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LITERATURE REVIEW

Leafminer parasitoids and pest management

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Abstract

A. Salvo, and G.R. Valladares. 2007. Leafminer parasitoids and pest management. Cien. Inv. Agr. 34(3):125-142. Leafminers are insects whose larvae live and feed within plant leaves, consuming mesophyll tissue without damaging the leaf epidermis. Several species are considered serious pests on intensive, horticultural, and ornamental crops. Natural enemies are the most frequent source of mortality for this herbivore insect guild, with parasitoids being the most effective and best represented source. This article provides an updated summary of the available research on leafminer parasitoids in relation to pest management. Parasitoids of leafminers are predominantly generalists, and can thus rapidly include in their host ranges newly introduced leafminer species, frequently achieving effective regulation a few years after the pest becomes established. Classical and augmentative biological control strategies are broadly used for leafminer pest management. Several studies have dealt with the simultaneous use of parasitoids together with chemical and cultural control. Many conventional insecticides have detrimental effects on parasitoids; however, others could be compatible with biological control. Although integrated pest management programs employing a combination of several control strategies have achieved success against leafminer pests, the effects of cultural practices that could boost parasitoid populations have been scarcely studied.

Key words: Biological control, chemical control, cultural control, leafminers, parasitoids, pest management.

Introduction

Parasitoids are insects with a complex and fascinating biology, whose larvae feed on other insects, killing them in order to complete their development. Although they are usually unnoticed due to their small size, this group of organisms has tremendous economic importance, as they regulate the population of their hosts and thereby represent useful tools for insect pest management. Leafminer parasitoids constitute an interesting and relatively well-studied group of species belonging to at least ten families of the Order Hymenoptera, Suborder Apocrita. These insects have adapted to their hosts' particular conditions of life, and have great potential in biological pest control programs (Hawkins *et al*., 1993).

This article includes a review of leafminer parasitoids in the context of their potential use in insect pest management. For this, we reviewed the ecological literature referring to both theoretical and practical aspects that must be considered when using leafminer parasitoids as population regulators. Likewise, other strategies used in the control of leafminers are discussed, with an emphasis on the relationship between these methods and the regulation exercised by the parasitoids. The subject is introduced with a brief characterization of leafminer insects, their economic importance, the reasons why several species reach pest status in various crops, and the relative importance of parasitoids for the regulation of their populations.

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The leafminers

Leafminers are insects whose larvae live and feed inside the leaves, consuming the mesophyll without damaging the leaf epidermis. Their feeding tracks ("mines") are externally visible in leaves, as whitish or grey areas with variable shapes that rangefrom narrow linear galleries to wide chambers (Hering, 1951). The leaf mining habit has been developed by a group of over 10,000 species of holometabolous insects, concentrated in four orders: Diptera, Coleoptera, Hymenoptera, and Lepidoptera (Connor and Taverner, 1997).

The galleries excavated by the leafminer larva can reduce the photosynthetic capacity of leaves, cause premature leaf abscission, and permit pathogen entry into plant tissue. Moreover, they reduce the esthetic value of ornamental plants or edible leaves (Spencer, 1973; Parrella and Jones, 1987; Minkenberg and Van Lenteren, 1986; Maier, 2001; Valladares, in press). Many species are considered pests in several parts of the world. Among these are the citrus leafminer *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), and more than 100 species of leaf mining flies (Diptera: Agromyzidae), especially *Liriomyza trifolii* (Burgess) and *Liriomyza huidobrensis* (Blanchard) in horticultural crops, and *Agromyza frontella* (Rondan) in alfalfa (Amalin, *et al.* 2002; Dempewolf, 2004).

Most authors agree that a leafminer species becomes a pest due to insecticide resistance development and the elimination of their natural enemies. The latter is a consequence of aggressive agricultural practices (i.e. plowing, breaking up, and burning of soils, etc.) and the use of agrochemicals (Spencer, 1973; Minkenberg and Van Lenteren, 1986). Furthermore, another two factors can importantly contribute to elevate leafminer population sizes: 1. Relative inconspicuousness, allowing them to go unnoticed until reaching high densities (Maier, 2001), and 2. The protection of their immature stages inside plant tissue, especially against the effects of contact insecticides. This last characteristic has promoted the indiscreet use of wide spectrum insecticides, which have decimated their natural enemy populations. At the same time, leafminer adults have developed resistance, going from being secondary pests to becoming primary pests (Murphy and La Salle, 1999; Civelek and Weintraub, 2003). Concrete examples of this are *Liriomyza sativae* (Hills and Taylor, 1951), *L. trifolii* (Reitz *et al.*, 1999), leafminers of the genus *Phyllonorycter* on fruit trees (Maier, 2001), and several leafminer pests on tomatoes (Gelenter and Trumble, 1999).

Another factor that could contribute to certain leafminer species becoming pests is the increase in monocultivation. Many parasitoids have preference for specific plants. Therefore, if the only crop present is not attractive for the parasitoids, leafminers may escape parasitoidism in this environment (Murphy and La Salle, 1999). Finally, the increase of extensive horticulture and plant commercialization without appropriate quarantine controls has also favored the expansion of leafminer pest distribution.

Causes of leafminer mortality

Intraspecific competition, both direct by interference, or indirect or exploitive, represents an important cause of mortality for the leafminer larvae (Faeth, 1990; Auerbach *et al.*, 1995; Eber, 2004). Leaf abscission has also been indicated as another important survival factor for leafminers (Potter, 1985; Faeth, 1990; Girardoz *et al.*, 2006a). Abscission can be interpreted as the plant defense induced by leafminer attack. Nevertheless, in some cases, it could benefit the leafminers by freeing them from potential parasitoid attack (Kahn and Cornell, 1989). On the other hand, some leaf mining larvae release cytokinins that maintain green areas ("green islands") in ageing leaves, which allows them to complete their development. Stiling and Simberloff (1989), after studying the mortality of some species that induce leaf abscission, conclude that this phenomenon must be seen, from a parsimonious point of view, as a simple response of the plant to the phytophagous damage. Other plant defense mechanisms, mostly related to chemical and physical aspects, have also been mentioned (Valladares and Lawton, 1991).

The action of natural enemies occurs by

predation and parasitoidism. Predation has been cited as the greatest cause of mortality at the beginning of the growing season of some crops, while parasitoidism is more important in more advanced stages of crop development (Queiroz, 2002; Urbaneja *et al*., 2000). Except for some leafminers, such as *Tuta absoluta* (Lepidoptera: Gelechiidae), very low mortality values due to parasitoidism (<1%) and high levels of larval mortality due to predation, which can reach up to 80% (Motta Miranda *et al*., 1998), have been reported.

Leafminer predators include birds, spiders and insects. Among the insects, there are predators in various families of Coleoptera (ej. Carabidae, Cicindelidae, Staphylinidae), Hemiptera (i.e. Anthocoridae, Nabidae, Lygaeidae), and Hymenoptera (i.e. ants) (Cisneros and Mujica, 1998; Motta Miranda *et al*., 1998; Arno *et al*., 2003; Grabenweger *et al*., 2005). The effect of predators sometimes surpasses the effect of parasitoidism (Memmott *et al*., 1993; Queiroz, 2002; Xiao *et al*., 2007); furthermore, they can even have an adverse effect on the mortality caused by parasitoids (Sato and Higashi, 1987).

Although the relative influence of predators and parasitoids in regulating different leafminer species is variable, the literature indicates that, in general, the parasitoids constitute the most important group (Parrella, 1987; Hespenheide, 1991). Parasitoids have a key function in leafminer population control in natural ecosystems and in cultivated areas with a rational use of insecticides (Lewis *et al*., 2002).

The leafminer parasitoids

The leafminers are in the phytophagous guild (group of organisms that consume the same resource in the similar manner), which has the greatest number of parasitoid species per host species, and has the highest average rate of parasitoidism (Hawkins, 1994). Characteristics of leafminer habits, such as the scarce mobility of the larvae, the clear visibility of the mines produced, and the scarce physical protection provided by the leaf epidermis, are the main causes of leafminers' vulnerability to parasitoids (Hochberg and Hawkins, 1992). On the other hand, leafminers are herbivorous insects characterized by a distinct homogeneity of both ecological and taxonomic aspects (Connor and Taverner 1997), which facilitates the development of a diverse community of parasitoids that share hosts, and would explain why this insect group as a whole has an elevated load of parasitic species (Godfray, 1994).

Most of the leafminer parasitoid species correspond taxonomically to the superfamilies Chalcidoidea (Families Eulophidae and Pteromalidae), Ichneumonoidea (Family Braconidae), and Cynipoidea (Family Figitidae) (Salvo, in press). These insects may be classified as idiobionts, when they permanently paralyze their host when ovipositing, or as koinobionts, which only temporarily paralyzes the host, allowing it to continue its development prior to provoking its death (Askew and Shaw, 1986). The idiobiont/koinobiont dichotomy would be associated with a series of differentiating characteristics related to their host group's preference, feeding specificity, reproductive strategy, development time, competitive capacity, presence of sexual dimorphism, etc. (Gauld and Bolton, 1988; Salvo and Valladares, 1999).

The idiobionts, by permanently paralyzing their hosts, risk the possibility that their food resource will later be attacked by other organisms, so they are more frequently associated with endophytophagous insects, which feed inside plant tissues and are better protected from unfavorable conditions (Quicke, 1997). On the other hand, by attacking a resource without physiological defenses, the idiobionts could consume a greater variety of hosts.

Conversely, the koinobionts must coexist for some time with an active organism and, therefore, are restricted to fewer host species. Since leafminers are endophagous insects, it is expected that their parasitic complexes will be dominated by idiobiont species (Hawkins, 1994), which is not always the case (Salvo, 1996).

In terms of food specificity, the literature contributes abundant evidence that leafminer parasitoids have ample food ranges, generally defined by the host ecology (Godfray, 1994; Salvo and Valladares, 1999). This wide food range has interesting consequences regarding introduced species management, since it allows the leafminer parasitoids present in an area to incorporate the invasive species into their spectrum of hosts in relatively short periods of time (Murphy and La Salle, 1999). In effect, when a leafminer species invades a new region and becomes a pest, it initially possesses a low number of associated parasitic species, and they are mostly generalist idiobionts with low rates of parasitoidism. However, the new leafminers are soon colonized by other parasitoids and reach total parasitoidism levels similar to that of native leafminers, which is often sufficient to achieve natural control. For example, this process has been observed in *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae) in diverse regions of the world (Uygun *et al.*, 1997; Urbaneja *et al.*, 2000; Amalin *et al.*, 2002; Vercher *et al.*, 2005; Diez *et al.*, 2006). However, on occasion, the recruiting of a parasitic complex similar to that of other leafminers is not accompanied by the expected mortality levels (Grabenweger, 2004), which may be due to poor synchronization between pests and parasitoids, or to the lack of density-dependent responses (degree of response dependent on population density) (Malausa, 1997; Girardoz *et al.*, 2006b).

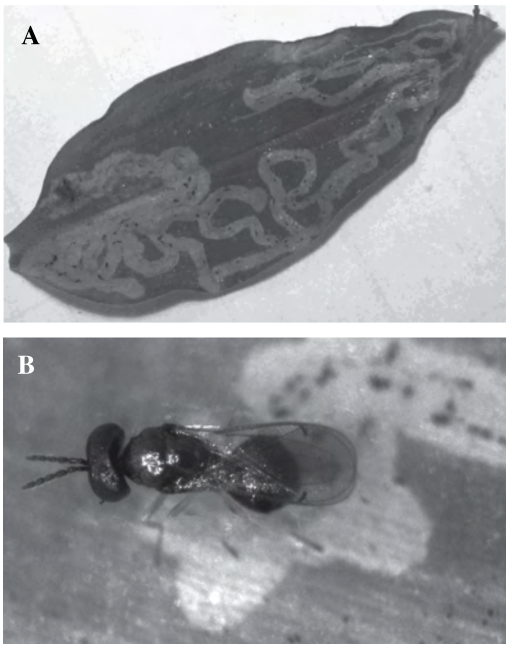

Figure 1. Leafmine of *Liriomyza commelinae* (Frost) (Diptera: Agromyzidae). A. Leafmine on *Commelina erecta* L. (Commelinaceae). B. Female parasitoid, *Chrysocharis flacilla* (Hymenoptera: Eulophidae) searching for its host.

The efficiency of parasitoids as agents of leafminer mortality varies depending on the species, and it may even vary between different larval stages of the same species, as well as in relation to environmental conditions (Grabenweger, 2003). For example, parasitoids are likely to be a more important cause of mortality in temperate zones than in the tropics (Hawkins *et al.*, 1997; Queiroz, 2002). Similarly, parasitoidism rates would be higher at the end of the growing season, at least in cultivated systems (Parrella, 1987; Murphy and La Salle, 1999; Urbaneja *et al.*, 2000). The presence of other organisms may also affect leafminer parasitoidism rates; in this regard, there is evidence of effects caused by other herbivorous insects, such as externally chewing herbivores (Faeth, 1985), and even by the presence of endophytic fungi (Preszler *et al.*, 1996).

Tritrophic plant-herbivore-parasitoid interactions are important in these systems (Price *et al.*, 1980). It has been observed that parasitoidism may also vary depending on plant species (Olivera and Bordat 1996; Rauf and Shepard, 1999), or even between cultivars or genotypes of the same plant species in which the leafminer develops (Fritz *et al.*, 1997; Braman *et al.*, 2005). For example, *L. huidobrensis* parasitoidism in potato is very low compared to that observed in other crops (Shepard *et al.*, 1998). According to Johnson and Hara (1987), effective biological control of certain leafminers may depend on the plant species on which the leafminer feeds. One aspect related to the leafminer host plant that may affect their parasitoidism level, mentioned earlier, is leaf abscission. In some cases, leaf abscission causes mortality to both the leafminer and parasitoid (Potter, 1985), while in other systems, the abscission reduces larvae parasitoidism due to the fact that parasitoids don't search for hosts in fallen leaves (Kahn and Cornell, 1989).

Finally, other factors that affect leafminer parasitoidism include: droughts (Staley *et al*., 2006), leaf age (Facknath, 2005), and leafminer position in the plant (Barrett, 1994; van der Linden 1994; Brown *et al*., 1997).

In parasitoid insects, as well as parasitoidism itself, there are two other behaviors that may increase leafminer mortality: 1. feeding on the host (host feeding) and 2. host paralyzation without oviposition or feeding (host stinging).

In the first case, adult wasps feed on a certain proportion of leafminer larvae, which may or may not be a previous requisite for egg laying (Jervis and Kidd, 1986). Some parasitoids use hosts of different sizes, either as a substrate for egg laying or to feed upon (Duncan and Peña, 2000). The magnitude of the mortality due to host feeding may be similar to, or even higher than, that caused by the parasitoidism itself (Amalin *et al*., 2002; Bernardo *et al*., 2006). However, the effect of host feeding, functionally comparable to predation, is frequently ignored. This may greatly underestimate the levels of mortality caused by parasitoid species (Cure and Cantor, 2003).

In some leafminer parasitoid species, particularly belonging to the genera *Diglyphus* Walker, Sympiesis Foerster and Pnigalio Schrank (Hymenoptera, Eulophidae), paralyzation and death of leafminer larvae are often observed without them being used as an ovipositon substrate or to feed on (Casas, 1989). This behavior, interpreted as a way to decrease the number of leafminer larvae in the plant to ensure the survival of the parasitized ones, varies with the size of the hosts availability, their density, the size of cages in which the parasitoids are reared, and temperature (Heinz and Parrella, 1989; Patel and Schuster, 1991; Patel *et al*., 2003).

Density-dependence in parasitoidism is a phenomena usually considered favorable for host population regulation to be effective (Connor and Beck, 1993; Eber *et al*., 2001). In some cases, the parasitoidism caused by native parasitoids is more coupled to the density of an exotic leafminer than the parasitoidism caused by the parasitoids introduced for their control (Amalin *et al*., 2002). The density of hosts can also affect other aspects in the parasitoid-leafminer relationship, like searching behavior (Connor and Cargain, 1994).

Biological control

Cases of leafminer biological control, cited in the literature, mainly report on the introduction and augmentative release of parasitoid insects, although other organisms have also been employed, such as nematodes and bacteria (Sher *et al*., 2000; van Mele and van Lenteren 2002; Cikman and Comelkcloglu, 2006). There are numerous successful examples of classic biological control (introduction of agents for the control of a native or foreign pest) with parasitoids for different species of leafminers, both in the open field (Dharmadhikari *et al*., 1977; Johnson *et al*., 2003; García-Marí *et al*., 2004) and in greenhouses (van Lenteren and Woets, 1988; Heinz and Parrella, 1990; Abd-Rabou, 2006). In these cases, studies prior to introduction are important and include tolerance to humidity, ability to recognize previously parasitized hosts, existence of alternative hosts, as well as synchronization with the host (Wang *et al*., 1999; Grabenweger, 2004; Girardoz *et al*., 2006b; Zappala and Hoy, 2004). Temperature constraints have also been shown to be an obstacle for a leafminer parasitoid to be successfully introduced in some regions (Klapwijk *et al*., 2005; Llácer *et al*., 2006).

Large-scale rearing of parasitoids for leafminer control has been considered in the literature (Parrella *et al*., 1989; Kharrat and Jerraya, 2005). Diverse factors have been mentioned as important at the time of carrying out large-scale rearing, among which can be highlight humidity, photoperiod, and temperature (Yoder and Hoy 1998; Urbaneja *et al*., 2001; Lim *et al*., 2006; Kafle *et al*., 2005; Haghani *et al*., 2007).

Large-scale rearing of parasitoids implies simultaneous management of three trophic levels, which can be difficult (Smith and Hoy, 1995). The costs and benefits for rearing parasitoids should be carefully analyzed, and various modifications have been proposed in order to get positive results based on conventional techniques (Rizqi *et al*., 1999). The overproduction of males in large-scale parasitoid rearing increases the costs of biological control because only females kill the hosts. For this, techniques have been developed to significantly increase the proportion of females by means of using different sized hosts (Ode and Heinz, 2002; Chow and Heinz, 2006).

The size of the leafminers may not only affect the sex ratio but also the size of the parasitoids reared on them, which could have consequences on their reproductive capacity (Abe *et al.*, 2005). Intraspecific differences in body size have been observed, for both parasitoids that develop in different host species (Salvo and Valladares, 1996), as well as for those that parasitoidize the same polyphagous leafminer species that reach different body sizes on different host plants (Salvo and Valladares, 2002). Studies on *Diglyphus websteri* (Crawford) (Hymenoptera: Eulophidae) laboratory rearing demonstrated the effects of temperature, host species, and sex ratio on the size and other growth parameters of the species reared. Complicated interactions between sex ratio-temperature, host-temperature, and host- sex ratio-temperature (Bazzocchi *et al.*, 2003) have been also observed. .

A decrease in the proportion of males can be induced through the use of bacteria (Argov *et al.*, 2000). Species of *Wolbachia* are one of the most ubiquitous bacteria in insects, which manipulates the reproduction of the host in several ways, among which can be mentioned cytoplasmic incompatibility, male death, feminization of genetic males, and induction of parthenogenesis (West *et al.*, 1998). It has been proposed that infected wasps could be more efficient as leafminer biological control agents (Tagami *et al.*, 2006a,b).

It is important to keep in mind that adults obtained in the laboratory may exhibit differences in parasitoidism and host-feeding capacity in relation to adults obtained in the field (Arno *et al.*, 2003). Therefore, quality control studies of parasitoids obtained through large-scale rearing methods are required.

A long debate, at the time of introducing natural enemies, consists in knowing if one single species would be more effective in regulating the pest than various species. Some studies using leafminer parasitoids indicate that two species released together do not control the host better than when releasing only one (Bader *et al.*, 2006). To establish *a priori* the feasibility of multiple introductions, various laboratory studies have been carried out to determine the role of competition and interference in leafminer parasitoids (Heimpel and Meloche, 2001; Urbaneja *et al.*, 2003; Mitsunaga and Yano, 2004), and also the possible interaction between predators and parasitoids (Wu and Lin, 1998).

The simultaneous introduction of parasitoids and nematodes has been analyzed, with conflicting results: in some cases, parasitized leafminer larvae were infected by the nematode, which reduced the survival of the leafminer and the parasitoid as well (Head *et al.*, 2003), while in other cases, there was compatibility between the parasitoids and nematodes (Shanower *et al.*, 1992). A crucial element could be the time at which each enemy is released in the field. There are examples in which the application of nematodes after the release of parasitoids increased the degree of control, but when applied before the impact was negative (Sher *et al.*, 2000). In the context of simultaneous use of parasitoids and other organisms, the use of *Bacillus thuringiensis* is worth mention, and has shown good results against some leafminer species (Khyami-Horani and Ateyyat, 2002), including some positive effects on the parasitoids (Cikman and Comelkcloglu, 2006).

Parasitoids and chemical control

In regard to chemical control, most leafminers are resistant to organophosphorates, carbamates, and pyrethroids, and at the same time, their natural enemies are severely damaged by these chemicals, which leave few options for their chemical control. Insecticides that do not penetrate the leaf surface are practically ineffective (Weintraub and Horowitz, 1999). For this reason, insecticides with good translaminar action (i.e. cyromazine and abamectin) are the most widely used against leafminers (Civelek and Weintraub, 2003). Growth inhibitors are useful in controlling leafminers, and at the same

Table 1. Studies evaluating the toxicity of several chemical substances for parasitoids of leafminers.

Pesticides	Toxicity[1]		
	High	Moderated	Low
Acetamiprid		Mafi and Ohbayashi, 2006	Hidrayani *et al*., 2005
Alanycarb	Mafi and Ohbayashi, 2006	Weintraub and Horowitz, 1998	Parrella and Kaspi, 2005
Abamectin	Schuster, 1994 Villanueva-Jiménez and Hoy, 1998 Weintraub, 1999; Shen *et al*., 2003 Bjorksten and Robinson, 2005 Parrella and Kaspi, 2005.	Prijono *et al*., 2004	
Bifenthrin		Mafi and Ohbayashi, 2006	
Carbosulfan	Hidrayani *et al*., 2005		
Cloropyrifos	Prijono *et al*.,2004		
Clothianidin		Mafi and Ohbayashi, 2006	Mafi and Ohbayashi, 2006
Cyromazin		Weintraub and Horowitz, 1998 Weintraub, 1999.	Weintraub, 1999; Shen *et al*., 2003; Prijono *et al*., 2004; Bjorksten and Robinson, 2005
Diflubenzuron		van Driesche *et al*., 1998	Villanueva-Jiménez and Hoy, 1998; Mafi and Ohbayashi, 2006
Dimetoato	Darvas and Andersen, 1999		
Dinotefuran	Mafi and Ohbayashi, 2006		
Etofenprox	Saito 2004		
Fenoxycarb			Parrella *et al*., 1983; Grenier and Grenier, 1993; Villanueva-Jiménez and Hoy, 1998.
Fenvalerato			Rathman *et al*., 1990
Flufenoxuron			Shen *et al*., 2003
Imidacloprid	Villanueva-Jiménez and Hoy, 1998; Tran *et al*., 2005	Mafi and Ohbayashi, 2006	Villanueva-Jiménez and Hoy, 1998.
Isoxathion	Mafi and Ohbayashi, 2006		
Lufenuron	Tran *et al*., 2005		
Mancozeb		van Driesche *et al*., 1998	Prijono *et al*., 2004; Bjorksten and Robinson, 2005
Methomyl	Saito, 2004	van Driesche *et al*., 1998	Rathman *et al*., 1990
Milbemectin			Ohno *et al*., 1999
Mineral oil		Conti *et al*., 2004, Mafi and Ohbayashi, 2006	Villanueva-Jiménez and Hoy, 1998
Neem and other natural products		Conti *et al*., 2004	Villanueva-Jiménez and Hoy, 1998; Immaraju, 1998; Abou-Fakhr Hammad *et al*., 2000; Banchio *et al*., 2003; Chen *et al*., 2003a; Shen *et al*., 2003.
Organophosphates	Villanueva-Jiménez and Hoy, 1998		Rathman *et al*., 1990
Othion	Villanueva-Jiménez and Hoy, 1998		
Oxamyl		van Driesche *et al*.,1998	Rathman *et al*., 1990
Permethrin	Saito 2004		Rathman *et al*., 1990
Pimetrozin	Tran *et al*., 2005		
Profenofos	Hidrayani *et al*., 2005		
Prothiofos	Saito, 2004		
Teflubenzuron			Mafi and Ohbayashi, 2006
Thiamethoxam		Mafi and Ohbayashi, 2006	

[1]Given the various approaches used in the studies, three qualitative levels of toxicity were considered: low, parasitoids are not significantly affected; high, parasitoids suffer high mortality and/or population reduction; and moderated, effects are noticeable, but they are not very strong, or are variable among generations, treatments, etc.

time, are potentially compatible with biological control agents due to their low toxicity and high specificity.

There are numerous studies on the susceptibility of leafminer parasitoids to different types of insecticides (Table 1). Some species of leafminer parasitoids have developed resistance, mainly to organophosphorates. For example, *Diglyphus begini* (Ashmead) (Hymenoptera: Eulophidae) is tolerant to oxamyl, methomyl, permethrin, and fenvalerate (Rathman *et al.*, 1990). Insecticide application time and method may affect the susceptibility of the parasitoids (Kaspi and Parrella, 2005; Weintraub, 1999), which varies between species (Mafi and Ohhayashi, 2006) and even between genders (Rathman *et al.*, 1992).

In studies with different leafminer species, crops treated with low doses or without insecticides had higher percentages of parasitoidism (Galantini Vignez and Redolfi de Huiza, 1992; van Driesche *et al.*, 1998; Adachi, 2002; Chen *et al.*, 2003a). Likewise, in organic crops, greater parasitoid species richness along with improved efficiency has been observed (Balázs, 1998). However, in other cases, there was no difference on leafminer parasitoid densities between plots treated and not treated with synthetic insecticides (Mafi and Ohbayashi, 2004).

Parasitoids and cultural control

It is possible to increase the action of leafminer enemies through habitat management (Price and Harbaugh, 1981). Different studies mention the importance of weed patches near crops as possible reservoirs of parasitoids (Murphy and La Salle, 1999). For this reason, it has been suggested that the management of weeds and other plants in or at the edge of an agroecosystem can improve the availability of pollen and nectar for leafminers' natural enemies (van Mele and van Lenteren, 2002). In some cases, the presence of flowering plants in habitats nearby produces an increase in leafminer parasitoidism (Chen *et al.*, 2003b). However, in other cases, the increase in plant diversity had no effect on leafminers or their parasitoids (Johnson and Mau, 1986; Letourneau, 1995).

Although some weeds may act as reservoirs of leafminer pests (Smith and Hardman, 1986; Schuster *et al.*, 1991), others give refuge to leafminer specialists, which do not harm crops. In the latter case, weeds provide alternative hosts for the parasitoids, thereby increasing the biological control in crops. These plant species could be used for the implementation of open-field rearing of parasitoids (Parkman *et al.*, 1989), which consist of favoring the presence of plants and harmless leafminers, in the same environment as the crop, to increase populations of natural enemies. Rearing parasitoids in the open field has been successful for controlling some leafminers (van der Linden, 1992). For this, the knowledge of leafminer host ranges and their parasitoids is critical (Parkman *et al.*, 1989; Chen *et al.*, 2003b; Rizzo, 2003). In some cases, the study of trophic webs in different environments has made possible the theoretical proposal of open-field rearing systems, taking into account the possible interactions between the species at three trophic levels (Valladares and Salvo, 1999).

Policultures and planting additional plant species with the main crop may also have a positive effect on parasitoids. For example, it has been observed that at the beginning of the sweet potato crop cycle, growing kidney bean plants in adjacent strips attracts *L. huidobrensis* parasitoids, and advances and increases their presence in the sweet potato crop (Da Paixão Pereira *et al.*, 2002). Likewise, potato cultivated along with wheat has less leafminer damage because wheat attracts parasitoids (Ebwongu *et al.*, 2001).

Adult parasitoid food provisioning, by means of sugar solutions or honey, is a conservation biological control practice that has been repeatedly used (Powell, 1986). However, in some cases, the provision of food for the parasitoids of a primary pest can have a negative impact on the control of secondary pests, to which leafminers generally belong to (Mitsunaga *et al.*, 2006).

Among biological control techniques that augment and conserve leafminers' natural enemies, physical devices have been designed to allow parasitoids to escape, which are generally smaller than their hosts, based on containers with mined leaves (Kehrli *et al.*, 2005). This apparatus serve to augment or conserve local or foreign parasitoid populations and could be a low cost alternative to the release of conventionally reared natural enemies. This method can be used where chemical control is forbidden, like in the case of organic agriculture. By making adjustments in screen size, diverse parasitoid and host systems can be managed in this way (Kehrli and Bacher, 2004).

It is important to keep in mind that although some practices recommended that leafminer control favor the increase of parasitoid populations, others harm them. For example, flooding to drown pupae of certain leafminers, or sunlight exposition of pupae to provoke their death also reduces populations of larvo-pupal parasitoids (Braun and Shepard, 1997).

Compost application to the crop may have an indirect effect on leafminers, increasing their predator's diversity and efficiency (Brown and Tworkoski, 2004). However, nitrogen fertilizers must be used with care because they can stimulate pest development, augmenting not only the plant's vigor, but also the survival of leafminer larvae and pupae (van Lenteren and Overholt, 1994). There might be fertilization thresholds above which the numbers of leafminer pupa are augmented and the parasitoidism diminishes, as shown in citrus leafminers (Ateyyat and Mustafa, 2001). On the other hand, elevated levels of nitrogen fertilization in kidney bean crops decreased the development time and increased the fertility of the parasitoid *Chrysocharis oscidinis* (Hymenoptera: Eulophidae) on the leafminer *Liriomyza trifolii* (Kaneshiro and Johnson, 1996). Other studies have evaluated the effect of fertilization on parasitoidism rates, without analyzing the mechanisms involved (Yarnes and Boecklen, 2006).

One practice recommended for reducing leafminer populations is the destruction of plant residues from the previous harvests that were attacked by pests, which can be burned or buried (Larraín, 2004), but this practice also reduces parasitoid populations (Vincent *et al.*, 2004). However, pruning during summer and placing the cut branches under the trees resulted in a decrease in the number of citrus leafminer larvae and pupae without affecting parasitoidism (Ateyyat and Mustafa, 2001).

Sticky traps, consisting usually of yellow sticky surfaces, play a double role, monitoring leafminer populations (to learn the appropriate time to apply some type of control), and at the same time, decrease the number of leafminers in a field (Larraín, 2004). These traps are used in integrated pest management programs for leafminer flies (Agromyzidae), where the number and surface area of traps for effective control is known in some detail (Braun and Shepard, 1997). However, there is a possibility that yellow sticky traps decrease parasitoid populations (Gonçalves, 2006). The combination of yellow traps with attractive substances for the leafminers, such as extracts of host plant leaves, notably decreases the capture of other insects and possibly also reduces the number of parasitoids trapped there (Harand *et al.*, 2004).

Integrated pest and leafminer management

The integration of various practices in integrated pest management programs has proven to be successful in the control of leafminers. The replacement of synthetic chemical pesticides by biopesticides (i.e. *Bacillus thuringiensis*) or the selective use of insecticides with low impact on the natural enemies, the decrease of disturbances imposed in the system (through less aggressive agricultural practices), and the implementation of the different types of biological control all increase the chances of controlling leafminers (Murphy and La Salle, 1999).

Laboratory experiments with cages demonstrate that the release of *Diglyphus isaea* together with the release of sterile male *L. huidobrensis* constitutes a more efficient method than the use of each technique separately (Kaspi and Parrella, 2006). Some parasitoids can develop in eggs laid by females sterilized by gamma rays, even over several generations (Harwalkar *et al.*, 1987).

Diverse studies have undertaken the implementation of integrated pest management programs for the control of leafminers, including models and detailed costs-benefit analyses (Dudley *et al.*, 1989; Shepard *et al.*, 1998; Gelernter and Trumble, 1999; Reitz *et al.*, 1999; Motta Miranda *et al.*, 2005). They agree that it is possible to markedly decrease the amount of pesticides applied compared to calendar applications. For example, the integrated pest management programs for *L. huidobrensis* in Perú include the use of resistant or tolerant varieties, irrigation management, elimination of harvest waste, sticky yellow traps, insecticides with low toxicity, and biological control (Palacios *et al*., 1995). In greenhouses, the application of adulticides (i.e. pyrethroids) to reduce the initial populations of the miner pest, in combination with two or three applications of selective insecticides, such as azadirachtin, minimizes the possibility of resistance and ensures the control of all the stages of the pest without obstructing the action of natural enemies, extending the control range (Immaraju, 1998).

Conclusion

As a conclusion, is important to emphasize that there are abundant bibliographic records that detail the relationship between parasitoids and leafminers. They include descriptive biological or ecological aspects without direct relation to the management of pest species, studies which were not included here because they were beyond the objective of this review. Also, there are numerous practical studies available that analyze the compatibility of parasitoid use combined with different chemical pesticides, as explained above.

The areas that are less developed are those that explore the importance of the different sources of mortality in leafminer life tables and the impact of agricultural practices on the parasitoid fauna. In this regard, the effect of nearby weeds on the parasitoids is practically unknown, and information referring to the interaction of pest parasitoids with other hosts in the agroecosystem is also scarce. To have this type of information available, especially incorporating information on the three trophic levels involved: plants (cultivation and spontaneous vegetation), leafminers (pest and alternative hosts), and parasitoids, would make the implementation of ecologically sound management strategies possible. Open-field parasitoid rearing systems, management of plant diversity, and other environmental manipulation methods, constitute, in this sense, alternatives that have been, up to now, scarcely employed for leafminer pest control.

Resumen

Los minadores de hojas son insectos cuyas larvas viven y se alimentan dentro de las hojas, consumiendo el mesófilo sin dañar la epidermis foliar. Varias especies son consideradas serias plagas de cultivos intensivos, hortícolas y ornamentales. Entre las fuentes de mortalidad más importantes para este gremio de fitófagos se citan a los enemigos naturales, de los que se destacan los parasitoides como el grupo más efectivo y mejor representado. Este artículo proporciona un resumen actualizado de la información disponible sobre parasitoides de minadores de hojas en relación al manejo de plagas. Por ser generalistas, los parasitoides de minadores de hojas pueden incluir rápidamente en su rango alimenticio a especies introducidas, muchas veces lográndose un control efectivo luego de unos pocos años de establecida la plaga. Control biológico clásico y aumentativo son estrategias ampliamente usadas para regular las poblaciones de minadores de hojas plaga. Numerosos estudios abordan la compatibilidad del uso de parasitoides con control químico y cultural. Si bien la mayoría de los insecticidas convencionales poseen efectos adversos para los parasitoides, otros serían compatibles con el control biológico. Se conoce que la combinación de diversas estrategias de control en programas de manejo integrado de plagas ha resultado efectivo contra minador de hojas plaga. Sin embargo, los efectos de prácticas culturales que podrían favorecer las poblaciones de parasitoides han sido escasamente estudiados.

Palabras clave: Control biológico, control cultural, control químico, minadores de hojas, parasitoides.

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