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Natural factors regulating mustard aphid dynamics in cabbage

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Abstract

Lipaphis erysimi (L.) Kaltenbach (Hemiptera: Aphididae) is one of the most important pests of brassica crops, mainly causing losses due to sap sucking, toxin injection and viral transmission. Knowledge about the main natural factors that regulate populations of this pest, as well as its critical mortality stage, is crucial for the development of integrated pest management of *L. erysimi*. Here, we determined the critical stage and key mortality factors for *L. erysimi* in cabbage using an ecological life table. Causes of mortality at each stage of *L. erysimi* development were monitored daily in the field for seven seasons. From the experimental data, we determined the key factor and critical stage of mortality through correlation and regression analyses. The nymphal stage, especially first instar nymphs, was critical for *L. erysimi* mortality. The key mortality factors were, in descending order of importance, physiological disturbances and predation by Syrphidae, Coccinellidae and *Solenopsis* ants. Therefore, control measures should target early stages of *L. erysimi* and the use of cabbage cultivars that have negative effects against *L. erysimi* may be a promising strategy for its management. Our results may be useful for plant geneticists who could develop new cabbage cultivars based on these findings. In addition, conservation measures of the main predators of *L. erysimi* may contribute to the natural control of this pest.

Keywords: conservation biological control, critical stage, key factor, life table, *Lipaphis erysimi*, plant resistance

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Introduction

The mustard aphid *Lipaphis erysimi* (L.) Kaltenbach (Hemiptera: Aphididae) is one of the most important pests of brassica crops, mainly in tropical and subtropical climate areas (Lamb *et al*., 1993; Liu & Meng, 2000; Rana, 2005). These aphids quantitatively and qualitatively affect plant production, through sap sucking, toxin injection and transmission of viruses from the Luteoviridae family, leading to leaf curling, shrivelling and yellowing (Sylvester, 1987). In addition, these aphids produce honeydew, a medium for the growth of sooty mold that negatively effects photosynthesis, leaf durability, and crop market value (Ram *et al*., 1989).

From a pest management standpoint, it is very important to know the main natural factors (i.e., key mortality factors) that regulate insect pest populations, since the magnitude of these factors (climatic elements, natural enemies or top-down forces, and host-plant attributes or bottom-up effects) varies considerably with the pest species (Pereira *et al*., 2007, 2018; Semeão *et al*., 2012; Silva *et al*., 2017). In addition, the application of control measures at the stages that most influence the size of a pest population (i.e., critical stages) increases control efficiency and allows the reduction of insecticide use and environmental impacts (Wilby & Thomas, 2002; D'Auria *et al*., 2016).

In this context, ecological life tables are very useful tools because, through the qualification and quantification of the mortality factors at each stage of a pest life cycle, they identify the

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key factors and the critical mortality stages (Harcourt, 1969; Podoler & Rogers, 1975; Southwood & Henderson, 2000). The information obtained by life table studies also allows the identification of new natural biological control agents and provides data to determine potential sources of plant resistance to pests.

In this study, we report the critical stage and key mortality factors for *L. erysimi* using an ecological life table aiming to better understand the population ecology and role of natural factors in regulating populations of this important pest.

Materials and methods

Study site

The study was carried out on cabbage crops (*Brassica oleracea* var. *capitata*, hybrid Sekai F1) in the experimental area of the university (20°46′10″S; 42°52′10″W; altitude 750 m), Minas Gerais state, Brazil. The climate of the study region is tropical and corresponds to the Köppen class Cwb (Peel *et al.*, 2007), with rainy summers and dry winters. The average annual temperature is 19.4°C, ranging between 13 and 30°C. The mean annual rainfall is 1170 mm with rains concentrated between October and March (INMET, 2017). The study site was located near fragments of native vegetation (seasonal semi-deciduous forest).

The cabbage crops were constituted by five rows of 30 plants spaced $1 \times 0.5\ m^2$. Cabbage seedlings were transplanted in the field 30 days after sowing. The fields were grown as recommended by Filgueira (2000). No pesticide was applied during the study.

Insects

The aphids used in the experiments were obtained from an established laboratory population. To carry out this rearing, cabbage leaves infested with *L. erysimi* were collected in commercial cabbage fields from Viçosa County, Minas Gerais, Brazil. Adults from these colonies were transferred to cabbage leaves and placed in wooden cages ($45 \times 45 \times 45\ cm^3$) covered with organza fabric. Twenty-four hours after the transfer, the females were removed and only the nymphs generated were left on the leaves, in order to avoid infestation of parasitoids and fungi during rearing. Every 3 days, new cabbage leaves were added to the cages and the yellow leaves were removed.

Cohort establishment

Life table data of *L. erysimi* were obtained in seven periods, as presented in table 1. These periods were selected to allow the evaluation of the factors regulating *L. erysimi* populations in all seasons of the year. The whole cycle of the aphids was monitored in the field to determine the critical stage and the mortality factors of these insects at each stage. The experimental design was completely randomized with 10 plots. Each plot consisted of two cabbage plants in stage 3 (6–8 leaves): one designated to evaluate the mortality caused by physiological disturbances and the other to determinate total mortality.

Table 1. Periods of data collection of *Lipaphis erysimi* life table in cabbage crops in Viçosa, MG, Brazil.

Period	Dates	Season
1	25 June 2007–18 August 2007	Winter
2	19 September 2007–24 October 2007	Spring
3	22 January 2008–04 March 2008	Summer
4	27 March 2008–15 April 2008	Autumn
5	07 July 2008–26 August 2008	Winter
6	07 October 2008–06 November 2008	Spring
7	22 January 2009–26 February 2009	Summer

Physiological disturbances are abnormalities observed in insects, such as incomplete molt and malformation of nymphs (Semeão *et al.*, 2012). These disorders are related to bottom-up forces, including plant phenology, nutritional quality and defense compounds produced by the plant (Godoy & Cividanes, 2002; Chattopadhyay *et al.*, 2005). The plants used to assess mortality caused by physiological disturbances were covered with organza-enclosed wooden cages ($45 \times 45 \times 45\ cm^3$) to prevent the action of natural enemies. The cages were protected from rain by canvas sheeting attached to wooden supports. These plants were previously inspected for removal of aphids and other arthropods present.

For the initial establishment of the cohort, 35 2-day-old females were equally distributed on two medium leaves of the plants using a fine brush. To prevent predation of females during the infestation period, all plants were covered with cages. After 24 h, the females were removed and the 1st instar nymphs generated (130, on average) were left on the plant. The aphid infested leaves were numbered to facilitate evaluation and the cages covering the plants used for the assessment of total mortality were removed.

Assessment of mortality factors

Causes of mortality at each stage of *L. erysimi* development were monitored daily in the field from the establishment of the cohort until the adults entered the reproductive phase. Aphids were counted three times a day (8 am, 12 am, and 5 pm) and only at 5 pm for plants used to evaluate total mortality and mortality due to physiological disturbances, respectively. *Lipaphis erysimi* fecundity was determined by counting the nymphs produced by females, daily, in the plants designated to evaluate the mortality caused by physiological disturbances.

Aphids were also counted immediately after the occurrence of rains and those that disappeared during this period or died covered by mud were considered dead due to this factor. Mortality due to parasitism was evaluated by counting parasitized mummies (smooth, shiny and swollen mummies). Mortality due to fungal infection was evaluated by counting mummies covered by mycelium or aphids with infection symptoms (pinkish mummies). The mortality of aphids during the molting process in the cage-covered plants was attributed to physiological disturbances. Nymphs that died attached to their exuviae were considered dead by this factor. The same mortality rates caused by physiological disturbances in caged plants was adopted for unprotected plants since, in the latter ones, these rates are obscured by other factors (predation and rainfall, for instance). Mortality due to predation was directly evaluated in the field through the observation of arthropods feeding on aphids. The plants were observed for 15 min, at each evaluation time (8 am, 12 am, and 5 pm), to identify the predators.

Exemplars of parasitized *L. erysimi* were collected in the evaluated plants and in other plants of the crop and placed in 100-ml plastic pots for the emergence of the parasitoids in the laboratory. Specimens of predators and parasitoids were maintained in 70% alcohol and identified according to the literature (Auad & Trevizani, 2005; Rakhshani *et al.*, 2008). Fungi

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infected aphids were mounted on microscope slides to identify the entomopathogens.

Construction and analyses of life tables

Standard methods were used to generate the life tables (Varley *et al*., 1974; Southwood & Henderson, 2000; Silva *et al*., 2017). Net reproductive rate (R_0) was estimated by dividing the number of first instar nymphs expected in the next generation (number of surviving adults from the original cohort × sex ratio × fecundity) by the initial number of 1st instar nymphs (l_0). Sex ratio (*sr*) was taken to be 1.0 since all individuals in the *L. erysimi* population are females, and fecundity (*f*) was obtained in the plants used to assess mortality from physiological disturbances.

Life tables were composed of the columns x, lx, dx, $100qx$, and $100rx$, where x is the developmental stage, lx is the number of individuals alive at the beginning of each stage, dx is the number of individuals that died during each stage, $100qx$ is the apparent mortality percentage ($100qx = 100 \times dx/lx$), and $100rx$ is the real mortality percentage ($100rx = 100 \times dx/l_0$).

Marginal mortality (the expected mortality of a factor as if this was the only acting factor) was calculated. This concept is important since mortality factors like rainfall and predation kill quickly and are easily observed while physiological disturbances, parasitism, and entomopathogens usually take longer to kill (Elkinton *et al*., 1992). Mortality due to rainfall and physiological disturbances was not obscured by any other factor and therefore their marginal mortality was considered equal to the apparent mortality. The same probability of predation of parasitized or fungi-infected aphids and healthy aphids was assumed.

For the subsequent analyses, mortality was expressed as a *k*-value ($k = -\log(1-MMx/100)$) where MMx is the marginal mortality (%) for a given factor at a given developmental stage. The use of *k*-value is convenient because it is additive through stages and mortality factors. The total mortality (K) of the developmental stage in question can be obtained by the sum of the *k*-values ($K = \Sigma k$). For the identification of critical stages and key mortality factors, correlation analyses were performed between partial mortality (k) and total mortality (K) (Varley *et al*., 1974). When a positive, significant correlation ($P < 0.05$) existed between mortality in a particular stage and total mortality, that stage was considered the critical mortality stage. When more than one stage showed significant correlation, partial mortality (k) were regressed on total K, and the critical stage was the one presenting the largest significant regression angular coefficient (slope) at $P < 0.05$ (Podoler & Rogers, 1975; Naranjo & Ellsworth, 2009; Pereira *et al*., 2018). Difference between slopes in the regression analyses was verified by the confidence interval at 95% probability. Key mortality factors were determined at the critical stage through the same procedures described above (Podoler & Rogers, 1975). Correlation and regression analyses were performed using PROC CORR and PROC REG (SAS 9.0, SAS Institute, Cary, USA). Assumptions of normality and homoscedasticity were checked using PROC UNIVARIATE and PROC GLM (SAS 9.0).

Results

Mortality factors of Lipaphis erysimi

The mean mortality of the entire *L. erysimi* cycle was 90.21%. Mortality was 45.38% in the 1st instar; 36.02% in the 2nd instar; 27.59% in the 3rd instar; 20.27% in the 4th instar; 36.77% in the 5th instar and 23.77% in the adult phase. On average, of 130 initial individuals, 17 reached adulthood and 13 reached the reproductive phase. Based on the fecundity obtained (46.42 nymphs/female), the net reproductive rate (R_0) of *L. erysimi* was 4.95 (table 2).

Mortality of 1st instar nymphs was caused by physiological disturbances, rainfall, Syrphidae larvae, Coccinellidae adults, and ants. In the 2nd instar, causes of mortality were physiological disturbances, rainfall, spiders, Syrphidae larvae, Coccinellidae larvae and adults, and ants. Mortality in the 3rd instar was caused by physiological disturbances, rainfall, spiders, *Chrysoperla externa* Hagen larvae (Neuroptera: Chrysopidae), *Aphidoletes* sp. larvae (Diptera: Cecidomyiidae), Syrphidae larvae and Entomophthorales fungi. In the 4th nymphal instar, mortality was caused by physiological disturbances, rainfall, spiders, Syrphidae larvae, Aphidoletes sp. larvae, Coccinellidae larvae and adults, Entomophthorales and parasitism by *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae). In the 5th instar, causes of mortality were physiological disturbances, rainfall, spiders, Syrphidae larvae, *Aphidoletes* sp. larvae, Coccinellidae larvae and adults, ants, Entomophthorales and parasitism by *D. rapae* and *Aphidius colemani* Viereck (Hymenoptera: Braconidae). In the adult phase, mortality factors were rainfall, spiders, Syrphidae larvae, *Aphidoletes* sp. larvae, Coccinellidae larvae, Entomophthorales, *D. rapae*, and *A. colemani* (table 2).

Critical mortality stage of Lipaphis erysimi

Lipaphis erysimi mortality curve during the nymphal stage was the one that best represented the total mortality curve, as indicated by the positive and significant correlation coefficient ($r = 0.93$, $P < 0.0001$, $n = 55$). Mortalities of all nymph stages showed positive and significant correlations ($P < 0.05$, $n = 55$) with the nymphal total mortality. The mortality curve with the largest significant slope (b) was that for 1st instar (table 3). Therefore, the critical mortality stage of *L. erysimi* was the 1st instar nymph.

Key mortality factors of Lipaphis erysimi

The mortality factors of 1st instar *L. erysimi* nymphs were physiological disturbances, predation, and rainfall. The *L. erysimi* partial mortality curve for physiological disturbances presented the largest significant slope (b), followed by the partial mortality curve for predation (fig. 1a, b).

Syrphidae larvae, ants, and Coccinellidae adults were the predators that caused mortality to 1st instar *L. erysimi* nymphs. The partial mortality curve for Syrphidae presented the largest significant slope (b), followed by the partial mortality curve for adults of Coccinellidae (fig. 2a, b). Therefore, the key mortality factor for 1st instar *L. erysimi* nymphs was physiological disturbances, followed by predation and rainfall. The predator that caused the highest mortality to *L. erysimi* was Syrphidae larvae.

Discussion

Knowledge about the natural mortality factors and their magnitude in the population dynamics of insect pests is fundamental for the development of efficient management systems of these organisms. Populations of *L. erysimi* are determined by biotic and abiotic factors that caused a 92%

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Table 2. Ecological life table of *Lipaphis erysimi* in cabbage crops in Viçosa, MG, Brazil.

Stage/Mortality factors	*Lx*	*Dx*	100*qx*	100*rx*	*MM* (*k*)
1st instar nymphs	130.13 ± 13.67	59.05 ± 6.33	45.38	45.38	(0.261)
Physiological disturbances		39.89 ± 4.54	30.66	30.66	35.95 (0.193)
Rainfall		1.09 ± 1.09	0.84	0.84	0.84 (0.004)
Larvae of Syrphidae		6.75 ± 1.56	5.19	5.19	7.57 (0.025)
Adults of Coccinellidae		5.01 ± 0.11	3.85	3.85	5.62 (0.034)
Ants		6.31 ± 0.38	4.85	4.85	7.08 (0.032)
2nd instar nymphs	71.07 ± 10.63	25.6 ± 5.04	36.02	65.06	(0.194)
Physiological disturbances		17.71 ± 4.61	24.92	13.61	24.92 (0.124)
Rainfall		0.07 ± 0.07	0.10	0.06	0.1 (0.0004)
Spiders		2.33 ± 0.12	3.28	1.79	4.38 (0.019)
Larvae of Syrphidae		2.10 ± 0.26	2.96	1.61	3.94 (0.017)
Adults of Coccinellidae		2.10 ± 0.15	2.96	1.61	3.94 (0.017)
Ants		1.28 ± 0.15	1.81	0.99	2.41 (0.011)
3rd instar nymphs	45.47 ± 6.6	12.55 ± 2.53	27.59	74.70	(0.137)
Physiological disturbances		3.62 ± 0.62	7.96	2.78	7.96 (0.036)
Rainfall		3.98 ± 1.69	8.76	3.06	8.76 (0.04)
Spiders		0.25 ± 0.04	0.55	0.19	0.66 (0.003)
Larvae of *Chrysoperla externa*		0.62 ± 0.09	1.37	0.48	1.64 (0.007)
Larvae of *Aphidoletes* sp.		1.74 ± 0.16	3.83	1.34	4.60 (0.020)
Larvae of Syrphidae		2.26 ± 0.16	4.97	1.74	5.96 (0.027)
Entomophthorales fungi		0.07 ± 0.06	0.16	0.06	0.22 (0.001)
4th instar nymphs	32.93 ± 5.64	6.67 ± 1.18	20.27	79.82	(0.098)
Physiological disturbances		0.64 ± 0.14	1.93	0.49	1.93 (0.008)
Rainfall		2.24 ± 0.86	6.79	1.72	6.79 (0.031)
Spiders		0.19 ± 0.03	0.58	0.15	0.64 (0.003)
Larvae of Syrphidae		1.15 ± 0.17	3.48	0.88	3.81 (0.017)
Larvae of *Aphidoletes* sp.		0.19 ± 0.04	0.58	0.15	0.64 (0.003)
Adults of Coccinellidae		0.84 ± 0.06	2.55	0.65	2.80 (0.012)
Larvae of Coccinellidae		0.95 ± 0.18	2.90	0.73	3.18 (0.014)
Entomophthorales fungi		0.45 ± 0.24	1.38	0.35	1.7 (0.007)
Diaeretiella rapae		0.02 ± 0.02	0.06	0.01	0.07 (0.0003)
5th instar nymphs	26.25 ± 4.9	9.73 ± 2.1	36.77	87.24	(0.176)
Physiological disturbances		1.36 ± 0.35	5.12	1.03	5.12 (0.023)
Rainfall		3.24 ± 1.16	12.19	2.46	12.19 (0.056)
Spiders		0.61 ± 0.07	2.32	0.47	2.81 (0.012)
Larvae of Syrphidae		2.28 ± 0.07	8.7	1.76	10.52 (0.048)
Larvae of *Aphidoletes* sp.		0.61 ± 0.09	2.32	0.47	2.81 (0.012)
Adults of Coccinellidae		0.80 ± 0.16	3.03	0.61	3.67 (0.016)
Larvae of Coccinellidae		0.23 ± 0.05	0.87	0.18	1.05 (0.005)
Ants		0.23 ± 0.05	0.87	0.18	1.05 (0.005)
Entomophthorales fungi		0.29 ± 0.12	1.11	0.22	1.73 (0.008)
Diaeretiella rapae		0.04 ± 0.04	0.07	0.01	0.11 (0.0005)
Aphidius colemani		0.02 ± 0.02	0.14	0.03	0.22 (0.001)
Adults	16.6 ± 3.28	3.95 ± 1.03	23.77	90.28	(0.115)
Rainfall		1.82 ± 0.77	10.95	1.40	10.95 (0.05)
Spiders		0.02 ± 0.02	0.12	0.02	0.14 (0.001)
Larvae of Syrphidae		0.12 ± 0.06	0.72	0.09	0.81 (0.003)
Larvae of *Aphidoletes* sp.		0.40 ± 0.15	2.41	0.31	2.70 (0.011)
Larvae of Coccinellidae		0.02 ± 0.02	0.12	0.02	0.14 (0.001)
Entomophthorales fungi		0.62 ± 0.13	3.72	0.48	4.66 (0.021)
Diaeretiella rapae		0.82 ± 0.30	4.93	0.63	5.79 (0.026)
Aphidius colemani		0.04 ± 0.04	0.22	0.03	0.26 (0.001)
Adults in reproductive stage	12.65 ± 2.42				
Fecundity = 46.42; Mortalidade total = 90.21%; R_0 = 4.95					

lx = number of insects alive at the beginning of each stage, *dx* = number of insects killed by each factor at each stage, 100*qx* = apparent or non-cumulative mortality (%), 100*rx* = actual mortality or cumulative mortality (%), *MM* = marginal mortality (%), $k = -\log(1-MM/100)$, and R_0 = net reproductive rate. The presented values represent an average of 55 life tables.

reduction in *L. erysimi* cohorts. However, in spite of this significant mortality, *L. erysimi* had a population increase during the year ($R_0 > 1$), principally due to the reproductive advantage of these organisms, that reproduce by parthenogenesis (Powell *et al.*, 2006). This shows that the causes of natural mortality are not sufficient to reduce densities of these insects. Therefore, other methods and management strategies should be adopted in order to maximize or complement the action of natural mortality factors in cabbage crops.

Lipaphis erysimi nymphs are more vulnerable than the adult stage. This is due to the longer development period of this stage compared with the adult phase. In addition, earlier

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Table 3. Pearson correlation and simple linear regression analyses for determination of the critical mortality stage of *Lipaphis erysimi* in cabbage crops in Viçosa, MG, Brazil.

	Correlation analysis		Regression analysis			
Stage	*r*	*P*	*b*	r^2	*F*	*P*
Adults	0.21	0.1165	0.12 (0.09–0.15)	0.50	54.05	<0.0001
Nymphs	0.93	<0.0001	0.88[1] (0.85–0.91)	0.98	2869.02	<0.0001
1st instar	0.46	0.0004	0.29[1] (0.25–0.33)	0.81	225.44	<0.0001
2nd instar	0.36	0.0068	0.18 (0.15–0.21)	0.70	124.07	<0.0001
3rd instar	0.53	<0.0001	0.17 (0.14–0.20)	0.69	119.74	<0.0001
4th instar	0.45	0.0005	0.12 (0.09–0.15)	0.59	79.06	<0.0001
5th instar	0.61	<0.0001	0.24 (0.19–0.28)	0.67	112.79	<0.0001

r, correlation coefficient; *b*, angular coefficient of the mortality curve; $CI_{95\%}$ = Confidence interval at 95% probability.
[1]Higher angular coefficient based on the confidence interval at 95% probability.

stages are more vulnerable to desiccation, low plant quality, and climatic variability, especially temperature (Aschehoug *et al.*, 2015; Sultana *et al.*, 2017). Thus, control measures should be taken early during *L. erysimi* development, since the critical mortality stage for this pest is the 1st instar nymph.

The most important mortality factor for 1st instar nymphs of *L. erysimi* is physiological disturbances. Plants defense compounds, including total phenols, O-OH phenols, glucosinolates, and lectins, have been shown to cause physiological disorders to *L. erysimi* (Rana, 2005; Newton *et al.*, 2009; Kumar *et al.*, 2011). Therefore, the use of resistant plants is a promising strategy to manage this pest. Since cultivated cabbage genotypes have a low content of defense compounds, wild brassica expressing high levels of lectins, such as *Brassica fruticulosa*, *B. montana*, and *Rorippa indica*, have been shown to be promising sources of resistance to *L. erysimi* (Kumar *et al.*, 2011; Bandopadhyay *et al.*, 2013). Our results may be a starting point for future research to determine which chemical(s) are responsible for the physiological disturbances.

The application of insect growth regulators (IGRs) is another tactic that can be adopted in *L. erysimi* management. The effect of juvenile hormone analogues, such as pyriproxyfen and methoprene, on this pest, has been studied (Rup & Gill, 1993; Liu & Chen, 2001). These products cause excessive molting and premature death of immature phases. When exposed to these molecules, nymphs of *L. erysimi* up to 3rd instar suffer the greatest effects, while nymphs of 4th instar normally molt to the adult phase (Liu & Chen, 2001). There are reports of side effects of these insecticides on some natural enemies (Mendel *et al.*, 1994; Hattingh & Tate, 1995), but not on others (Liu & Stansly, 2004; Cloyd & Dickinson, 2006). In general, growth regulators are safer to beneficial organisms than the molecules commonly applied in the management of *L. erysimi* (pyrethroids, carbamates, and organophosphates) (Naranjo *et al.*, 2004; Cloyd *et al.*, 2009; Naranjo & Ellsworth, 2009;

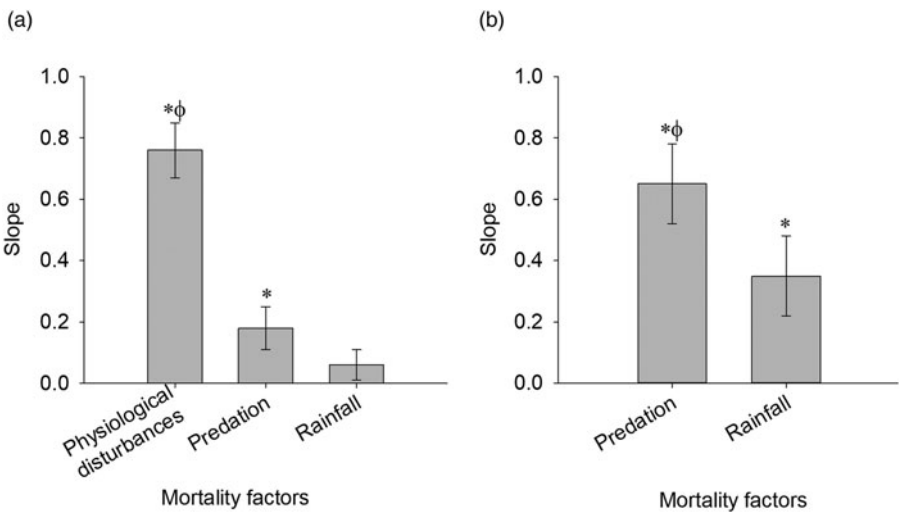

Fig. 1. Slopes (*b*) of the simple linear regression curves for determination of key mortality factors for 1st instar nymphs of *Lipaphis erysimi* in cabbage crops (Viçosa, MG, Brazil). (a) The factor with significant and greater slope based on confidence interval at 95% probability was selected. Physiological disturbances: $b = 0.76$ (0.67–0.85), $r^2 = 0.85$, $F = 296.09$, $P < 0.0001$; Predation: $b = 0.18$ (0.11–0.26), $r^2 = 0.32$, $F = 24.95$, $P < 0.0001$; Rainfall: $b = 0.06$ (0.00–0.12), $r^2 = 0.06$, $F = 3.29$, $P = 0.08$. (b) The key mortality factors were submitted again to this analysis, excluding the previously selected factor. Predation: $b = 0.65$ (0.52–0.78), $r^2 = 0.65$, $F = 99.04$, $P < 0.0001$; Rainfall: $b = 0.35$ (0.22–0.48), $r^2 = 0.35$, $F = 29.44$, $P < 0.0001$. Numbers in parentheses represent 95% confidence interval for the slope of the curves. *Significant angular coefficient ($P < 0.05$); ϕGreater slope based on confidence interval at 95% probability. $n = 55$.

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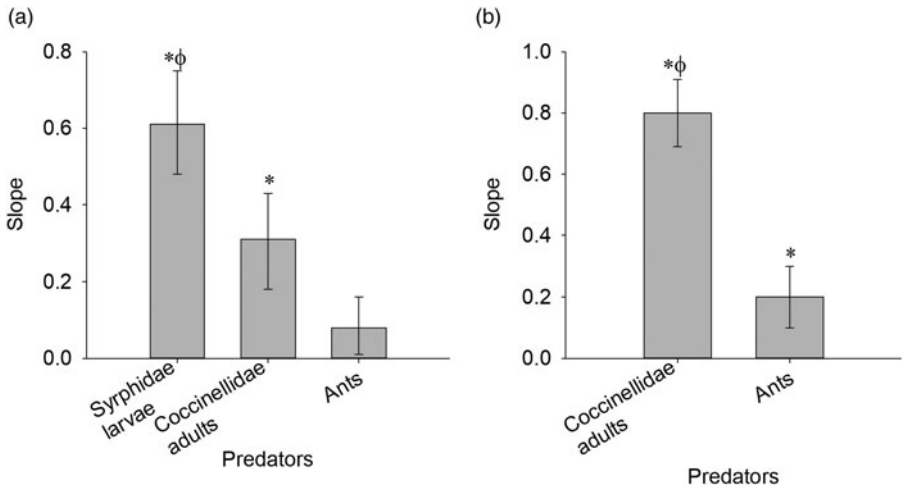

Fig. 2. Slopes (*b*) of the simple linear regression curves for determination of the main predators of 1st instar nymphs of *Lipaphis erysimi* in cabbage crops (Viçosa, MG, Brazil). (a) The predator with significant and greater slope based on confidence interval at 95% probability was selected. Syrphidae larvae: $b = 0.61$ (0.48–0.75), $r^2 = 0.61$, $F = 86.12$, $P < 0.0001$; Coccinellidae larvae: $b = 0.31$ (0.18–0.43), $r^2 = 0.31$, $F = 24.24$, $P < 0.0001$; Ants: $b = 0.08$ (0.00–0.14), $r^2 = 0.08$, $F = 4.42$, $P = 0.04$. (b) The predators were submitted again to this analysis, excluding the previously selected predator. Coccinellidae larvae: $b = 0.65$ (0.52–0.78), $r^2 = 0.65$, $F = 99.04$, $P < 0.0001$; Ants: $b = 0.35$ (0.22–0.48), $r^2 = 0.35$, $F = 29.44$, $P < 0.0001$. Numbers in parentheses represent 95% confidence interval for the slope of the curves. *Significant angular coefficient ($P < 0.05$); ϕGreater slope based on confidence interval at 95% probability. $n = 55$.

Echegaray & Cloyd, 2012). Since IGRs act primarily at the critical mortality stage of *L. erysimi* and are safer to natural enemies when compared to conventional alternatives, they fit well in this pest management.

Among the predators, Syrphidae larvae, Coccinellidae adults and ants were the most important organisms regulating *L. erysimi*. *Ocyptamus gastrostactus* Wiedemann, *Allograpta exotica*, and *Pseudodorus clavatus* Fabricius were the species of Syrphidae found. In Brazil, there are several reports of Syrphidae causing mortality of aphids including *Allograpta neotropica* Curran, O. *gastrostactus*, *Syrphus phaetostigma* Wiedemann, *Ocyptamus dimidiatus* Fabricius, and *P. clavatus* predating aphids in citrus, kale, cucumber, wheat and potato (Auad & Trevizani, 2005). In general, Syrphidae larvae feed on 660 to 1140 third instar nymphs during their larval development (Tenhumberg & Poehling, 1995; Soleyman-Nezhadiyan & Laughlin, 1998) and play an important role in aphid regulation (Michaud & Belliure, 2001). The species of Coccinellidae found predating *L. erysimi* were *Cycloneda sanguinea* (L.), *Eriopis connexa* (Germar) and *Harmonia axyridis* (Pallas). Adults and larvae of ladybugs are highly mobile and voracious predators. Although they are generalists, ladybugs are often associated with aphids (Snyder & Ives, 2003). Predation by ladybugs may also cause aphids to drop from the plants, an anti-predation behavior observed in several aphid species (Kunert *et al.*, 2005; Francke *et al.*, 2008). As aphids have a thin cuticle layer and few defense strategies, this dropping can be advantageous as a defense strategy against ladybugs. However, once on the ground, they can be preyed on by soil-dwelling arthropods or die due to desiccation (Gish & Inbar, 2006). The ant species found preying on *L. erysimi* are from the genus *Solenopsis*. Mutualism of *L. erysimi* with these ants not being verified. In fact, the predation on aphids on the soil by these organisms was often observed during the evaluations.

In order to maximize the natural control of *L. erysimi*, habitat management strategies can be adopted to provide resources for its main natural enemies. More complex agroecosystems (e.g., bands of flowering plants near brassica plantations and intercropping) favor Coccinellidae and Syrphidae adults, and consequently *L. erysimi* suppression, since these organisms feed on pollen and nectar (White *et al.*, 1995; Hickman & Wratten, 1996; Obrycki *et al.*, 2009; Ramsden *et al.*, 2014). Maintenance of weed coverage and soil moisture, in turn, are measures that favor *S. saevissima* in brassica crops (Harvey & Eubanks, 2004; Wang *et al.*, 2016). Additionally, the use of selective insecticides, aiming to reduce the ecological impacts of these chemicals and insecticide applications (e.g., adoption of sampling and action thresholds) can contribute to the biological control of *L. erysimi*.

In conclusion, the nymphal stage, especially first instar nymphs, is critical for *L. erysimi* mortality. The key mortality factors during this stage in order of decreasing importance are physiological disturbances and predation by Syrphidae, Coccinellidae, and *Solenopsis* ants. Therefore, control measures should target early stages of *L. erysimi* and research aimed at developing cabbage varieties resistant to *L erysimi* should be prioritized. Finally, strategies aiming to maintain the action of the biological control agents might contribute to *L. erysimi* suppression in brassica crops.

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