

# Brassica aphid (Hemiptera: Aphididae) populations are conditioned by climatic variables and parasitism level: a study case of Triângulo Mineiro, Brazil

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## Abstract

Cosmopolitan pests such as *Brevicoryne brassicae*, *Lipaphis pseudobrassicae*, and *Myzus persicae* (Aphididae) cause significant damage to Brassicaceae crops. Assessment of the important biotic and abiotic factors that regulate these pests is an essential step in the development of effective Integrated Pest Management programs for these aphids. This study evaluated the influence of leaf position, precipitation, temperature, and parasitism on populations of *L. pseudobrassicae*, *M. persicae*, and *B. brassicae* in collard greens fields in the Triângulo Mineiro region (Minas Gerais state), Brazil. Similar numbers of *B. brassicae* were found on all parts of the collard green plants, whereas *M. persicae* and *L. pseudobrassicae* were found in greatest numbers on the middle and lower parts of the plant. While temperature and precipitation were positively related to aphid population size, their effects were not accumulative, as indicated by a negative interaction term. Although *Diaeretiella rapae* was the main parasitoid of these aphids, hyperparasitism was dominant; the main hyperparasitoid species recovered from plant samples was *Alloxysta fuscicornis*. Parasitoids seem to have similar distributions on plants as their hosts. These results may help predict aphid outbreaks and gives clues for specific intra-plant locations when searching for and monitoring aphid populations.

**Keywords:** *Brevicoryne brassicae*, *Lipaphis pseudobrassicae*, *Myzus persicae*, parasitism, climatic variables, hurdle models

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## Introduction

The aphid species *Brevicoryne brassicae* (L.), *Lipaphis pseudobrassicae* (Davis), and *Myzus persicae* (Sulzer) are cosmopolitan pests that cause substantial damages to plants in the Brassicaceae family (Blackman & Eastop 2000; Micic, 2005; Collier & Finch, 2007; Gu *et al.*, 2007).

Aphid–parasitoid interactions on Brassica crops constitute a complex system that has been much studied because of its

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importance to biological control (Waterhouse & Sands, 2001, Cividanes, 2002; Akhtar *et al.*, 2010). For instance, the endoparasitoid *Diaeretiella rapae* (McIntosh) (Braconidae, Aphidiinae) may significantly affect the biotic regulation of aphid populations (Pike *et al.*, 1999; Sullivan & Völkl, 1999) including those of *B. brassicae*, *L. pseudobrassicae*, and *M. persicae*, all known hosts of *D. rapae* (Stary *et al.*, 2007). Nonetheless, it is well known that both abiotic and biotic factors regulate insect populations (Price *et al.*, 2011) and so assessing the relative effects of these factors on natural pest populations is as difficult as it is essential for improving future controls of these aphid species (Dent, 1995). For example, studies aimed to establish whether or not hyperparasitoids interfere with the impact of primary parasitoids on aphid populations (Höller *et al.*, 1993), works dealing with the effect of environmental conditions on the parasitism rate (Zamani *et al.*, 2006), and research into the feasibility of the Integrated Pest Management of certain parasitoids that naturally occur under fluctuating conditions (Desneux & Ramirez-Romero, 2009) have all been widely conducted in the Northern Hemisphere. However, a broader perspective of the maintenance of natural aphid–natural enemy interactions in tropical regions is lacking. Thus, the study of Brassica aphids appears to be a suitable model for further exploring the effect of abiotic conditions on aphid–parasitoid interactions. This approach is particularly interesting, as few studies have ever been carried out under field conditions in the Tropical region.

The research reported here aimed to examine the influence of abiotic and biotic variables on Brassica aphids under field conditions. We first investigated the influence of leaf position, precipitation (estimated as 7-day accumulated values), and average temperature on populations of *L. pseudobrassicae*, *M. persicae*, and *B. brassicae*. We hypothesized that the response of aphid species to temperature would follow the same gradient in the field as it had under laboratory conditions. In addition, we expected that leaf position would also have an effect on aphid distribution and that species colonizing the lower leaves of the plant would be less affected by precipitation than those colonizing upper leaves. Secondly, we investigated the influence of abiotic and biotic variables on the communities of *L. pseudobrassicae*, *M. persicae*, and *B. brassicae* parasitoids in collard fields.

## Materials and methods

### Experiment setup

Our study was conducted in the fields of the Glória Experimental Farm of the Federal University of Uberlândia in southeastern Brazil (18°57'07"S, 48°12'27"W). This farm is in the Triângulo Mineiro region and lies in the Brazilian Savannah ecosystem, locally known as the Cerrado. This ecosystem occupies about 20% (206 million ha) of Brazil's land surface, although in the past 30 years 50% of the natural vegetation has been replaced by agricultural crops and cultivated pastures (Assunção & Chiavari, 2015). The agriculture of the Cerrado provides 60% of Brazilian grain (mainly soybean and corn), 75% of its cotton, and 19% of its sugar cane, and also harbors 50% of its cattle, which demand large areas of pastureland (CONAB, 2015). The Cerrado includes a great diversity of habitats, from open fields to dense forest formations, and has two well-defined seasons (dry winter and rainy summer). Although its soils' morphological and physical characteristics vary widely, the predominant soils (about 54%) are

latosols that are generally nutrient-poor (especially phosphorus) and highly weathered, and have a low cation exchange capacity and high acid and aluminum toxicity (Malavolta & Kliemann, 1985).

The farm's fields are surrounded by cropland (corn and soybean) and pastures. The crops are rotated and the position of each crop is changed every year. The rotation schedule includes collard greens, cabbages, cauliflowers, lettuces, beet and carrots. Taking into account the crop rotation system adopted in the fields, the study was conducted in a similar matrix structure in two enclosed areas (100 m apart) inside the fields. Collard greens *Brassica oleracea* var. *acephala* L. was chosen as the aphids' host plant due to its importance as a food crop in Brazil and the peculiarities of the disposition of its leaves. This species constantly produces new leaves from the top of the plant, which allows the plant's aphid distribution to be observed for longer than on other Brassica crop species. By contrast, other Brassica crops such as cabbage, cauliflower and broccoli stop producing new leaves in order to form flowering heads (Filgueira, 2003).

Seedlings were taken from the lateral shoots of the mother plants of the Talo Roxo cultivar and kept in 2-liter plastic bags with organic substrate in a greenhouse for 1 month. Afterwards, seedlings were transplanted into the field. The plants in the experiment in area 1 were planted in July 2005 and sampling was carried out in August 2005–March 2006. This experimental field consisted of two rows, each of 35 plants, and one row of 19 plants, giving a total of 89 collard green plants. The second study site (area 2) was planted in September 2006 and sampling was carried out in October 2006–January 2008. In this case, the experimental field had three rows, each of 25 plants, giving a total of 75 collard green plants. In both areas, the spacing between plants was constant: one meter between rows and 0.5 m between plants.

In both experimental areas, only organic fertilizer was applied (at 10 kg cattle manure per meter) and no insecticides were used. Sprinkler irrigation was performed daily and lateral shoots were manually removed each week.

In southeastern Brazil, where this study was conducted, the highest temperatures and rainfall occur in September–March (IBGE, 2010). We counted aphid populations in 101 samples taken in the hot rainy season, since the chief aim of the study was to assess the effects of high temperatures and precipitation on aphid populations. Climatic data were obtained from a meteorological station located about 500 m from the experimental areas.

### Sampling of insects and species identification

To quantify aphid population dynamics, samples were taken on a weekly basis (32 samples over the course of the experiment for area 1 and 69 for area 2). Each sample consisted of three randomly selected plants, one from each row in each plot. A total of three leaves per plant were removed and examined, one from each of the three positions (upper, middle, and lower). Upper leaves were considered to be upright and still expanding; middle leaves were fully expanded but not yet senescent; and lower leaves had already reached senescence. All samples were taken from plants that had been in the field for at least 1 month, enough time to permit aphid colonization. In order to guarantee the independence of the samples taken from a plant, the sampling design includes a restriction that the same plant would not be sampled again for another 4 weeks.

In the laboratory, the parasitized and non-parasitized individuals of each of the three aphid species were counted and studied under a stereoscopic microscope. After identifying the parasitized aphid species, including mummified individuals and empty mummies (bearing the parasitoid's exit hole), mummies were removed from leaves and placed in separate Eppendorf tubes. These tubes were kept for up to a year to allow primary and secondary parasitoids to hatch. However, practically all parasitoids and hyperparasitoids emerged within 2 weeks and were identified to family, genera, or species levels whenever possible following (Pike *et al.*, 1997; Powell, 1982).

#### Data analyses

Since aphids tend to congregate, when monitoring aphid population dynamics in crops it is not unusual to find no aphids on successive samples, but then find a very large concentration once a colony is encountered (Maunder & Punt, 2004). One solution to this clumping is to adopt what are generally known as 'hurdle models' since sampling rates of zero can complicate calculations and, in addition, if not properly modeled the presence of many zero rates can invalidate an analysis' assumptions and jeopardize the integrity of the inferences (Potts & Elith, 2006). The use of hurdle models is particularly suited to data sets with many zeros (Maunder & Punt, 2004; Mayer *et al.*, 2005).

Hurdle modeling combines two components that are simply two particular examples of generalized linear models (McCullagh & Nelder, 1989). For the binary component of the conditional model, we used a logistic model assuming a binomial distribution given the binary nature (presence/absence) of the zero catch rates (O'Neill & Faddy 2003; Mayer *et al.*, 2005; Potts & Elith, 2006). By contrast, for the second component of the conditional model we used a log-normal distribution (conditional upon their presence), the most commonly selected distribution model (Maunder & Punt, 2004; Potts & Elith, 2006), after checking the normal distribution of the residuals of the obtained data set.

In order to meet the assumption of the dependence of simultaneously taken observations, the analyses of the biotic and abiotic factors affecting aphids' density and parasitism rates were tested using generalized linear mixed models (Bates *et al.*, 2008).

Analyses were conducted for the three main aphid species, *B. brassicae*, *L. pseudobrassicae*, and *M. persicae*. In all analyses, leaf position (upper, middle, and lower), average weekly temperature, 7-day accumulated precipitation, and the interaction between average temperature and accumulated precipitation were included as fixed factors. The sampling period was included as a random effect term to account for the fact that samples taken at the same time were not independent.

In the analyses, aphid density was taken as the number of parasitized aphids + the number of non-parasitized aphids, while the parasitism rate was the number of mummified aphids/aphid density. All mummified aphids are used in the analyses, including both empty mummies and mummies from which parasitoids did not emerge.

*Ad hoc* contrasts from ANOVA variance were evaluated for the three species of aphid to compare their relative abundance after adjusting for leaf position.

All analyses were performed on R 3.0.2 (R Development Core Team, 2013); library lme4 (Bates *et al.*, 2008) was used for model fitting and library lmerTest (Kuznetsova *et al.*, 2013) was used for inference methods with mixed models.

## Results

### Aphid, parasitoid and hyperparasitoid abundance

A total of 469,795 Brassica aphids were counted during the 101 sampling sessions. With a total individual of 303,200, *B. brassicae* was the most abundant aphid species found, followed by *L. pseudobrassicae* (153,364) and *M. persicae* (13,231). In terms of the average population density of the three aphid species, *B. brassicae* was more abundant than both *L. pseudobrassicae* ( $t = -3.58$ ,  $P < 0.001$ ) and *M. persicae* ( $t = -6.93$ ,  $P < 0.001$ ); the population of *L. pseudobrassicae* was greater than that of *M. persicae* ( $t = 3.35$ ,  $P < 0.002$ ). The population dynamics of each aphid species was distinct: while *L. pseudobrassicae* was abundant throughout the sampling period, *B. brassicae* was all but absent in October 2005–August 2007 and *M. persicae* in December 2006–August 2007. Aphid species have their own endogenous intra-annual rhythm: *B. brassicae* is mostly unimodal, while *M. persicae* and *L. pseudobrassicae* are both bimodal (fig. 1).

The relative abundance of the hyperparasitoids that emerged from the mummies of the three aphid species was greater than that of the primary parasitoids (table 1). The most abundant primary parasitoid was *D. rapae*, while *Alloxysta fuscicornis* (Hartig) was the most abundant hyperparasitoid. However, a large number of *Syrphophagus* hyperparasitoids also emerged from *L. pseudobrassicae* and *M. persicae* mummies. Hyperparasitoids belonging to the genus *Pachyneuron* were infrequent and parasitoids of the genus *Aphelinus* and hyperparasitoids of the genera *Dendrocerus* and *Tetrastichus* only occurred sporadically (table 1).

Aphid parasitism of *B. brassicae* averaged  $16.2 \pm 2.28\%$ , with a maximum of 87.5% from a single sampling sessions. For *L. pseudobrassicae*, parasitism averaged  $0.8 \pm 0.19\%$ , with a maximum parasitism of 11.1%, while for *M. persicae* parasitism averaged  $8.5 \pm 1.44\%$ , with a maximum of 72.2%.

### Influence of climatic factors on aphids and parasitism

During the sampling period, climatic conditions followed the typical pattern for southeastern Brazil in the rainy season (September–March). The highest temperatures were registered during this period (fig. 1). A common feature of the three aphids' populations was the occurrence of a population peak between September and November (spring) at the beginning of the rainy season. Aphid population patterns are also correlated with peaks in the populations of primary and secondary parasitoids, which was especially obvious in the case of *B. brassicae* (fig. 1).

Responses to temperature and precipitation in these Brassica aphids varied according to species. Higher temperatures benefited the presence of *B. brassicae* and *M. persicae*, and favored their abundances whenever they were present (tables 2 and 3). Similarly, precipitation positively affected the presence of *B. brassicae* and *M. persicae*, although only the abundance of *B. brassicae* seems to be determined by precipitation patterns. By contrast, the presence and range of abundance of these two species was negatively related to the interaction between temperature and precipitation (tables 2 and 3). Variation in *L. pseudobrassicae* colonies was not significantly related to any of those climatic variables.

In turn, parasitism rates of the three species varied in relation to climatic variables. Although both precipitation and temperature increased the parasitism rates in these species,

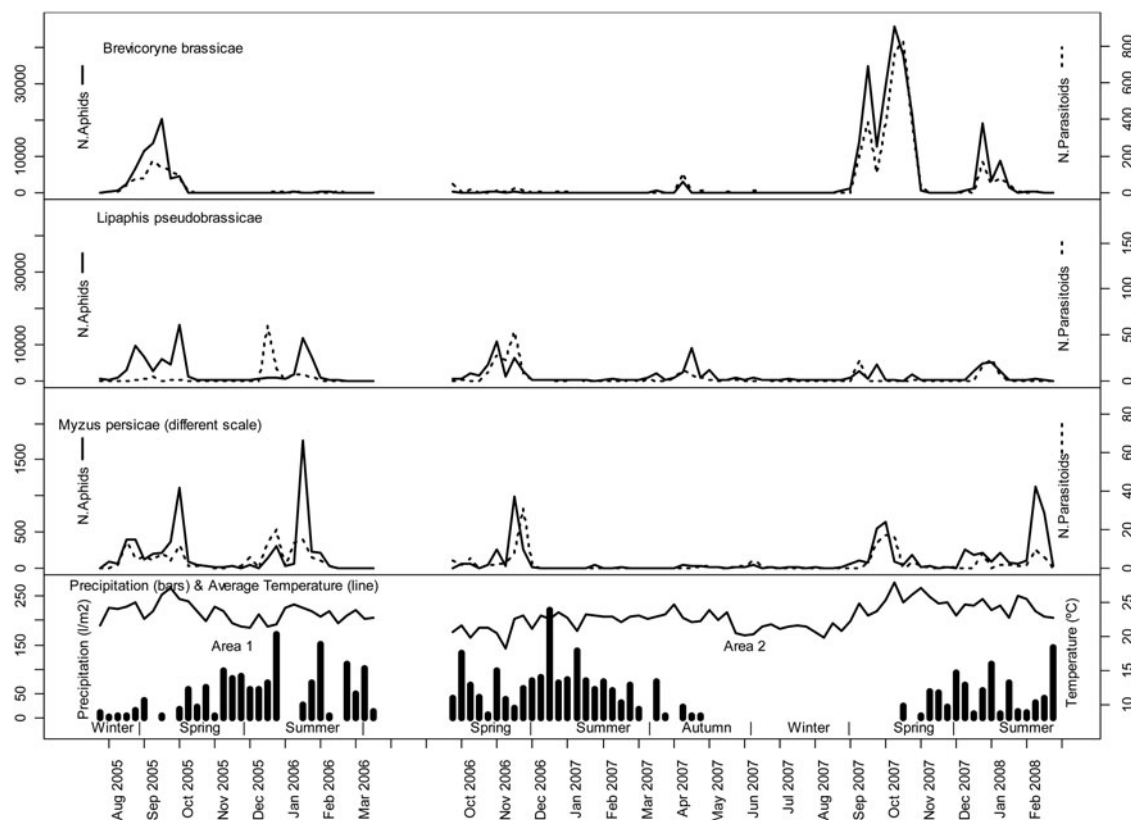


Fig. 1. Total weekly population of *Brevicoryne brassicae*, *Lipaphis pseudobrassicae* and *Myzus persicae* (in a lower scale) on collard green (black straight lines) in relation to their primary and secondary parasitoids (dotted black line), to precipitation (bars) and average temperature (line) from August 2005 to March 2006 and from October 2006 to January 2008 in Uberlândia-MG (Brazil).

Table 1. Relative and absolute abundances (in brackets) of primary parasitoids and hyperparasitoids (Hymenoptera) emerging from mummified *B. brassicae*, *L. pseudobrassicae*, and *M. persicae*.

| Hymenoptera emerged                             | Species of host aphid |                           |                    |
|---|-----------------------|---------------------------|--------------------|
|   | <i>B. brassicae</i>   | <i>L. pseudobrassicae</i> | <i>M. persicae</i> |
| <b>Primary parasitoids</b>                      |                       |                           |                    |
| <i>Aphelinus</i> sp.                            | 0.04% (2)             | 0.33% (1)                 | 0% (0)             |
| <i>Diaeretiella rapae</i>                       | 8.61% (389)           | 13.16% (40)               | 15.75% (46)        |
| Total parasitoids                               | 8.65% (391)           | 13.49 (41)                | 15.75% (46)        |
| <b>Secondary parasitoids (Hyperparasitoids)</b> |                       |                           |                    |
| <i>Alloxysta fuscicornis</i>                    | 72.30% (3,267)        | 43.75% (133)              | 38.01% (111)       |
| <i>Dendrocerus</i> spp.                         | 0.04% (2)             | 0.33% (1)                 | 0.34% (1)          |
| <i>Pachyneuron</i> spp.                         | 2.79% (126)           | 10.53% (32)               | 11.99% (35)        |
| <i>Tetrastichus</i> sp.                         | 0.02% (1)             | 0% (0)                    | 0% (0)             |
| <i>Syrphophagus</i> spp.                        | 16.20% (732)          | 31.91% (97)               | 33.90% (99)        |
| Total hyperparasitoids                          | 91.35% (4,128)        | 86.52% (263)              | 84.24% (246)       |

Uberlândia-MG, Brazil, August 2005–March 2006 and October 2006–January 2008.

the interaction between these two climatic variables had a negative effect on the parasitized aphids' presence (tables 5–7).

#### *Intra-plant distribution effects on aphids and parasitism*

Both *L. pseudobrassicae* and *M. persicae* populations were significantly related to leaf position. The logistic model

showed that there was a greater probability of finding colonies of both species on the middle and lower leaves than on the upper leaves. Nevertheless, the lognormal model indicates that when colonies of these species are present the number of individuals is also positively related with those positions, with greater populations on middle and lower leaves than on upper leaves (tables 3 and 4). The presence of parasitized aphids of these two species followed the same pattern as for

the aphid species themselves: more on middle and lower leaves than on upper leaves (tables 6 and 7).

By contrast, neither the presence nor density of *B. brassicae* was significantly affected by intra-plant location, a phenomenon that might be explained by the greater abundance of *B. brassicae*, a species that forms larger colonies with more individuals than the other two species. Nonetheless, intra-plant locations do explain the greater range of *B. brassicae* parasitism on the bottom leaves than on the upper ones, as the significant effect indicates (table 5). However, the probability of finding parasitized individuals showed no significant relation to leaf position.

### Discussion

Our results add to a growing body of work that indicates that both abiotic and biotic factors play an important role in Brassica aphid regulation (Waterhouse & Sands, 2001; Cividanes & Souza, 2004; Micic, 2005; Akhtar *et al.*, 2010). However, the particular effects of these factors differed between species.

During each of the 101 weekly sampling periods 303 plants and 909 leaves were inspected and in total 469,795 Brassica aphids were counted. Of the three aphid species monitored, *B. brassicae* and *L. pseudobrassicae* were the most abundant. Although *B. brassicae* reaches higher population levels than the other two aphid species, its populations may decline in number and even disappear for several months. According to Micic (2005), *B. brassicae* tends to colonize heavily single plants or small groups of plants and create 'hot spots' within crops. High aphid populations may reduce plant quality and, according to Dixon (1977) and Karley *et al.* (2004), such a reduction may negatively influence aphid population size.

#### *Effects of intra-plant distribution on aphids*

*B. brassicae* was the only species that was evenly distributed across all three plant strata. Both *L. pseudobrassicae* and *M. persicae* were more abundant in the middle and lower regions of the collard plants. A greater concentration of defensive compounds is expected to exist in young upper-region collard leaves due their importance in areas with greater photosynthetic activity (Brown *et al.*, 2003; Reifenrath & Müller, 2007). Thus, their ability to avoid Brassicaceae defense compounds, i. e. glucosinolates (MacGibbon & Beuzenberg, 1978; Weber *et al.*, 1986; Bridges *et al.*, 2002), may explain differences in the intra-plant distributions of the aphid species that colonize Brassica species. Both *B. brassicae* and *L. pseudobrassicae* can synthesize the enzyme myrosinase and thus hydrolyze glucosinolates as a defense against their toxic effects (MacGibbon & Beuzenberg, 1978; Weber *et al.*, 1986; Bridges *et al.*, 2002); conversely, *M. persicae* cannot (Weber *et al.*, 1986). According to MacGibbon & Beuzenberg (1978), *B. brassicae* has higher levels of myrosinase activity than *L. pseudobrassicae*, which may allow it to colonize young leaves with greater glucosinolate levels. Other feasible explanations for the presence *B. brassicae* on higher leaves is that its greyish-white powdery wax covering offers greater waterproofing, or that the color of its wax makes it less obvious to would-be predators (Pope, 1983).

These varying intra-plant distributions of the aphid species that colonize Brassica indicate that the upper leaves of these plants are the best for searching for and monitoring *B. brassicae* populations; on the other hand, the middle leaves are the most useful for searching for populations of all three aphid species.

#### *Abiotic factors effects on aphids*

A rise in temperature provoked a population increase in *B. brassicae* and *M. persicae* without seeming to affect *L. pseudobrassicae*. Constant-temperature laboratory studies of the biology of aphids that attack Brassica suggest that *L. pseudobrassicae* has a greater tolerance (Liu & Meng, 2000; Godoy & Cividanes, 2002) to higher temperatures than either *M. persicae* (Liu & Meng, 1999; Kanegae & Lomônaco, 2003) or *B. brassicae* (Cividanes, 2003; Satar *et al.*, 2005). However, at a constant temperature of 30°C, *M. persicae* did not develop and all individuals died (Kanegae & Lomônaco, 2003). At the same temperature, *B. brassicae* merely showed a reduction in its development speed that did not affect its relative mortality rate (Cividanes, 2003). By contrast, at 30°C the development rate of *L. pseudobrassicae* continued with no negative effects (Godoy & Cividanes, 2002), thereby suggesting that *L. pseudobrassicae* has the greatest tolerance of these three aphid species to high temperatures. That there was no negative effect of high temperature on these three aphid species indicates that the average temperature during the sampling period was optimal for the development of Brassica aphids.

As in the case of temperature, a rise in precipitation increased the populations of both *B. brassicae* and *M. persicae* but did not influence those of *L. pseudobrassicae*. The mechanical effect of precipitation – for example, during intense rainstorms – may cause aphid populations to fall or even disappear from a crop (Pinto *et al.*, 2000; Karley *et al.*, 2004), and is likely to affect most of all the species that use the plant's apical leaves (Hughes *et al.*, 1962) since the upright position of these leaves offers little protection. Although other studies have observed a reduction in *B. brassicae* populations coinciding with an increase in precipitation (Dixon, 1977; Cividanes, 2002), we observed no such reduction in *B. brassicae* in our study. Thus, the effect of rain and its relationship with upper leaf colonization needs to be more fully investigated for this aphid species.

The significant negative interaction between temperature and precipitation indicating that the combination of high temperatures and precipitation has a negative impact on aphid populations could be interpreted in biological terms (as we discuss below) or from a more technical standpoint.

In spring and summer, heavy rains and high temperatures are common in the study region. The positive effect of precipitation and temperature on aphid populations suggests that increases could be represented by a straight line. However, this pattern is only true for a certain range of values and will not increase indefinitely, since extreme temperatures will not have a positive effect on any aphid population. Thus, when these continually increasing variables begin to approach an asymptote, their interaction should be understood as a small negative correction or adjustment of their sum.

#### *Population dynamics of aphids and parasitoids*

*B. brassicae* peaked once a year between the second week of September and the second week of October. Conversely, *L. pseudobrassicae* and *M. persicae* peaked twice a year, with one peak in September–November and another in January–March.

It is impossible to determine when aphid species reach the fields in Uberlandia because they are almost always there and so it is rare to fail to find aphids in, for example, a 2-week sampling period. Unlike in temperate regions, where aphids

Table 2. *Brevicoryne brassicae* abundance: hurdle models.

|                | Logistic model |   |      |       |              | Lognormal model |   |      |       |              |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|--------------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | T     | P value      |
| Intercept      | -13.62         | ± | 5.54 | -2.46 | <b>0.014</b> | -16.47          | ± | 3.76 | -4.38 | <b>0.000</b> |
| M leaf         | 0.35           | ± | 0.40 | 0.86  | 0.392        | 0.24            | ± | 0.24 | 1.00  | 0.317        |
| B leaf         | 0.17           | ± | 0.40 | 0.43  | 0.671        | -0.02           | ± | 0.24 | -0.10 | 0.920        |
| Av. temp       | 0.68           | ± | 0.25 | 2.77  | <b>0.006</b> | 0.87            | ± | 0.16 | 5.42  | <b>0.000</b> |
| PPT            | 0.26           | ± | 0.12 | 2.13  | <b>0.033</b> | 0.19            | ± | 0.09 | 2.06  | <b>0.043</b> |
| Av. temp × PPT | -0.01          | ± | 0.01 | -2.16 | <b>0.031</b> | -0.01           | ± | 0.00 | -2.11 | <b>0.038</b> |

Two complementary models were used: a logistic model to test for presence/absence and a lognormal model to assess the type of abundance of count data. In both models the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

Table 3. *Myzus persicae* abundance: hurdle models.

|                | Logistic model |   |      |       |              | Lognormal model |   |      |       |              |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|--------------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | t     | P value      |
| Intercept      | -10.39         | ± | 3.93 | -2.65 | <b>0.008</b> | -6.28           | ± | 2.24 | -2.79 | <b>0.006</b> |
| M leaf         | 2.32           | ± | 0.38 | 6.16  | <b>0.000</b> | 1.37            | ± | 0.24 | 5.60  | <b>0.000</b> |
| B leaf         | 3.19           | ± | 0.43 | 7.44  | <b>0.000</b> | 1.69            | ± | 0.24 | 7.02  | <b>0.000</b> |
| Av. temp       | 0.43           | ± | 0.17 | 2.55  | <b>0.011</b> | 0.33            | ± | 0.10 | 3.45  | <b>0.000</b> |
| PPT            | 0.22           | ± | 0.10 | 2.28  | <b>0.023</b> | 0.05            | ± | 0.06 | 0.89  | 0.376        |
| Av. temp × PPT | -0.01          | ± | 0.00 | -2.33 | <b>0.020</b> | -0.00           | ± | 0.00 | -0.86 | 0.390        |

Two complementary models were used: a logistic model to test for the presence/absence and a lognormal model to assess the type of abundance of count data. In both models, the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

Table 4. *Lipaphis pseudobrassicae* abundance: hurdle models.

|                | Logistic model |   |      |       |              | Lognormal model |   |      |       |              |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|--------------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | T     | P value      |
| Intercept      | 8.68           | ± | 4.55 | 1.91  | 0.056        | -0.51           | ± | 2.94 | -0.18 | 0.862        |
| M leaf         | 1.36           | ± | 0.48 | 2.82  | <b>0.005</b> | 2.14            | ± | 0.22 | 9.95  | <b>0.000</b> |
| B leaf         | 1.64           | ± | 0.51 | 3.20  | <b>0.001</b> | 3.25            | ± | 0.21 | 15.29 | <b>0.000</b> |
| Av. temp       | -0.29          | ± | 0.19 | -1.48 | 0.139        | 0.13            | ± | 0.13 | 0.99  | 0.320        |
| PPT            | 0.03           | ± | 0.11 | 0.23  | 0.819        | 0.13            | ± | 0.07 | 1.75  | 0.083        |
| Av. temp × PPT | -0.00          | ± | 0.00 | -0.31 | 0.755        | -0.01           | ± | 0.00 | -1.85 | 0.067        |

Two complementary models were used: a logistic model to test for the presence/absence and a lognormal model to assess the type of abundance of count data. In both models, the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

Table 5. *Brevicoryne brassicae* parasitism rate: hurdle models.

|                | Logistic model |   |      |       |              | Lognormal model |   |      |       |              |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|--------------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | t     | P value      |
| Intercept      | -20.36         | ± | 4.48 | -4.55 | <b>0.000</b> | 3.70            | ± | 2.60 | 1.43  | 0.159        |
| M leaf         | 0.14           | ± | 0.35 | 0.40  | 0.690        | 0.42            | ± | 0.22 | 1.91  | 0.059        |
| B leaf         | 0.62           | ± | 0.35 | 1.78  | 0.075        | 0.91            | ± | 0.22 | 4.18  | <b>0.000</b> |
| Av. temp       | 0.86           | ± | 0.19 | 4.46  | <b>0.000</b> | -0.09           | ± | 0.11 | -0.88 | 0.381        |
| PPT            | 0.36           | ± | 0.10 | 3.56  | <b>0.000</b> | 0.04            | ± | 0.06 | 0.61  | 0.543        |
| Av. temp × PPT | -0.02          | ± | 0.00 | -3.52 | <b>0.000</b> | -0.00           | ± | 0.00 | -0.53 | 0.597        |

Two complementary models were used: a logistic model to test for presence/absence and a lognormal model to assess the type of abundance of count data. In both models the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

Table 6. *Myzus persicae* parasitism rate: hurdle models.

|                | Logistic model |   |      |       |              | Lognormal model |   |      |       |         |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|---------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | t     | P value |
| Intercept      | -21.89         | ± | 4.84 | -4.52 | 0.000        | 2.17            | ± | 2.58 | 0.84  | 0.402   |
| M leaf         | 3.16           | ± | 0.65 | 4.82  | <b>0.000</b> | -0.40           | ± | 0.52 | -0.78 | 0.440   |
| B leaf         | 5.11           | ± | 0.68 | 7.50  | <b>0.000</b> | 0.31            | ± | 0.51 | 0.62  | 0.539   |
| Av. temp       | 0.74           | ± | 0.20 | 3.69  | <b>0.000</b> | -0.02           | ± | 0.11 | -0.16 | 0.870   |
| PPT            | 0.34           | ± | 0.11 | 3.02  | <b>0.002</b> | 0.10            | ± | 0.06 | 1.58  | 0.119   |
| Av. temp × PPT | -0.01          | ± | 0.01 | -2.97 | <b>0.003</b> | -0.00           | ± | 0.00 | -1.57 | 0.122   |

Two complementary models were used: a logistic model to test for presence/absence and a lognormal model to assess the type of abundance of count data. In both models the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

Table 7. *Lipaphis pseudobrassicae* parasitism rate: hurdle models.

|                | Logistic Model |   |      |       |              | Lognormal Model |   |      |       |         |
|----------------|----------------|---|------|-------|--------------|-----------------|---|------|-------|---------|
|                | X              | ± | SE   | Z     | P value      | X               | ± | SE   | t     | P value |
| Intercept      | -19.96         | ± | 6.23 | -3.20 | <b>0.001</b> | 1.02            | ± | 4.75 | 0.21  | 0.831   |
| M leaf         | 3.61           | ± | 1.05 | 3.45  | <b>0.000</b> | 1.35            | ± | 0.78 | 1.73  | 0.101   |
| B leaf         | 5.99           | ± | 1.07 | 5.61  | <b>0.000</b> | 1.46            | ± | 0.78 | 1.88  | 0.075   |
| Av. temp       | 0.57           | ± | 0.26 | 2.19  | <b>0.028</b> | -0.14           | ± | 0.20 | -0.72 | 0.473   |
| PPT            | 0.51           | ± | 0.15 | 3.29  | <b>0.000</b> | 0.03            | ± | 0.10 | 0.29  | 0.770   |
| Av. temp × PPT | -0.02          | ± | 0.00 | -3.25 | <b>0.001</b> | -0.00           | ± | 0.00 | -0.21 | 0.833   |

Two complementary models were used: a logistic model to test for presence/absence and a lognormal model to assess the type of abundance of count data. In both models the effects of leaf position were assessed: [M leaf = Aphid density on middle vs. upper leaves], [B leaf = Aphid density on bottom vs. upper leaves], average temperature (Av. temp), accumulated precipitation (PPT), and the interaction between average temperature and PPT (Av. temp × PPT). Statistically significant results are indicated in bold text (<0.05).

disappear for some months, this pattern is common in the Tropics. Of the total of samples taken, in 67% *L. pseudobrassicae* was present, in 48% *B. brassicae* was present, and in 33% *M. persicae* was present. Similarly, Auad *et al.* (1997) found aphids on peach leaves throughout the year in Brazil, while Jenkins *et al.* (2011) report that aphids could be a problem in canola in Australia in autumn, winter and spring, that is, almost the whole year.

A whipsaw effect in parasitoid populations can generally be explained by fluctuations in host populations (Haddad *et al.*, 2001; Caballero-López *et al.*, 2012); thus, the response of *D. rapae* to temperature and precipitation was quite similar to patterns in their hosts. Likewise, the spatial distribution of parasitism across plants followed the same trend as that of the host aphid, with an increase in the percentage of parasitism wherever aphid density was greatest. These findings can be linked to observations that the parasitoid *D. rapae* prefers to search and increase patch time on plant parts with hosts or where they find cues such as honeydew indicating the presence of hosts (Ayal, 1987; Sheehan & Shelton, 1989). Additionally, as Shaltiel & Ayal (1998) have reported, the number of aphids attacked by *D. rapae* is greater in large host populations. Nonetheless, the emergence rates of primary parasitoids for *L. pseudobrassicae* is very low, 11% parasitism being much lower than the 60% previously reported (Jeon *et al.*, 2005; Akhtar *et al.*, 2010). Conversely, emergence rates of secondary parasitoids are astonishingly high. Thus, our findings support previous studies that suggest that primary parasitoids may be constrained by the presence of secondary parasitoids (Mackauer & Völkl, 1993; Sullivan & Völkl, 1999),

which may also significantly affect the biotic regulation of aphid populations. According to our results, the impact of *D. rapae* on aphid regulation is limited due to the abundance of secondary parasitoids such as *A. fuscicornis*. The low parasitism rate of *L. pseudobrassicae* could be explained by a resistance effect in the aphid population to *D. rapae*. Laboratory studies have detected high mortality rates in immature *D. rapae*, which seems to indicate the presence of aphid clones of *L. pseudobrassicae* that are resistant to this parasitoid (Oliveira *et al.*, 2013). Aphid resistance to certain parasitoid species has been attributed to the presence of a secondary symbiont (Leclair *et al.*, 2016; Rothacher *et al.*, 2016) but in some cases the cause of this resistance remains unknown because it occurs in the absence of any secondary symbiont (Martinez *et al.*, 2014). Nonetheless, we were unable to identify which was the most relevant factor for explaining the pattern of secondary parasitoid dominance or the low rate of parasitism on *L. pseudobrassicae*.

## Conclusions

Our results show that an increase in either precipitation or temperature favors an increase in aphid populations. Nevertheless, high levels of precipitation combined with high temperatures did seem to act as a brake on Brassica aphid populations. The close match between the distribution of parasitoids and that of their hosts also suggests that there is an important biotic element in aphid population control. Thus, an efficient monitoring system taking both abiotic and biotic factors into account has the potential to improve

Integrated Pest Management strategies and reduce the risk of Brassica aphid outbreaks.

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### Author Contribution

M.V.S. conceived and designed the research. M.V.S., J.E.A.H., S.E.F., S.O.A., D.M.B., and C.M.G. conducted the experiments. M.V.S. and J.P.V. identified the insects. B.C.L. and J.A.S.E. analyzed the data. M.V.S., A.P.K., and B.C.L. wrote the manuscript. All authors have read and approved the manuscript.

### References

- Akhtar, M.S., Dey, D., Usmani, M.K. & Choudhury, R.A. (2010) Seasonal abundance of *Diaeretiella rapae* (M'Intosh) (Braconidae: Aphidiinae) parasitizing *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae) in *Brassica juncea* variety Pusa bold. *Munis Entomology and Zoology* **5**, 692–696.
- Assunção, J. & Chiavari, J. (2015) Towards efficient land use in Brazil. The New Climate Economy. Available online at <http://2015.newclimateeconomy.report/wp-content/uploads/2015/09/Towards-Efficient-Land-Use-Brazil.pdf> (accessed 20 October 2015).
- Auad, A.M., Bueno, V.H.P., Kato, C.M. & Gamarra, D.C. (1997). Ocorrência e Flutuação Populacional de Predadores e Parasitóides de *Brachycaudus* (Appelia) *schwartzi* (Börner) (Homoptera: Aphididae), em Pessegueiro, em Jacu-MG. *Anais da Sociedade Entomológica do Brasil* **26**(2) 257–263.
- Ayal, Y. (1987) The foraging strategy of *Diaeretiella rapae*. *Journal of Animal Ecology* **56**, 1057–1068.
- Bates, D., Maechler, M. & Dai, B. (2008) Lme4: linear mixed-effects models using S4 classes. R package version 0.999375–28 (CD.ROM).
- Blackman, R.L. & Eastop, V.P. (2000) *Aphids on the World's Crops: an Identification and Information Guide*, 2nd edn. New York, J. Wiley & Sons.
- Brown, P.D., Tokuhisa, J.G., Reichelt, M. & Gershenzon, J. (2003) Variation of glucosinolate accumulation among different organs and developmental stages of *Arabidopsis thaliana*. *Phytochemistry* **62**, 471–481.
- Bridges, M., Jones, A.M.E., Bones, A.M., Hodgson, C., Cole, R., Bartlet, E., Wallsgrove, R., Karapapa, V.K., Watts, N. & Rossiter, J. (2002) Spatial organization of the glucosinolate-myrosinase system in brassicae specialist aphids is similar to that of the host plant. *Proceedings of the Royal Society of London B* **269**, 187–191.
- Caballero-López, B., Blanco-Moreno, J.M., Pérez, N., Michelena, J.M., Pujade-Villar, J., Guerrero, E., Sánchez-Espigares, J.A. & Sans, F.X. (2012) Weeds and aphid-parasitoid communities benefit differently from organic and conventional cropping of spring cereals. *Journal of Pest Science* **85**(1), 81–88.
- Cividanes, F.J. (2002) Impacto de inimigos naturais e de fatores meteorológicos sobre uma população de *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae) em couve. *Neotropical Entomology* **31**, 249–255.
- Cividanes, F.J. (2003) Exigências térmicas de *Brevicoryne brassicae* e previsão de picos populacionais. *Pesquisa Agropecuária Brasileira* **38**, 561–566.
- Cividanes, F.J. & Souza, V.P. (2004) Distribuição vertical de pulgões (Hemiptera: Aphididae) em couve. *Arquivos do Instituto Biológico* **71**, 254–256.
- CONAB (2015) (Companhia Nacional de Abastecimento). Séries Históricas. Open source. Available online at <http://www.conab.gov.br/conteudos.php?a=1252&>. (accessed 20 October 2015).
- Collier, R.H., Finch, S. (2007) IPM case studies: brassicas. pp. 549–559 in van Emden, H., Harrington, R. (Eds) *Aphids as Crop Pests*. Wallingford, UK, CABI.
- Dent, D. (1995) *Insect Pest Management*. London, Chapman & Hall.
- Desneux, N. & Ramirez-Romero, R. (2009) Plant characteristics mediated by growing conditions can impact parasitoid's ability to attack host aphids in winter canola. *Journal of Pest Science* **82**, 335–342.
- Dixon, A.F.G. (1977) Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology, Evolution and Systematics* **8**, 329–353.
- Figueira, F.A.R. (2003) *Novo manual de olericultura: agrotecnologia moderna na produção e comercialização de hortaliças*, 2nd edn. Viçosa, UFV.
- Godoy, K.B. & Cividanes, F.J. (2002) Tabelas de esperança de vida e fertilidade para *Lipaphis erysimi* (Kalt.) (Hemiptera: Aphididae) em condições de laboratório e campo. *Neotropical Entomology* **31**, 41–48.
- Gu, H., Fitt, G.P., & Baker, G.H. (2007) Invertebrate pests of canola and their management in Australia: a review. *Australian Journal of Entomology* **46**, 231–243.
- Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knopa, M.H. (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *The American Naturalist* **158**, 17–35.
- Höller, C., Borgemeister, C., Haardt, H. & Powell, W. (1993) The relationship between primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field data. *Journal of Animal Ecology* **62**, 12–21.
- Hughes, R.D. (1962) A method for estimating the effects of mortality on aphid populations. *Journal of Animal Ecology* **31**, 389–396.
- IBGE (Instituto Brasileiro de Geografia e Estatística) (2010) Open source. Available online at <http://www.ibge.gov.br> (accessed 7 December 2011).
- Jenkins, L., Brill, R. & McCaffery, D. (2011) Managing aphids in flowering canola in central west NSW. p. 82 in *Proceedings of Seventeenth Australian Research Assembly on Brassicas (ARAB) organized by the Australian Oilseeds Federation*, 15–17 August 2011, Wagga Wagga, New South Wales, Australia.
- Jeon, H.Y., Kim, H.H., Lee, Y.H., Chang, Y.D. & Yiem, M.S. (2005) Biological control of the turnip aphid (*Lipaphis erysimi*



- K.) using the braconid wasp (*Diaeretiella rapae* M.). *Korean Journal of Horticultural Science and Technology* **23**, 337–341.
- Kanegae, A.P. & Lomônaco, C.** (2003) Plasticidade morfológica, reprodutiva e assimetria flutuante de *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) sob diferentes temperaturas. *Neotropical Entomology* **32**, 37–43.
- Karley, A.J., Parker, W.E. & Pitchford, J.W.** (2004) The mid-season crash in aphid populations: why and how does it occur? *Ecological Entomology* **29**, 383–388.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B.** (2013). lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R-Version:1.1–0. Available online at <http://cran.rproject.org/web/packages/lmerTest/index.html>
- Leclair, M., Pons, I., Mahéo, F., Morlière, S., Simon, J.C. & Outreman, Y.** (2016) Diversity in symbiont consortia in the pea aphid complex is associated with large phenotypic variation in the insect host. *Evolutionary Ecology* **30**, 925–941.
- Liu, S.S. & Meng, X.D.** (1999) Modeling development time of *Myzus persicae* (Hemiptera: Aphididae) at constant and natural temperatures. *Bulletin of Entomological Research* **89**, 53–63.
- Liu, S.S. & Meng, X.D.** (2000) Modeling development time of *Lipaphis erysimi* (Hemiptera: Aphididae) at constant and variable temperatures. *Bulletin of Entomological Research* **90**, 337–347.
- MacGibbon, D.B. & Beuzenberg, E.J.** (1978) Location of glucosinase in *Brevicoryne brassicae* and *Lipaphis erysimi* (Aphididae). *New Zealand Journal of Science* **21**, 389–392.
- Mackauer, M. & Völkl, W.** (1993) Regulation of aphid populations by aphidian wasps: does parasitoid foraging behaviour or hyperparasitism limit impact? *Oecologia* **94**, 339–350.
- Malavolta, E. & Kliemann, H.J.** (1985) *Desordens nutricionais nos cerrados*. 136p, Piracicaba, POTAFOS.
- Martinez, A.J., Ritter, S.G., Doremus, M.R., Russell, J.A. & Oliver, K.M.** (2014) Aphid-encoded variability in susceptibility to a parasitoid. *BMC Evolutionary Biology* **14**, 127.
- Maunder, M.N. & Punt, A.E.** (2004) Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* **70**, 141–159.
- Mayer, D., Roy, D., Robins, J., Halliday, I. & Sellinet, M.** (2005) Modelling zero-inflated fish counts in estuaries: a comparison of alternative statistical distributions. pp. 2581–2587 in Zenger, A., Argent, R.M. (Eds) International Congress on Modelling and Simulation, Anaheim, Nano Science and Technology Institute.
- McCullagh, P. & Nelder, J.A.** (1989) *Generalized Linear Models*. London, Chapman & Hall.
- Micic, S.** (2005) *Identification and Cultural Control of Insect and Applied Pests of Canola*. Bulletin 4650. South Perth, Western Australia, Australia, Department of Agriculture.
- Oliveira, R.S., Sampaio, M.V., Ferreira, S.E., Ribeiro, L.C.M. & Tannús-Neto, J.** (2013) Low parasitism by *Diaeretiella rapae* (Hym.: Braconidae) of *Lipaphis pseudobrassicae* (Hemip.: Aphididae): pre- or post-ovipositional host resistance? *Biocontrol Science and Technology* **23**, 79–91.
- O’Neill, M.F. & Faddy, M.J.** (2003) Use of binary and truncated negative binomial modeling in the analysis of recreational catch data. *Fisheries Research* **60**, 471–477.
- Pike, K.S., Starý, P., Miller, T., Allison, D., Boydston, L., Graf, G. & Gillespie, R.** (1997). Small-grain aphid parasitoids (Hymenoptera: Aphelinidae and Aphidiidae) of Washington: distribution, relative abundance, seasonal occurrence, and key to known North American species. *Environmental Entomology* **16**, 1299–1311.
- Pike, K.S., Starý, P., Miller, T., Allison, D., Graf, G., Boydston, L., Miller, R. & Gillespie, R.** (1999) Host range and habitats of the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae) in Washington state. *Environmental Entomology* **28**, 61–71.
- Pinto, R.M., Bueno, V.H.P. & Santa-Cecília, L.V.C.** (2000) Flutuação populacional de afídeos (Hemiptera: Aphididae) associados à cultura da batata *Solanum tuberosum* L., no plantio de inverno em Alfenas, Sul de Minas Gerais. *Anais da Sociedade Entomologica do Brasil* **29**, 649–657.
- Pope, R.D.** (1983) Some aphid waxes, their form and function (Homoptera: Aphididae). *Journal of Natural History* **17**, 489–506.
- Potts, J.M. & Elith, J.** (2006) Comparing species abundance models. *Ecological Modelling* **199**, 153–163.
- Powell, W.** (1982) The identification of hymenopterous parasitoids attacking cereal aphids in Britain. *Systematic Entomology* **7**, 465–473.
- Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. & Kaplan, I.** (2011) *Insect Ecology: Behavior, Population and Communities*. Cambridge, UK, Cambridge University Press.
- R Development Core Team, R.** (2013) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. In: *R Development Core Team*. Vienna, Austria. Open source. Available online at <http://www.R-project.org>
- Reifenrath, K. & Müller, C.** (2007) Species-specific and leaf-age dependent effects of ultraviolet radiation on two Brassicaceae. *Phytochemistry* **68**, 875–885.
- Rothacher, L., Ferrer-Suay, M. & Vorburger, C.** (2016) Bacterial endosymbionts protect aphids in the field and alter parasitoid community composition. *Ecology* **97**, 1712–1723.
- Satar, S., Kersting, U. & Ulusoy, M.** (2005) Temperature dependent life history traits of *Brevicoryne brassicae* (L.) (Hom., Aphididae) on white cabbage. *Turkish Journal of Agriculture and Forestry* **29**, 341–346.
- Shaltiel, L. & Ayal, Y.** (1998) The use of kairomones for foraging decisions by an aphid parasitoid in small host aggregations. *Ecological Entomology* **23**, 319–329.
- Sheehan, W. & Shelton, A.M.** (1989) Parasitoid response to concentration of herbivore food plants: finding and leaving plants. *Ecology* **70**, 993–998.
- Starý, P., Sampaio, M.V., Bueno, V.H.P.** (2007) Aphid parasitoids (Hymenoptera, Braconidae, Aphidiinae) and their associations related to biological control in Brazil. *Revista Brasileira de Entomologia* **51**, 107–118.
- Sullivan, D.J. & Völkl, W.** (1999) Hyperparasitism: multitrophic ecology and behavior. *Annual Review of Entomology* **44**, 291–315.
- Waterhouse, D.F. & Sands, D.P.A.** (2001) *Classical Biological Control of Arthropods in Australia*. Canberra, Australia, CSIRO Entomology, Australian Centre for International Agricultural Research.
- Weber, G., Oswald, S. & Zollner, U.** (1986) Suitability of rape cultivars with different glucosinolate content for *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). *Journal of Plant Diseases and Protection* **93**, 113–124.
- Zamani, A.A., Talebi, A.A., Fathipour, Y. & Baniameri, V.** (2006) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science* **79**, 183–188.