

GENERAL DISCUSSION AND CONCLUSIONS

The current study forms part of a larger research project on self-sustaining pest management strategies for *Liriomyza* species in Kenyan horticultural systems. It specifically investigated factors related to biological control of agromyzids, specifically *Liriomyza* species, with hymenopteran parasitiods. However, the apparent paucity of information on the Agromyzidae, which include a number of pest species of horticultural importance, and their associated natural enemies in Kenya and the Afrotropical region at large, limits our knowledge concerning biological control, data on distribution of agromyzids, host plant records and associated parasitoid species in this region was collated from museum collections, available literature and own observations.

This is the first study in the Afrotropical region that summarizes available literature and provides a snapshot of our current knowledge. The review is critical in advancing biological control research and allows for a more informed approach towards biocontrol projects involving agromyzid species. Agromyzid and parasitoid records (Chapter 1) also provide a framework for collection of additional data on host plant, leafminer, parasitoid associations in the Afrotropical region and can be of great value to agromyzid and biocontrol workers in Africa and elsewhere.

Based on the review in Chapter 1, a wide diversity of agromyzid leafminers has been documented in the Afrotropical region with collection efforts mainly centered on the East and Southern African sub-regions. In contrast to agromyzids, few parasitoid species have been recorded. The number of parasitoid species is approximately 1/6 of the recorded agromyzid species, highlighting either a possible lack of parasitoid diversity associated with agromyzid species or perhaps most likely a lack of sampling effort in the Afrotropical region. There is, therefore, a need for more intensive collaborative research in the afrotropics to identify the causes of the observed pattern.

There are several reports on biological invasions and natural control of *Liriomyza* species from outside the Afrotropical region (Sivapragasam *et al.*, 1999; Shepard *et al.*, 1998; Murphy & LaSalle, 1999; Rauf & Shepard, 1999; Thang, 1999; Chen *et al.*, 2003). According to these reports, local parasitoid species are capable of controlling leafminers in areas they invaded because agromyzid parasitoids, especially



eulophids, are generally not host specific (Murphy & LaSalle, 1999). Unlike in regions outside the Afrotropics, only 14 parasitoid species have been recorded from *Liriomyza trifolii* (Burgess), three parasitoid species from *L. huidobrensis* (Blanchard) and only one species from *L. sativae* Blanchard (Chapter 1). Most of these records are likely to be a result of deliberate introduction from other parts of the world, e.g. *Diglyphus isaea* (Walker) (Hymenoptera: Eulophidae) and *Dacnusa sibirica* Telenga (Hymenoptera: Braconidae) from the Palearctic region, for classical biological control programmes or augmentative releases (Minkenberg & van Lenteren, 1986; Neuenschwander *et al.*, 1987; Minkenberg, 1989). On the other hand, a sizeable number of parasitoids have been recorded on *Ophiomyia phaseoli* (Tryon), a widely distributed agromyzid pest of legumes in the Afrotropical region. The relationship between the parasitoid species of *O. phaseoli* and the invasive *Liriomyza* species needs further investigation through more parasitoid collection efforts in this region.

According to previous studies, pest problems with *Liriomyza* species arose because of the use of broad-spectrum pesticides (Hills & Taylor, 1951; Spencer, 1973; Johnson *et al.*, 1980; Parrella *et al.*, 1984; Keil *et al.*, 1985; Macdonald, 1991; Kotzee & Dennill, 1996; Murphy & LaSalle, 1999). According to the limited documentation available on pesticides, mostly broad-spectrum insecticides have been used for control of agromyzids in the Afrotropical region (Abate, 1990; Davies, 1998; Musundire, 2002). It is likely that in this region negative impact on natural enemies of *Liriomyza* species is associated with the indiscriminate use of insecticides in the agro-ecosystems while biological control of leafminers in the natural ecosystems is taking place but escaping notice. In light of this hypothesis, the recommendations made in Chapter 1, that there should be more concerted sampling efforts and capacity building in parasitoid taxonomy, are crucial in advancing biological control of agromyzid pests in the Afrotropical region.

In addition, parasitoid records of *L. huidobrensis*, *L. sativae* and *L. trifolii*, indicate that the presence of some of the parasitoid species is likely a result of deliberate introductions by humans (Neuenschwander *et al.*, 1987), showing a willingness by stakeholders in agriculture to approach invasive *Liriomyza* control in a non-chemical way. Due to the ongoing large-scale disturbance of the natural ecosystems within some parts of the Afrotropical region because of expansion of land under agricultural



production, it is unlikely that natural control of invasive *Liriomyza* species by parasitoids attacking sister agromyzid species in natural ecosystems will be realized in agro-ecosystems without human intervention. This provides a firm basis for advocating crop diversification and habitat management in Afrotropical agro-ecosystems while also providing an opportunity for implementing augmentative biological control techniques where parasitoids can be mass-reared and introduced into agro-ecosystems through inundative or inocultive releases.

Conservation biological control programmes have been successful in suppressing *Liriomyza* species to non-economic levels in celery, cucurbits, potatoes and tomatoes whose produce are not directly attacked by leafminers (Johnson *et al.*, 1980; Heinz & Chaney, 1995; Murphy & LaSalle, 1999; Liu *et al.*, 2009). On the other hand, augmentative releases of natural enemies have been successfully applied in greenhouses (van der Linden, 2004; van Linteren *et al.*, 2006). Within the context of the existing large-scale commercial agricultural practices in some parts of the Afrotropical region, augmentative biological control seems suitable as the release of parasitoids can be synchronized with other management strategies within the agro-ecosystems, maximizing the efficiency of parasitoids during periods of their release. However, additional surveys of parasitoid candidates suitable for biological control are recommended to widen the base of parasitoids that can be used as biological control agents.

Production of sufficient and high quality hosts is essential for mass-rearing parasitoids (Liu *et al.*, 2009). One of the requirements for successful rearing of *Liriomyza* species is production of good quality host plants under suitable environmental and nutritional conditions (Liu *et al.*, 2009). The ideal host plants should be easily propagated and maintained, be attractive to females for oviposition and support high numbers of leafminer larvae (Liu *et al.*, 2009). Results of the current study showed differences in host plant suitability for *L. trifolii* and to some extent for *L. sativae* but not *L. huidobrensis*, and as well as differences in host plant – host preference for *D. isaea*. These results highlight the importance of selecting suitable host plant species for mass- rearing leafminers for subsequent mass rearing of parasitoids. This is in accordance with Johnson & Hara (1987) that the best results for field application of *D. isaea* are obtained by matching the parasitoid with suitable host and



host plant species. However, under field conditions and for mass rearing of *Liriomyza*, larval density per leaf may well exceed the larval densities/cm² leaf area used in this study. There are, therefore, research opportunities to investigate the effect of different larval densities on the size of the resulting leafminer and implications at the third trophic level.

Various host plants have been used to rear *Liriomyza* species including lima beans (Webb & Smith, 1970; Petitt & Wietlisbach, 1994), tomato (Ushchekov, 1994) and cowpea (Jeyakumar & Uthamasamy, 1997). In the current study the underlying factors of host plant preferences of *Liriomyza* species was not determined. Host plant characteristics, e.g. plant chemistry (Isman, 1992; Martin *et al.*, 2005) and nutrition (Minkenberg & Ottenheim, 1990), affect life history parameters of *Liriomyza* as well as parastioid species. Future studies on *Liriomyza* and host plant interactions should involve methods that assess variation in larval size by using measurements of the cephalopharyngeal skeleton (Head *et al.*, 2002) or measurements of pupal lengths (Via, 1984a,b; Via, 1986), combined with analyses of the nutritional content of the host plants.

Results of current study suggest that larval size of *Liriomyza* is not necessarily positively linked with parasitism by *D. isaea* (Chapters 2 and 3). It is likely that plant related factors other than size of the *Liriomyza* larvae influenced parasitism. Apart from indirectly affecting the quality of host larvae, host plants have also been shown to influence the degree of parasitism of *D. isaea* by affecting cues for parasitoids, which include visual, acoustic, contact, taste and olfactory cues (Feeny, 1976; Bergman & Tingey, 1979; Price *et al.*, 1980; Elzen *et al.*, 1983; Visser, 1986; Johnson & Hara, 1987; Gross & Price, 1988; Liu *et al.*, 2009).

Olfaction is one of the many important factors involved in the search for a host by *D. isaea* (Zhao & Kang, 2002). Results from this study (Chapter 4) showed a positive response by parasitoids to all *L. huidobrensis*-damaged plant species evaluated. Although there was some variation in the response by parasitoids to plant species infested with *L. sativae* and *L. trifolii* (Chapter 4), overall parasitoids were attracted to leafminer-damaged plants. In addition, results show that indirect defensive compounds (allomones) were emitted by leafminer-damaged plants (Chapter 5). However, there is no discernable pattern between parasitoid response to damaged plants and parasitism



and host feeding on the same plants. This suggests that olfactory preference is not necessarily linked with parasitism.

The apparent discrepancy between attraction of parasitoids to leafminer damaged host plants and parasitism or host feeding in the current study indicates that, while volatile cues are important in successful host location by *D. isaea*, a combination of other signals such as visual, acoustic, gustatory, and touch may be involved in successful parasitism or host feeding by the parasitoid. Therefore, the successful use of *D. isaea* in the field and mass rearing may depend on using suitable host plants for leafminers and parasitoids.

Using plant mixtures for manipulating host feeding, parasitism and sex allocation by *D. isaea* can contribute towards improving biological control of *Liriomyza* species. Firstly, crop mixtures are planted in many agro-ecosystems where *Liriomyza* species pose a problem for subsistence and small-scale farmers. It is, therefore, important to determine the dynamics of *D. isaea* in mixed cropping systems. Secondly, previous studies have shown that *D. isaea* adjusts the rate of parasitism according to the host size encountered previously (Ode & Heinz, 2002). Further research on manipulating *D. isaea* behaviour to maximize its efficiency in agro-ecosystems and improve female biased populations for mass-rearing using plant mixtures should be undertaken.

In conclusion, the current study showed that the suitability of *D. isaea* for controlling *Liriomyza* species is variable and depends mostly on host plant species and leafminer size. A need exists for more intensive regional collaborative research to identify other suitable biological control candidates.

References

- Abate, T. (1990) Studies on genetic, cultural and insecticidal controls against the bean fly *Ophiomyia phaseoli* (Tyron) (Diptera: Agromyzidae) in Ethiopia. PhD Thesis, Simon Fraser University, USA.
- Bergman, J.M., & Tingey, W.M. (1979) Aspects of interaction between plant genotypes and biological control. *Bull. Entomol. Soc. Am.* **25**, 275-279.



- Chen, X.X., Lang, F., X.U. Zhi-hong, Jun-hua, H.E. & Yun, M.A. (2003) The occurrence of leafminers and their parasitoids on vegetables and weeds in Hangzhou area, Southeast China. *BioControl* 48, 515-527.
- Davies, G. (1998) Pest status and ecology of bean stem maggot (*Ophiomyia* spp.: Diptera: Agromyzidae) on the Niassa Plateau, Mozambique. *Int. J. Pest. Manag.* 44, 215-223.
- Elzen, G.W., Williams, H.J., & Vinson, S.B. (1983) Response by the parasitoid *Campolitis sonorensis* (Hymenoptera: Ichneumonidae) to chemicals (synomones) in plants: Implications for host habitat location. *Environ. Entomol.* 12, 1872-1876.
- Feeny, P.P. (1976) Plant apparency and chemical defense. In: Gross, P. & Price, P.W. (1988). Plant influences on parasitism of two leafminers: a test of enemy- free space. *Ecology* 69, 1506-1516.
- Gross, P. & Price, P.W. (1988) Plant influences on parasitism of two leafminers: a test of enemy- free space. *Ecology* 69, 1506-1516.
- Head, J., Walters, K.F.A & Langton, S. (2002) Utilisation of morphological features in life table studies of Liriomyza huidobrensis (Dipt., Agromyzidae) developing in lettuce. J. Appl. Entomol. 126, 349-354.
- Heinz, K.M. & Chaney, W.E. (1995) Sampling for *Liriomyza huidobrensis* (Diptera: Agromyzidae) larvae and damage in celery. *Environ. Entomol.* **109**, 213-220.
- Hills, O.A. & Taylor, E.A. (1951) Parasitization of dipterous leafminers in cantaloups and lettuce in Salt River Valley, Arizona. J. Econ. Entomol. 44, 759-762.
- Isman, M.B. (1992) A physiological perspective. In: Roitberg, B. & Isman M.B. (eds.), Insect chemical ecology. Chapman& Hall, New York. pp 156-176.
- Jeyakumar, P. & Uthamasamy, S. (1997) Mass rearing of American serpentine leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae). *Entomon.* 22, 243-245.
- Johnson, M.W. & Hara, A.H. (1987) Influence of host crop on parasitoids (Hymenoptera) of *Liriomyza* spp. (Diptera: Agromyzidae). *Environ. Entomol.* 6, 339-344.



- Johnson, M.W., Oatman, E.R. & Wyman, J.A. (1980) Effects of insecticides on populations of the vegetable leafminer and associated parasites on summer pole tomatoes. J. Econ. Entomol. 73, 61-66.
- Keil, C.B., Parrella, M.P. & Morse, J.G. (1985) Method for monitoring and establishing baseline data for resistance to permethrin by *Liriomyza trifolii* (Burgess). J. *Econ. Entomol.* 78, 419-422.
- Kotzee, D.J. & Dennill, G.B. (1996) The effect of *Liriomyza trifolii* (Burgess) (Dipt., Agromyzidae) on fruit production and growth of tomatoes, *Solanum lycopersicum* L. (Solanaceae). *J. Appl. Entomol.* **120**, 231-235.
- Liu, T., Kang, L., Heinz, K.M. & Trumble, J. (2009) Biological control of *Liriomyza* leafminers: progress and perspective. CAB Reviews: *Persp. Agric., Vet Sci, Nutr. Nat. Resour.* 4, 1-16.
- Martin, A.D., Stanley-Horn, D. & Hallett, R.H. (2005) Adult host preference and larval performance of *Liriomyza huidobrensis* (Diptera: Agromyzidae) on selected hosts. *Environ. Entomol.* 34, 1170–1177.
- Mcdonald, O.C. (1991) Responses of the alien leafminers *Liriomyza trifolii* and *Liriomyza huidobrensis* (Diptera, Agromyzidae) to some pesticides scheduled for their control in the UK. *Crop Prot.* **10**, 509-513.
- Minkenberg, O.P.J.M. (1989) Temperature effects on the life history of the eulophid wasp *Diglyphus isaea*, an ectoparasitoid of leafminers (*Liriomyza* spp.), on tomatoes. *Ann. Appl. Biol.* **115**, 381–397.
- Minkenberg, O.P.J.M. & van Lenteren, J.C. (1986) The leafminers *Liriomyza bryoniae* and *L. trifolii* (Diptera: Agromyzidae), their parasites and host plants: a review.
 Agricultural University Wageningen Papers, Agricultural University, Wageningen, Netherlands. pp 86-92.
- Minkenberg, O.P.J.M. & Ottenheim J.J.G.W. (1990) Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. *Oecologia* 83, 291-298.
- Murphy, S.T. & LaSalle, J. (1999) Balancing biological control strategies in the IPM of New World invasive *Liriomyza* leafminers in field vegetable crops. *Biocontrol News Inf.* 20, 91-104.



- Musundire, R. (2002) Evaluation of certain aspects of chemical, varietal and biological control methods against broad bean (*Vicia faba*) leafminers (*Liriomyza huidobrensis*). Msc Thesis University of Zimbabwe.
- Neuenschwander, P., Murphy, S.T. & Coly, E.V. (1987) Introduction of exotic parasitic wasp for the control of *Liriomyza trifolii* (Diptera, Agromyzidae) in Senegal. *Trop. Pest Manag.* 33, 290-297.
- Ode, P.J. & Heinz, K.M. (2002) Host-size-dependent sex ratio theory and improving mass reared parasitoid sex ratios. *Biol. Control* **24**, 31-41.
- Parrella, M.P., Keil, C.B. & Morse, J.G. (1984) Insecticide resistance in *Liriomyza* trifolii. Calif. Agric. **38**, 22-23.
- Petitt, F.L. & Wietlisbach, D.O. (1994) Laboratory rearing and life history of *Liriomyza sativae* (Diptera: Agromyzidae) on lima bean. *Environ. Entomol.* **23**, 1416-1421.
- Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.* 11, 41-65.
- Rauf, A. & Sherpard, B.M. (1999) Leafminers in vegetables in Indonesia: surveys of host crops, species composition, parasitoids and control practices. In: Lim, G.S., Soetikno, S.S. & Koke. W.H. (eds). Proceedings of a workshop on leafminers of vegetables in Southeast Asia, Tanah Rata, Malaysia, 2-5 February 1999. Serdang, Malaysia; CAB International Southeast Regional Centre, pp 22-25.
- Shepard, B.M., Samsudin, R. & Braun, A.R. (1998). Seasonal incidence of *Liriomyza huidobrensis* (Diptera: Agromyzidae) and its parasitoids on vegetables in Indonesia. *Int. J. Pest Manag.* 44, 43-47.
- Sivapragasam, A., Syed, A.R., LaSalle, J. & Ruwaida, M. (1999) Parasitoids of invasive agromyzid leafminers on vegetables in Peninsular Malaysia. Proceedings of Symposium on Biological Control in the Tropics, MARDI Training center, Serdang, Selangor, Malaysia, 18-19 March 1999, pp 127-128.
- Spencer, K.A. (1973) Agromyzidae (Diptera) of economic importance. Series Entomologica 9, Dr W Junk The Hague
- Thang, V.T. (1999) Surveys of leafminers (*Liriomyza*) and their parasitoids on vegetables in Vietnam 1998. In: Lim, G.S., Soetikno, S.S. & Loke, W.H. (Eds),



Proceedings of a workshop on leafminers of vegetables in South East Asia, Tanah Rata, Malaysia, 2-5 February 1999. CAB International Southeast Asia Regional Centre, Serdang, Malaysia, pp 42-53.

- Ushchekov, A.T. (1994) *Diglyphus* as an efficient parasitoid of mining flies. *Zashchita i Karantin Rastenii*. **3**, 56-57.
- van der Linden, A. (2004) Biological control of leafminers on vegetable crops. In: Heinz, K.M., van Driesche, R.G., Parella, M.P., (eds). Biocontrol in protected culture. B. ball Publishing, Batavia, IL; 2004. pp 235-251.
- van Lenteren, J.C., Bale, J., Bigler, F., Hokkanen, H.M.T. & Loomans, A.J.M. (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annu. Rev. Entomol.* 51, 609-634.
- Via, S. (1984a) The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interaction in larval performance on different host plant species. *Evolution* 38, 881-895.
- Via, S. (1984b) The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution* 38, 896-905.
- Via, S. (1986) Genetic covariance between oviposition preference and larval performance in an insect herbivore. *Evolution* **40**, 778-785.
- Visser, J.H. (1986) Host odour perception in phytophagous insects. *Annu. Rev. Entomol.* 32, 121-144.
- Webb, R.E. & Smith, F.F. (1970) Rearing a leafminer, *Liriomyza munda*. J. Econ. Entomol. 63, 2009-2010.
- Zhao, Y.X. & Kang, L. (2002) The role of plant odours in the leafminer *Liriomyza* sativae (Diptera: Agromyzidae) and its parasitoid *Diglyphus isaea* (Hymenoptera: Eulophidae): orientation towards the host habitat. *Eur. J. Entomol.* **99**, 445-450.