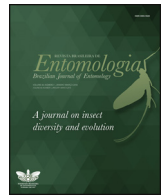




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Parasitism rate of *Myzus persicae* (Sulzer) by *Diaeretiella rapae* (McIntosh) in the presence of an alternative, resistant host

Samira Evangelista Ferreira^a, Marcus Vinicius Sampaio^{a,*}, Reinaldo Silva de Oliveira^{a,b}, Heraldo Luís de Vasconcelos^c

^a Universidade Federal de Uberlândia, Instituto de Ciências Agrárias, Uberlândia, MG, Brazil

^b Instituto Federal de Educação, Ciência e Tecnologia do Triângulo Mineiro, Uberlândia, MG, Brazil

^c Universidade Federal de Uberlândia, Instituto de Biologia, Uberlândia, MG, Brazil

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ABSTRACT

The aphids *Lipaphis pseudobrassicae* (Davis) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) are important Brassicaceae pests, occurring worldwide and causing significant damage to crops. Interspecific variations in the resistance to natural enemies can potentially impact the interaction among aphid populations. Here we evaluated the hypothesis of associational resistance by determining if the presence of resistant aphids (*L. pseudobrassicae*) reduces the rate of parasitism by *Diaeretiella rapae* (McIntosh) on non-resistant aphids (*M. persicae*). The experiment was conducted using collard green plants infested with *M. persicae* and *L. pseudobrassicae* either resistant or susceptible to *D. rapae*. The percentage of parasitism by *D. rapae* was greater on *L. pseudobrassicae* in the susceptible than in the resistant treatment, but parasitism rates on *M. persicae* did not differ between the treatments. There was no difference in average growth rate between *M. persicae* and susceptible *L. pseudobrassicae* populations, but resistant *L. pseudobrassicae* had greater growth rate than *M. persicae*. These results suggest that over a short period of time the presence of resistant *L. pseudobrassicae* does not affect the rate of parasitism by *D. rapae* on *M. persicae*.

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Introduction

Interactions involving a shared and limited resource may result in exploitative competition, when individuals use available resources and thus deprive competitors of these resources, or in interference competition, in which individuals inflict damage to each other through direct contact, thus depriving competitors of access to the resource (Price et al., 2011; Schoener, 1983).

When two species do not compete for a resource, their population can be changed by a shared predator, parasite, or pathogen – a phenomenon known as “competition mediated by parasites or natural enemies” or “apparent competition”. This type of competition was defined as a reduction in population of a species when the population of a second species increases through its interaction with a third species of a higher trophic level (Chaneton and Bonsall, 2000; Holt, 1977; Holt and Lawton, 1994). Competition mediated by parasites and natural enemies are very common in nature and

can be considered one of the main types of interaction in ecological systems (Bhattacharai et al., 2017; Kaplan and Denno, 2007; Price et al., 1986).

There are several cases where the parasitoid species are the same for two hosts, but the impact of this natural enemy is different in each one (Frost et al., 2016; Holmes, 1982; Rice and Westoby, 1982). For instance, a host species with a large population may sustain a large parasitoid population and, thus, indirectly affect the parasitism rate of a second host species (Asgari et al., 1998; Blumberg, 1997; Price et al., 1986; van Veen et al., 2006).

On the other hand, the theory of optimal foraging predicts that parasitoids should oviposit preferentially in hosts of better quality for the development of their offspring (Emlen, 1966; Fellowes et al., 2007; MacArthur and Pianka, 1966; MacArthur and Wilson, 1967). However, some aphid parasitoids (Braconidae: Aphidiinae) may not be able to recognize the best hosts (Henry et al., 2005; Sampaio et al., 2008) or may even oviposit in hosts unsuitable for the development of their offspring (Sampaio et al., 2008; Starý, 1989). As a result, eggs are likely to be deposited in both, resistant and susceptible hosts (Ferrari et al., 2001; Oliver et al., 2003; Oliveira et al., 2013).

* Corresponding author.

E-mail: mvsampaio@ufu.br (M.V. Sampaio).

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Some parasitoid species are able to recognize the resistant hosts (Oliver et al., 2012). *Diaeretiella rapae* (McIntosh) (Hymenoptera: Braconidae: Aphidiinae), however, deposit its eggs in resistant hosts at the same frequency as it does in susceptible ones, indicating that this parasitoid species cannot recognize the resistant ones (Oliveira et al., 2013). This way, the presence of a resistant host can potentially reduce the parasitoid population, thus favoring the susceptible aphid competitor through indirect resistance (Meisner et al., 2007), which may lead to serious consequences for the biological control of aphid pests that share the same parasitoid.

The aphids *Lipaphis pseudobrassicae* (Davis) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) are important Brassicaceae pests, occurring worldwide and causing significant damage to crops (Blackman and Eastop, 2007). Studies reveal that the population of *L. pseudobrassicae* in Uberlândia, southeastern Brazil, has individuals resistant to *D. rapae* (Oliveira et al., 2013), which is the main parasitoid present in *Brassica* in the region (Sampaio et al., 2017).

The cause of the resistance of *L. pseudobrassicae* to *D. rapae* is still under investigation, but resistant individuals are more abundant than susceptible ones in Uberlândia's population, which makes *D. rapae* ineffective in controlling *L. pseudobrassicae* (Oliveira et al., 2013; Sampaio et al., 2017). In contrast, the parasitoid *D. rapae* has been found as the main natural enemy of *L. pseudobrassicae* in regions where the aphid is susceptible, with high rates of parasitism in the laboratory (Silva et al., 2011) and in field and greenhouse conditions (Desh and Chand, 1998; Jeon et al., 2005).

Here we evaluated if resistant *L. pseudobrassicae* populations can change the parasitism rate of a second host species, *M. persicae*, through indirect resistance to their shared parasitoid (*D. rapae*).

Material and methods

Host plant material

Collard green seedlings (*Brassica oleracea* var. *acephala* L., cultivar *Manteiga da Georgia*) were grown in a greenhouse in plastic pots containing the commercial organic substrate Bioplant[®]. Plants used for rearing the aphids and parasitoids were kept in 3-L plastic pots (15 cm tall and 20 cm diameter), whereas plants used for the experiment were kept in 14.5 L plastic pots (27 cm tall and 30 cm diameter). Leaves were detached from plants and taken to the laboratory to obtain leaf discs, which were then placed on Petri dishes with agar solution to rear the aphids. Thirty five days old seedlings, with six expanded leaves, were covered with an anti-aphid cage for the experiment. The experiment was conducted in a greenhouse from November 10 to December 1, 2012, with an average temperature of 28 °C, and the minimum and maximum averages of 19 °C and 37 °C, respectively.

Aphid rearing

Two clones of *L. pseudobrassicae*, B3 (resistant) and B6 (susceptible), were collected in collard green plants, selected and rearing for five months in laboratory prior to the experiment (Ferreira, 2013). Aphids were grown on collard green leaf disks placed on 1% agar/water solution in Petri dishes (10 cm diameter). The Petri dishes were maintained in a climate controlled chamber (23 ± 1 °C, 12 h photoperiod, 50–55% humidity) and aphids were transferred to new Petri dishes containing fresh foliage every four days to ensure a good quality of the host plant.

To confirm the resistance of the clone B3 in comparison with the susceptible B6, 60 second instar nymphs of *L. pseudobrassicae* of each clone were placed individually in Petri dishes with a collard green leaf disk. A mated *D. rapae* female was released on every Petri dish until it oviposited on six *L. pseudobrassicae* nymphs. A

total of ten *D. rapae* females were used to parasitize 60 aphids of each clone. Subsequently, these nymphs were kept in a climatic controlled chamber and observed daily. None of the B3 nymphs parasitized by *D. rapae* mummified, indicating that all individuals were resistant. In contrast, 40 out of the 60 parasitized B6 nymphs were mummified, confirming the susceptibility of B6.

The resistant clone B3 was then reared in the laboratory for five months and used to obtain susceptible individuals within its population. Resistance to parasitoids in aphids, associated with the presence of secondary symbionts, may be lost in some individuals even if they are clones from a single resistant female. This happens because secondary symbionts associated with aphids are transmitted via mother's ovaries to her offspring; however, this transmission is not perfect, which results in resistance loss by some individuals (Chen and Purcell, 1997; Fukatsu et al., 2000; Oliver et al., 2010; Dykstra et al., 2014). Even though the cause of the resistance of *L. pseudobrassicae* to *D. rapae* is still unknown, it was possible to obtain susceptible individuals from the clone B3. To obtain susceptible individuals, 60 nymphs of *L. pseudobrassicae* of fourth instar were placed individually in Petri dishes with a collard green leaf disk and were subjected to a single oviposition of *D. rapae* (as previously described above). Parasitized *L. pseudobrassicae* nymphs of fourth instar are able to reproduce before dying, even the susceptible ones. When the parasitized aphid (four aphids) developed to a regular mummy (normal development of the parasitoid), her offspring was selected and kept for colony formation of susceptible *L. pseudobrassicae*. Similarly, nymphs produced by a parasitized aphid whose parasitoid did not develop (49 aphids) were used to form colonies of resistant *L. pseudobrassicae*. After the test, the B3 offspring population was divided between those that lost resistance and those that were still resistant. These two groups were maintained in Petri dishes (100 mm) to be used in the experiment.

Myzus persicae aphids were collected in collard green plants in a greenhouse of the Federal University of Uberlândia and reared in Petri dishes, as previously described. A colony of approximately 50 individuals of various instars was kept in each Petri dish. Thirty Petri dishes with *M. persicae* were used in the experiment and two dishes of this aphid species were used for rearing *D. rapae*.

Parasitoid rearing

The parasitoids were obtained from *Brevicoryne brassicae* L. mummies collected in a commercial collard green crop at the Federal University of Uberlândia. The mummies were taken to the laboratory, placed individually in Eppendorf tubes and kept at 23 °C and photoperiod of 12 h. Once parasitoids emerged, they were fed with 50% honey and water. Two Petri dishes with approximately 50 individuals of *M. persicae* were used for rearing *D. rapae*. One mated female of *D. rapae* was released in each Petri dish and maintained for 24 h for oviposition. After this period, the females were removed and parasitized aphids kept at 23 ± 1 °C, 50–55% RH and photoperiod of 12 h. The mummified aphids were placed in Eppendorf tubes and, after emergence, the parasitoids fed and mated. After mating was observed, males were removed from the tubes and the females were used in the experiment 24 h after emergence.

Experimental protocol

On the first day of the experiment, the aphid colonies were reduced to 30 individuals of several instars. To ensure a uniform stand, smaller nymphs (1st and 2nd instar) were removed, leaving only the largest nymphs (3rd and 4th instars) and adults. The leaf disk containing the aphids was removed from the Petri dish and placed on a plant inside an anti-aphid cage. Two leaves in opposite positions were infested per plant. Each plant received a leaf

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