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Biological Control and Crop Protection

## Biotic factors are more important than abiotic factors in regulating the abundance of *Plutella xylostella* L., in Southern Brazil



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### ABSTRACT

The serious economic loss caused *Plutella xylostella* L., 1758 in several regions of the world has prompted a demand for alternative management strategies. In this context, understanding the key factors governing the population dynamics of the pest is important for development of management strategies. This study aimed to identify the larval parasitoids associated with *P. xylostella* and investigate the biotic (crop subspecies, plant age and parasitism) and abiotic factors (minimum and maximum temperatures, rainfall, relative humidity and planting season) affecting the population dynamics of the pest in organic crops located in Southern Paraná State, Brazil. Despite the continuous and abundant availability of host plants throughout the year, *P. xylostella* occurred between June and November, and the largest peaks of abundance were observed between August and September, when low temperatures and rainfall were recorded. According to the stepwise regression analysis, *P. xylostella* was more abundant in broccoli during winter. Neither temperature, nor rainfall significantly influenced pest abundance. Four species of larval parasitoids were identified associated with the pest, of which *Diadegma leontinae* (Brèthes) (Hymenoptera: Ichneumonidae), *Apanteles piceotrichosus* Blanchard (Hymenoptera: Braconidae) and *Siphona* sp. Meigen (Diptera: Tachinidae) were abundant, while *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae) was rarely found. Parasitism was the major factor influencing population dynamics of *P. xylostella*, contributing to 48% of the variation in pest abundance. These results show the importance of larval parasitoids complex in regulating *P. xylostella* population and that the temperature and rainfall recorded during field experiments did not influenced pest abundance.

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### Introduction

The diamondback moth, *Plutella xylostella* L., 1758 (Lepidoptera: Plutellidae) is an important pest of brassicas that causes significant losses in yield in several regions of the world (Talekar and Shelton, 1993; Zalucki et al., 2012). Recent analysis showed that the worldwide annual cost associated with its management is estimated in US\$ 4 billion (Zalucki et al., 2012). Several factors are responsible for this situation in different regions of the world, such as the diversity and availability of host plants, lack of effective natural enemies, high tolerance to a wide range of temperatures, and high reproductive potential and genetic plasticity, which combined favors the rapid evolution of resistance to insecticides (Talekar and Shelton, 1993; Mohan and Gujar, 2003). Frequent failure in the control of *P. xylostella* has made the economical

production of brassicas impracticable in certain regions of the world (Talekar and Shelton, 1993; Sarfraz et al., 2006). This scenario is not much different in some regions of Brazil, where insecticide resistant populations cause serious economic damage (Castelo-Branco et al., 2001; Zago et al., 2013). This condition has prompted a demand for alternative management strategies, particularly those based on biological and cultural control (Sarfraz et al., 2005, 2006).

Several parasitoid species were identified associated with *P. xylostella* worldwide, and some of which are considered important for the regulation of pest population (Sarfraz et al., 2005). Eight species were found parasitizing larvae of *P. xylostella* in Brazil (Feronato and Becker, 1984; Guilloux et al., 2003; Silva-Torres et al., 2010), representing a low diversity when compared to other regions of the world (Kfir, 1997; Liu et al., 2000; Mosiane et al., 2003; Ayalew and Ogol, 2006). However, the role they play in regulating pest population was not investigated, despite the importance of this information for bioprospection of parasitoid species to be used as biocontrol agents against *P. xylostella*.

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In addition to the biological interactions, abiotic factors, such as temperature and rainfall, and the plant used as host are known to affect insect population dynamics (Wallner, 1987). Understanding the factors governing the population dynamics of insects is an important issue of insect ecology (Andrewartha and Birch, 1954), and is a practical concern with regard to species that produce economic damage (Baskauf, 2003). The recognition of the key mortality factors of insect pests is particularly important because they can be used in the development of management strategies (Baskauf, 2003). Biological conservation practices that improve parasitoid effectiveness may be sensibly adopted when larval parasitoid complex is an important mortality factor regulating an insect pest population.

Here, data obtained in field surveys carried out in different host plants were used to answer a series of questions involving the ecology of *P. xylostella*. Initially, we investigated the population dynamics of the pest in commercial crops located in Southern Brazil. Also, the larval parasitoids associated with *P. xylostella* and their role in regulating the abundance of the pest was assessed. Finally, we investigated whether factors such as host plants, temperature conditions and rainfall influence the abundance of the pest in the field. Together, this information can be used for management purposes, particularly those involving biological control.

## Material and methods

### Study area

The study was conducted on organic commercial crops located in the county of Colombo, Paraná State, Southern Brazil (S 25° 17', W 49° 13', 950 m altitude) between June 2007 and June 2008. Seasonal abundance of the diamondback moth was evaluated on broccoli (*Brassica oleraceae* var. *italica*) and cauliflower (*B. oleraceae* car. *botrytis*) crops. The same hybrid of broccoli (BRO 68) was cultivated throughout the seasons, while the cauliflower variety "White A" was grown in spring, summer and autumn, and the hybrid "Barcelona" in winter. Seedlings of broccoli and cauliflower were transplanted to plots of ca. 700 m<sup>2</sup> each, with a distance of 0.50 m between plants and 0.80 m between rows. The cropping system followed the protocol recommended for organic farming. After harvesting, the area passed through a fallow period, when wild radish and remains of previous crops were incorporated into the soil as green manure. Additionally, fertilization during planting was made with chicken manure. There was no pesticide application during field surveys. The experimental site was surrounded by other vegetable crops that are not used by *P. xylostella* as host (tomato, lettuce and pepper) and fragments of native vegetation, which is considered an important characteristic providing shelter and alternative hosts to natural enemies when the primary host is not available (Thomson and Hoffmann, 2009).

According to the Köppen–Geiger climate classification, the region is within subtropical highland climate (cfb), characterized by cold and relatively dry winters, and moderately warm and wet summers. Meteorological data were obtained from weather stations of the Meteorological Institute of Paraná State during the sampling period. These data comprise daily minimum and maximum temperature (°C), daily rainfall (mm) and daily relative humidity (%). Average temperatures recorded during field surveys ranged from 13 °C in the colder months of winter to 20 °C in summer. Minimum and maximum temperatures were recorded in July 2007 (5 °C) and March 2008 (28 °C), respectively. Rainfall ranged from 136 mm in the driest months (June to August) to 398 mm in the rainy months (December to February) (Fig. 1).

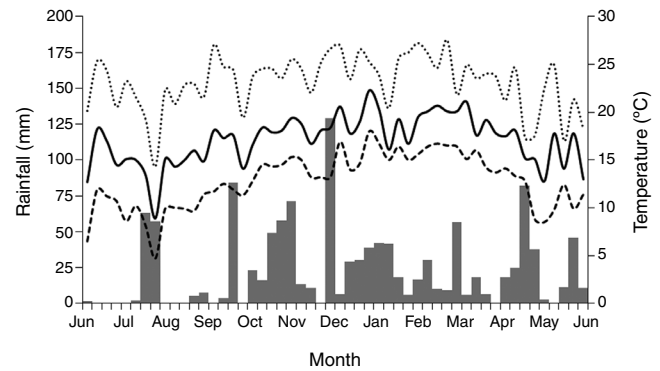


Fig. 1. Climatic variables recorded during field surveys in the county of Colombo, Paraná State, Southern Brazil. Climate data shown are: rainfall (column), mean temperature (solid line), minimum temperature (dashed line) and maximum temperature (dotted line).

### Population dynamics of *P. xylostella*

Samplings were taken weekly, allowing the record of the abundance of *P. xylostella* in all plant phenological stages. In each survey, 30 plants per crop were examined; and second to fourth instar larvae and pupae were collected through visual observation of all plant leaves. First instar larvae were not collected because at this stage they are leaf-mining, which makes their observation and sampling difficult. Surveys initiated always two weeks after seedling transplant, but the number of samples varied due to differences in plant cycle length. In spring, summer, autumn and winter 8, 10, 9 and 13 samples were respectively carried out on broccoli and 9, 9, 10 and 10 on cauliflower.

### Abundance of larval parasitoids

In order to identify the larval parasitoids associated with *P. xylostella*, all larvae observed during samplings were collected, taken to the laboratory and individually kept in polyethylene vials (4 cm × 7 cm) maintained in environmental chambers (FANEM® Ltd., model 347 CDG) regulated at 20 °C, and L12:D12 photoperiod. Larvae were fed on fresh leaves of the crop on which they were collected until the emergence of adult moths or parasitoids. Host plant leaves provided to the larvae were previously washed in 0.5% solution of sodium hypochlorite to avoid larval contamination with entomopathogens. Emerged parasitoids were properly preserved in alcohol 95% and sent to taxonomists for identification. The percentage of parasitism was determined based on the total number of larvae collected and the number of parasitized larvae. Additionally, the parasitism level by each parasitoid in the absence of others, here called potential parasitism (Ayalew et al., 2006), was estimated following Dreyer and Baumgärtner (1995).

### Statistical analysis

The role biotic and abiotic factors on the abundance of *P. xylostella* were assessed using stepwise multiple linear regression analysis (Draper and Smith, 1981). The biotic factors evaluated included crop subspecies (dummy variable  $C=0$  for broccoli and 1 for cauliflower), plant age (days after transplantation) and the parasitism by three species, while the abiotic factors assessed were minimum and maximum temperatures, rainfall, relative humidity and planting season (dummy variable  $E=0$  for spring and 1 for winter). Multiple linear regression analysis was conducted considering only the period of pest occurrence in the field. This analysis allows the ranking of the biotic and abiotic variables based on their explanatory importance. The contribution of each variable

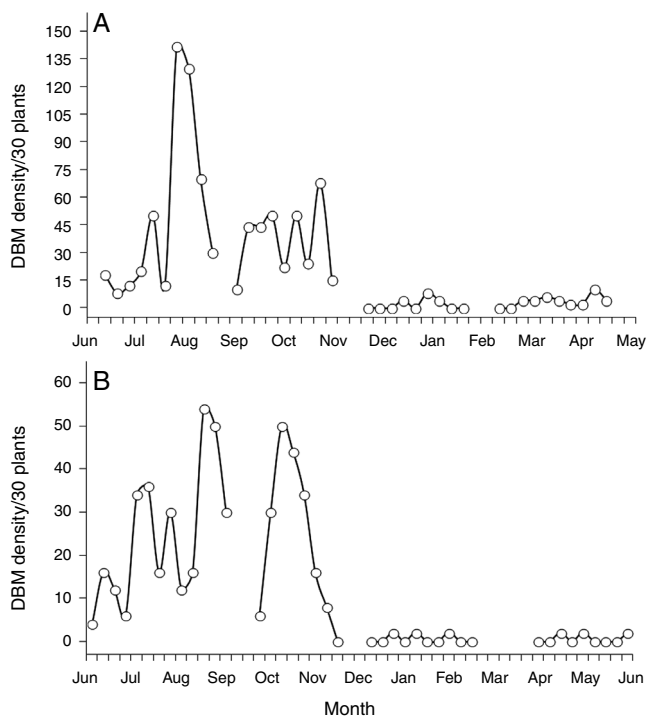


Fig. 2. Abundance of *Plutella xylostella* on broccoli (A) and cauliflower crops (B) in the county of Colombo, Paraná State, Southern Brazil.

was determined by the coefficient of determination ( $r^2$ ) and the  $p$  value. In the stepwise multiple regression the abundance of *P. xylostella* was selected as the dependent variable and the biotic and abiotic factors as independent variables.  $F$ -values higher than 1.0 were used as a criterion for a variable to enter in the final model. Chi-square test was used to compare the frequency of occurrence of larval parasitoids ( $p < 0.05$ ).

## Results

### Population dynamics of *P. xylostella*

Seasonal abundance of the diamondback moth on broccoli and cauliflower is shown in Fig. 2A and B, respectively. Despite the abundant and continuous availability of food sources throughout the year, *P. xylostella* showed a clear seasonality. Its occurrence was restricted to June–November, coinciding with the periods of lower temperature and rainfall (Fig. 1). One peak of abundance was recorded in August on broccoli, while on cauliflower two peaks were recorded, one in September and another in October. Considering both winter and spring, a mean of 1.4 and 0.8 larvae per plant were recorded on broccoli and cauliflower, respectively. The mean number of larvae sampled in winter was slightly lower than in spring on both broccoli (winter:  $49.2 \pm 15.7$ ; spring:  $36.3 \pm 6.4$  immatures/30 plants) and cauliflower (winter:  $24.3 \pm 4.4$ ; spring:  $23.5 \pm 6.6$  immatures/30 plants).

### Larval parasitoids of *P. xylostella*

Four species of larval parasitoids comprising two orders and four families were identified associated with *P. xylostella* (Table 1). The abundance of parasitoids was different on broccoli ( $\chi^2_{(3)} = 71.71$ ,  $p < 0.001$ ) and cauliflower ( $\chi^2_{(3)} = 45.50$ ,  $p < 0.001$ ). *Diadegma leontinae* (Brèthes) was the most abundant parasitoid on broccoli, accounting for 58% of the overall parasitism recorded, followed by *Apanteles piceotrichosus* (Blanchard) with 26% and *Siphona* sp.

Table 1  
Larval parasitoids of *Plutella xylostella* identified at Colombo, Paraná, Brazil.

Order: Family	Species	Frequency (%)	
		Broccoli	Cauliflower
Hymenoptera: Icheumonidae	<i>Diadegma leontinae</i>	58.4a	27.5b
Hymenoptera: Braconidae	<i>Apanteles piceotrichosus</i>	26.0b	47.5a
Hymenoptera: Eulophidae	<i>Oomyzus sokolowskii</i>	1.3c	0.0c
Diptera: Tachinidae	<i>Siphona</i> sp.	14.3b	25.0b

Values followed by the same letter in columns are not statistically different according chi-square test ( $p > 0.05$ ).

Table 2  
Probabilities of *Plutella xylostella* parasitism by its larval parasitoids in the presence (observed parasitism in bold) and in the absence of other parasitoid species (potential parasitism in regular font) in broccoli and cauliflower crops during winter and spring season.

Crop and season	<i>D. leontinae</i>	<i>A. piceotrichosus</i>	<i>Siphona</i> sp.	Total	
Broccoli					
	Winter	<b>0.052</b>	<b>0.085</b>	<b>0.010</b>	<b>0.147</b>
		0.054	0.088	0.010	0.278
Spring	<b>0.169</b>	<b>0.073</b>	<b>0.020</b>	<b>0.262</b>	
		0.181	0.077	0.020	0.278
Cauliflower					
	Winter	<b>0.074</b>	<b>0.080</b>	<b>0.012</b>	<b>0.166</b>
		0.77	0.084	0.012	0.173
Spring	<b>0.021</b>	<b>0.239</b>	<b>0.137</b>	<b>0.397</b>	
		0.021	0.267	0.152	0.440

Table 3  
Regression statistics for abundance of *Plutella xylostella*.

Variable	Slope $\pm$ SE	$t$ value	$p$ value	Cumulative $r^2$
Intercept	1.042 $\pm$ 1.633	0.648	0.528	–
<i>D. leontinae</i>	0.308 $\pm$ 0.111	2.770	0.009	0.384
<i>A. piceotrichosus</i>	0.304 $\pm$ 0.110	2.767	0.009	0.440
<i>Siphona</i> sp.	0.597 $\pm$ 0.162	3.686	<0.001	0.479
Crop subspecies	–0.535 $\pm$ 0.219	–2.442	0.020	0.568
Planting season	0.626 $\pm$ 0.269	2.324	0.027	0.602
Relative humidity	0.024 $\pm$ 0.017	1.458	0.155	0.642
Minimum temperature	–0.078 $\pm$ 0.055	–1.413	0.167	0.664

Meigen with 14%. The most abundant parasitoid on cauliflower was *A. piceotrichosus*, accounting for 47% of the overall parasitism, followed by *D. leontinae* and *Siphona* sp., with 27% and 25% of the total parasitism, respectively (Table 1). The gregarious endoparasitoid *Oomyzus sokolowskii* (Kurdjumov) was rarely found.

### Observed and potential parasitism

Slight differences were recorded between observed and potential parasitism (Table 2). Highest percent increment in parasitism was estimated for *A. piceotrichosus* (7.3%), followed by *D. leontinae* (5.8%) and *Siphona* sp. (5.0%).

### Factors influencing abundance of *P. xylostella*

Multiple regression analysis showed that parasitism by *D. leontinae*, *A. piceotrichosus* and *Siphona* sp., crop and planting season affected the abundance of *P. xylostella*. Together these variables explained 60.2% of the variation in the pest abundance (Table 3). The most important factors were the parasitism by *D. leontinae* (partial  $r^2 = 0.38$ ) and *A. piceotrichosus* (partial  $r^2 = 0.06$ ) and crop subspecies (partial  $r^2 = 0.05$ ) (Table 3).

According to the multiple regression analysis, parasitism by *D. leontinae*, *A. piceotrichosus* and *Siphona* sp. was positively related to host abundance, indicating a density–dependent relationship. Neither temperature, nor rainfall and relative humidity influenced the

abundance of *P. xylostella*. Among the abiotic factors, only planting season affected the abundance the diamondback moth. The negative slope of crop and the positive slope of planting season indicate higher abundance of *P. xylostella* on broccoli during winter.

## Discussion

Seasonal cycles in insect communities are often attributed to variations in quality and availability of resources according to climatic conditions (Wolda, 1988; Pinheiro et al., 2002). If climatic conditions are not a limiting factor, and environmental resources are available throughout the year, it is expected that a highly flexible species like *P. xylostella* would be able to use continuously these resources. Neither temperature (Marchioro and Foerster, 2011), nor availability of food resources are factors that prevent the occurrence of *P. xylostella* throughout the year in Southern Brazil. Nevertheless, our study demonstrates a clear seasonal variation in the abundance of the insect pest.

A similar seasonal pattern in the population dynamics of *P. xylostella* was recorded in Southeastern and Midwestern Brazil, where the pest occurred between July and December (Guilloux et al., 2003; Campos et al., 2006). In southeastern Brazil, the influx of migrants was suggested as the possible cause of population increase in the beginning of July (Campos et al., 2006). The same population trend recorded in different regions of Brazil suggests that the migration pattern identified by Campos et al. (2006) may be an isolated sample of a larger event. Several studies have demonstrated the migratory capacity of *P. xylostella*, in some cases for distances longer than 3000 km using air currents (Talekar and Shelton, 1993; Chapman et al., 2002). In this context, it is reasonable to suppose that migration is the possible cause of seasonality in the neotropical populations of *P. xylostella* (Campos et al., 2006).

If influx of *P. xylostella* adults is the cause of population increase, one can question the reasons of population decline in the beginning of December. Several mortality factors have been proposed as possible causes of population decline, such as the reduction of host plant quality, higher temperature, migration, increase in rainfall and suppressive effect of parasitoids (Campos et al., 2006). In this context, the identification of key mortality factors related to variation in the abundance of *P. xylostella* is important not only for management purposes, but also to elucidate the factors that may be related to population collapse in the beginning of December.

Parasitism was the major factor influencing the abundance of *P. xylostella*. Among the larval parasitoids identified in the study area, *D. leontinae*, *A. piceotrichosus* and *O. sokolowskii* were previously recorded in other regions of Brazil (Ferronato and Becker, 1984; Guilloux et al., 2003; Silva-Torres et al., 2010). However, as far as we know, this is the first report of the tachinid *Siphona* sp. parasitizing *P. xylostella*. Similarly to found in our study, *D. leontinae* and *A. piceotrichosus* were previously recorded as the most abundant parasitoids of *P. xylostella* in Midwestern Brazil (Guilloux et al., 2003). Although *O. sokolowskii* was rarely found in the study area, it was the most abundant larval parasitoid of *P. xylostella* in surveys carried out in the county of Porto Alegre, Southern Brazil (Ferronato and Becker, 1984). Differences in the abundance of *O. sokolowskii* among regions with similar climatic conditions are probably explained by local factors influencing the parasitoid establishment. It is known that factors such as temperature (Wang et al., 1999), interspecific competition (Talekar and Hu, 1996; Liu et al., 2000; Shi and Liu, 2003) and management practices (Furlong et al., 2004; Ayalew and Ogol, 2006) may influence the parasitism by *O. sokolowskii*.

Although the diversity of larval parasitoids found in different regions of Southern Brazil is similar, it is lower when compared to those found in Midwestern Brazil (Guilloux et al., 2003) and other regions of the world (Goodwin, 1979; Kfir, 1997; Liu et al., 2000; Mosiane et al., 2003; Ayalew and Ogol, 2006). Interestingly, greater

diversity of larval parasitoids does not necessarily mean higher rates of parasitism. In Midwest Brazil, seven larval parasitoids and six species of hyperparasitoids were identified associated with *P. xylostella*, but the average parasitism rate (23%) was similar to the one recorded in our study (Guilloux et al., 2003). Moreover, under higher diversity of parasitoids, few species usually are responsible for more than 90% of larval parasitism (Mosiane et al., 2003; Ayalew and Ogol, 2006; Guilloux et al., 2003), with the remaining species showing lower parasitism rates.

Parasitism was consistently higher in the absence of other parasitoid species, but the difference between observed and potential parasitism was quite subtle. Similar results were obtained in a study investigating the population dynamics of the diamondback moth and its larval parasitoids in Ethiopia (Ayalew et al., 2006). These findings indicate that competition among parasitoids is limited.

Multiple regression analysis showed that parasitism by *D. leontinae*, *A. piceotrichosus* and *Siphona* sp. was positively related to host abundance, indicating the existence of a density-dependent relationship. This is important because density-dependent relationship between parasitoid and its host generally results in a more efficient regulation of the host population. Highly positive correlation like the observed in our study indicates parasitoid specificity and a rapid numerical response to variations in host density (Jervis and Kidd, 1996), two desired attributes for biocontrol agents.

The key role that the larval parasitoids complex showed as a mortality factor of *P. xylostella* in southern Brazil demonstrate the feasibility of biological conservation practices to improve parasitoid effectiveness. Several attributes of agroecosystems may affect parasitoids' abundance, some improving and others reducing their effectiveness, and this information can be used for the development of control strategies. For instance, larval parasitoids of the genus *Apanteles* Förster and *Diadegma* are positively affected by intercropping (Asman et al., 2001; Ayalew and Ogol, 2006). Also, studies have demonstrated the importance of natural enemies' interaction with landscape, showing that both diversity and abundance of parasitoids can be linked with landscape complexity (Thies and Tschamtkke, 1999; Tschamtkke et al., 2007). Indeed, there are several studies demonstrating that adjacent vegetation near to crops tend to improve parasitoid effectiveness through supply of food resources and microhabitats that serve as refuge for parasitoids (Griffiths et al., 2008; Wade et al., 2008; Thomson and Hoffmann, 2009). On the other hand, it is well known that pesticides used against *P. xylostella* are a major cause of reduction in larval parasitoid populations (Talekar and Shelton, 1993), and therefore should be used with caution in order to avoid reductions in parasitoids population.

The meteorological factors evaluated did not affect the abundance of *P. xylostella* in the study area. This is unexpected considering that previous studies have reported rainfall as one of the most important abiotic factors causing mortality in eggs and small larvae of *P. xylostella* (Harcourt, 1963; Annamalai et al., 1988; Kobori and Amano, 2003), and often differences in the abundance of *P. xylostella* among regions are explained as a result of variations in rainfall (Martínez-Castillo et al., 2002; Ayalew et al., 2006). On the other hand, other studies have shown that rainfall did not affect the population dynamics of *P. xylostella*, and these findings were attributed to host plant morphology conferring less exposure of small larvae and pupae to rain (Muckenfuss et al., 1992). Furthermore, both rainfall duration and intensity are important factors causing egg and larval mortality (Kobori and Amano, 2003). In light of these findings, it is possible that precipitation recorded during the period of pest occurrence in the field may not have been intense enough to cause significant mortality on the immatures.

Temperature is another important abiotic factor known to influence the development time and survival of insects, including *P. xylostella* (Liu et al., 2002; Golizadeh et al., 2007; Marchioro

and Foerster, 2011). Its influence on insect abundance is easily noticed when temperature extrapolates lower and upper development thresholds causing insect mortality; and/or when higher temperatures accelerate development resulting in an increase in the number of generations of the species. The latter situation can be easily detected when comparing the abundance of an insect species over time in regions where temperature varies widely throughout the year. Although this climate condition is found in the study area, we probably did not detect the influence of temperature on *P. xylostella* abundance because the analysis was performed considering the period that *P. xylostella* occurred in the field, when large variations in temperature were not recorded. Also, in this period both minimum and maximum temperatures recorded rarely extrapolated the lower development threshold ( $\cong 6^\circ\text{C}$ ), and never reached the upper threshold ( $\cong 37^\circ\text{C}$ ) (Marchioro and Foerster, 2011).

Although this study has shown that temperature and rainfall are less important that biotic interaction in the population regulation of *P. xylostella*, these parameters may indirectly affect pest abundance. Both temperature and rainfall may affect the abundance of the larval parasitoids associated with *P. xylostella*, reducing their ability to regulate pest population. This is not unexpected considering that the response to abiotic factors can be sensibly different between parasitoids and their hosts (Hence et al., 2007; de Sassi and Tylianakis, 2012). In fact, under extreme conditions, such as climate change, these divergences may lead to a disruption of temporal and/or geographical synchronization, increasing the risks of pest outbreak (Hence et al., 2007).

In conclusion, our study investigated the factors that affect the population dynamics of *P. xylostella* in the field. Despite the availability of food resources throughout the year, the occurrence of *P. xylostella* in the study area was restricted between June and November. Four species of larval parasitoids were found associated with *P. xylostella*, and three of these parasitoids play a major role on pest population regulation. In addition to parasitism, crop subspecies was another biotic factor that influenced pest population dynamics. Among the abiotic factors evaluated, only plant season influenced pest abundance. This study provides a valuable contribution to the knowledge about the mechanisms underlying the population regulation of the diamondback moth. These findings indicate that conservation practices may be adopted to improve parasitoid effectiveness and reduce pest population.

## Conflicts of interest

The authors declare no conflicts of interest.

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## References

Andrewartha, H.G., Birch, L.C., 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.

- Annamalai, S., Itô, Y., Saito, T., 1988. Population fluctuations of the diamondback moth, *Plutella xylostella* (L.) on cabbages in *Bacillus thuringiensis* sprayed and non sprayed plots and factors affecting within-generation survival of immatures. *Res. Popul. Ecol.* 30, 329–342.
- Asman, K., Råmert, B., Ekbom, B., 2001. Effect of intercropping on oviposition and emigration behavior of the leek moth (Lepidoptera, Acrolepiidae) and the diamondback moth (Lepidoptera, Plutellidae). *Environ. Entomol.* 30, 288–294.
- Ayalew, G., Ogol, C.K.P.O., 2006. Occurrence of the diamondback moth (*Plutella xylostella* L.) and its parasitoids in Ethiopia: influence of geographical region and agronomic traits. *J. Appl. Entomol.* 130, 343–348.
- Ayalew, G., Baumgärtner, J., Ogol, K.P.O.C., Löhr, B., 2006. Analysis of population dynamics of diamondback moth, (*Plutella xylostella* (Lepidoptera: Plutellidae)) at two sites in central Ethiopia, with particular reference to parasitism. *Biocontrol Sci. Technol.* 16, 607–618.
- Baskauf, S.J., 2003. Factors influencing population dynamics of the southwestern corn borer (Lepidoptera: Crambidae): a reassessment. *Environ. Entomol.* 32, 915–928.
- Campos, W.G., Schoereder, L.H., DeSouza, O.F., 2006. Seasonality in neotropical populations of *Plutella xylostella* (Lepidoptera): resource availability and migration. *Popul. Ecol.* 48, 151–158.
- Castelo-Branco, M., França, F.H., Medeiros, M.A., Leal, J.G.T., 2001. Uso de inseticidas para o controle da traça-do-tomateiro e traça-das-crucíferas: um estudo de caso. *Hortic. Bras.* 19, 60–63.
- Chapman, J.W., Reynolds, D.R., Smith, A.D., Riley, J.R., Pedgley, D.E., Woiwod, I.P., 2002. High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: a study using radar aerial netting and ground trapping. *Ecol. Entomol.* 27, 641–650.
- de Sassi, C., Tylianakis, J.M., 2012. Climate change disproportionately increases herbivore over plant or parasitoid biomass. *PLoS ONE* 7, e40557.
- Draper, N.R., Smith, H., 1981. *Applied Regression Analysis*. John Wiley and Sons, New Delhi.
- Dreyer, H., Baumgärtner, J., 1995. The influence of post-flowering pests on cowpea seed yield with particular reference to damage by Heteroptera in southern Benin. *Agric. Ecosyst. Environ.* 53, 137–149.
- Ferronato, E.M., Becker, M., 1984. Abundância e complexo de parasitoides de *Plutella xylostella* (Linnaeus, 1758) (Lepidoptera: Plutellidae) em *Brassica oleracea* L. var. *acephala* D.C. *An. Soc. Entomol. Bras.* 13, 261–278.
- Furlong, M.J., Shi, Z.H., Liu, Y.Q., Guo, S.J., Lu, Y.B., Liu, S.S., Zalucki, M.P., 2004. Experimental analysis of the influence of pest management practice on the efficacy of an endemic arthropod natural enemy complex of the diamondback moth. *J. Econ. Entomol.* 97, 1814–1827.
- Golizadeh, A., Kamali, K., Fathipour, Y., Abbasipour, H., 2007. Temperature-dependent development of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) on two brassicaceous host plants. *Insect Sci.* 14, 309–316.
- Goodwin, S., 1979. Changes in numbers in the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera) in Victoria. *Aust. J. Zool.* 27, 981–989.
- Griffiths, G.J.K., Holland, J.M., Bailey, A., Thomas, M.B., 2008. Efficacy and economics of shelter habitats for conservation biological control. *Biol. Control* 45, 200–209.
- Guilloux, T., Monnerat, R., Castelo-Branco, M., Kirk, A., Bordat, D., 2003. Population dynamics of *Plutella xylostella* (Lep., Yponomeutidae) and its parasitoids in the region of Brasília. *J. Appl. Entomol.* 127, 288–292.
- Hence, T., Baaren, J.V., Vernon, P., Boivin, G., 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. *Ann. Rev. Entomol.* 52, 107–126.
- Harcourt, D.G., 1963. Major mortality factors in the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). *Mem. Entomol. Soc. Can.* 95, 55–66.
- Jervis, M., Kidd, N., 1996. Population dynamics. In: Jervis, M., Kidd, N. (Eds.), *Insect Natural Enemies. Practical Approaches to their Study and Evaluation*. Chapman and Hall, London, pp. 232–292.
- Kfir, R., 1997. Parasitoids of *Plutella xylostella* (Lep. Plutellidae) in South Africa: an annotated list. *Entomophaga* 42, 517–523.
- Kobori, Y., Amano, H., 2003. Effect of rainfall on a population of the diamondback moth, *Plutella xylostella* (Lepidoptera, Plutellidae). *Appl. Entomol. Zool.* 38, 249–253.
- Liu, S.S., Wang, X.G., Guo, S.J., He, H.J., Shi, Z.H., 2000. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. *Bull. Entomol. Res.* 90, 221–231.
- Liu, S.S., Chen, F.Z., Zalucki, M.P., 2002. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. *Environ. Entomol.* 31, 221–231.
- Marchioro, C.A., Foerster, L.A., 2011. Development and survival of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) as a function of temperature: effects on the number of generations in tropical and subtropical regions. *Neotrop. Entomol.* 40, 533–541.
- Martínez-Castillo, M., Leyva, J.L., Cibrián-Tovar, J., Bujanos Muniz, R., 2002. Parasitoid diversity and impact on populations of the diamondback moth *Plutella xylostella* (L.) on *Brassica* crops in central México. *BioControl* 47, 23–31.
- Mohan, M., Gujar, G.T., 2003. Local variation in susceptibility of the diamondback moth, *Plutella xylostella* (Linnaeus) to insecticides and detoxification enzymes. *Crop Prot.* 22, 495–504.
- Mosiane, S.M., Kfir, R., Villet, M.H., 2003. Seasonal phenology of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and its parasitoids on canola, *Brassica napus* (L.), in Gauteng province, South Africa. *Afr. Entomol.* 11, 277–285.

- Muckenfuss, A.E., Shepard, B.M., Ferrer, E.R., 1992. Natural mortality of diamondback moth in Coastal South Carolina. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifers Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Taiwan, pp. 27–36.
- Pinheiro, F., Diniz, I.R., Coelho, D., Bandeira, P.S., 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecol.* 27, 132–136.
- Sarfraz, M., Keddie, A.B., Dossall, L.M., 2005. Biological control of the diamondback moth, *Plutella xylostella*: a review. *Biocontrol Sci. Technol.* 15, 763–789.
- Sarfraz, M., Dossall, L.M., Keddie, B.A., 2006. Diamondback moth–host plant interactions: implications for pest management. *Crop Prot.* 25, 625–639.
- Shi, Z.H., Liu, S.S., 2003. Interspecific competition between *Cotesia plutellae* Kurdjumov (Hymenoptera: Braconidae) and *Oomyzus sokolowskii* Kurdjumov (Hymenoptera: Eulophidae), two major parasitoids of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). *Chin. J. Appl. Ecol.* 14, 949–954.
- Silva-Torres, C.S.A., Pontes, V.A.F., Torres, J.B., Barros, R., 2010. New records of natural enemies of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) in Pernambuco, Brazil. *Neotrop. Entomol.* 39, 835–838.
- Talekar, N.S., Hu, W.J., 1996. Characteristics of parasitism of *Plutella xylostella* (Lep., Plutellidae) by *Oomyzus sokolowskii* (Hym., Eulophidae). *Entomophaga* 41, 45–52.
- Talekar, N.S., Shelton, A.M., 1993. Biology, ecology, and management of the diamondback moth. *Annu. Rev. Entomol.* 38, 275–301.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.N., van Nouthuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309.
- Thies, C., Tscharntke, T., 1999. Landscape structure and biological control in agroecosystems. *Science* 285, 893–895.
- Thomson, L.J., Hoffmann, A.A., 2009. Vegetation increases the abundance of natural enemies in vineyards. *Biol. Control* 49, 259–269.
- Wade, M.R., Zalucki, M.P., Wratten, S.D., Robinson, K.A., 2008. Conservation biological control of arthropods using artificial sprays: current status and future challenges. *Biol. Control* 45, 185–199.
- Wallner, W.E., 1987. Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annu. Rev. Entomol.* 32, 317–340.
- Wang, X., Liu, S., Guo, S., Lin, W., 1999. Effects of host stages and temperature on population parameters of *Oomyzus sokolowskii*, a larval-pupal parasitoid of *Plutella xylostella*. *Biocontrol* 44, 391–402.
- Wolda, H., 1988. Insect seasonality: why? *Ann. Rev. Ecol. Syst.* 19, 1–18.
- Zago, H.B., Siqueira, H.A.A., Pereira, E.J.G., Picanço, M.C., Barros, R., 2013. Resistance and behavioural response of *Plutella xylostella* (Lepidoptera: Plutellidae) populations to *Bacillus thuringiensis* formulations. *Pest Manag. Sci.* 70, 488–495.
- Zalucki, M.P., Shabbir, A., Silva, R., Adamson, D., Shu-Sheng, L., Furlong, M.J., 2012. Estimating the economic cost of one of the world's major insect pests, *Plutella xylostella* (Lepidoptera: Plutellidae): just how long is a piece of string? *J. Econ. Entomol.* 105, 1115–1129.