

The Tritrophic System *Hyptis suaveolens* (Lamiaceae) - Agromyzid Leafminers (Diptera: Agromyzidae) - Parasitoids (Hymenoptera): Effects of Herbivore Density, Host Plant Patch Size, and Habitat Complexity on Parasitism Rate

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ABSTRACT

*In this study a tritrophic system was evaluated to measure the contributions of the insect host density and its host plant concentration in simple and diversified habitat on the rate of parasitism. The system was composed of the plant *Hyptis suaveolens*, two species of agromyzid leafminers, and three morphospecies of parasitoids. The parasitism rate, patch size, and habitat complexity were found to be interdependent. If only the habitat complexity or patch size was taken into account the differences in parasitism rate are not significant, although habitat diversity seemed to contribute more than the host plant concentration to increase the parasitism rate. The leaves or plants with different number of mines were equally attacked by the parasitoids. The results were representative of what happened to the leafminers at different host plant densities under the homogeneous and heterogeneous habitat condition. This work could help to reinforce the idea of the importance of the plant diversity for enhancing the biological control of the pests by the parasitoids in the managed ecosystems.*

Key words: Habitat heterogeneity, *Calycomyza*, *Chrysocharis*, Biological control

INTRODUCTION

It seems reasonable that the density and dispersion of the herbivore hosts among the plants are factors related to the rate at which they are attacked by the parasitoids. Stiling (1987) reported that in only about 25% of the cases studied, the parasitoid response was directly dependent on the host density, while in 52% of the cases, no relation between the parasitism rate and host density was observed. Other factors, such as the host plants

(Barbosa and Benrey, 1998; Gratton and Welter, 2001; Till et al., 2002), habitat and environmental factors (Kareiva, 1983; Nichols and Altieri, 1994; Gurr et al., 2003), as well as variation in the foraging behavior among the herbivore host species (Hawkins, 1994) and parasitoid species (Stiling, 1987; Casas, 1989; Lewis et al., 1990) seem to be important in explaining the variations in the parasitism rate. Therefore, although obviously relevant, the host density, by itself, is

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not enough to determine the parasitism rate on the phytophagous insects.

For each particular phytophagous species, both intrinsic factors to the host plant-herbivore-parasitoid system and extrinsic habitat factors must be taken into account when analyzing the role of the parasitoids in herbivore's population dynamics. Barbosa and Benrey (1998) observed that the high resource availability of the diversified habitats could increase a parasitoid's fecundity, longevity, survival, and rate of the parasitism. Such a positive correlation has been ascribed to the higher availability of the resources provided by a more diverse plant community, such as the shelter and food supplies (*e.g.* nectar, pollen, and honeydew) (Root 1973, Powell 1986). Also, the habitat structure, particularly the plant species dispersion and composition, affect the parasitoids by interfering with the host location mechanisms, which are mainly based on the detection of the chemical and visual signals directly emanating from the host plants or mediated by the herbivores feeding on them (Vinson, 1976; Price et al., 1980; Whitam and Eller, 1990; Vet and Dicke, 1992; Godfray, 1995). Because of the higher concentration of the specific volatiles, the places where the host plants are concentrated, such as monocultures, would be expected to attract more parasitoids particularly associated with the herbivores feeding on these plants (Vet and Dicke, 1992). However, it has been demonstrated that not only the parasitoid richness, but the parasitoid abundance as well, tend to be higher in more complex habitats (Risch, 1979; Botelho et al., 1994).

Usually, a guild of the herbivores, such as the agromyzid leafminers, is attacked by a complex of parasitoids. The relative contribution of a particular species or group of the parasitoid species, through mortality, to a leafminer guild's population dynamics may depend on a combination of factors, which includes the density of the host herbivores, concentration of their host plants, and other features of the habitat where the insect hosts are found (Price et al., 1980; Damman, 1990). However, most of the studies aiming to analyze the insect host-parasitoid interactions refer to oversimplified systems of one host – one parasitoid species, or deal more with the community approaches to complex food webs. Despite the relevance of these approaches, in many systems the focus of one is too broad, and of the other too narrow to optimally measure the

effects of the increased plant density and/or diversity on the tritrophic interactions in the agroecosystems.

Focusing on the systems having an intermediate level of the complexity, such as those composed of one plant species, and multiple insect species depending on it, constitutes an interesting approach to investigate the effects of the host plant dispersion, herbivore density and habitat factors on the parasitism rate. This kind of information on the basic aspects of the tri-trophic interactions can help guide the biological control programs (Dyer and Gentry, 1999).

The present study aimed to evaluate the effects of the insect host density and host plant concentration at the simple and diversified habitat on the parasitism rate of the agromyzid leafminers living on *Hyptis suaveolens* Poit.

MATERIALS AND METHODS

The system studied

The system *Hyptis suaveolens* Poit. (Lamiaceae)–agromyzid leafminers – parasitoids was studied from November 1994 to August 1995, in the Serra do Japi (23° 11'S, 46° 52'W), Brazil, hereafter referred to as Japi. Japi is a protected area, with 300 Km², covered by a semideciduous forest, near the City of São Paulo. Patches of *H. suaveolens* are commonly found on the borders of the trails and roads crossing the area. *Hyptis suaveolens* is a native annual herbaceous plant commonly found in agricultural systems and in the open areas (Leitão Filho et al., 1972; Lorenzi, 1991).

The leafminers from the genus *Calycomyza* Hendel (Diptera: Agromyzidae) were found attacking *H. suaveolens* at Japi. The blotch mines containing the last instar (third) can measure up to 1.5 cm². The adults, ca. 2 mm long, can be seen on either surface of *H. suaveolens* leaves.

Parasitism of agromyzid leafminers in natural conditions

A total of 344 mined leaves of *H. suaveolens* was collected from November 1994 to May 1995. During this period of the year, the host plant occurred at the highest abundance and looked most vigorous. The collections took place along a 5 km trail, representing an altitudinal gradient from 800 m to 1100 m above the sea level. The collection was done at six different areas where *H. suaveolens* was abundant, three at 800 m, one at

900 m, one at 1000 m, and one at 1100 m altitude. In each area, a total of 10 random collections of mined leaves were made distributed as follows: one in Nov/94, two in Dec/94, two in Jan/95, one in Feb/95, one in Mar/95, two in Apr/95, and one in May/95. The collected leaves were individually separated in small plastic bags, which were labeled and taken to the laboratory where they were kept at room temperature. The emerged adults of both the leafminers and parasitoids were recorded and preserved for later identification.

Effect of leafmine density on parasitism in natural conditions.

During April and May 1995, 95 plants of *H. suaveolens*, occurring isolated from each other in the forest border, were inspected. Only the plants carrying at least one leafminer larvae at the last instar were sampled. The collection was restricted to larvae at this stage to guarantee that these mines had been exposed to the parasitoids during the similar amount of time, and also to reduce the variability in the survival rate of both the host and parasitoids. The inspections were carried out along a trail at 800 m altitude. The number of mined leaves per plant and the number of mines per leaf were recorded. The mined leaves were separated in the plastic bags, labeled, and taken to the laboratory where the same methodology, as described above, was followed.

Effect of host plant patch size and habitat heterogeneity on parasitism.

Three experiments were set between April and August 1995 at the Japi Field Station at 800 m altitude. About 1000 seedlings from *H. suaveolens* were collected from the forest border and transplanted in the plastic bags containing one part of the potting soil and two parts of the soil from the experimental area. These seedlings were initially left to grow close to the experimental area. All the seedlings were continuously inspected and all the mined leaves were removed before installing the experiment. For all the experiments different numbers of the potted plants were taken at random (about 20 cm) to establish the different sized patches of the treatments.

Two areas were used as the arenas for the experiment. One was a grass field of 450 m² (area A), representing an homogeneous habitat, and the other was an old orchard of 525 m² (area B), representing an heterogeneous habitat. The exact position of each patch in the arena in each

experiment, was determined randomly. Each patch was installed at least 5 m apart from the nearest patch. The pots composing the same patch were joined together and Tanglefoot® was applied to avoid attack of the plants by *Atta* sp. (Hymenoptera, Formicidae). Each day for the following 10 days, the plants were inspected and all mines were removed. This procedure was adopted to guarantee that all mines and parasitoids recorded had colonized the plants after the experiment had been installed. After this period, the number of mines per plant and per leaf in each patch was counted. The mined leaves were collected and the mines were raised in laboratory using the same technique previously described.

The experiments differed in the patch sizes and distribution pattern of the treatments. In the area A (grass field) two trials were made. The first one had four patch sizes: 1, 10, 20, and 30 plants/patch, with 13 replicates for the isolated plant treatment and 5 replicates for the other patch size treatments. The inspections were carried out five times from April to May. For the second trial in the area A, the largest patch size was increased, using patches of 1, 10, and 50 plants each, with 18 replicates for isolated plants and five replicates for each of the other patch size treatments. The inspections were carried out five times from June to August. In the area B (old orchard) only two patch sizes were used: 1 and 20 plants each, with 20 replicates for the isolated plants and six for the aggregated plants. Inspections were carried out nine times from April to August.

Statistical analysis

The total number of insects, both leaf-miners and parasitoids, which emerged from the leaves, were used to calculate the percent parasitism (similar methodology was applied by Friedlander et al., 1985 and by Kahn and Cornell, 1989). Other mortality factors were not considered. Although the mortality due to abortion of the mines in the laboratory could differ between the parasitized and not parasitized mines, this source of the error was evenly distributed among the patch sizes and habitats treatments. The statistical tests applied to compare the differences in the frequency and proportion of the agromyzids and parasitoids emerged from the mines per plant and per leaf and from the aggregated and isolated plants in simple (grass field) and complex habitat (old orchard). The analyses were carried out using Qui-Square

test, G test, and multidimensional contingency table analysis as described by Zar (1996).

RESULTS

The System *H. suaveolens*-Agromyzidae-parasitoids.

The *H. suaveolens*-agromyzid-parasitoids system in Southeast Brazil is composed of two species of agromyzid, *Calycomyza hyptidis* (L.) Poit. and another *Calycomyza* species (unidentified) (*Calycomyza* sp2), and three morphospecies of the parasitoids, *Chrysocharis* sp1, *C.* sp2 (Eulophidae), and one species from the family Eucoilidae (Eucoilidae sp1). No other species of leafminer or leafminer parasitoid on *H. suaveolens* was found. At all the places surveyed, the *Calycomyza* sp2 was more common than *C. hyptidis* (Fig. 1), and often the both species co-occurred in the same leaf. The two agromyzid species were easily distinguished from each other. *Calycomyza* sp2 formed a blotch mine located on the basal portion of the leaf, usually on the side of the mid vein, while *C. hyptidis* produced a star shape mine located on the apical portion of the leaf, often exactly over the mid vein.

Overall parasitism in natural conditions

From the 344 mined leaves collected along the altitudinal transect, between November 1994 and May 1995 (summer and autumn), 58 adult *Calycomyza* (about 84% *C.* sp2. and 16% *C. hyptidis*) and 83 parasitoids (41% from *C.* sp2 mines and 59% from the *C. hyptidis*) mines were obtained. Among the emerged parasitoids, *Chrysocharis* sp1 was the most common (39 adults), followed by *Chrysocharis* sp2 (29) and the least common was Eucoilidae sp1 (15) (Fig. 1).

Effect of leafminer density on parasitism rate.

Of the 95 colonized plants that were naturally occurring isolated in the forest border, 52 had only one individual leafmine of *Calycomyza*, while 43 plants had more than one leafmine and the maximum was 15 leafmines per plant. Although the leafmines on the plants carrying more than one

mine suffered about 10% more parasitism than the ones occurring isolated, this difference was not statistically significant (Fisher modified test, $P = 0.159$).

The maximum number of the mines per leaf was six, and the leafmines occurring alone (one per leaf) and aggregated (more than one per leaf) were almost equally attacked by the parasitoids (Fisher modified test, $P = 0.472$). Therefore, neither the leafminer density per plant, nor the leafminer density per leaf seemed to be clearly related with the parasitism rate of *Calycomyza* on the leaves of *H. suaveolens* in the natural conditions.

Effect of host plant patch size and habitat complexity on parasitism of leafmines.

From the total of 764 leafmines that colonized the plants in the experimental arenas, 127 adult insects emerged, 39 flies and 88 parasites, giving a parasitization rate of 69%. The absolute frequencies of the parasitoids successfully raised were not independent of the combined effects of patch size and habitat condition (Table 1, $G = 22.88$; $DF = 1$; $P < 0.001$). The numbers of the agromyzid parasitized, patch size, and habitat complexity were shown to be interdependent variables (Table 2, χ^2 for the mutual independence = 32.45, $DF = 4$; $P < 0.001$). However, taking into account only the habitat complexity, although the parasitism rate was about 14% higher in the heterogeneous habitat, this difference was not significant (Fisher modified test, $P > 0.05$). Otherwise, when taking into account only the patch size, the parasitism rate was even more similar between isolated and aggregated plants (64% and 72%, respectively) (Fisher modified test, $P = 0.31$). The parasitism rate proved to be only marginally dependent of the other two variables together (Table 2, $\chi^2 = 7.269$, $DF = 3$; $P < 0.10$).

The final result of this interaction on the third trophic level, when the effects of host plant patch size and habitat on the herbivore and on its parasitoids were combined, was that the parasitism rate was the lowest (44%) for the leafminers in the isolated plants in the homogeneous habitat, and the highest (85%), for the leafminers in the grouped plants in the heterogeneous habitat (Table 3).

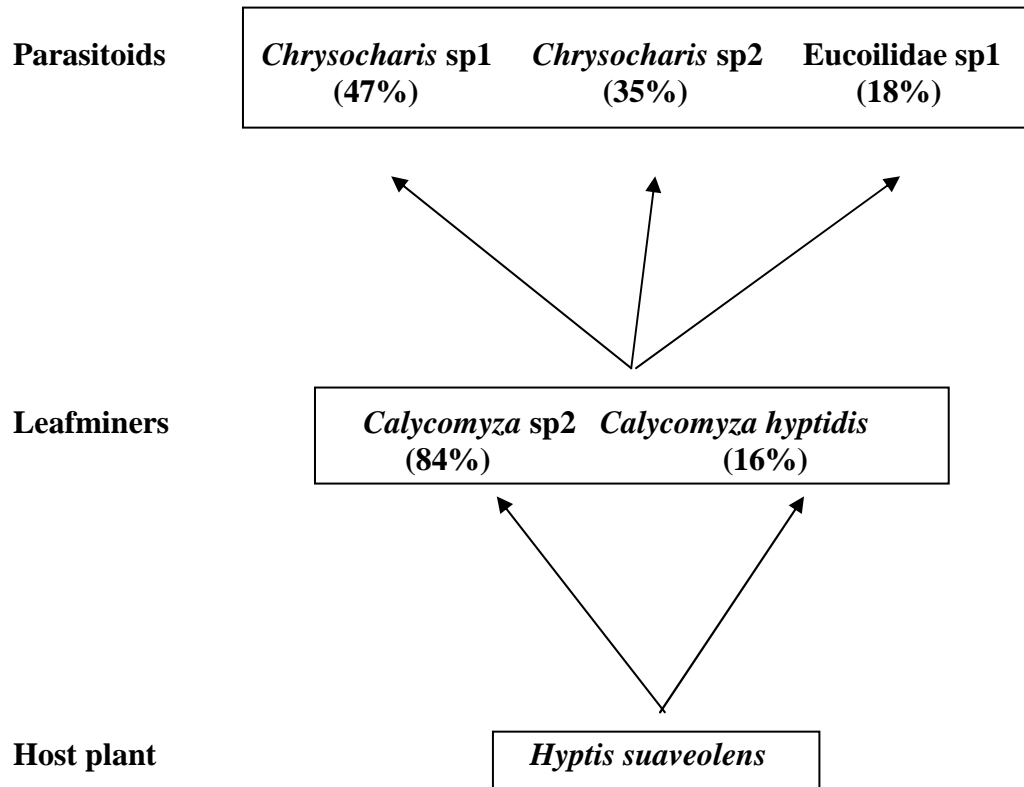


Figure 1 - Tritrophic system *Hyptis suaveolens* – *Calycomyza* leafminers – parasitoids in the Serra do Japi, Southeast, Brazil.

Table 1 - Frequency of microhymenoptera parasitoids emerging from *Calycomyza* leafminers in experiments with isolated and aggregated host plant *Hyptis suaveolens* in homogeneous (grass field) and heterogeneous habitats (old orchard).

	Homogeneous habitat	Heterogeneous habitat	Total	G	P
Isolated plant	8	22	30	22.88	<0.001
Aggregated plants	47	11	58		
Total	55	33	88		

*P for $\chi^2_{0.05, 1}=3,841$

Table 2 - Three-dimensional contingency table for mutual and partial independence analysis among parasitism (parasitized x not parasitized), host plant density (isolated x patched), and habitat (homogeneous x heterogeneous) in the system *Hyptis suaveolens* - *Calycomyza* spp. leafminers - microhymenoptera parasitoids.

	Homogeneous habitat		Heterogeneous habitat		Total
	Isolated plants	Aggregated plants	Isolated plants	Aggregated plants	
Parasitized	8	47	22	11	88
Not parasitized	10	20	7	2	39
Total	18	67	29	13	127

χ^2 for total independence

$\chi^2=32.453$ P<0.001 ($\chi^2_{0.05, 4}=9.488$)

χ^2 for parasitism independent of habitat and plant density

$\chi^2=7.269$ 0.05<P<0.10 ($\chi^2_{0.05, 3}=7.815$)

DISCUSSION

Parasitism rate on leafminers

The leafminer parasitoids certainly exert strong effect on the insect host population dynamics. The high parasitism rate observed for *Calycomyza* species on *H. suaveolens* in Southeast Brazil, reinforced the idea, which had already been reported for the insect-plant systems studied in the temperate regions that parasitoids represented an important top-down mortality factor for the herbivore insects (Price, 1992). Esposito (1990), working in the same region reported 43% of parasitism rate for agromyzid pupae collected from the herbaceous plants community. In the natural habitats of Central Argentina, Valladares and Salvo (2001) also found high rates of the parasitism on the agromyzid leafminers, particularly during the summer (December to March), when over 70% of the leafmines had been parasitized.

Density dependence and habitat heterogeneity effects on parasitism rate

While the density of the leafminers per plant and per leaf seemed not to be related to parasitism rate, the patch size of the herbivore's host plant, as well as the habitat heterogeneity seemed to affect parasitoid numbers. It was found that *Calycomyza* species are more prone to escape from parasitoids when in isolated plants in the homogeneous habitat, and that the parasitism rate tended to be the highest when the leafminers occurred in the patched host plants in more diversified habitat. The habitat heterogeneity seemed to be relatively more important than the host plant density for explaining the differences in the parasitism rate in this tritrophic system. The presence of other herbs, shrubs and trees in the heterogeneous habitat probably contributed additional resources that might have positively affected the parasitoids, resulting in higher parasitism rate.

A possible, but not exclusive explanation, could be the well known positive role of the complementary and supplementary food sources and microclimate conditions in a more complex environment on the parasitoid efficiency (Barbosa and Benrey, 1998; Marino and Landis, 1996). Landis et al.(2000) suggested that the spatial and temporal management of the resources such as the alternative food, alternative prey, and shelter in the habitat was a key factor for the improvement of

the herbivore population control by the natural enemies.

Therefore, although the parasitism rate considered in this study did not take into account the differences among agromyzid and parasitoid species involved, the proportion of both the agromyzid hosts did not differ between areas (*Calycomyza* sp. is always more abundant, about 85% of the total) and that the combined species analyzed represented a common interactive situation. From the point of view of the response of the parasitoids as a top-down factor, the results were representative of what happened to the leafminers at different host plant densities under the homogeneous and heterogeneous habitat condition. Thus, it could be concluded that: 1. the number of mines per plant and per leaf had marginal or no effect on parasitism rate; 2. the patch size of the herbivore's host plant, as well as the habitat heterogeneity seemed to affect the parasitism rate; 3. habitat diversity seemed to contribute more than the host plant concentration for increasing the parasitism rate. These conclusions reinforced the idea of the importance of the flora diversity for enhancing the biological control of the specialist pests by the parasitoids in the agroecosystems. If this is true, the conservation of the biodiversity of the parasitoids in one tropical region could be more directly dependent on the conservation of the plant diversity.

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RESUMO

Foi avaliado um sistema tritrófico para medir os efeitos da densidade de insetos minadores e a concentração da planta hospedeira em habitats simples e diversificados sobre a taxa de parasitismo. O sistema era composto pela planta *Hyptis suaveolens*, duas espécies de agromizídeos

minadores de folhas e três morfoespécies de parasitóides. A taxa de parasitismo, tamanho da mancha e a complexidade do habitat foram interdependentes. Se levarmos em consideração apenas a complexidade ou tamanho de mancha, as diferenças na taxa de parasitismo não foram significativas, embora a diversidade de habitat pareça ter contribuído mais do que a concentração da planta hospedeira para aumentar a taxa de parasitismo. Folhas ou plantas com diferentes números de minas foram igualmente parasitadas. Nossos resultados são representativos do que acontece com insetos minadores em diferentes densidades de plantas e condição do ambiente – homogêneo ou heterogêneo. Este trabalho ajuda a reforçar a idéia de que a diversidade de plantas no sistema ajuda a aumentar o controle biológico de pragas por parasitóides.

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