for these species will be increased.	*Chrysocharis flacilla* *Closterocerus purpureus* *Halticoptera arduine* *Lamprotatus tubero*
Possibly host specific. But there is even some doubt as to the specificity of this species, and it is likely that it will have a wider host range than a single species.	*Quadrastichus liriomyzae*

Table 7. An indication of some host crop "preferences"[1] of some common parasitoids of *Lirimoyza* spp. (from Johnson & Hara, 1987).

Parasitoid	Crop
Diglyphus begini	celery/tomato/beans/cucumber/cabbage
Diglyphus intermedius	celery/spinach
Neochrysocharis diastatae	tomato/watermelon
Chrysocharis oscinidis	tomato

[1] Measured as most abundant parasitoid; these species do occur in other crops.

First, some species (e.g. the eucoilid *Ganaspidium utilis* Beardsley) have restricted distributions whilst others have a very wide distribution in the New World, e.g. *Diglyphus begini* (Ashmead) and *Diglyphus intermedius* (Girault). Climatic biotypes may exist within the widely distributed species.

Second, there is little concrete evidence that *Liriomyza* parasitoids display any high degree of host specificity. Although it may appear that species can be specific, this often merely reflects a lack of knowledge of the species involved. Taking the world records in Table 3 we find a total of 30 species names of chalcid parasitoids which attack at least one of these species. Of these 30, there are 18 species (60%) on this list that attack only one of the three species (Table 5). Thus, on the surface, it might appear that over half of these *Liriomyza* parasitoids are host specific. However, a more careful look at these parasitoids indicates that most are not specific. The parasitoids from Table 5, which appear to be specific when examining information based on only three hosts, are listed again in Table 6 under several different categories. Several of these species are actually seen to be quite polyphagous when all host records are examined, and others are known from at least some other hosts. Additionally, the specificity of some species can be questioned owing to the fact that there is some ambiguity as to their actual identity, or they come from areas that are extremely poorly known. There is only one species of parasitoid that might actually be considered as specific, and even this may not be so specific when more is learned about it. Thus, it appears that specific chalcid parasitoids of agromyzids might actually be rather rare, and one should assume, in general, that *Liriomyza* parasitoids are not host specific.

Finally, although many species within the communities are polyphagous, attacking several dipterous leafminer species, some are strongly influenced by the host plant or vegetable crop. For example, Johnson & Mau (1986) were unsuccessful in attempts to augment the impact of parasitoids on *L. huidobrensis* in onion by planting beans, which is a favoured host. Johnson & Hara (1987) listed some host crop preferences of some of the common parasitoids (Table 7).

Similar trends in parasitoid community composition and structure have been found within the adventive ranges of the leafminers. Thus, the parasitoid genera *Opius* (Braconidae), *Chrysocharis* and *Diglyphus* (Eulophidae) and *Halticoptera* (Pteromalidae) and others all have global distributions and species from these genera have been recorded from the leafminers from almost all the regions invaded. Table 8 shows the parasitoids that have been recorded from the three leafminers from Malaysia, Indonesia, Vietnam, China and Japan. Records for Malaysia, Indonesia and Vietnam are largely taken from recent studies (Rauf & Shepard, 1999; Sivapragasam & Syed, 1999; Thang, 1999); other records are from Hansson & LaSalle (1996), Arakaki & Kinjo (1998), Konishi (1998), Noyes (1998) and unpublished information based on recent identifications by LaSalle from China. Several points from these studies are worth noting and further illustrate some of our earlier comments. First, there are numerous indigenous parasitoids of agromyzids already present in Asia. Second, the number of parasitoids recorded from a country may reflect the amount of study that has been done in that country. Note that the largest number of parasitoids is from Japan, which has had the largest number of published studies on the subject. Lastly, the polyphagous nature of these parasitoids explains why they can readily exploit the alien invasive leafminers.

Table 8. Asian parasitoids of *Liriomyza trifolii; L. huidobrensis* and *L. sativae.*

Parasitoid	Country				
	Malaysia	Indonesia	Vietnam	China	Japan
EULOPHIDAE					
Apleurotropis kumatai (Kamijo)					+
Asecodes delucchii (Bouček)					+
Asecodes erxias (Walker)				+	+
Asecodes spp.	+	+	+		
Chrysocharis pentheus (Walker)	+		+	+	+
Chrysocharis phryne (Walker)				+	
Chrysocharis pubicornis (Zetterstedt)					+
Cirrospilus ambiguus Hansson & LaSalle	+	+	+		
Closterocerus lyonetiae (Ferrière)				+	+
Closterocerus sp.			+		
Closterocerus trifasciatus Westwood				+	+
Diglyphus albiscapus Erdös				+	+
Diglyphus isaea (Walker)				+	+
Diglyphus minoeus (Walker)					+
Diglyphus pusztensis (Erdös & Novicky)					+
Hemiptarsenus varicornis (Girault)	+	+	+	+	+
Neochrysocharis formosa (Westwood)	+		+	+	+
Neochrysocharis okazakii Kamijo			+	+	+
Neochrysocharis sp.	+	+	+		+
Pediobius sp.					+
Pnigalio katonis (Ishii)				+	
Pnigalio sp.		+			+
Quadrastichus liriomyzae Hansson & LaSalle				+	+
Quadrastichus sp.		+	+		+
Stenomesius japonicus (Ashmead)					+
Zagrammosoma sp.		+			
PTEROMALIDAE					
Halticoptera circulus (Walker)				+	+
Sphegigaster hamugurivora Ishii					+
Sphegigaster sp.					+
Trichomalopsis oryzae Kamijo & Grissell					+
BRACONIDAE					
Dacnusa nipponica Takada					+
Dacnusa sibirica Telenga					+
Opius spp.	+			+	+
EUCOILIDAE					
Kleidotoma sp.					+
Gronotoma micromorpha (Perkins)					+
Gronotoma sp.	+	+			+
Nordlanderia sp.			+		

The diversity of parasitoids on islands is clearly less than in mainland areas and Waterhouse & Norris (1987) made the point that on islands many species have probably been introduced.

Natural enemies in the population dynamics of the leafminers

What then is the evidence that these parasitoids and other natural enemies can limit the distribution and incidence of these leafminers? Evidence comes from a number of sources:

- Studies on leafminer dynamics on particular crops in North America. For example, Johnson *et al*. (1980) and Palumbo *et al*. (1994) have shown the importance of parasitoids in the regulation of *Liriomyza* spp. In the former study, parasitism of *L. sativae* on tomato by the eulophid *Chrysocharis oscinidis* Ashmead (= *C. parksi* Crawford) was found to be density dependent. In general and under natural conditions, parasitism is usually low early in crop development and gradually increases as the crop matures (Parrella, 1987).
- The differential destruction of natural enemies through insecticide use during the first leafminer outbreaks in North America. In the early 1950s, Hills & Taylor (1951) showed that repeated applications of DDT against *Liriomyza* sp. prob. *sativae* were largely ineffective but reduced the parasitoid population, which resulted in a pest outbreak. Subsequent studies with many chlorinated hydrocarbon and organophosphorus insecticides have confirmed this conclusion (e.g. Oatman & Kennedy, 1976).
- Observations on leafminer dynamics in their adventive ranges. As we have seen, many local species of parasitoids have extended their host range to include the invading species. Interestingly, invading leafminer populations have sometimes been observed to decline naturally after a few years and it has been hypothesized that this is due to the action of local natural enemies. Also, the rate at which local leafminer parasitoids can expand their host range can be quite fast. These points were illustrated after the invasion of *L. trifolii* in Senegal in the early 1980s (Neuenschwander *et al.*, 1987). In Indonesia, *L. huidobrensis* and *L. sativae* (reported as *L. trifolii*) are relatively new invasives; the former was reported for the first time in 1994 (Shepard *et al*., 1998). Surveys for parasitoids in 1998 revealed eight species (Table 8; Rauf & Shepard, 1999) although only one has been found to be common at the present time. Similar diversities have been found on these leafminers in Malaysia (Sivapragasam & Syed, 1999) and Vietnam (Thang, 1999); in Vietnam several species of parasitoids have become common on the leafminers. Unfortunately no detailed studies have been conducted (in insecticide-free fields) on the impact of these communities of parasitoids or other local polyphagous arthropod predators, but there are some indications. Rauf & Shepard (1999) reported that in Indonesia, parasitism varies among crops and locations and is also affected by crop phenology; parasitism was high on French bean, eggplant, soybean and beet (50–90%) but very low on potato, celery and Welsh onion (generally less than 10%). However, in Malaysia, Sivapragasam & Syed (1999) reported that larval parasitoids could be an important within-generation mortality factor in the population dynamics of leafminers. A few years after the invasion of the leafminer in Vietnam, parasitism of *L. huidobrensis* was observed to increase in winter vegetable crops grown after summer crops (Thang, 1999). This effect could be seasonal and/or due to more parasitoids exploiting the leafminer. In general the results for South-East Asia are dependent on the invasion dynamics of the leafminers and the time since the first establishment of the flies. Similar parasitoid impacts have been found in Venezuela (F. Garaud-Pouey, pers. comm.).

Thus, the evidence is that the initial outbreaks of *Liriomyza* spp. in the southern USA were induced because of the excessive use of insecticides in the 1950s and 1960s and the high susceptibility to these chemicals of parasitoids keeping the leafminers in check. Another factor that may have contributed to the disruption of parasitoids is the increase in vegetable crop monocultures; some of the major parasitoids have particular crop ‘preferences’ and thus their impact may be reduced on ‘non-preferred’ crops. In conclusion, there is good evidence that natural enemies, particularly parasitoids, regulate leafminers in their native ranges. Furthermore, the polyphagous nature of leafminer parasitoids means that leafminers may come under relatively quick control in their adventive ranges.

Previous Biological Control Programmes

Observations on natural control by communities of parasitoids have stimulated a lot of effort in biological control. Research and implementation have largely been focused in two cropping situations: open fields and glasshouses. Work on biological control in glasshouses has mostly been developed in horticultural industries in western Europe and North America. In general, biological control efforts under glass have focused on augmentative methods and these have been successful because of the closed conditions and regulated climate. For example, in France, in the Rhone Valley delta, *Diglyphus isaea* (Walker) was mass reared and used successfully on a large scale under glass against *L. trifolii* (Minkenberg & van Lenteren, 1986). Other biological programmes against *Liriomyza* spp. under glass are also reviewed by these authors.

Of more relevance here are the biological control programmes that have been conducted against *Liriomyza* spp. in open field systems or in under partly covered crops. Interestingly, although many parasitoid species have been recorded from the leafminers in particular areas in their adventive ranges, little work has been done to put this to use in IPM, i.e. in the development of conservation biological control. One exception is the work of CIP (the International Potato Centre) in Peru, where the conservation of local natural enemies has been assessed in station trials as part of the development of IPM (CIP, 1994).

Most effort in the biological control of invasive leafminers in open fields has focused on the classical approach, i.e. the introduction of natural enemies from the area of origin of the pest. In the case of *Liriomyza* spp. this has sometimes been in the belief that exotic parasitoids will be more tolerant of insecticides than local ones (e.g. Lai, 1983). To date, most classical biological control has been targeted against *L. trifolii* and *L. sativae* (Table 9). Hawaii has had a particularly active programme of parasitoid introductions against *L. trifolii* and *L. sativae* over the last few decades. Overall, in Hawaii and elsewhere, the success of these programmes has been mixed. In many cases, an introduced parasitoid has failed to establish or the result of the introduction is not known. However, a few notable successes on vegetables have been achieved. In Hawaii, the eucoilid *Ganaspidium utilis* (originally identified as *Cothonaspis* n. sp.), introduced in 1977, has a major impact on *L. trifolii* and *L. sativae* on watermelons and may be important on *L. trifolii* on celery (Johnson, 1993). Also, the eulophid *Neochrysocharis diastatae* (Howard) (= *Chrysonotomyia punctiventris* (Crawford)) was found to have a significant impact on both leafminers on watermelon, beans and tomato. Likewise, in Tonga, *G. utilis* and the eulophid *Chrysocharis oscinidis* were released in 1988 for the control of *L. trifolii* on watermelon, pumpkin, tomato, bean and Irish potato. These species successfully controlled the leafminer to the extent that chemical control was no longer necessary (Johnson, 1993).

Table 9. Previous biological control programmes against *Liriomyza trifolii/L. sativae.* Data from BIOCAT (Greathead & Greathead, 1992; Johnson, 1993).

Country[1]	Crop	Date	Parasitoid[2]	Family	Outcome[3]
Senegal[a]	okra, potato	1982-3	*Opius dimidiatus* (Ashmead)	Braconidae	F
		?	*Opius dissitus* Muesebeck	Braconidae	N
		1982-83	*Disorygma* sp.[c]	Eucoilidae	F
		1982-83	*Chrysocharis oscinidis* Ashmead[c]	Eulophidae	F
		1982-83	*Neochrysocharis diastatae* (Howard)[c]	Eulophidae	F
		1982-83	*Chrysonotomyia* sp. W	Eulophidae	F
		1982-83	*Diaulinopsis callichroma* Crawford	Eulophidae	F
		1982-83	*Diglyphus intermedius* (Girault)	Eulophidae	F
		1982-83	*Halticoptera circulus* (Walker)	Pteromalidae	F
Hawaii[b]	chrysanthemum	1976	*Opius dimidiatus* (Ashmead)	Braconidae	F
		1981	*Opius dissitus* Muesebeck	Braconidae	E
		1977	*Opius montanus* (Ashmead)	Braconidae	F
		1977	*Opius* sp.	Braconidae	F
		?	*Opius* sp.	Braconidae	N
		1976	*Ganaspidium utilis* Beardsley[c]	Eucoilidae	E
		1976	*Chrysocharis giraulti* Yoshimoto	Eulophidae	F
		1976, 82	*Chrysocharis oscinidis* Ashmead[c]	Eulophidae	E
		1976	*Chrysocharis* sp.	Eulophidae	F
		1980, 82	*Chrysocharis* sp.	Eulophidae	F
		1980, 82	*Chrysocharis* sp. nr. *giraulti* Yoshimoto	Eulophidae	F
		1977	*Neochrysocharis diastatae* (Howard)[c]	Eulophidae	E
		1976, 77	*Neochrysocharis diastatae* (Howard)[c]	Eulophidae	E
		1976	*Closterocerus trifasciatus* Westwood[c]	Eulophidae	F
		1981	*Diaulinopsis* sp.	Eulophidae	F
		1977	*Diglyphus begini* (Ashmead)	Eulophidae	N
		1975	*Diglyphus intermedius* (Girault)	Eulophidae	E
		1975	*Diglyphus isaea* (Walker)	Eulophidae	F
		1976	*Diglyphus pulchripes* (Ashmead)	Eulophidae	F
		1977	*Diglyphus* sp.	Eulophidae	E
		1977	*Pediobius metallicus* (Nees)[c]	Eulophidae	F
		1977	*Sympiesis* sp.	Eulophidae	N
		1980	*Halticoptera circulus* (Walker)	Pteromalidae	E
	vegetable	1982	*Chrysocharis oscinidis* Ashmead[c]	Eulophidae	N
		1982	*Halticoptera patellana* (Dalman)	Pteromalidae	N
		1976	*Ganaspidium utilis* Beardsley[c]	Eucoilidae	C
		1977	*Neochrysocharis diastatae* (Howard)[c]	Eulophidae	S
Barbados[b]	vegetable	1972-75	*Opius* sp.	Braconidae	N
		1972-75	*Chrysocharis* sp.	Eulophidae	N
		1972-75	*Diglyphus minoeus* (Walker)	Eulophidae	N
		1972-75	*Diglyphus ?isaea* (Walker)	Eulophidae	N
Marianas[a]	bean	1990	*Ganaspidium utilis* Beardsley[c]	Eucoilidae	S
		1990	*Chrysocharis* sp.	Eulophidae	S
		1985	*Ganaspidium utilis* Beardsley[c]	Eucoilidae	E
		1983	*Diglyphus begini* (Ashmead)	Eulophidae	F
Tonga[a]	vegetable	1988	*Ganaspidium utilis* Beardsley[c]	Eucoilidae	C
		1988	*Chrysocharis oscinidis* Ashmead[c]	Eulophidae	C
Taiwan[a]	chrysanthemum/vegetable	1988	*Dacnusa sibirica* Telenga	Braconidae	F
Guam[a]	vegetable	1986	*Diglyphus begini* (Ashmead)	Eulophidae	F
			Ganaspidium utilis Beardsley[c]	Eucoilidae	C

[1] Programmes against [a]*L. trifolii* only, [b]*L. trifolii* and *L. sativae.*

[2] Species marked [c] were originally cited as follows: *Disorygma* sp. as *Disorygyna* sp.; *Chrysocharis oscinidis* Ashmead as *Chrysocharis parksi* Crawford; *Neochrysocharis diastatae* (Howard) as *Chrysonotomyia punctiventris* (Crawford); *Ganaspidium utilis* Beardsley as *Cothonaspis*; *Closterocerus trifasciatus* Westwood as *Closterocerus tricintus* (Ashmead); *Pediobius metallicus* (Nees) as *Pediobius acantha* (Walker).

[3] Outcome: F, failed to become established; N, result not known; E, permanently established; S, substantial control reported; C, complete control.

There seem to be several reasons why success was not achieved in some of the other programmes listed in Table 9. In the Senegal programme, there was a high mortality in the shipments of parasitoids and thus it was difficult to establish healthy cultures (Neuenschwander *et al.*, 1987). More generally there is the observation that some parasitoid species seem to be better adapted to particular crop plants. Johnson & Hara (1987) emphasize that effective biological control may depend on matching the most effective natural enemies with a given *Liriomyza* host and crop.

The Prospects for Biological Control in the IPM of *Liriomyza* spp.

As a starting point, any insect management programme must be based on the correct identification of the species and biotypes involved, their distribution and incidence across different geographical areas and land use systems/crops, and an understanding of the ecology of the population outbreak. This information is essential to define research and implementation needs. IPM could involve elements of quarantine, surveillance, monitoring, cultural techniques, host plant resistance and biological control, together with reduced chemical sprays. Also, successful implementation will require the involvement of several different sectors of workers: researchers, quarantine personnel, extension workers and farmers.

Our reviews of the biogeography, ecology and previous biological control programmes of the New World invasive *Liriomyza* spp. have shown that the prospects for the development of biological control as a component IPM are good. In most vegetable crops, *Liriomyza* spp. only affect the leafy, non-marketable parts of the plant.

Biological control strategies appropriate for *Liriomyza* spp. in field vegetables could include conservation or enhancement of local natural enemies and/or the introduction of appropriate natural enemies from the area of origin of the pests or from related leafminers from other areas. However, these strategies are not mutually exclusive, as it is clear that any introductions should take into account the existing local natural enemy community. Conserved biodiversity contains a pool of potential biological control agents (LaSalle, 1993; LaSalle & Gauld, 1993). Thus regional biodiversity can contain indigenous parasitoids that will contribute to the control of invading pests. With respect to invading *Liriomyza* spp., initial surveys indicate that this certainly is occurring in South-East Asia and other countries, although high levels of pesticide usage make this difficult to quantify. Despite the difficulties in quantifying the effect of indigenous parasitoids, they should be considered as a resource and protected as much as possible. Also, one of the largest threats to indigenous species is introduced species (Reid & Miller, 1989), and there is concern about the possible effects of introduced biological control agents on non-target organisms (Howarth, 1991). One possibility is introduced parasitoids out-competing, and thus eliminating, indigenous parasitoids, and there is some indication that this has already happened with fruitfly parasitoids in Hawaii (Duan *et al.*, 1996). Of particular concern when considering introductions are generalists species which show little discrimination in switching hosts, and most agromyzid parasitoids seem to fall into this category.

In light of these points we now consider the relative roles that conservation/enhancement and classical biological control might play in an IPM programme for *Liriomyza* spp. in field crops.

Conservation biological control

There is circumstantial evidence that in continental areas, local natural enemies can reduce the incidence of the invading *Liriomyza* spp. after a period of a few years. This is similar to evidence which has been seen for another invasive species, the Asian citrus leafminer (*Phyllocnistis citrella* Stainton; Lep., Gracillariidae), which was regulated to some extent by indigenous natural enemies in Central and South America (LaSalle & Peña, 1997; Schauff *et al*, 1998). A biological control strategy would seek to conserve or enhance these local natural enemies, particularly parasitoids. Such a strategy would need to be developed hand-in-hand with a campaign to reduce insecticide spraying, or the use of selective insecticides and the implementation of other IPM components. The urgency of taking environmental issues into consideration in IPM programmes has been highlighted in recent volumes on the subject (Altieri, 1994; Barbosa, 1998; Wood & Lenné, 1999). Where *Liriomyza* spp. form part of a pest complex, and synthetic chemicals are used against other species, efforts could be made to replace these chemicals with mycopesticides (e.g. *Bacillus thuringiensis*).

At the beginning of a management programme, it is important to determine the species composition (in terms of host stage attacked, seasonality, etc.) and impact of the local parasitoid communities on different crops and to gain some understanding of the main factors limiting the small-scale distribution of the parasitoids across crop and plant species. In particular, applications of chemical insecticides frequently destroy these communities of parasitoids and thus studies need to take this into account.

It may be possible to enhance the action of *Liriomyza* parasitoids through habitat management. For example, several authors have pointed to the importance of weed patches near crops as being important reservoirs for parasitoids (e.g. Genung, 1981; Schuster *et al*., 1982). These weed patches are unlikely to be major sources of leafminer adults (Schuster *et al*., 1982) or invasive weeds (Genung, 1981). Particular plant species are also very likely to influence the incidence of particular parasitoids (Coll, 1998) and this subject needs further research.

It may, under some circumstances, be possible to augment local *Liriomyza* parasitoid populations. For example, in Western Sumatra, Indonesia, extension workers have successfully worked with farmers in areas of low pesticide usage to redistribute parasitized leafminers on crops such as cauliflowers to fields where parasitoids are absent or have low activity (Zamzami, 1999). This last example also illustrates the need for extension staff and researchers to work with farmers in order to maximize the potential of local parasitoids and other natural enemies.

Base-line studies on local natural enemies may reveal that some attacked crops have low levels of parasitism. For example, in Java and Sumatra, Indonesia, Shepard *et al*., (1998) have shown that parasitism of *L. huidobrensis* on potato crops is very low in comparison with other crops. Under these circumstances, and on some islands, where diverse leafminer natural enemy communities, particularly parasitoids, may not exist, it is important to determine ‘gaps’ in the parasitoid guilds before considering introductions of exotic parasitoids.

Classical biological control

Some notable successes in the control of *Liriomyza* spp. have been achieved on some of the Pacific Ocean islands – Hawaii, Tonga and Guam. Nonetheless, most parasitoid introductions have failed on these islands and elsewhere. Part of the failure relates to shipping techniques but other factors are important. For example, an examination of the biogeography and ecology of leafminer parasitoid communities raises a number of issues that need to be addressed in future programmes:

- Surveys for further parasitoids and other natural enemies. Although much is know about the communities of parasitoids associated with *L. sativae* and *L. trifolii* in North America, relatively little is known about the parasitoids of *L. huidobrensis*, although some studies have been undertaken in Peru. This is partly because the endemic focus of this leafminer is unclear. In the past, problems of leafminer identification have made the study of natural enemies difficult (Parrella & Keil, 1984). Also, little is known about the predators that feed on these leafminers. Thus further work needs to be undertaken to resolve these issues.
- Number of parasitoid species to introduce. As mentioned above, this needs to be based on local parasitoid guild structure. Also, relatively little seems to be known about the climatic or other environmental tolerances of the 'major' parasitoids used in the introduction programmes to date. For example, some of the species have a wide distribution in North America and thus climatic biotypes may well exist. There is also the issue of the relative attractiveness of different vegetable crops to different parasitoids but this subject is still poorly understood. In summary, it is likely that new introduction programmes will need to consider a suite of parasitoids.
- Parasitoid resistance to insecticides. Studies have shown that some parasitoids are relatively tolerant of insecticides (e.g. Trumble & Toscano, 1983). For example, in Hawaii, there are geographical biotypes of *Diglyphus begini* that are tolerant to oxamyl, methomyl, permethrin and fenvalerate (Rathman *et al*., 1990). Laboratory selected strains of *Ganaspidium utilis* that are resistant to fenvalerate have also been produced in Hawaii (Rathman *et al*., 1995).

Conclusions

The three New World *Liriomyza* spp. are clearly still invading new regions and causing serious damage to a wide range of crops and ornamental flowers. Also, within their current ranges, a wide range of insecticides is used to manage these species but insecticide-resistant populations are fast developing and this has added a new problem for farmers. The diversity of natural enemies and, in particular, the regulatory impact of parasitoids in North America seem clear. However, the general polyphagous nature of *Liriomyza* spp. and other agromyzid parasitoids means that these have been able to exploit readily the alien invasive leafminers. But, to some extent, it has been difficult to determine whether these parasitoids can effectively control the *Liriomyza* spp. because of the high levels of pesticide usage in these regions. Nonetheless, there is circumstantial evidence that local parasitoids can have a significant impact. Other natural enemies (e.g. predatory flies) may also be important but these have not received much attention. Clearly, the invasion dynamics of *Liriomyza* and the impact of indigenous natural enemies needs further research. To date, biological control has not featured significantly in the management of invasive *Liriomyza* spp. in field situations and, where it has, the focus has been on the introduction approach. However, more effort should be made in continental areas to understand, conserve and enhance local natural enemies before the introduction of exotic parasitoids is considered. In particular, gaps should be identified in local parasitoid guilds such that ecologically compatible exotic agents can be identified. In islands, local natural diversity may be depauperate and thus the introduction of exotic parasitoids will be the most appropriate biological control strategy in this case. The final point should be, though, that continued excessive pesticide usage may be a larger threat to local biodiversity than importing non-specialist leafminer parasitoids.

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