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THE LEAFMINERS *LIRIOMYZA*
BRYONIAE AND *L. TRIFOLII*
(DIPTERA: AGROMYZIDAE), THEIR
PARASITES AND HOST PLANTS:
A REVIEW.

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ABSTRACT

The leafminer *Liriomyza trifolii* has become an important pest organism in ornamentals and vegetables throughout the world. This leafminer poses a threat to the current pest control system in greenhouse vegetables in the Netherlands, which employs parasitic wasps, predators and selective chemicals. Chemical control of *L. trifolii* is problematic due to the rapid development of resistance against insecticides. Application of biological control may help to overcome both the difficulty of control of *L. trifolii* and integration problems with other biological pest control methods. Ideally, a biological control method for *L. trifolii* should also be effective against another leafminer species, *L. bryoniae*, which also occurs as a pest in greenhouses. In this paper, the current situation with regard to control of *L. bryoniae* and *L. trifolii* is evaluated. The relationships between these leafminer species, their parasites, their host plants, and factors influencing these relationships are reviewed. A list of parasites and predators is provided with some notes on their biology. Finally, procedures for evaluation of the effectiveness of parasites are discussed.

1 INTRODUCTION

Agromyzid leafminers cause serious pest problems in ornamentals and vegetables throughout the world. The larvae feed in leaf mesophyll tissue, which may cause reductions in crop value or yield (SPENCER 1973).

The polyphagous leafminers, *Liriomyza bryoniae* (Kaltenbach) and *L. trifolii* (Burgess), are important greenhouse pests in the Netherlands; *L. bryoniae* is long known as a pest of tomato, while *L. trifolii* was reported for the first time in 1976 (VAN FRANKENHUYZEN and VAN DE BUND 1979). *L. trifolii* has become a cosmopolitan species and is reported as a pest for chrysanthemum (LINDQUIST et al. 1980; PRICE 1981; PARRELLA et al. 1981a; BROADBENT 1983), gerbera (D'AGUILAR et al. 1980), gypsophila (PRICE and STANLEY 1983), celery (GENUNG and JANES 1975; LEIBEE 1981a; TRUMBLE 1981; GRILL 1984), tomato (ZEHNDER and TRUMBLE 1984), cowpea (SINGH and MERRETT 1980), bean and potato (VERCAMBRE 1980; FAGOONEE and TOORY 1983).

Under natural conditions agromyzid larvae are heavily parasitized by a diverse parasite-complex (e.g., 15 species parasitize *Phytomyza ranunculi* Schrank (SUGIMOTO et al. 1983) and 21 species parasitize *Chromatomyia syngenesiae* Hardy (CORNELIUS and GODFRAY 1984)), which may explain the often low abundance of leafminers in unsprayed crops (HILLS and TAYLOR 1951; MICHELBACHER et al. 1951; FRICK 1952; LANGE et al. 1957; OATMAN 1959; HARDING 1965; OATMAN and PLATNER 1969; BRAGG 1974; HAFEZ et al. 1974; GENUNG and JANES 1975; GREATHEAD 1975; MUSGRAVE et al. 1975a,b, 1976; PRICE and POE 1976; HENDRICKSON 1980; JOHNSON et al. 1980a; TRUMBLE 1981; CHANDLER 1982; MACCOLLUM et al. 1982; PRICE and DUNSTAN 1983). The use of non-selective chemicals is generally considered as the main cause of leafminer damage, because the parasites of leafminers are very susceptible to these chemicals (SPEYER and PARR 1948; WENE 1955; GETZIN 1960; WOLFENBARGER 1962; SHOREY and HALL 1963; JENSEN and KOEHLER 1970; BRAGG 1974; GENUNG and JANES 1975; MUSGRAVE et al. 1975b; WADDILL 1978; JOHNSON et al. 1980b,c; LANGE et al. 1980; FALCÓN et al. 1983). OATMAN and KENNEDY (1976) clearly demonstrated the elimination of beneficial parasites by broad spectrum insecticides. The combined effect of elimination of natural enemies and the development of resistance of leafminers against commonly used insecticides leads to increasing control problems.

This paper reviews the current situation with regard to the control of *Liriomyza* spp. To obtain a good insight into the pest problems and possibilities for biological control, the relationships between leafminer species, parasites and host plants, and factors influencing these relationships are also reviewed.

1.1 THE LEAFMINER PROBLEM IN THE NETHERLANDS

The area of heated greenhouses in the Netherlands comprises ca. 8000 ha

in 1985; 4109 ha with ornamentals such as rose, chrysanthemum, gerbera and gypsophila, and 3868 ha with vegetables such as lettuce, tomato, cucumber and sweet pepper. Tomato covers 1959 ha, of which 45% is rockwool cultivation. The main vegetable cropping period for tomato starts in mid winter (Dec./Jan.) and extends over 6 to 10 months.

For more than a decade, the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), is being controlled successfully with the parasitic wasp *Encarsia formosa* Gahan in 25-30% of the total area of greenhouse tomatoes (VAN LENTEREN et al. 1980). Against other insect or mite pests, control methods compatible with this biological control method are available (RAVENSBERG et al. 1983). *L. bryoniae* was reported as a pest in the Netherlands in 1965 and 1966 (DE BROUWER and VAN OFFEREN 1966), but since 1976 *L. bryoniae* occurs in large numbers in tomatoes. A biological control programme against the leafminer did not exist, so growers had to apply chemicals. As a consequence, biological control of the whitefly was disturbed. This prompted research into the possibilities of controlling *L. bryoniae* biologically. The parasite *Opius pallipes* Wesmael proved to be the most promising candidate (HENDRIKSE et al. 1980) and trials in commercial greenhouses were reasonably successful (WOETS and VAN DER LINDEN 1983). However, since 1980 a second leafminer species, *L. trifolii*, appeared as a pest on vegetables. Biological control by *O. pallipes* is ineffective against this species, because the parasite eggs are encapsulated when deposited in *L. trifolii* larvae (WOETS and VAN DER LINDEN 1982a). Chemical control of *L. trifolii* requires pyrethroids, methomyl and other compounds, the use of which upsets

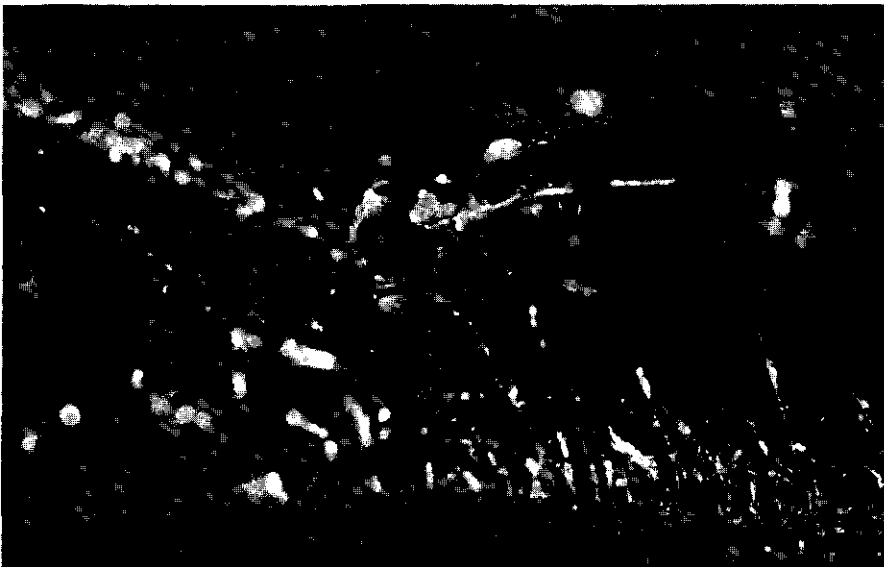


PHOTO 1: The agromyzid fly (*Liriomyza bryoniae*) sucking the contents of mesophyl cells after having macerated them by its ovipositor. The protruding ovipositor-sheath of the female is clearly visible (photo: J. C. VAN LENTEREN).

the current system of integrated control (RAVENSBERG et al. 1983). Leafminers of both species are common in greenhouse tomatoes, although *L. trifolii* thrives only in summer. Leafminers are able to flourish due to the year-round cultivation and the use of rockwool as substrate, which does not require soil disinfection. Another contributing factor to fast population development is immigration in winter and spring with young plants and during summer via open windows, because most of the greenhouses are located in close vicinity to each other.

For cutflower producers *L. trifolii* has presented a recurrent problem on chrysanthemum, gerbera and gypsophila (VAN DE VRIE and DIRKSE 1982). In 1982, an intensive information campaign was started by the Extension Service, the Glasshouse Crops Research and Experiment Station and Research Station for Floriculture to improve control of *L. trifolii*. Eradication was impossible. Finland prohibited the importation from the Netherlands of several host plants of *L. trifolii* in 1980 and British plant health authorities demanded more stringent inspections. In 1981, a pre-export inspection system for cutflowers, the 'green corner', was set up. For export to be allowed it is required that the registered nursery is completely free from *L. trifolii* infestation and not a single mine is allowed. This has resulted in an intensive chemical control programme in ornamentals (1-2 sprays per week).

1.2 DAMAGE

The damage caused by *Liriomyza* spp. can be divided into two categories (direct and indirect):

1. The most serious damage is caused by larval feeding. The mining activity of larvae can reduce the photosynthetic capacity of the plant. Heavy infestation will cause desiccation and premature fall of leaves. In (sub)tropical areas this can lead to sunburning of fruits, e.g. melons and tomatoes (MICHELBACHER et al. 1951; MUSGRAVE et al. 1975b). Feeding punctures made by the adult females can also cause damage. Total destruction of seedlings and young plants has been reported.
2. The feeding punctures can be invaded by fungi and bacteria. PRICE and HARBAUGH (1981) observed an increase of bacterial leafspot disease, probably *Pseudomonas cichorii* (Swing) Stapp, in chrysanthemum infested by *L. trifolii*, which aggravated the conditions of the mined leaves remarkably. Transmission of viruses by *Liriomyza* flies has been demonstrated by COSTA et al. (1958) (tobacco and soybean mosaic virus) and ZITTER and TSAI (1977) (celery and watermelon mosaic virus).

Surprisingly little research has been done to determine injury levels, especially when one considers the many decisions on control measures which are taken regularly. The accurate assessment of economic thresholds in vegetables is difficult. The relation between size of leafminer population, leaf injury and reduction of yield are influenced by a complex of factors like season, cultivation method

and host-plant susceptibility. Especially the effect of low infestations, when complete compensation by the host plant can be expected, is unknown.

Researchers have not been able to correlate leafminer injury with yield loss (WOLFENBARGER and WOLFENBARGER 1966; LEVINS et al. 1975; SCHUSTER et al. 1976). In tomato, the position of leafminer injury in relation to the development stage of the adjacent trusses seems important. The economic injury level was assessed to be 15 mines of *L. bryoniae* per leaf, if the leaves were adjacent to fruit at an early to mid stage of swelling (LEDIEU and HELYER 1982a). WYATT et al. (1984) found the highest correlation between the yield of a truss and *L. bryoniae* infestations on the six leaves surrounding that truss when the fruit is half grown; the loss was directly proportional to the number of mines (30 mines/leaf: 10% loss; 60 mines/leaf: 20% loss). Defoliation experiments showed that removal of lower leaves hardly affects yield. Also, removing a quarter of each leaflet or one leaf between each truss causes no loss. Thus the tomato plant can tolerate at least 25% defoliation before any loss occurs (STACEY 1983). Nevertheless, LEDIEU and HELYER (1985) stress that picking off the lower leaves too early will result in loss of yield. JOHNSON et al. (1983) and TRUMBLE et al. (1985) proved that photosynthesis rates in leaves mined by *Liriomyza* spp. are greatly reduced. An increase of the net photosynthesis in the remaining leaves after removal of a leaf from a tomato plant was shown by WOLK et al. (1983).

1.3 CONTROL MEASURES

Different cultural control methods, such as good sanitation, removal of weeds (PRICE and HARBAUGH 1981; SCHUSTER et al. 1983), manual removing of mined leaves (PRICE 1983), specific substrates (OETTING 1983), film mulches (WOLFENBARGER and MOORE 1968; PRICE and POE 1976; CHALFANT et al. 1977) or intercropping (HERBERT et al. 1984) will usually not control a leafminer population sufficiently. Some authors reported on the usefulness of yellow sticky traps in greenhouses to control leafminers (MCCLANAHAN 1983; NUCIFORA et al. 1983; HERBERT et al. 1984; VAN DE VEIRE and VACANTE 1984), but this method has not yet shown to be sufficiently reliable and is not commercially feasible.

1.3.1 Chemical control

The history of chemical control of agromyzid leafminers has been described by SPENCER (1973, p. 2-4, p. 342-350). He concludes that 'In view of the greater toxicity to hymenopterous parasites of many of the chlorinated hydrocarbons and organophosphorous compounds currently recommended for use against leafminers, the search for effective selective insecticides clearly demands the highest priority'. Broad spectrum chemicals are most commonly used for leafminer control while research efforts for new insecticides are continuing.

Many authors report on the development of resistance in *Liriomyza* populations against insecticides, including chlorinated hydrocarbons, organophosphates, carbamates and pyrethroids (GENUNG 1957; WOLFENBARGER 1958; GEN-



PHOTO 2: The larvae of *L. trifolii* mining a tomato leaflet. Feeding punctures made by the adult females are also shown (photo: W. J. SANDERS).

UNG and HARRIS 1961; WOLFENBARGER and GETZIN 1963; JANES and GENUNG 1975; MUSGRAVE et al. 1975b; PARRELLA et al. 1981a). In a review on chemical control, LEIBEE (1981b) pointed out the shortening of 'effective life' of insecticides till approximately 3 years. To minimize this problem, a change of insecticide-use policy is necessary (KEIL and PARRELLA 1983), e.g. rotating insecticides (TRUMBLE 1985a).

In guided chemical control programmes, where pesticide use is based on monitoring the leafminer population and economic thresholds, the levels of infestation were reduced for gypsophila (PRICE et al. 1980a,b; PRICE and STANLEY 1983), celery (GENUNG et al. 1978; VAN STEENWIJK and TOSCANO 1982; TRUMBLE 1983), tomato (POHRONEZNY and WADDILL 1978; JOHNSON et al. 1980d; SCHUSTER et al. 1980) and bean (WADDILL et al. 1981). The effect of an insecticide on the parasite complex of the leafminer should be examined and taken into account before it is used (POE et al. 1978; WADDILL 1978; TRUMBLE and TOSCANO 1983; TRUMBLE 1985b).

Aqueous neem extracts from leaves of the neem tree *Azadirachta indica* A. Juss. are quite effective in controlling *L. trifolii* (FAGOONEE and TOORY 1984). WEBB et al. (1983) showed that neem seed solutions had an anti-ovipositional effect on *L. trifolii* females in contrast with *L. sativae* Blanchard. Larval mortality of both species was high: 100% for *L. trifolii* and 98.2% for *L. sativae*. These effects on *L. trifolii* were confirmed by STEIN and PARRELLA (1985). Neem seed extract used as a soil drench to chrysanthemum proved also to be effective against *L. trifolii*: 98% mortality of pupae (LAREW et al. 1985). But neem extract

was also toxic to the parasite *Hemiptarsenus semialbiclava*: (Girault) (FAGOONEE and TOORY 1984).

Insect growth regulators (IGR's) have a more selective insecticidal action than broad-spectrum insecticides. Two IGR's effective against *Liriomyza* spp., triprene ZR-619 and kinoprene ZR-777, were found to be harmful to the important parasite *Opius dimidiatus* (Ashmead) (POE 1974; LEMA and POE 1978). PARRELLA et al. (1983a) and ROBB and PARRELLA (1984) found that two IGR's, providing more than 80% control of *L. trifolii*, cyromazine 75W and Ro 13-5223 1E, are compatible with *Chrysocharis parksi* Crawford under specific conditions. The results of these compounds are promising, but tests on the whole parasite-complex are necessary to determine whether the beneficial effects of natural control are affected.

1.3.2 Biological control

Biological control of agromyzid leafminers was reviewed by SPENCER (1973, p. 350-354). Natural control of *Liriomyza* populations by a complex of parasites is regularly observed to occur in agriculture, which increases the probability that efficient parasites for biological control of *Liriomyza* pests will be found.

Parasites can be used in different ways in biological control programmes (VAN LENTEREN 1983):

1. Inoculative release method. Parasites are collected in an exploration area and introduced in the area where the pest occurs. Only a limited number of parasites is released; the aim is a long-term control effect. A good example is the control of *Agromyza frontella* (Rondani) (the alfalfa blotch leafminer, accidentally imported into North America) by *Dacnusa dryas* (Nixon) and *Chrysocharis punctifacies* Delucchi (HENDRICKSON and PLUMMER 1983). Introductions of different species of parasites were made for control of *Liriomyza* spp. in Hawaii (LAI et al. 1982; LAI and FUNASAKI 1985).
2. Inundative release method. Parasites are collected, mass reared and periodically released in large numbers to obtain an immediate control effect. This method is usually applied against univoltine pests in annual crops. As *Liriomyza* is multivoltine, this type of release method is not feasible.
3. Seasonal inoculative release method (combination of methods 1 and 2). Parasites are released periodically in short-term crops (6-9 months) where multivoltine pests occur. A relatively large number of parasites is released to obtain both an immediate control effect and also a build-up of a parasite population for control later during the same growing season. This introduction method seems most suitable for biological control of *Liriomyza* spp. in greenhouse crops.

Biological control is only successful when the economic threshold is not exceeded during the entire growing season. But as mentioned earlier, few data on injury levels are available and decisions by growers are taken more on a psychological basis than on criteria based on research data. Success was defined by DE LARA (1981) as at least 90% parasitization with less than one mine per

plant on chrysanthemum and no mines on tomato from next generation of the pest, which normally occurs 4-6 leaves up the plant.

It is evident that before biological control of leafminers can be applied, the use of broad spectrum pesticides has to be discarded and no residues should be present. In the Netherlands, several parasite species have been tested from 1977 to 1985 in experimental and commercial tomato greenhouses (ZUCCHI and VAN LENTEREN 1978; HENDRIKSE et al. 1980; WOETS and VAN DER LINDEN 1982b, 1983, 1985; HENDRIKSE 1983). It was found that:

1. in most greenhouses (> 60%) *L. bryoniae* is present and can cause problems,
2. natural control of *L. bryoniae* by *O. pallipes* and/or *Dacnusa sibirica* Telenga may occur, if sufficient overwintering parasitized pupae are present in the greenhouse,
3. when there are no parasites present or parasitism is too low – ca. 30% in April – depending on numbers of mines per plant, it is necessary to release parasites,
4. introduction of parasites should be made at regular intervals instead of only once, and as soon as possible after appearance of leafminers in spring,
5. *Opius pallipes* showed a slightly faster population increase than *D. sibirica* and *O. pallipes* was observed to control *L. bryoniae* faster than *D. sibirica*. *Chrysocharis parksi* only gave some promising results in experimental greenhouses,
6. a leafminer infestation appearing after mid May can be controlled by naturally occurring parasites, mainly *Diglyphus isaea* (Walker), which invade the greenhouse in May/June.

The commercial producer of natural enemies prefers *Dacnusa sibirica* as biological control agent, because of a practical reason: it can be reared without infection by other parasite species. *D. sibirica* can also be effective against *L. trifolii* (RAVENSBERG pers. comm.). Since 1980, biological control of *Liriomyza* spp. has been practised in the Netherlands on ca. 30 ha per year. Nowadays, *D. sibirica* is commercially introduced in greenhouses under integrated control (60 ha in 1985; a total of 10,000-20,000 parasites/ha; > 1 ♀ per 4 plants). This number of parasites proved to be sufficient to control *Liriomyza* spp. during the growing season.

In the U.K. and Sweden, sometimes bad control results were reported using *D. sibirica* (DE LARA 1981; NEDSTAM 1983; WARDLOW 1983, 1984a). This is probably due to immigration of flies, incorrect timing of release of parasites, insufficient introduction rates or bad quality of the parasites. In Ohio (U.S.A.), *O. dimiatus* (cited as *O. bruneipes* Gahan) was unable to control *Liriomyza* spp., despite a high introduction rate (4.5 parasite/plant) (LINDQUIST and CASEY 1983). Poor results were also obtained with *O. dimiatus* in Ontario (Canada), but the performance of *Diglyphus begini* (Ashmead) was promising (MCCLANAHAN 1980). In the Rhône delta (France), *D. isaea* was mass-reared and used successfully on a large scale; *L. trifolii* is no longer a pest problem in this area (LYON pers. comm.). In English greenhouses, positive results were obtained us-

ing *D. sibirica* or *O. pallipes* combined with *D. isaea* later on, against *C. syngenesiae* on chrysanthemum (LEDIEU and HELYER 1982b; WARDLOW 1983; CROSS et al. 1983).

In 1985, biological control of *Liriomyza* spp. with parasites has been carried out in greenhouses in Belgium, Denmark, France, the F.R.G., the Netherlands, Sweden and the U.S.A. on an estimated area of 460 ha.

In floricultural crops, biological control of leafminers by parasites is presently not feasible, because of the zero tolerance level for leafminer symptoms and the frequent applications of non-selective insecticides. In gerbera, where only the flowers are harvested, are perhaps possibilities for biological control of leafminers by inundative releases of parasites.

1.3.3 Integrated control

The aim of integrated control of insects is to minimize disturbance of the control effect of natural components of the agroecosystems (LEVINS and WILSON 1980; ALTIERI et al. 1983). Integration of chemical with biological control can be achieved by the use of selective chemicals and chemicals with short-term residual activity, or by choosing the appropriate moment or place of application. The use of chemicals can be further decreased by selecting insect-resistant host plants and including cultural control methods.

An IPM programme for Dutch greenhouse tomatoes consists of the following control measures: *E. formosa* against greenhouse whiteflies, fenbutatinoxide (selective insecticide) or predatory mites (*Phytoseiulus persimilis* Athias-Henriot) against two-spotted spider mites (*Tetranychus urticae* Koch), pirimicarb (selec-



PHOTO 3: The braconid wasp *Dacnusa sibirica* parasitizing a leafminer (*L. bryoniae*) (photo: J. C. VAN LENTEREN).

tive insecticide) against aphids, *D. sibirica* against *Liriomyza* spp. and *Bacillus thuringiensis* Berliner against caterpillars (Woets and VAN DER LINDEN 1982; RAVENSBERG et al. 1983). A recent IPM programme for greenhouse tomatoes in the U.K. is given by WARDLOW (1984b).

2 *LIRIOMYZA BRYONIAE* (KALTENBACH)

2.1 SYSTEMATICS

Liriomyza bryoniae (Kaltenbach 1858) was originally described as *Agromyza bryoniae* and belongs to the genus *Liriomyza* Mik; synonyms are *L. solani* Hering 1927 and *L. citrulli* Rohdendorf 1950 (SPENCER 1973, p. 209).

2.2 ORIGIN AND DISTRIBUTION

The fly is a palaeartic species, occurs commonly outdoors in southern Europe, whereas in the rest of Europe it is only found in greenhouses (SPENCER 1973). In the Netherlands, *L. bryoniae* was never found outdoors. Reports outside Europe are from Egypt (ABUL-NASR and ASSEM 1961), Israel (BERLINGER et al. 1983) and Japan (KAMIJO 1978).

2.3 HOST PLANTS

Liriomyza bryoniae is a polyphagous species attacking, e.g. tomato, cucumber, lettuce, melon and other vegetables. Polyphagy was defined by SPENCER (1964) as the indiscriminate feeding on a number of different plant orders. Only a few agromyzid species are polyphagous. This species has been reared from many host plant genera in almost 35 families (BUHR 1954 in SPENCER 1973, p. 210).

2.4 LIFE HISTORY

The following description of *L. bryoniae* is based on SPENCER (1973, p. 209-211); the description of its life history on HENDRIKSE (1983). The adult is a small fly (length of ♂♂ 1.5 mm; of ♀♀ 2.0-2.3 mm). They have a shining black mesonotum, largely yellow femora, and both vertical bristles on yellow background. The flies can easily be sexed by the clearly visible black abdominal tip (last 3 segments) of the female. Rearing data revealed a fifty-fifty sex ratio (♀♀:♂♂ = 518:493). Ca. 30% of the males emerge 1 day before most females emerge. Before copulation, both female and male are rhythmically bending their legs and vibrating their wings. Then the male mounts the abdomen of the female,

separating her wings and grasping the thorax. The abdomen of the male is brought forward to connect the copulatory organs. During copulation the female stands still. Copulation takes about 14 minutes (6-31 min.; N=10). Non-fertilized females are not able to oviposit and on average live longer than mated females. Adult females feed on leaf mesophyll. They scrape an opening, feeding punctures, in the leaf with their ovipositor and ingest the fluid. These feeding punctures resemble egg punctures, but feeding punctures are round and egg punctures are oval shaped (on tomato plants). Egg punctures contain one egg each (opaque and ellipsoidal; 0.15×0.25 mm). In *Liriomyza* there are three larval stages, which can be distinguished by the size of the sclerotized mouth hooks (OATMAN and MICHELbacher 1958). The first larval stage of *L. bryoniae* is ca. 0.57 mm, length mouth hooks 95μ ($75-113\mu$; N=15), the second larval stage measures ca. 1.55 mm, length mouth hooks 188μ ($150-250\mu$; N=15) and the last larval stage is ca. 2.50 mm, length mouth hooks 323μ ($300-350\mu$; N=15) (on tomato). Their posterior spiracles each have an ellipse of 7-12 pores. The older larvae have a yellow front part and a white hind part, by which they are quite different from entirely yellow *L. trifolii* larvae. If a leaf is not large enough to provide sufficient food, larvae can move up in the stem into a second leaf. The larva is unable to penetrate leaves from the outside. Prior to pupation, the third instar larva cuts a characteristic semi-circular exit slit in the epidermis of the mine. Then the third instar leaves the mine to pupate in the soil down to a depth of 5 cm and forms a puparium (0.9×2 mm). The colour of the pupae varies from gold-yellow to darkbrown-black. Under rearing conditions, ca. 10% of the pupae were found attached to mines, leaves or stems. The longevity of the males was less than 3 days and females lived for more than one week. On alternative food, like sugar water, honey and flowers of the tomato plant, none of the females lived longer than 3 days. During autumn and winter only few flies emerge. Low temperatures rather than short photoperiod appeared responsible. It is not yet clear whether this is diapause or a retarded development.

3 *LIRIOMYZA TRIFOLII* (BURGESS)

3.1 SYSTEMATICS

Liriomyza trifolii (Burgess 1880) was originally described as *Oscinis trifolii* and collected from white clover (*Trifolium repens* L.). The holotype got lost, which led to confusion about the status of this species and related ones in the genus *Liriomyza* Mik. SPENCER (1965) designated a neotype and clarified the situation by distinguishing species by the structure of the male genitalia. Despite of this, the identification in this genus remained confused partly due to the occurrence of mixtures of species on the same host plant species (e.g. in LINDQUIST and CASEY (1983), POE and MONTZ (1981a) and CHANDLER (1985)). Diagnosis of *L. trifolii* and other *Liriomyza* spp. is possible by gel electrophoresis (ZEHNDER



PHOTO 4: The larvae of the eulophid wasp *Diglyphus isaea* feeding on a leafminer (*L. trifolii*) (photo: K. DEN BRABER).

et al. 1983) also for the larval and pupal instars (MENKEN and ULENBERG 1983, 1986). Morphological characteristics of the female genitalia are useful in identification (KNODEL-MONTZ and POE 1983). SPENCER (1973, p. 226) gives the following synonyms of *L. trifolii*: *Oscinis trifolii* Burgess (1880), *L. trifolii* de Meijere (1925) and *L. allivora* Frick (1955).

3.2 ORIGIN AND DISTRIBUTION

Originally, *L. trifolii* is a nearctic and neotropical species, but now it is cosmopolitan. Florida is thought to be its endemic focus (SPENCER 1965). The population range has extended northwards through the eastern United States as far as Ontario in Canada and southwards the Bahamas, Guyana and Venezuela. According to SPENCER (1973), 'This species can survive in areas where the winters are invariably severe with sub-zero temperatures for extended periods, but it only thrives in subtropical and tropical conditions'. In 1968, the Colombian flower industry began importing chrysanthemum cuttings from Florida and the leafminer was first noticed there in 1974-1975. The first severe outbreak of *L. trifolii* occurred in Colombia in 1977 (PRICE 1983). In 1975-1976, this species was imported on plant material from Florida into California (PARELLA 1982), the Netherlands (VAN FRANKENHUYZEN and VAN DE BUND 1979) and Kenya (DE LIMA 1979). In Kenya, augmentation of chrysanthemum cuttings occurred and in 1977, cuttings were exported to the U.K., the F.R.G., Denmark and

the Netherlands (Anon. 1978). The farms on the Canary Islands and Malta could also be an indirect source of *L. trifolii*. *L. trifolii* has occurred on the Canary Islands since 1973 (PEÑA ESTÉVEZ and RODRIQUEZ 1983). In the U.K., it was first seen in 1977 at a nursery where chrysanthemums were being grown from cuttings imported from Kenya and Malta. In 1978, infestations were found on chrysanthemum cuttings from Kenya and Canary Islands and on gerbera from the Netherlands (BARTLETT and POWELL 1981). In Canada, it was also introduced on chrysanthemum cuttings from Florida (MCCLANAHAN 1983). In Japan, *L. trifolii* was recorded for the first time in 1949 and still occurs on leguminous plants (NAKAZAWA pers. comm.). A distribution map of *L. trifolii* is given by the Commonwealth Institute of Entomology (Anon. 1984a). So the dispersion of the leafminer *L. trifolii* throughout the world by the flower industry is a fact due to misidentification of species and failure of quarantine procedures (LINDQUIST 1983; PARRELLA and KEIL 1984). Several countries have eradication campaigns whenever the pest is found, e.g. the U.K. and Finland. Now it seems that *L. trifolii* has not been established outside the greenhouses in northern and eastern Europe and Canada and its significance as a pest decreases in these areas (MCCLANAHAN, HANSEN and NEDSTAM pers. comm.; PÉNZES 1983). In southern Europe and Israel, *L. trifolii* occurs outdoors during the whole year (BERLINGER et al. 1983; LYON pers. comm.).

3.3 HOST PLANTS

Liriomyza trifolii is a polyphagous species, attacking ornamentals, crops and weeds. STEGMAIER (1966a) has listed fortyseven plant genera in ten families in which the leafminer has been observed. Among the crops are melon, cucumber, squash, bean, pea, onion, pepper, tomato, egg plant, potato, celery, lettuce and carrot and among the ornamentals are chrysanthemum, gerbera, gypsophila and marigold. The number of recorded host plants is still increasing and now about 120 species in 21 families are known (STEGMAIER 1968; GENUNG and JANES 1975; POWELL 1981; SPENCER 1981). Host plants are found in 27 genera of the Compositae which is almost 40% of the total number of host plant genera. The next preferred family are the Leguminosae, in which 10 genera (almost 15%) contain host plants of *L. trifolii*.

3.4 LIFE HISTORY

The adult *L. trifolii* is a small fly (about 2 mm long). The head is yellow with plum-red eyes; the thorax and abdomen are greyish-black with a noticeable yellow patch at the hind end of the mesonotum. The underside and legs are mostly pale yellow. Peak emergence of the adults occurs before midday (CHARLTON and ALLEN 1981). Mating usually takes place within the day of emergence and single mating is sufficient to ensure fertilization of all eggs laid. Unfertilized

females are unable to oviposit. Female flies feed by cutting the leaf epidermis with their ovipositor (for description of ovipositor see HENDEL 1938; KNODEL-MONTZ and POE 1983) and sucking the contents of the macerated mesophyll cells (feeding punctures: 0.15-0.3 mm). SPENCER (1973, p. 19) writes: 'The feeding by the adult female appears to have a threefold function, firstly to confirm that the host plant is correct, second to ingest proteins specific to the host plant which are necessary for maturation of the eggs and without which they are unable to oviposit, and finally actual feeding on the available carbohydrates'. CHARLTON and ALLEN (1981) found that *L. trifolii* feed throughout the daylight hours but feed and oviposit most frequently around midday. Males are unable to puncture leaves but have been observed feeding at punctures produced by females. Both males and females take nectar from flowers or honeydew and feed in the laboratory on diluted honey. The punctures also serve as sites for oviposition (egg punctures). The eggs are oval, originally translucent and later become creamy. Their size is ca. 0.2×0.1 mm and they are inserted just below the epidermis. The number of feeding punctures and eggs varies considerably. The larva feeds in the leaf on the mesophyll layer producing a contorting mine. In chrysanthemum, *L. trifolii* larvae prefer the palisade mesophyll (PARRELLA et al. 1985). Shape and form of the mine are variable and depend on the host plant-species and cultivar. The larva, which is initially colourless, darkens to yellow as it matures. There are three larval stages. The third instar leaves the mine by cutting an opening at the end of the mine. The larval emergence from leaves also occurs primarily in the morning (CHARLTON and ALLEN 1981). The opening can be in the upper or lower surface of leaves. The larva drops on the ground and normally pupates in the soil or in the darkest accessible area. The pupa is orange-yellow and turns brown as it gets older. Both the larva and pupa have an anterior and posterior pair of distinctively shaped tricorn spiracles. The duration of the life cycle is highly variable. This species is not known to enter diapause. The above description of the life history is mainly based on data given by SPENCER (1973, p. 226), ANONYMOUS (1984b), BARTLETT and POWELL (1981) and FAGOONNEE and TOORY (1984). The males of *L. trifolii* live only a few days (δ : 2.3 d; f : 7.2 d) (CHARLTON and ALLEN 1981). ZEHNDER and TRUMBLE (1983) found that a fifty-fifty sex ratio existed in the field. Adult flies of *L. trifolii* can cover distances of 100 m within a few hours (VAN DE VRIE and DIRKSE 1982).

4 NATURAL ENEMIES OF *LIRIOMYZA* SPP.

4.1 PARASITES OF *L. bryoniae*

The following palaeartic parasite species of the families Braconidae and Eulophidae are mentioned by SPENCER (1973, p. 212):

1. *Dacnusa hospita* (Förster)

2. *D. maculipes* Thomson
3. *D. sibirica* Telenga
4. *Chorebus daimenes* (Nixon)
5. *Opius pallipes* Wesmael
6. *Chrysocharis pubicornis* (Zetterstedt)
7. *Hemiptarsenus zilahisebessi* Erdős
8. *Pediobius acantha* (Walker)

Aphidius ervi Haliday, also mentioned by SPENCER (1973), is presumably not a parasite of *L. bryoniae* but of certain aphid species (MACKAUER and STARÝ 1967). Besides *O. pallipes* and *D. sibirica*, *D. isaea* and *Halticoptera crius* (Walker) also occur as parasite of *L. bryoniae*. *C. parksi* has been introduced in European greenhouses. In Sweden, the braconid *Dacnusa areolaris* (Nees), the eulophid *Pnigalio soemius* (Walker) and the pteromalid *Cyrtogaster vulgaris* Walker, which parasitizes the pupae of *L. bryoniae*, were reported (NEDSTAM pers. comm.):

9. *Diglyphus isaea* (Walker)
10. *Chrysocharis parksi* Crawford
11. *Dacnusa areolaris* (Nees)
12. *Pnigalio soemius* (Walker)
13. *Cyrtogaster vulgaris* Walker.
14. *Halticoptera crius* (Walker)

The most important taxonomic literature on palaearctic parasites is for the Braconidae (key to subfamilies): VAN ACHTERBERG (1976); (Alysiinae): GRIFFITHS (1968, 1984) and SHENEFELT (1974); (Opiinae): FISHER (1973); (immature stages): ČAPEK (1973); Eulophidae: BOUČEK and ASKEW (1968); Pteromalidae: GRAHAM (1969) and ASKEW (1972). Results of biological studies of some parasite species are summarized below.

4.1.1 *Opius pallipes* Wesmael

Opius pallipes Wesmael 1835 belongs to the subfamily of Opiinae (Braconidae), which live as endoparasites of dipteran larvae and pupate within the puparium of the host. *Opius pallipes* is very similar to *Opius dissitus* Muesebeck (WHARTON 1984). As hosts are reported *C. syngenesiae* on chrysanthemum (CORNELIUS and GODFRAY 1984), *A. spiraeae*, *L. bryoniae* and *L. strigata* (SPENCER 1973).

Opius pallipes is a solitary endoparasite of *L. bryoniae*. It oviposits in all instars. The adult parasite emerges in the puparium of the host and escapes by making a hole with its mandibles. The sexes can be separated; the protruding ovipositor of the females is visible. Rearings were hampered by a sex ratio shifting from 50% to 90% or more males. At 22°C the total development took 18.3 days (± 1.4 ; N=30; Table 5). The average longevity was 8.7 days (± 5.4 ; N=6) in which an average of 89.2 eggs (± 57.7 ; N=6; Table 6) were laid (HENDRIKSE 1983).

The searching behaviour of *O. pallipes* is as follows: the female hovers around the leaves. After landing on a leaf, she starts scanning the leaf surface with her antennae and stings it rhythmically with her ovipositor. If a mine is encountered, the wasp follows it; again, the antennae and ovipositor are used for scanning. The female tries to determine the position of the larva. When the host is found, she inserts her ovipositor into the larva. She may reject it or will lay an egg in it (HENDRIKSE and ZUCCHI 1979). Older larvae are found faster than younger ones. Host feeding is never observed. Experiments indicated that *O. pallipes* is able to distinguish plants infested with *L. bryoniae* from uninfested plants. *Opius pallipes* accepts all larval stages of *L. bryoniae* for oviposition and can discriminate between parasitized and unparasitized hosts (HENDRIKSE et al. 1980).

4.1.2 *Dacnusa sibirica* Telenga

Dacnusa sibirica Telenga 1934 belongs to the subfamily of the Alysiinae (Braconidae). Almost all species are solitary endoparasites of dipteran larvae. *Dacnusa sibirica* has a palaearctic distribution: Europe and Siberia. This parasite has been introduced into Cleveland, Ohio (U.S.A.) (RAVENSBERG pers. comm.). As hosts are reported *P. asteris*, *P. autumnalis*, *P. plantaginis*, *P. ranunculi* and *L. bryoniae* (Griffith 1966, 1968), *C. syngenesiae* on chrysanthemum (CORNELIUS and GODFRAY 1984) and *L. trifolii* on tomato.

D. sibirica is a solitary endoparasite and can be sexed by the difference in colour of the pterostigma on the wing. It is black for the male, whereas in the female it is pale grey. Sometimes the protruding ovipositor of the female is visible. Copulation takes only 1-2 minutes. The searching behaviour of *D. sibirica* is similar to that of *O. pallipes*, although the frequency of stinging the leaf and the mine is higher than in *O. pallipes*. The female parasitizes all instars. The development takes place inside the host, including the pupal stage. The adult emerges from the host puparium in the soil. At 22°C the total development took 15.7 days (± 1.5 ; N=30). The average longevity was 6.1 days (± 2.6 ; N=7) and the fecundity was 71.7 eggs (± 48.1 ; N=7) (HENDRIKSE 1983).

Experiments showed that *D. sibirica* can not distinguish plants infested with *L. bryoniae* from uninfested plants from a distance. Older larvae are found faster than younger ones by the wasp. Host feeding was never observed. *Dacnusa sibirica* does not select larvae of a specific age. It can distinguish unparasitized from parasitized larvae. It was also found that *D. sibirica* can distinguish a previously visited leaf from a leaf that was not visited before by conspecifics (HENDRIKSE et al. 1980). The results indicate that besides marking the host, a marking pheromone is applied to the leaf. A marking pheromone was also found for *Dacnusa* sp., a parasite of *P. ranunculi*, by SUGIMOTO (1984). PETITT (1984) observed *Opius dissitus* marking the visited leaf, mainly the mine and larva.

4.1.3 *Diglyphus isaea* (Walker)

The genus *Diglyphus* (Eulophidae) belongs to the subfamily Eulophinae. This subfamily, including the genera *Hemiptarsenus* and *Pnigalio*, comprises larval

ectoparasites only. *Diglyphus* spp. are primary parasites. *Diglyphus isaea* (Walker 1838) is holarctic. Its taxonomy is discussed by GORDH and HENDRICKSON (1979) and hybridization tests between *D. isaea* and *D. intermedius* showed that reproductive isolation between them was not complete.

Diglyphus isaea is an abundant species in Europe, North Africa and Japan and has been reared from a wide variety of leafminers. It is generally associated with hosts on herbaceous plants and scarce on trees. Eighteen host species in 5 genera of Agromyzidae and the lepidopteran *Lyonetia clerckella* are recorded (BOUČEK and ASKEW 1968). New host data are *Liriomyza crucifericola*, *Cerodontae lateralis* (SPENCER, 1973), *Napomyza carotae* on chicory, carrots and camomille (VAN 'T SANT et al. 1975), *Agromyza albipennis*, *Agromyza oryzae*, *Phytomyza horticola*, *P. ranunculi* (KAMIJO 1978), *L. bryoniae*, *L. trifolii* on tomato (HENDRIKSE et al. 1980). *Diglyphus isaea* is a facultative gregarious parasite of leafmining insects. After paralysing the host, the female usually lays one egg, in exception 2-5 eggs, near or on the host. The eggs are cylindrical and slightly curved; their size is 0.3×0.1 mm. The young parasite larvae are colourless but become green as they mature. Three larval stages can be distinguished (IBRAHIM and MADGE 1979). The leafminer becomes flaccid and brown after a few days. The last larval instar displays a characteristic behaviour before pupation. It consolidates its pupal chamber with meconial pillars presumably serving as structural support when the leaf dries out. The parasite larva pupates in the leaf and the nymph has a length of ca. 1.5 mm. It is greenish until sclerotisation occurs and its eyes are red. The wasp emerges through a round hole which it cuts through the epidermis of the mine. The sex of the wasps can be determined using the colour of the hind tibia. In the female there is one median black mark on the hind tibia, but in the male there are two smaller black marks (ASKEW 1968). The sex ratio is variable. Mortality in leafminer population, besides through parasitization is caused by the host-feeding activities of adult females. Host feeding in the laboratory accounted for almost half of the number of larvae killed (IBRAHIM and MADGE 1979). Only the third instar of *L. trifoliarum* Spencer and second and third instars of *C. syngenesiae* are selected for oviposition by *D. isaea* (HENDRICKSON 1975; IBRAHIM and MADGE 1979). Sometimes the parasite eggs or larvae are killed by a conspecific.

Inoculative releases in 1975-1976 were done in Hawaii against *Liriomyza* spp. (NAKAO and FUNASAKI 1979) and in the north-eastern U.S.A. and Canada against *A. frontella* (HENDRICKSON and BARTH 1979; GUPPY et al. 1984). However, establishment of *D. isaea* in North America is uncertain.

Natural control of agromyzid leafminers in greenhouses in Europe usually occurs during summer. As it overwinters outdoors, *D. isaea* enters the greenhouse in spring. Control of the leafminer population may occur within a few generations (SCOPES 1972; WOETS and VAN DER LINDEN 1983; WARDLOW 1984a; NUCIFORA and CALABRETTA 1985). In Japan, *Chrysocharis pentheus* (Walker), which also acts as a hyperparasite, is possibly an important mortality factor of *D. isaea* populations (TAKADA and KAMIJO 1979).

TABLE I. Parasites reared from *Liriomyza* spp. in the nearctic region.

Parasite	Host		<i>L. trifolii</i>													<i>L. sativae</i> ^a									
	reference ^b		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
<i>Dacnusa</i> sp.																									
<i>D. maculipes</i> ^d			+																						
<i>Chorebus misella</i> ^e			+																						
<i>Oenogastra microthopala</i> ^f											\$										+				
<i>Opius</i> sp.			+																						+
<i>O. aridis</i>																									
<i>O. dimidiatus</i>			+																						
<i>O. dissitus</i>			+																						
<i>Cothonaspis</i> sp.																									
<i>Ganaspidium</i> sp. ^g																									
<i>Mirzagrammosoma lineaticeps</i>			+																						
<i>Zagrammosoma americanum</i>			+																						
<i>Prigatio flavipes</i>			+																						
<i>Diglyphus</i> sp.			+																						
<i>D. begini</i>			+																						
<i>D. intermedius</i>			+																						
<i>D. pulchripes</i>			+																						
<i>D. websteri</i>			+																						
Eulophinae (genus unknown)			+																						
<i>Chrysocharis</i> sp.			+																						
<i>C. ainsliei</i>			+																						
<i>C. mallochi</i>																									
<i>C. parksii</i>																									
<i>C. viridis</i>																									
<i>Chrysonotomyia</i> sp. ^h			+																						
<i>C. formosd</i>			+																						
<i>C. punctiventris</i> ^j			+																						
<i>Closterocerus</i> sp.			+																						
<i>C. cinctipennis</i>			+																						
<i>C. utahensis</i>			+																						
<i>Tetrastichus</i> sp.			+																						
<i>Halticoptera</i> sp.			+																						
<i>H. circulus</i>			+																						
<i>H. patellano</i> ^k			+																						

Total number of species

Place of sampling^l

12 16 3 4 2 3 4 1 4 5 1 7 8 4 8 5 14 10 4 2 9 5
 F F C F O F F F O F F C T O T C C On F On C F

- a. probably mixture of species (see POE and MONTZ 1981a; LINDQUIST and CASEY 1983; CHANDLER 1985)
- b. references:
- | | |
|--------------------------------|------------------------------------|
| 1. STEGMAIER (1966a, 1972). | 12. TRUMBLE and NAKAKIHARA (1983). |
| 2. POE and MONTZ (1981b). | 13. CHANDLER (1982). |
| 3. PARRELLA et al. (1982). | 14. LINDQUIST et al. (1979, 1980). |
| 4. GENUING and JANES (1975). | 15. CHANDLER (1984). |
| 5. LINDQUIST and CASEY (1983). | 16. JOHNSON et al. (1980a). |
| 6. PRICE and STANLEY (1983). | 17. OATMAN and JOHNSON (1981). |
| 7. PRICE (1981). | 18. McCLANAHAN (1977). |
| 8. MURPHY (1984). | 19. GENUING et al. (1978). |
| 9. FOGG (1981). | 20. McCLANAHAN (1975). |
| 10. POE et al. (1978). | 21. OATMAN and KENNEDY (1976). |
| 11. POE (1974). | 22. STEGMAIER (1966b). |
- ad 5: the parasite species is cited as *Opius bruneipes* Gahan. Specimens were identified as *O. dimidiatus* by VAN ACHTERBERG (VAN DER LINDEN pers. comm.) and by WHARTON (LINDQUIST pers. comm.).
- ad 13 and 15: Leafminer species (mentioned as *L. sativae*) is a mixture of *L. trifolii* (>95%) and *L. sativae* (CHANDLER 1985).
- ad 22: the leafminer species (mentioned as *L. munda*) is presumably *L. sativae* (SPENCER 1973, p. 221).
- c. + = present; \$ = tomato as host plant; ? = presence doubtful.
- d. formerly *Rhizarcha* (FITTON et al. 1978).
- e. *C. misella* is presumably a misidentification; its distribution is palaeartic (SHENEFELT 1974, p. 1056).
- f. mentioned as parasite of *L. trifolii* on greenhouse chrysanthemums in Georgia (OETTING and BODRI 1984).
- g. possibly *Disorygma* sp.; this generic group including *Ganaspidium* sp. and *Disorygma* sp. has not been revised taxonomically (CHANDLER 1984).
- h. formerly *Achrysocharella* sp. and *Derostenus* sp. (YOSHIMOTO 1978).
- i. formerly *Derostenus variipes* (YOSHIMOTO 1978).
- j. formerly *Derostenus arizonensis* and *Derostenus agromyzae* (YOSHIMOTO 1978).
- k. formerly *Halticoptera aenea*; *H. patellana* and *H. aenea* only occur in Europe; Canadian and U.S.A. records of *H. aenea* presumably refer to *H. circulus* (GRAHAM 1969, p. 165). The palaeartic species of *Halticoptera* have been revised by ASKEW (1972).
- l. A = Arizona, C = California, F = Florida, H = Hawaii, O = Ohio, On = Ontario, T = Texas.

4.2 PARASITES OF *Liriomyza trifolii*

Many authors have made surveys of parasites of *Liriomyza* spp. The parasite species differ for the various crops and geographical areas. Only the identified species are listed below. The parasites which have been recorded in different states of the nearctic region are mentioned in table 1. Sixteen hymenopteran species in the families Braconidae (Alysiinae and Opiinae), Eulophidae (Elachertinae, Eulophinae, Entedontinae and Tetrastichinae) and Pteromalidae parasitize *L. trifolii*. With the exception of two species, they were all found in Florida (U.S.A.):

1. *Chorebus misella* (Marshall)

Florida

2. <i>Dacnusa maculipes</i> (Ashmead)	Florida
3. <i>Oenonogastra microrhopalae</i> (Ashmead)	Georgia/Ohio/Ontario
4. <i>Opius dimidiatus</i> (Ashmead)	Florida/California/Ohio/ Ontario
5. <i>O. dissitus</i> (Muesebeck)	Florida
6. <i>Mirzagrammosoma lineaticeps</i> (Girault)	Florida
7. <i>Diglyphus begini</i> (Ashmead)	California/Ontario
8. <i>D. intermedius</i> (Girault)	Florida/California/Texas/ Ontario
9. <i>D. pulchripes</i> (Crawford)	Florida/Ohio/Ontario
10. <i>D. websteri</i> (Crawford)	Florida
11. <i>Chrysocharis parksi</i> (Crawford)	Florida/California
12. <i>Chrysonotomyia formosa</i> (Westwood)	Florida/Ohio
13. <i>C. punctiventris</i> (Crawford)	Florida/California
14. <i>Closterocerus cinctipennis</i> (Ashmead)	Florida/Texas
15. <i>Halticoptera circulus</i> (Walker)	Florida/Texas/California/ Ohio
16. <i>H. patellana</i> (Dalman)	Florida/California/Ontario

In the neotropical region, surveys were made by PRIETO and CHACÓ DE ULLOA (1982), VÉLEZ ANGEL et al. (1982) and MURPHY (1984):

(7) <i>D. begini</i>	Colombia/Trinidad
17. <i>Diaulinopsis callichroma</i> Crawford	Trinidad
18. <i>Chrysocharis caribea</i> Bouček	Trinidad
19. <i>Closterocerus purpureus</i> (Howard)	Trinidad
(15) <i>H. circulus</i>	Trinidad

In the ethiopian region VERCAMBRE and THIERY (1983a) and BOURDOUXHE (1982) sampled five parasite species of *L. trifolii* in Reunion and two in Senegal, respectively. The only identified species was an eulophid:

20. *Hemiptarsenus semialbiclava* Girault

In Israel FREIDBERG and GIJSWIJT (1983) made a survey in greenhouse ornamentals infested with *L. trifolii* and found 9 eulophids and one braconid parasite. The completely identified species were:

- 21. *Diglyphus isaea* (Walker)
- 22. *D. crassinervis* Erdős
- 23. *Ratzeburgiola incompleta* Bouček
- 24. *Hemiptarsenus dropion* (Walker)
- 25. *Pnigalio soemius* (Walker)
- 26. *Chrysocharis pentheus* (Walker)
- (12) *C. formosa*

In the Netherlands, three species were found to parasitize *L. trifolii* in greenhouses, namely *Dacnusa sibirica*, *Diglyphus isaea* and *Halticoptera crius* (VAN DER LINDEN and GIJSWIJT pers. comm.). The British species of *Halticoptera* are revised by ASKEW (1972):

27. *Dacnusa sibirica* Telenga

(21) *D. isaea*

28. *Halticoptera crius* (Walker)

A total of 28 parasite species of *L. trifolii* have been identified. The most important literature on nearctic parasites is for the Braconidae (Alysiinae): WHARTON (1980, 1984); Chalcidoidea (key to subfamilies): YOSHIMOTO (1984); Eulophidae: PECK (1963) and BOUČEK (1977), *Diglyphus*: GORDH and HENDRICKSON (1979), *Zagrammosoma*: GORDH (1978), *Chrysonotomyia*: YOSHIMOTO (1978), *Pnigalio*: YOSHIMOTO (1983), *Chrysocharis*: YOSHIMOTO (1973a) and *Pediobus*: PECK (1985). Detailed biological studies have been conducted on some species only. Results of these studies are summarized below.

4.2.1 *Diglyphus begini* (Ashmead)

Diglyphus begini (Ashmead 1904) is nearctic and neotropical. It is numerically the most abundant species of the genus in Canada. In the U.S.A., it appears to be more common in the western states than elsewhere (GORDH and HENDRICKSON 1979). It is reported on *Liriomyza* spp. from Ontario, Ohio, Arizona, California (Table 1), Puerto Rico (PÉREZ PÉREZ 1973) and Colombia (PRIETO and CHACÓ DE ULLOA 1982). DOUTT (1957) mentions that the host range of *D. begini* includes 19 species in 5 genera of Agromyzidae. This species is mentioned as parasite of *L. trifolii* on chrysanthemum (ALLEN and CHARLTON 1981; PRIETO and CHACÓ DE ULLOA 1982; PARRELLA et al. 1982) and of *L. trifolii* and *L. sativae* on tomato and celery (ZEHNDER and TRUMBLE 1984).

Life history studies were done by HILLS and TAYLOR (1951), DOUTT (1957), ALLEN and CHARLTON (1981). *Diglyphus begini* is facultative gregarious. Development time, longevity and fecundity of *D. begini* are given in tables 5 and 6. The longevity is greatly increased when parasites are provided with honey. The adults could be kept for months at 5°C (ALLEN and CHARLTON 1981). The number of larvae killed by host feeding is impressive: from a total of 716 killed larvae, 448 were killed by host feeding (ALLEN and CHARLTON 1981).

In field studies of *Liriomyza* spp., *D. begini* is often found to be quite abundant in relation to other parasite species. HILLS and TAYLOR (1951) mentioned *D. begini* as numerically one of the most important parasites of leafminers infesting cantaloups and lettuce, besides *H. aenea* and *C. punctiventris* in Arizona. OATMAN (1959) conducted a study of natural control of *Liriomyza* sp. (probably *L. sativae* (SPENCER 1973, p. 203)) on melon. He reports that parasitization was low early in the year, but increased rapidly and that the two most numerous species were *D. begini* and *H. patellana*. Natural control of *L. brassicae* on cabbage in southern California is important. OATMAN and PLATNER (1969) reported

that the leaf injury caused by this leafminer was insignificant and the parasitization varied from 26.7% in January to 84.1% in October. *Diglyphus begini* is mentioned as by far the commonest larval parasite and *H. patellana* as the dominant pupal parasite. Populations of *C. syngenesiae* in artichokes in California remained consistently below economic damage levels due to parasitization by *C. amslei*, *D. websteri* and *D. begini* in order of importance (BRAGG 1974). On alfalfa infested by *Liriomyza* spp. in California, *D. begini* was present in moderate numbers throughout the season (JENSEN and KOEHLER 1970). Parasitization of *L. sativae* on tomato averaged 62.8% from mid June till September. *Diglyphus begini* was by far the most numerous species, representing 80.7% of the total number of parasites reared (OATMAN and KENNEDY 1976). JOHNSON et al. (1980c) reported that *D. begini* and *C. punctiventris* were the most abundant parasites reared from tomato. ZEHNDER and TRUMBLE (1984) found that *D. begini* was the most numerous species from *L. sativae* and *L. trifolii* infesting tomatoes; in celery, *D. begini* and *D. intermedius* were the commonest parasites.

In Canadian greenhouses, *D. begini* is an important parasite of *L. sativae* on tomatoes later in the year. This parasite caused up to 67% parasitism in 1973, together with the less numerous *O. dimiatus*. In 1974, *D. begini* was not abundant and only one individual of *O. dimiatus* was recorded (MCCLANAHAN 1975). MCCLANAHAN (1980) mentions successful biological control of *L. sativae* in a greenhouse experiment in autumn using *D. begini*. The released *O. dimiatus* and *Chrysochardis viridis* (Provancher) failed to control the leafminers.

4.2.2 *Diglyphus intermedius* (Girault)

Diglyphus intermedius (Girault 1916) is nearctic and neotropical. It is reported on *Liriomyza* spp. from Ontario, Texas, Florida and California (table 1) and has been introduced into Hawaii (NAKAO and FUNASAKI 1979). Eight host species in 3 genera of Agromyzidae are mentioned by GORDH and HENDRICKSON (1979).

Although usually solitary, *D. intermedius* is probably occasionally gregarious (HENDRICKSON and BARTH 1978). Biological notes for *D. intermedius* are provided by HENDRICKSON and BARTH (1978) and PATEL and SCHUSTER (1983). This parasite species uses all three instars of its host for host feeding and prefers third instar for oviposition; development of *D. intermedius* on second instars of *L. trifoliarum* was not possible probably due to inadequate food supply. The parasite has three larval stages, distinguishable by mouth-hook length. The shortest development time (ca. 9 days) occurs at 27°C (Table 5).

Diglyphus intermedius was the dominant parasite of *Liriomyza* sp. on tomato in California besides *H. patellana* (SHOREY and HALL 1963). *D. intermedius* was also reported as the dominant parasite of *Liriomyza* sp. on melon (MICHELBA-CHER et al. 1951). In north-eastern states of the U.S.A., *D. intermedius* is the commonest parasite of *A. frontella* in alfalfa (HENDRICKSON and BARTH 1978). In Florida, this parasite is the most abundant one on *L. sativae* on tomato (POE et al. 1978; SCHUSTER et al. 1979) or on *L. sativae* on celery together with *C. formosa* (TRYON and POE 1981). In California, *D. intermedius* is nowadays less

abundant on tomato (OATMAN and KENNEDY 1976) and it shows a clear preference for celery infested by *L. trifolii* (ZEHNDER and TRUMBLE 1984).

4.2.3 *Diglyphus pulchripes* (Crawford)

Diglyphus pulchripes (Crawford 1912) is nearctic and it is similar to the palearctic species *D. crassinervis* (GORDH and HENDRICKSON 1979). This parasite is recorded on *Liriomyza* spp. from Ontario, Ohio, California, Florida (table 1) and Massachusetts (MILLER and JENSEN 1970). It has been introduced into Hawaii (NAKAO and FUNASAKI 1979). It is known on 7 species in 5 genera of Agromyzidae (GORDH and HENDRICKSON 1979).

D. pulchripes is reported as the most abundant and a successful parasite on leafminers together with *O. dimidiatus* in greenhouses in Ohio (LINDQUIST et al. 1979). In autumn, *L. trifolii* on greenhouse tomatoes could be controlled by *D. pulchripes* when the parasites were either introduced or naturally invaded the greenhouse (LINDQUIST and CASEY 1983).

4.2.4 *Diglyphus websteri* (Crawford)

Diglyphus websteri (Crawford 1912) is nearctic and neotropical (GORDH and HENDRICKSON 1979). It is recorded on *Liriomyza* spp. from Florida, Texas, Arizona, California (table 1) and Peru (CAMPOS 1982).

CAMPOS (1982) reported that *Liriomyza huidobrensis* (BLANCHARD) on potato was held in check by *D. websteri* and other parasites early in the season. *D. websteri* was reported as parasite of *C. syngenesiae* in artichokes besides *D. begini* and *C. ainslei* (BRAGG 1974).

4.2.5 *Chrysocharis parksi* Crawford

Chrysocharis parksi Crawford 1912 belongs to the Entedontinae of the family Eulophidae. The subfamily also includes the genera *Pediobus*, *Chrysonotomyia* and *Closterocerus*; the latter probably being a synonym of *Chrysonotomyia* (ASKEW 1979). This subfamily are internal or external parasites. *Chrysocharis* spp. are primary, rarely secondary, endoparasites of larvae and pupae (BOUČEK and ASKEW 1968). The North American species of this genus have been revised by YOSHIMOTO (1973a,b). *Chrysocharis parksi* is nearctic. This parasite species has been introduced into the Netherlands (WOETS and VAN DER LINDEN 1985) and France (RAVENSBERG pers. comm.). YOSHIMOTO (1973a) lists 9 host species in 6 genera of Agromyzidae. It is reported on *Liriomyza* spp. from California and Florida (Table 5) and has been introduced into Hawaii (LAI and FUNASAKI 1985). The female has a blue-green colour and is 1.4-1.5 mm long. The legs beyond the coxae are pale except the terminal tarsal segment, which is brown. The males, which are 1.3-1.4 mm long, can be distinguished by the form of the abdomen. The male abdomen is shrunken and triangular in form; the abdomens of females are round.

Chrysocharis parksi is an endoparasite. The female injects her eggs into the larvae; the host larvae are usually able to pupate normally and the adult parasites emerge from the puparia formed by the agromyzid larva. *Chrysocharis parksi*

parasitizes the late third instars of *L. sativae* (JOHNSON et al. 1980a). Parasitized *L. trifolii* pupae can be instantly separated from those unparasitized, because of a difference in colour. *Chrysocharis* females feed from the host (PARRELLA et al. 1982).

On *Liriomyza* spp. in alfalfa in California, *C. parksi* occurred in moderate numbers and only during the early part of the season (JENSEN and KOEHLER 1970). In tomatoes on *L. sativae*, *C. punctiventris* (60%) and *D. begini* (24%) were the dominant (ecto)parasites; *C. parksi* had only a minor part in parasitism (7.2%) (JOHNSON et al. 1980a). Also in Florida on *L. sativae* in tomato, *C. parksi* is insignificant (POE et al. 1978). However, ZEHNDER and TRUMBLE (1984) found that *C. parksi* is the predominant parasite on *L. sativae* on tomato in mid to late season. It has been demonstrated that *C. parksi* prefers either this host or this habitat over *Liriomyza* spp. in celery. Experiments in greenhouses using *C. parksi* as biological control agent yielded promising results (WOETS and VAN DER LINDEN 1985).

4.3 PREDATORS OF *Liriomyza* spp.

HENDEL (1938) observed that some leafminers are eaten by predatory insects such as ants, true bugs and lacewings. The agromyzid adults may be killed by other dipteran species like *Drapetis subaenescens* (Collin), *Tachydromia annulata* Fallén (?) (Empididae) and *Coenosia attenuata* (Zetterstedt) (?) (Muscidae) (FREIDBERG and GIJSWIJT 1983). A *Draperis* sp. (Empididae) was described by VERCAMBRE and THIERY (1983). PRIETO and CHACÓ DE Ulloa (1982) observed ants (Ponerinae) attacking the larvae and spiders (Oxyopidae) and flies (Dolichopodidae) attacking the adults of *L. trifolii*. Biological studies were conducted with the tomato bug, *Cyrtopeltis modestus* (Distant), a facultative predator of leafminers (PARRELLA and BETHKE 1983). This insect, which is also considered as a pest organism, feeds primarily on tomato stems and only the older stages use leafminers as a food source. Another possibility for leafminer control is the predaceous nematode, *Neoplectana carpocapsae* (Weiser). This nematode may be effective against the stages of *Liriomyza* occurring in the soil (PARRELLA et al. 1982). Birds, e.g. titmice, sometimes prey on agromyzid larvae and pupae.

4.4 METHODS FOR REARING PARASITES AND THEIR HOSTS

Several laboratory rearing methods of leafminers (FREEMAN and GUYTON 1957; GRIFFITH 1962; HENDRICKSON and BARTH 1977; WEBB and SMITH 1970a; KETZLER and PRICE 1982) and parasites (GRIFFITH 1962) has been described. Methods for mass production of both hosts and endoparasites (HENDRIKSE 1980) and of ectoparasites (HENDRICKSON 1975) have also been described. The effect of density of *L. trifolii* larvae on the production of flies has been examined (PARRELLA 1983). Intraspecific competition, caused by depletion of leaf resour-

ces, and larval cannibalism adversely affected larval survival and pupal size. Pupal size was found to be an indicator of longevity and oviposition of adult flies. Competition in *A. frontella* on alfalfa has been investigated extensively (QUIRING and McNEIL 1984, 1985).

5 FACTORS INFLUENCING THE POPULATION DEVELOPMENT OF LEAFMINERS AND THEIR PARASITES

In spring at the start of the cultivation period, the predominantly warm and sheltered greenhouse environment and the abundant high-quality food supply can lead to a rapid increase in leafminer populations, especially in the absence of natural enemies. But the greenhouse environment is also favourable for a fast development of the parasites. The host-parasite interaction can proceed at a quite predictable speed, because of the densely planted crops, the relatively small changes in abiotic conditions, and the absence of hyperparasites and unwanted predators. Nevertheless, there are still many factors that can influence the host-parasite relationship and the rate of parasitism, and thus the success of a biological control programme. The size and growth of both the host and parasite populations are determined by:

1. abiotic factors -such as temperature, humidity and light- and biotic factors -such as host plant quality-,
2. biological characteristics of host and parasite species.

The influence of various factors on the relationships between host plant, flies and parasites is summarized below.

5.1 TEMPERATURE

Temperature has a direct influence on the growth rate of the host and parasite populations. Population growth rate is determined by development time, mortality of immature stages, and longevity and fecundity of the adult. Table 2 gives some data for *L. bryoniae*. The influence of different constant temperatures on the total development time of *L. trifolii* is shown in table 3. The development time decreases as temperatures increase from 11.5°C to 30°C. Above 30°C development time is near the upper threshold and an air temperature of 35°C is almost the upper lethal limit. Reductions in population levels of *L. huidobrensis* (mentioned as *L. langei*, but see SPENCER 1973, p. 216) occurred when the maximum daily temperature rose to 40.5°C (LANGE et al. 1957). The theoretical development thresholds are different for each instar and species and apparently also depend on the host-plant species. The real temperature thresholds are probably lower, because the theoretical ones are extrapolated and it is commonly found that linear extrapolations lead to values that are too high. The calculated deve-

TABLE 2A. The mean development time of *L. bryoniae* (days) at different constant temperatures; 2B. The mean longevity (days) and the mean total fecundity^a per female (eggs) of *L. bryoniae* at 22°C.

Host plant	Temperature (°C)				reference
	15	20	22	25	
A. <i>Lycopersicon esculentum</i> Mill. cv. 'Moneydor'	40	24	—	17	VAN DER LINDEN 1983
<i>L. esculentum</i> cv. 'Moneydor'	—	—	19.6	—	HENDRIKSE et al. 1980
B. <i>L. esculentum</i> cv. 'Moneydor'	—	—	8.7(67)	—	HENDRIKSE et al. 1980

^a in parentheses.

lopment thresholds of *L. trifolii* determined from regression equations for development rate, are on bean 7.5°C (VERCAMBRE and THIERY 1983); on chrysanthemum, 9°C for pupal stage (PARRELLA et al. 1981b), 10.1°C for egg-larva, 10.8°C for pupal stage (MILLER and ISGER 1985); on tomato 7.8°C for larval stage (SCHUSTER and PATEL 1985) and on celery 12.9°C for egg stage, 8.4°C for larval stage and 10.3°C for pupal stage (LEIBEE 1984). These differences may be due to different experimental set-up, host plant species and cultivars, and different origin of *L. trifolii* strains. The data should be treated with care.

The optimum temperature for development, defined as the temperature with the lowest mortality is near 25°C. On chrysanthemum, 68%, 80%, 92.5%, 75.5% and 0% emergence from pupae occurred at 15.6°C, 21.2°C, 26.7°C, 32.2°C and 37.8°C respectively (PARRELLA et al. 1981b) and on the same host-plant species, 33%, 56%, 61%, 75% and 74% pupal emergence was found at 16°C, 18°C, 20°C, 26°C and 30°C respectively (MILLER and ISGER 1985). On celery, these data were 80%, 83%, 87%, 83% and 9% pupal survival at 15°C, 20°C, 25°C, 30°C and 35°C, respectively (LEIBEE 1984). The mortality of immature stages of *L. trifolii* rises sharply at temperatures above 30°C and at low temperatures. Some data on the development time of *L. trifolii* at fluctuating temperatures have been collected (FAGOONEE and TOORY 1984; MILLER and ISGER 1985). However, more research is necessary for evaluating the effects of alternating temperatures on the development and the mortality of immature stages of *L. trifolii*.

Legumes are more suitable host plants than chrysanthemums considering development time and mortality (CHARLTON and ALLEN 1981). This seems to be in contrast with the number of suitable genera in Leguminosae and Compositae (see section 3.3). The total survival from larvae and pupae on blackeyed pea, pinkbean, chrysanthemum cultivars 'Show Off' and 'Yellow Knight' was 73%, 73%, 47% and 1%, respectively (23.8°C). Resistance against *L. trifolii* can be quite variable in chrysanthemums. WEBB and SMITH (1969) examined the effect of temperature on larval development time and mortality of *L. trifolii* (cited as *L. munda*, but see SPENCER 1973, p. 203). Mortality in tomato and chrysanthemum (not in lima bean) increased significantly with decreasing temperatures.

TABLE 3. The mean development time (days) of *L. trifolii* at different constant temperatures.

Host plant	Temperature (°C)											reference	
	11.5	13.8	14.8	15	16	18	20	23.8	25	30	32.5		35
<i>Phaseolus vulgaris</i> L. (pinkbean)	>115.5	64.7	51.2	-	-	-	20.3	16.1	15.8	12.5	12.2	-	CHARLTON and ALLEN 1981
<i>P. vulgaris</i> (bean)	-	-	-	61	-	-	23	-	17	15	-	+ ^a	VERCAMBRE and THIERY 1983
<i>Chrysanthemum morifolium</i> Ramat.	-	-	-	-	-	29.0	-	-	-	-	-	-	PRIETO and CHACÓ DE ULLOA 1982
<i>C. morifolium</i> cv. 'Show Off' ^b	-	-	-	-	-	-	24.1	-	16.7	13.8	14.3	-	CHARLTON and ALLEN 1981
<i>Lycopersicon esculentum</i> Mill. cv. 'Moneydot' (tomato)	-	-	-	44.5	-	-	26.3	-	16.9	-	-	-	MINKENBERG (in prep.)
<i>Apium graveolens</i> L. cv. 'Florida 2-14' (celery)	-	-	-	64.0	-	-	29.8	-	18.7	15.9	-	14.0	LEIBEE 1984
<i>C. morifolium</i> cv. 'Fandago'	-	-	-	-	50.8	39.2	29.6	-	-	18.6	14.4	-	MILLER and ISGER 1985

^a 100% mortality of immature stages.

^b this cultivar is considered susceptible.

Mortality was highest in the first instar, intermediate in the second and lowest in the third instar. With chrysanthemum, there was a correlation between the longer larval development time and the higher larval mortality in those cultivars considered resistant; such a correlation was not found with tomato cultivars.

Cold storage can be an important phytosanitary measure. In cold storage at 0°C, newly laid eggs of *L. trifolii* survived 3 weeks, but all stages of larvae were killed after 1-2 weeks in the chrysanthemum cuttings at 0°C (WEBB and SMITH 1970b). In quarantine, the chrysanthemum cuttings can be freed of leafminers in this way after incubation of the eggs combined with a chemical fumigation treatment (MORTIMER and POWELL 1984). Storage at 1.1°C for at least 16 days is also effective in controlling *L. trifolii* in celery, if no pupae are present (LEIBEE 1985).

The longevity and fecundity of *L. trifolii* decrease above 35°C. The upper oviposition threshold is near 40°C (Table 4). The maximum feeding per day per female occurred at 32.2°C, while the highest number of eggs per day per female was found at 26.7°C on chrysanthemum. The calculated oviposition threshold determined from regression equations for oviposition rate was 12.2°C. Experimentally, the oviposition threshold was established at 10.0°C and using this base temperature, degree-days were calculated. There was a strong relationship between the cumulative percent oviposition and the calculated cumulative degree-days (°D), and on the basis of such data it is possible to predict when and how much a female will oviposit. Ninety percent of all oviposition on chrysanthemum occurred within 550°D of adult life (PARRELLA 1984). The maximum population growth of *L. trifolii* on chrysanthemum and celery can be expected between 25° and 30°C. When the average temperature is about 15°C, there will be almost no increase. However, in the used set-up the longevity and fecundity of *Liriomyza* spp. were strongly influenced by the availability of honey to the adult female (e.g., in FREEMAN and GUYTON 1957). *L. trifolii* females on black-eyed pea provided with honey lived more than three times longer and produced a threefold number of eggs. The longevity and fecundity without and with honey were 7.2 d and 117 eggs and 22.7 d and 439 eggs respectively at 23.8°C (CHARLTON and ALLEN 1981). It is likely that some honeydew produced by whiteflies or aphids and nectar will be present in the field but it is not known whether the flies utilize these food sources.

More research needs to be done to characterize the microclimate conditions in which the immature and adult stages of *L. trifolii* exist in order to make a better prediction of the population growth possible (LEIBEE 1984). As these predictions will usually be based on experiments done at constant temperatures in climate rooms, the effects of fluctuation of the temperature and differences in host-plant quality on the biology of *L. trifolii* must also be determined.

TABLE 4. The mean longevity (days) and the mean total egg capacity^a per female (viable eggs) of *L. trifolii* at different constant temperatures.

Host plant	Temperature (°C)										reference
	15	15.6	20	21.1	25	26.7	30	32.2	35	37.8	
<i>Chrysanthemum morifolium</i> Ramat. cv. 'White Hurricane' ^b	-	16.7(42)	-	14.6(234)	-	12.8(279)	-	12.3(189)	-	3.1(1)	PARRELLA 1984
<i>C. morifolium</i> cv. 'White Hurricane' ^b	-	-	-	-	-	13.7(298)	-	-	-	-	PARRELLA et al. 1983b
<i>Apium graveolens</i> L. cv. 'Florida 2-14' (celery) ^b	27.7(24)	-	28.3(182)	-	16.8(288)	-	14.6(406)	-	13.0(240)	-	LEIBER 1984
<i>A. graveolens</i> cv. 'Tall Utah 5270-R' ^b	-	-	-	-	-	12.1(212)	-	-	-	-	PARRELLA et al. 1983b
<i>Lycopersicon esculentum</i> Mill. cv. 'Dwarf Patio Hybrid' (tomato) ^b	-	-	-	-	-	10.0(40)	-	-	-	-	PARRELLA et al. 1983b
<i>L. esculentum</i> cv. 'Moneydor'	6.2(3)	-	14.2(75)	-	5.4(55)	-	-	-	-	-	MINKENBERG (in prep.)

^a in parentheses

^b the flies were provided with honey

TABLE 5. The mean total development time (days) of parasites of *Liriomyza* spp. at different constant temperatures.

Parasite	Temperature (°C)										host and host plant				
	15	15.5	20	21.1	22	23	25	25.5	26.7	30		32.2	35		
<i>Opisus pallipes</i>	-	-	-	-	18.3	-	-	-	-	-	-	-	-	<i>L. bryoniae</i> bean	HENDRIKSE et al. 1980
<i>Dacnusa sibirica</i>	-	-	-	-	15.7	-	-	-	-	-	-	-	-	<i>L. bryoniae</i> tomato	HENDRIKSE et al. 1980
<i>Diglyphus isaea</i>	-	-	14.5	-	-	-	-	-	-	-	-	-	-	<i>C. syngenesiae</i> chrysanthe- mum	IBRAHIM and MADGE 1979

TABLE 5. (continued)

Parasite	Temperature (°C)										host and host plant	reference		
	15	15.5	20	21.1	22	23	25	25.5	26.7	30			32.2	35
<i>D. isaea</i> (♀)	26.0	-	16.6	-	-	-	10.5	-	-	-	-	-	<i>L. bryoniae</i> tomato	MINKENBERG (in prep.)
<i>O. dimidiatus</i>	-	-	-	-	-	20.4	-	-	-	-	-	-	<i>L. sativae</i> tomato	MCCLANAHAN 1983
<i>Pnigalio flavipes</i>	-	-	-	-	-	16.0	-	-	-	-	-	-	<i>L. sativae</i> tomato	MCCLANAHAN 1983
<i>D. begini</i>	-	-	-	-	-	-	-	11	-	-	-	-	<i>P. atricornis</i> <i>Sonchus oleraceus</i>	DOUTT 1957
<i>D. begini</i>	-	-	-	-	-	-	10.4	-	-	-	-	-	<i>L. trifolii</i> chrysanthemum	ALLEN and CHARLTON 1981
<i>D. begini</i>	-	-	-	-	-	14.3	-	-	-	-	-	-	<i>L. sativae</i> tomato	MCCLANAHAN 1983
<i>D. intermedius</i>	-	-	-	-	-	-	-	11	-	-	-	-	<i>L. trifoliarum</i> artificial mine	HENDRICKSON and BARTH 1978
<i>D. intermedius</i>	-	22.8	-	12.7	-	-	-	-	8.9	-	10.0	-	<i>L. sativae</i> artificial mine	PATEL and SCHUSTER 1983
<i>Chrysocharis parksi</i> (♀)	-	-	-	22.7	-	-	-	-	14.5	-	14.4	-	<i>L. trifolii</i> chrysanthemum	CHRISTIE 1984
<i>C. viridis</i>	-	-	-	-	-	22.4	-	-	-	-	-	-	<i>L. sativae</i> tomato	MCCLANAHAN 1983
<i>Halticoptera patellana</i>	-	-	-	-	-	24.6	-	-	-	-	-	-	<i>L. sativae</i> tomato	MCCLANAHAN 1983
<i>Hemiptarsenus semi-biclava</i>	-	-	16.5	-	-	-	11.5	-	-	8.5	-	6.5	<i>L. trifolii</i> bean	VERCAMBRE and THIERY 1983

5.2 HUMIDITY

The significance of humidity is quite different for the various stages of *L. trifolii*. Except for extreme drought or extreme moisture affecting the condition of the plant, the eggs, larvae and adults are insensitive to relative humidity (RH). The larger number of feeding punctures made by the adult female at high temperatures is probably due to the necessity for taking up more water. The influence of humidity and free moisture on the pupal stages of *L. trifolii* was studied at a range of constant temperatures (CHARLTON and ALLEN 1981). There was an increasing pupal emergence when the air over the pupae became more moist (RH 11%, 15%, 32%, 51%, 62%, 76%, 94%, 100% yielded emergences of 6%, 22%, 40%, 64%, 65%, 65%, 72%, 88%, respectively). In sand, when no water was added, the emergence was still 49% and in peat, it was as high as 79%. When newly formed pupae were submerged in water for 4 hours (h), 24h or 75h, 96%, 50% and 0% survived, respectively. Although the pupal stage is very sensitive to drought, humidity seems to play a minor role on the population growth of *Liriomyza* spp. under greenhouse conditions (RH 40-60%).

The influence of the relative humidity on the population growth of parasites has not yet been examined.

5.3 LIGHT

Little research on the effect of light intensity and duration on the development of the leafminers and parasites and on the behaviour of the adults has been done. *Liriomyza* spp. show a positive phototactic response. Therefore, a slowly rotating cage was constructed to eliminate any directional bias due to light or other environmental factors during oviposition experiments (SMITH et al. 1970). In darkness, *L. trifolii* adults do not feed or oviposit (L:D = 16:8, MINKENBERG in prep.). In greenhouses, higher densities of mines are observed along paths, borders and at the south side. Further research on the effect of light on the dispersal of agromyzid flies is necessary for understanding the distribution patterns of leafminers and the changes in these patterns. Some authors assumed that the efficiency of the parasite *D. isaea*, introduced against *C. syngenesiae* in greenhouse chrysanthemum in England, was impaired by the low light intensity or short day in spring, autumn and winter (SCOPES and BIGGERSTAF 1973). The effect of diminished radiation on the body temperature of the insect at lower light intensity could be a cause of reduced parasitization.

5.4 HOST-PLANT SUITABILITY

The host plant can be of great influence on the population growth of leafminers and parasites and their interactions. The suitability of host plants for phytophagous insects can be determined by comparing the growth, survival, ovipo-

sition or feeding on various host plants. Data presented in tables 3 and 4 clearly demonstrate the large variability of these characteristics of *L. trifolii* on different host-plant species or cultivars.

Liriomyza trifolii, introduced in Europe on ornamentals, occurred in large numbers in vegetables only a few years afterwards. The imported individuals fed, laid eggs, and the offspring survived on these plants. Evidently, a genetic basis for this step was present. The questions are now: 1) Are there 'host races' of *L. trifolii*, in other words are there genetically different forms? 2) Do the female flies have a preference for the host plant on which they bred and is this preference genetic or is it caused by conditioning of adults or larvae? 3) Will offspring which developed on the host plant that was preferred by their parents have a higher fitness than offspring which developed on other host-plant species? (for a review of these problems, see FUTUYMA and PETERSON 1985).

A sympatric host-associated variation in host preference was demonstrated in the polyphagous species *L. brassicae*(Riley) (TAVORMINA 1982). He found that flies produced a significantly greater proportion of their offspring on the host plant from which they were collected as larvae. A laboratory strain showed even a greater tendency to lay their eggs on the host plant on which they were reared, than wild flies from the host-plant species. According to TAVORMINA (1982): 'This fact demonstrates there is selection for an increased tendency to produce mines on the host plant an individual develops on and these results are consistent with the hypothesis that selection accounts for the divergence in mine-production behaviour observed in the wild population and that further divergence in the wild population is being inhibited by gene flow'. He concluded further that conditioning was not the only factor responsible for the differences in mine production behaviour, but that there was a genetic basis as well. There was no evidence that larval mortality was lower on the parental host plant and some evidence that larval growth is slightly faster on parental host plants. For another polyphagous leafminer, *L. sativae*, it was found that samples from closely adjacent fields of pea and tomato differed in host-plant preference phenotypically, and genetically in pupal weight (VIA 1984a,b). There is no significant genetic correlation of development time across host plants. There was a genetic correlation between oviposition preference and development time on the two host plants, but the 'populations' differed very little in average responses to the two plant species indicating that population divergence has not occurred in this system. The absence of 'host races' in this species may be due to frequent migration among crops, given the close spatial proximity of the test fields and yearly crop rotation. In choice experiments with the oligophagous leafminer, *P. matricariae* Hendel, it was found that maximum numbers of feeding punctures occurred on the plant on which flies were bred, but the number of eggs laid were not significantly higher than on some other plant species (SEGHAL 1971). The existence of host races or sibling species in *L. trifolii* could have important consequences for the development of control programmes.

For adult flies of *L. trifolii*, chrysanthemum and celery were more favourable hosts than tomato (PARRELLA et al. 1983b). Significantly fewer punctures and

eggs were found on tomato, and females lived for a shorter time. In the field, *L. trifolii* demonstrated a preference for celery in adjacent plantings of tomato and celery (ZEHNDER and TRUMBLE 1984). A comparison of the oviposition rate and development on tomato and three weed species showed that *L. trifolii* laid significantly more eggs on tomato and nightshade, whereas the percentage emergence and pupal weight on the different host plants did not differ significantly; the larval development time was significantly shorter on nightshade (ZOEBISH et al. 1984). These oviposition and feeding preferences of the females correspond with some biological characteristics of their offspring on the different host-plant species, e.g. larval mortality was significantly higher on tomato (PARRELLA et al. 1983b). However, the development time on tomato was the same as on chrysanthemum while on celery it was longer than on tomato and chrysanthemum (Table 3).

Thirty weed species are listed as host plants for *L. trifolii* with notes on their level of infestation and abundance (GENUNG and JANES 1975). The relative susceptibility of different varieties of chrysanthemum (WEBB and SMITH 1969; SCHUSTER and HARBAUGH 1979a,b; ALVERSON and GORSUCH 1982; OETTING 1982; BROADBENT and BLOM 1984) and of tomato (KELSHEIMER 1963; WOLFENBARGER 1966; WEBB et al. 1971; SCHUSTER et al. 1979, 1981) for *Liriomyza* spp can vary remarkably. No significant differences in leafminer tolerance among cantaloup cultivars were found (CHANDLER and THOMAS 1983). A comprehensive review on resistance of chrysanthemum and tomatoes to *Liriomyza* spp., including a discussion of the possibilities for breeding programmes, has been given by SCHUSTER et al. (1981).

The feeding puncture/egg ratio could be used as an indicator of host-plant preference for agromyzid leafminers, assuming that on a more nutritious host plant a female fly needs less feeding to produce eggs (HUSSEY and GURNEY 1962). Comparing the relative susceptibility of several chrysanthemum varieties for *C. syngenesiae*, they found a positive relation between the feeding puncture/egg ratio and the number of mines/10 cm² leaf. However, in choice experiments to compare different host-plant species or cultivars, the feeding puncture/egg ratio seemed unsatisfactory as an index for host-plant preference (IBRAHIM and MADGE 1977).

Increased plant nitrogen may either cause an increase or decrease in insect development rate, fecundity and numbers (SCRIBER 1984). On lettuce supplied with increasing concentrations of nitrogen, an increasing number of eggs were laid by *C. syngenesiae* (HUSSEY and GURNEY 1962). Increased fertilization which results in a heavier attack by *Liriomyza* sp. was previously shown (WOLTZ and KELSHEIMER 1958). A lower larval mortality of *L. sativae* occurred in chrysanthemum with a higher level of fertilization (POE et al. 1976). A linear relationship between fertilizer rate and the density of *L. trifolii* on chrysanthemum was established (PRICE and HARBAUGH 1981; HARBAUGH et al. 1983). These authors stressed that a surplus of nitrogen contributes to the leafminer problem.

Physical barriers like the leaf surface structure of the plant can be of great influence on the insect. The hooked trichomes on pink bean caused premature

death of leafminer flies (CHARLTON and ALLEN 1981). Higher density of hairs on plants negatively affects the oviposition by agromyzid flies (LIN and MITCHELL 1981; MACLEAN and BYERS 1983). Further investigations on the influence of host plants on fly and parasite development and behaviour are necessary.

6 THE DEVELOPMENT OF A BIOLOGICAL CONTROL PROGRAMME

After listing parasite species of *Liriomyza* spp. and summarizing information from the literature, an evaluation of the importance of these species for biological control of *Liriomyza* spp. in the desired crops and under the required climatic conditions should be made.

In greenhouse research the following procedure is recommended (VAN LENTEREN 1980):

1. literature research on pest and natural enemies,
2. collection of natural enemies,
3. laboratory experiments to study,
 - a) influence of temperature on biological parameters,
 - b) behavioural characteristics,
4. trials in experimental greenhouses,
5. trials in commercial greenhouses,
6. development of a mass-rearing programme for parasites,
7. development of an introduction method for parasites.

Steps 4 to 7 are not always performed in this sequence, but may be carried out concurrently. This approach has led to the development and application of biological control against several important greenhouse pests in vegetables (VAN LENTEREN 1986).

The usual method for evaluating parasites for biological control is still highly empiric: the trial-and-error method. To find an efficient natural enemy, this method takes about 3-5 years. However, it is difficult to find growers, who will give permission for trials in their greenhouses, when the control result can not be predicted.

Further, only a few parasite species are tested and the chosen species are not per se the most effective. In the Netherlands, a biological control method against leafminers in greenhouse tomatoes has been developed; only four parasite species are evaluated, while dozens of leafminer parasites are known. It has been demonstrated that two species are effective (a parasite is effective when it prevents a pest from crossing the economic injury level during the whole growing season). The need for an efficient evaluation method prior to introduction is stressed by most biocontrol workers and ecologists.

The aim of our research is to evaluate the capacity of some parasite species to control both leafminer species (*L. bryoniae* and *L. trifolii*). A general goal is to develop proper evaluation techniques for screening the control potential of parasite species prior to their use in practical situations. A compilation of

the literature describing the characteristics of an effective natural enemy was made (VAN LENTEREN 1980). The choice of criteria is determined by the system that we will examine (in our case the control of *Liriomyza* spp. in greenhouse tomatoes in the Netherlands by seasonal inoculative release of parasites). The characteristics which are useful as criteria for our selection process of parasite species for greenhouses are:

1. internal synchronisation with development of host,
2. no negative effects,
3. easy culture method,
4. sufficient reproductive potential,
5. good density responsiveness.

Several of these criteria are absolute, e.g. internal synchronisation with development of host. The reproductive potential and density responsiveness are hardly defined. It is necessary to quantify the latter criteria; otherwise, comparison of parasite species will not be possible.

An index for the reproductive potential is the intrinsic rate of increase (r_m). The r_m values at different temperatures depend on the development rate, mortality, longevity, sex ratio and fecundity and can be estimated under laboratory conditions. If host feeding occurs, the 'host kill rate' has to be measured, i.e. the combined value of r_m and the additional mortality caused by host feeding. The r_m values may be used to compare parasite species mutually and to compare parasites with their hosts. It seems to be a prerequisite for seasonal inoculative release systems, that an effective parasite has r_m values equal to or larger than those of its host. The realized rates of increase of parasites are lower in the greenhouse situation than the r_m values, because in greenhouses host densities should remain low. But estimating r_m values is useful for comparing potential population development.

The density responsiveness criterion is only loosely defined and contains aspects like functional and numerical response, aggregation, interference, intrinsic searching capacity, handling time, dispersal and spatial heterogeneity. This criterion can be defined as that part from the reproductive potential what is realised under the given circumstances. The searching behaviour of a parasite, involving the time spent in different phases of host location and the stimuli used, can be investigated in the laboratory. But experiments in greenhouses are necessary, e.g. to estimate migration capacities.

To verify the validity of the examined criteria, the combination of values for different parasite species should be related to their control capacities in commercial greenhouses. Effective as well as ineffective parasite species should be subjected to critical studies in order to establish a more reliable selection procedure of parasites species for biological control.

In the near future we hope to present such a reliable selection procedure for natural enemies in seasonal inoculative release systems, based on our studies with parasites of leafminers.

TABLE 6. The mean longevity (days) and the mean total fecundity^a per female (eggs) of parasites of *Liriomyza* spp. at different constant temperatures.

Parasite	Temperature (°C)						reference
	21.1	22	25	25.5	26.7	host and host plant	
<i>Opius pallipes</i>	-	8.7(89)	-	-	-	<i>L. bryoniae</i> tomato	HENDRIKSE 1983
<i>Dacnusa sibirica</i>	-	6.1(72)	-	-	-	<i>L. bryoniae</i> tomato	HENDRIKSE 1983
<i>Chrysocharis parksi</i> ^b	11.4(58)	-	-	-	14.7(135)	<i>L. trifolii</i> chrysanthemum	CHRISTIE 1984
<i>Diglyphus begni</i>	-	-	17.0(268)	-	-	<i>L. trifolii</i> chrysanthemum	ALLEN and CHARLTON 1981
<i>D. intermedius</i> ^b	-	-	-	24(40)	-	<i>L. trifoliarum</i> bean	HENDRICKSON and BARTH 1978

^a in parentheses^b parasites provided with honey solution

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