BIOLOGICAL CONTROL

Predators Impairing the Natural Biological Control of Parasitoids

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Predadores Prejudicando Parasitóides no Controle Biológico Natural

RESUMO - Foi analisado um caso bem conhecido de insucesso técnico no controle biológico natural: a coexistência enigmática do bicho-mineiro-do-cafeeiro, *Leucoptera coffeellum* (Guérin-Mèneville), e seus inimigos naturais. Apesar de ser uma presa adequada a oito espécies de parasitóides e três espécies de vespas predadoras, todas ocorrendo simultaneamente, o bicho-mineiro-do-cafeeiro apresenta, muito frequentemente, populações acima do nível de dano econômico para o cafezal. Foi demonstrado que vespas predadoras e parasitóides interagem negativamente, possivelmente porque vespas matam as lagartas de bicho-mineiro-do-cafeeiro parasitadas. Fazendo assim, vespas predadoras matam parasitóides indiretamente, prejudicando a eficiência do controle biológico natural. Conclui-se que programas de controle biológico deveriam estar baseados em conhecimentos de interações tróficas, ao invés de simplesmente se basearem em estratégias que envolvam a introdução de inimigos naturais exóticos.

PALAVRAS-CHAVE: Insecta, Interação intraguilda, *Leucoptera coffeellum*, café.

ABSTRACT - A well known case of ineffective natural biological control: the puzzling coexistence of the coffee leaf miner, *Leucoptera coffeellum* (Guérin-Mèneville), and its natural enemies was analyzed. Despite being a suitable prey to eight parasitoid species and three wasp species, all occurring simultaneously, the coffee leaf miner too often presents populations far above the damaging level for the coffee plantation. It is demonstrated that predatory wasps and parasitoids interact negatively, possibly because predatory wasps kill parasitized miner's larvae. In doing so, predatory wasps indirectly kill parasitoids, thereby impairing the efficacy of the natural biological control. It is warned that biological control programs should be based on knowledge of food web interactions, rather than simply on strategies involving introduction of exotic natural enemies.

KEY WORDS: Insecta, Interguild interaction, *Leucoptera coffeellum, coffee.*

There are many situations in which strategies of the natural biological control are not effective, failing to keep insect pest populations below damaging levels. For such cases, the critics often recommend a complete switch to "more reliable" strategies, such as chemical control. More ecologically concerned professionals, on the other hand, would recommend some kind of improvement to the system at hand, aiming to hopefully correct the faults. Solutions, apparently, tend to be based on a general assumption that when biological control fails, it happens simply because the natural enemies are not killing the pest. Ideas such as those are so deeply rooted, that importation of natural enemies have too often been regarded as trivial. That is, since native natural enemies are assumed to be ineffective, the easiest solution would be to bring along some "effective" ones. The scenario is somewhat more complex, however. Whether they attack or not a prey population, natural enemies may fail to keep pests at acceptable levels (Fig. 1).

This paper analyses a well known case of agronomic lack of success in biological control: the puzzling coexistence of the coffee leaf miner, *Leucoptera coffeellum* (Guérin-Mèneville), and its natural enemies. Despite being a suitable prey of nine species of parasitoids and two species of predatory wasps, all occurring simultaneously (Avilés 1991), the coffee leaf miner too often presents populations far above the damaging level. This fact has generated much controversy regarding the real role of natural enemies as controllers of the coffee leaf miner. Some authors (e.g. Souza 1979) consider that predatory wasps, rather than parasitoids, play the significant role in the natural biological control of the coffee leaf miner. Others (Konnorova 1985, Konnorova 1986, Campos *et al*. 1989, Avilés 1991) believe that parasitoids do play an important role, but their effect is overlooked by the current sampling procedures. Shedding lighting on this issue, Avilés (1991) observes that predatory wasps often do not kill all larvae in the attacked mine, and hypothesizes that these wasps may be attacking only parasitized larvae.

We present a test for such an hypothesis, which conforms to one branch of Fig. 1: by attacking parasitized larvae, predatory wasps limit the population of parasitoids by preying indirectly on them.

Theoretical Considerations. Natural enemies may not attack the prey when they are not adapted to it (Fig. 1; box A); this is the simplest reason for the failure of biological control programs. On the other hand, natural enemies may fail to kill the prey when they are not able to locate, fight, or subdue it (Fig. 1; box B). This may happen when the natural enemy does not fulfil all phases of a predator's foraging dynamics, which include search, pursuit, and domain of the prey (Griffiths 1980). Accomplishing these phases is not only a matter of how finely tuned are the biologies of the natural enemy and the prey, but also depends on the idiosyncrasies of the environment in which biocontrol agents are introduced. Since conventional agroecosystems do not resemble natural systems, failing natural enemies are not at all surprising because the dynamics of predation (*sensu latu*) may be easily impaired by the novel plant community composition and spatio-temporal arrangement (Altieri *et al*. 1993).

Natural enemies may also fail to keep pests at acceptable levels when they promote a moderate attack to the pest population, killing fewer individuals than would be needed for a successful biological control program. This may happen when several species of suitable prey coexist in the same area, thereby diverting the natural enemy from the target of the biological control program (Fig. 1, box C). Sometimes, even though when the pest is the primary prey available, the success is not achieved (Fig. 1, box D). Firstly, if the population of natural enemies oscillates too asynchronically relative to that of the prey, chances are increased that not enough natural enemies will be present at appropriate times to suppress populations prey. Normally, one would assign such fluctuations to climatic factors (Villacorta 1980, Campos *et al.* 1989, Nestel *et al*. 1994). Mostly overseen, and perhaps more important than climate, are the oscillations which are originated intrinsically, as the consequence of a reproductive rate "r" greater than 3.0. A population presenting such values of "r" will most likely show a fluctuation pattern that, although absolutely similar

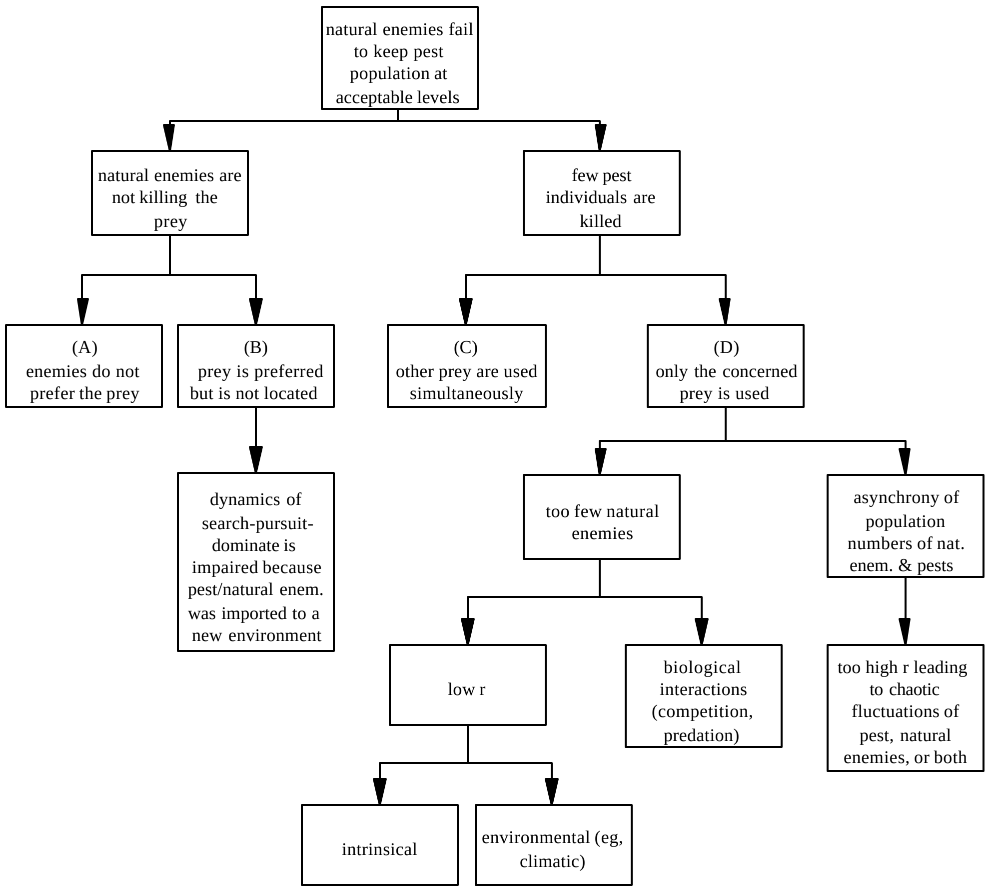

Figure 1. Theoretical reasons for technical failure in biological control programs. Boxes represent hypothetical biological mechanisms/processes which prevent natural enemies to keep pest population at technical acceptable levels. Boxes are kept apart for the sake of reasoning only, but several of these processes may occur simultaneously.

to climatic effects, obey a chaotic dynamics which does not depend on external factors (Miramontes & Rohani 1998). Therefore, if either natural enemies or pest present high "r" values, their population will fluctuate in a chaotic manner, establishing thereby an asynchrony deleterious to any biological control program. Therefore, reproductive rate should be one of the first traits to be examined when deciding whether or not a given natural enemy is suitable as a biological control agent.

Secondly, natural enemies may not achieve population numbers high enough to significantly lower the pest population. Low numbers of natural enemies can be a consequence of low "r" which arise from genetic and/or environmental factors. In such cases, massal rearing and releasing of natural enemies may improve the success of biological control programs. However, when the population of natural enemies is limited by biological interactions, low numbers of natural enemies may not be totally overcome by mass rearing and releasing. For instance, when natural enemies are under severe predation pressure. Therefore, before recommending a given natural enemy as a biological control agent, it is imperative to verify the occurrence of potential negative biological interactions in the environment into which the organism is going to be inserted.

Thus, when biological control programs fail, the assumption that native natural enemies need to be replaced (or other natural enemy species must be added to the system) may prove to be an oversimplified, if not a naïve, approach. There are many theoretical reasons, other than unsuitability of the natural enemy, for the lack of success of pest management programs based on biological control strategies.

Material and Methods

The system under study was composed of the coffee plants (*Coffea arabica* L), its leaf miner (*L. coffeellum*), and its set of natural enemies: predaceous wasps (*Protonectarina sylveirae* (de Saussure), *Polybia scutellaris* (White) and *Brachygastra lecheguana* (Latreille); and parasitoids (*Mirax* sp., *Colastes* sp., *Horismenus* sp., *Closterocerus* sp., *Proacrias* sp., *Eubadizon* sp., *Cirrospilus* sp. and *Tetrastichus* spp.) (Zucchi *et al*. 1979, Avilés 1991).

Leaves of coffee plants, containing mines of the coffee leaf miner, were marked in the field, prior to the beginning of the experiment. Leaves were chosen so as to contain only mines which presented no sign of attack by predatory wasps. Mines which have been attacked by predatory wasps are easily distinguishable by their torn lower surface (Souza 1979). Twenty of those leaves were collected in a 100 m long row of contiguous trees, on four occasions, 4, 8, 12, and 16 days after marking them; thus totaling 80 leaves per row. Leaves were taken to the laboratory, individualized in plastic bags previously perforated with a micropin, and kept for 30 days, or until the emergence of parasitoids. The technique to keep coffee leaves viable in the laboratory is described by Reis Jr. *et al.* (in press). Percent of predation was defined as the number of leaves containing torn mines divided by the total number of leaves collected, either in a row or for the whole experiment. Similarly, percent of parasitoidism was defined as the number of leaves from which parasitoids emerged, divided by the total number of leaves collected. The area of all mines was estimated as the area of an ellipse, using the formula pr_1r_2 where r_1 and r_2 are the biggest and the smallest diameter.

The experiment was carried out in three commercial coffee plantations in the region of Viçosa County, state of Minas Gerais, Southeastern Brazil. The coffee leaf miner had not been subjected to any non-natural kind of control in these plantations for the last 10 years. A total of 13 (100m) rows of continuous coffee plants were chosen within the selected plantations, so that three rows were located in the smaller plantation and the other two plantations held five rows each. Rows were chosen so as to cover the widest spatial range within each plantation, observing a minimum inter-row distance of 100m along lines of coffee plants, and 50m across lines.

Statistical analyses inspected the relationship between presence of predators and presence of parasitoids, at the local scale, and the pattern of resource exploitation by predators and parasitoids. Regression lines were fitted to the data, along with control variables, as appropriate.

Results and Discussion

Predation upon coffee leaf miner is inversely related to parasitoidism: low levels of parasitoidism are detected in places presenting high rates of predation, and vice-versa ($F_{[1;11]}$ = 7.98; P= 0.0165; Fig. 2); and this phenomenon does not depend on the plantation where the data were collected ($F_{[2;9]}$= 1.41; P=0.29). This suggests some kind of nega-

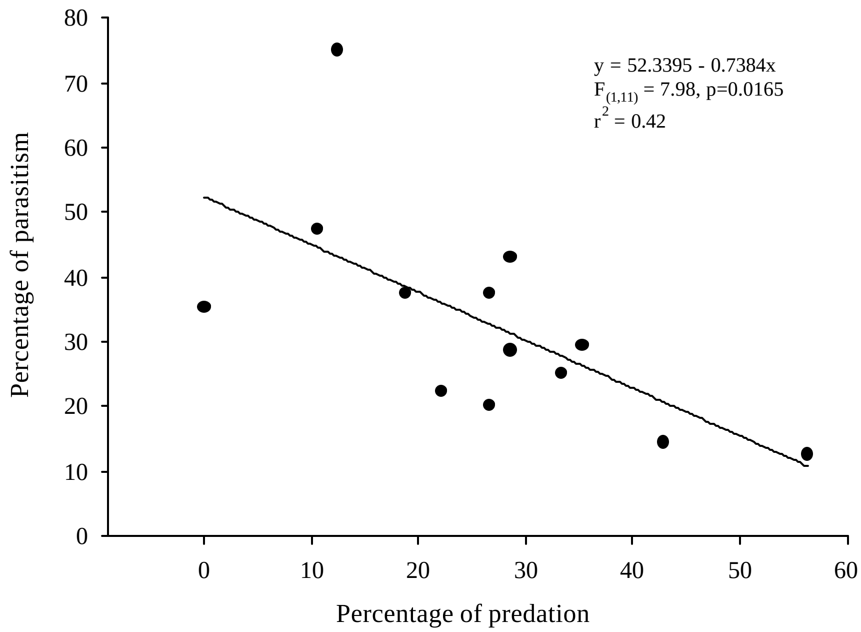

Figure 2. Local inverse relationship between predation and parasitism of *L. coffeellum* attacking coffee plantations. Each dot represents one 100m long row of contiguous coffee plants. Percents of predation and parasitism are defined as the number of leaves containing torn mines (predation), or the number of leaves from whose mines parasitoids emerged, divided by the total of leaves inspected. Data were collected within three disjunct plantations. Statistical analysis included plantations as a blocking factor ($F_{[2;9]}$= 1.41; P= 0.29), thereby extracting such effects from the observed trend.

tive interaction between predatory wasps and parasitoids regarding their action upon coffee leaf miner. Patterns of resource exploitation by predators and parasitoids overlap partially, with predators exploiting mines which are slightly larger than the mines attacked by the parasitoids (Predators: $F_{[1;6]}$= 43.99; P= 0.0006; r^2= 0.88. Parasitoids: $F_{[1;6]}$= 1165.18; P< 0.0001; r^2= 0.99. Fig. 3).

Biological control programs are not necessarily improved by assuring the coexistence of several species of natural enemies. The notion that natural enemies sum their effects upon a prey species population is shown to be false, at least for the case of the coffee leaf miner (Figs. 2 and 3).

In fact, in such a system, predators seem to be impairing the action of parasitoids. Such an idea is based on three facts: (i) predators and parasitoids are inversely related (Fig. 2); (ii) predators and parasitoids partially overlap in their resource exploitation (Fig. 3); and (iii) predators prey on larvae in mines which are slightly larger than those attacked by

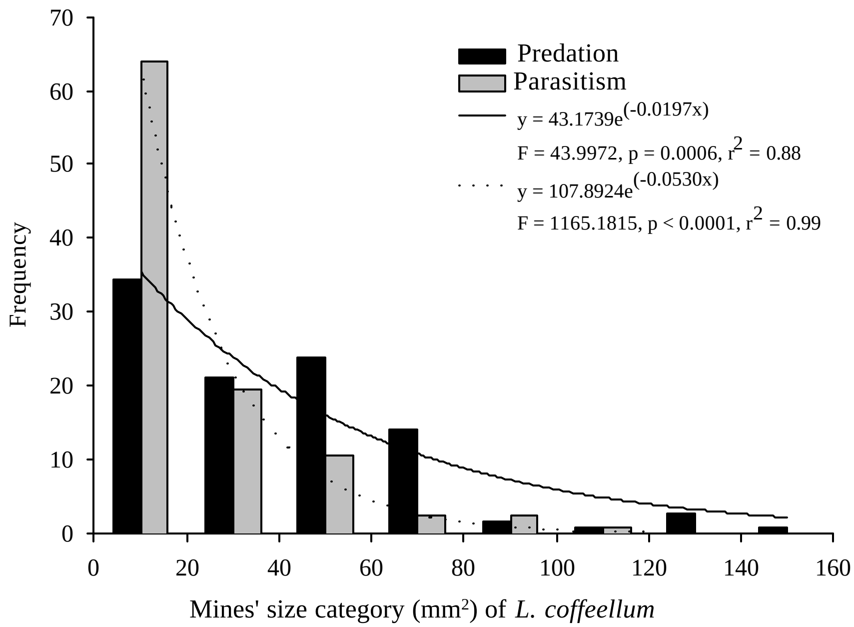

Figure 3. Resource partitioning among predators and parasitoids of the coffee leaf miner (*L. coffeellum*). Mines have been categorized in arbitrary classes of size. Frequency of occurrence of predators and parasitoids is defined as the number of leaves containing torn mines (predation), or the number of leaves from whose mines parasitoids emerged, divided by the total of leaves inspected (n= 1040) in three commercial coffee plantations.

parasitoids (Fig. 3). The picture that emerges is rather simple: by attacking a larvae in a mine, a predator makes it unavailable to parasitoids because the larvae is removed. The opposite is not true, however: larvae attacked by parasitoids remain in the mine, being therefore potentially available to predators. Thus, predators may kill both parasitoids and the leaf miner. We are not in position to state whether or not predators look for parasitized mines, but our data allow the suspicion that when predators attack their "preferred" mines (Fig. 3), many of these mines have been previously parasitized (otherwise Fig. 2 would not present the inverse pattern). Similar results have already been reported by Moreira & Becker (1986, 1987), working with *Nezara viridula* (Linnaeus) attacking soybean. In such a system, parasitized eggs of *N. viridula* suffer higher predation rate than non-parasitized ones, but the authors refrain from stating that the predators prefer such eggs. Rather, they showed that parasitized eggs are available to predators longer than are healthy eggs, which therefore increases their chances of being attacked.

For the coffee leaf miner, when a predator attacks parasitized mines, the parasitoid is consequently killed, which weakens the reproductive success of the latter. Only parasitoids escaping such a fate would contribute to the next generation. Therefore, the next generation of parasitoids would be guaranteed if (i) remaining parasitoids present relatively high reproductive rate, (ii) predators are not too abundant, or (iii) coffee leaf miner populations are so large that many parasitized miners are not preyed upon. In fact, despite the pressure from predatory wasps on these parasitoids, the system remains relatively stable: predatory wasps, parasitoids and the coffee leaf miner coexist in the field (Le Pelley 1973, Parra *et al*. 1981, Reis & Souza 1996). Apparently, such a stability is sustained by a combination of the above three reasons. The coffee leaf miner is known to present low abundance during summer (Nestel *et al*. 1994, Souza *et al*. 1998), when predatory wasps in general tend to present higher activity. In this scenario, the probability of a parasitized larvae being attacked is very high, which suppresses the population of parasitoids in the summer. As the winter approaches, the abundance of the coffee leaf miner reaches its maximum (Souza *op.cit*.), far beyond damaging levels for coffee plants (Villacorta & Tornero 1982, Souza *et al*. 1998). Because of the heavy losses suffered by parasitoids in the summer, their attack upon the miner is not severe enough to control this pest in the winter, but at least the population of parasitoids is able to rebound in the next generation.

Success of biological control programs of the coffee leaf miner would, thus, depend on correct manipulations of the impacts from some of the above items. It is important to realize that importation of new species is not among such strategies. Perhaps, the most effective strategy would be getting the best of the complete suite of natural enemies. Firstly, parasitoid abundance's should be increased right in the beginning of the miner's infestation, when mostly small mines are present (as shown in Fig. 3, small mines are attacked more intensely by parasitoids than by predators). As time elapses and mines get bigger, the abundance of predatory wasps need to be increased in large proportions, so that there are enough predators to attack healthy and parasitized mines. Specific techniques for such releases are yet to be developed, which could certainly open up several lines of research.

Specifically for such a system, introducing new highly specific parasitoid species may prove ineffective, unless such parasitoids present explicit strategies to avoid the attack by predatory wasps.

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