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ORIGINAL RESEARCH ARTICLE

Seasonality but not photoperiodism affects pesticide toxicity to the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae)

Zhenguo Yang[1] · Zinan Wang[3,4] · Jing Ni[1] · Aisi Da[1] · Daoyan Xie[1] · Henry Chung[3,4] · Yanjie Luo[1,2]

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Abstract

Understanding how endogenous and exogenous factors such as annual seasonal rhythm and photoperiodism affect pesticide toxicity is important to designing integrated pest management strategies. The two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), a worldwide phytophagous pest species distributed across different zones with contrasting environmental conditions, is a good model for exploring how photoperiodism and seasonality affect their responses against pesticides. In this study, we conducted a laboratory experiment from March 2017 to November 2018 in which *T. urticae* populations were reared under three photoperiod regimes (10L:14D, 12L:12D, and 18L:6D) in environmentally controlled incubators, and assessed the toxicity of the two pesticides, diafenthiuron and propargite, on *T. urticae* every month. To determine potential mechanisms underlying the changes in pesticide toxicity, we measured body size and total GSTs activity of *T. urticae* along with the toxicity measurements in 2018. Our results showed that the photoperiod regime did not significantly affect the toxicity of each of the two pesticides to *T. urticae*. However, unlike photoperiodism, the toxicity of both pesticides was found to be season-dependent, being higher during spring and summer and lower during the winter. This suggests that seasonality could induce in those *T. urticae* populations, an endogenous mechanism that influenced their susceptibility to the tested pesticides. Pearson's correlation analyses showed that only the body size had a weak negative correlation with pesticide toxicity, thereby suggesting that pesticides could have higher toxicity on smaller *T. urticae*. Taken together, our study showed that seasonality can affect pesticide toxicity, thereby providing practical insights into the management strategies against *T. urticae*.

Keywords Body size · Glutathione S-transferases (GSTs) · Propargite · Diafenthiuron

Introduction

Understanding factors underlying toxicity of chemical application to pest species under different rhythmicity such as photoperiodism and seasonality can lead to better pest management strategies (Gottlieb 2019). Biological rhythmicity is one of the most important systems that arthropods use to coordinate their development and physiology (Bradshaw and Holzapfel 2010; Khyati and Seth 2017). Together with the daily or seasonal alterations, changes in different abiotic factors such as photoperiod, temperature, and humidity could shape the adaptations of arthropods and lead to changes in their behavior and physiology (Goto 2016). Such cascading effects could indirectly influence the efficacy of pest control measures such as the use of pesticides in the field (Khyati and Seth 2017). For example, both the temperature and photoperiod have been found to induce diapause signals to prolong the nymphal development

Zhenguo Yang and Zinan Wang contributed equally for this work.

✉ Yanjie Luo
yanjieluo@126.com

1 Sericulture and Apiculture Research Institute, Yunnan Academy of Agricultural Sciences, Yunnan, China

2 Key Laboratory of Green Prevention and Control of Agricultural Transboundary Pests of Yunnan Province, Yunnan Academy of Agricultural Sciences, Yunnan, China

3 Department of Entomology, Michigan State University, East Lansing, MI, USA

4 Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI, USA

of two spider mite species, *Tetranychus kanzawai* Kishida and *T. urticae* Koch (Acari: Tetranychidae) (Suzuki and Takeda 2009; Shah et al. 2011), which further alters their capability of metabolizing multiple toxicants and pesticides (Hooven et al. 2009). Several studies reported that some insects and mites display a circadian rhythm of susceptibility to a toxic agent. For example, the toxicity of pesticides such as dimethyl 2, 2-dichlorovinyl phosphate (DDVP) (Polcik et al. 1964), dicofol (Fisher 1967), methyl parathion (Cole and Adkisson 1964), and permethrin (Beaver et al. 2010) has been reported to correlate with the circadian rhythm in diverse pest species. This suggests that circadian rhythm such as photoperiodism is an important factor to be considered in pest management.

Defined as the annually cyclic changing pattern (Wolda 1988; Altizer et al. 2006), seasonality is another rhythmic factor regulating arthropods' physiology which can affect their sensitivity to pesticides. However, this is rarely investigated under laboratory conditions where the majority of abiotic factors are maintained at a constant level. The understanding of how seasonality affects pesticide toxicity on arthropods mainly comes from measures on field-collected organisms across the season, e.g., the seasonal susceptibility of honeybee workers (*Apis mellifera* L.) to several commonly used pesticides such as organophosphate, benzoylphenyl urea, carbamate, oxadiazine (Piechowicz et al. 2013) and pyrethroid (Piechowicz et al. 2016). The measurements in these studies usually include the physiological changes induced by seasonally changing abiotic factors. Consequently, it is not clear whether seasonality could induce endogenous factors to regulate arthropods' physiological adaptations and whether such adaptations affect pesticide toxicity on these arthropods.

One way to investigate the endogenous effects of seasonality is to control abiotic factors such as temperature, humidity, and photoperiod in the laboratory when monitoring the physiological changes in arthropods and in their sensitivity to pesticide toxicity. Integration of the rhythmicity of pesticide toxicity into pest management has received much theoretical attention but this integration is less applied to pest controls in practical (Miyazaki et al. 2007; Hooven et al. 2009; Gottlieb 2019). This could be due to difficulties in applying and controlling biological rhythms in the field. Few applications were made only with Lepidopteran storage pests, in which the timing and dosage of insecticide applications were based on circadian rhythm to minimize the potential development of insecticide resistance (Singh and Das 2016).

The two-spotted spider mite, *T. urticae*, is a worldwide phytophagous pest known to cause significant yield losses in several crops, including fruits, cotton, vegetables, and ornamentals (Grbic et al. 2011; Van Leeuwen et al. 2015). Due to its wide host range, small body size, short developmental time, and high fecundity, it has become one of the most serious pests to manage (Sparks and Nauen 2015). Chemical control has become the foundation of tactics adopted by farmers to manage *T. urticae*, with propargite and diafenthiuron among the most effective and used pesticides in the field (Sparks and Nauen 2015). A previous study conducted in summer showed no differences in the toxicity of the two pesticides (propargite and diafenthiruon) among three *T. urticae* populations reared under different photoperiod regimes (Yang et al. 2020). However, it is still unknown whether the different photoperiod regimes across the seasons could induce physiological responses of *T. urticae* to affect pesticide toxicity.

In this study, we investigated the effects of photoperiod and season on the toxicity of two commonly used pesticides, diafenthiruon, and propargite, on *T. urticae* under laboratory conditions. We hypothesized that pesticide toxicity on *T. urticae* could have an intrinsic rhythm controlled by both photoperiodism and seasonality. We also included the body size of mites and glutathione S-transferases (GSTs) quantification inside the mites along with the toxicity assays to explore whether these factors correlate with the changing pesticide toxicity. Body size can be treated as a proxy of fitness (Jakob et al. 1996; Danielson-Francois et al. 2002). The glutathione S-transferases (GSTs) is a super-family of the detoxification enzyme and the toxicity of different pesticides appeared to be under circadian control of this enzyme in several arthropods (Krishnan et al. 2008; Yang et al. 2010; Pohl et al. 2013; Pavlidi et al. 2018). Our previous study also showed the GSTs to be involved in the propargite-resistance of *T. cinnabarinus*, another spider mite speices (Luo et al. 2014). Results from this study can provide a new perspective in the development of integrated pest management strategies.

Materials and methods

Mite sources

All experiments in this study were conducted on laboratory populations of *T. urticae* that were initiated from specimens collected from a rose tree plantation at Kunming, China (25.15°N, 102.76°E) in 2010. The populations were maintained on kidney bean leaves (*Phaseolus vulgaris* L.) in the temperate-controlled incubator (GXZ-250A, Ningbo Jiangnan Instrument Co., Ltd., Zhejiang, China) at 25 ± 0.5 °C, and a relative humidity of 75 ± 5%. White light-emitting diodes (LEDs) were used with light intensity of 500 – 700 Lx. For this study, three laboratory populations were established in 2015 at three photoperiod regimes including 10L:14D, 12L:12D, and 18L:6D. All other abiotic conditions were kept constant. In our setup, none of the three *T. urticae* populations entered diapause. All assays and measurements were conducted on female adults sampled every month from March 2017 to November 2018. None of the populations reared in the incubators were exposed to any pesticide.

Bioassay

The Potter spray tower bioassay method (Herron et al. 1998) was used to determine the toxicity of propargite (90%, Yisheng Chemical Technology Co., Ltd., Shanghai, China) and diafenthiuron (98%, Qingdao Pesticide Factory, Shandong, China). We sampled *T. urticae* female adults from the three populations under different photoperiod regimes every month, from March to December 2017 and January to November 2018. Both diafenthiuron and propargite were diluted using double-distilled water (ddH$_2$O) to five different concentrations, including 3.125, 6.25, 12.5, 25, and 50 μg/mL for diafenthiuron, and 62.5, 125, 250, 500, and 1000 μg/mL for propargite, while ddH$_2$O was used as the control. Each concentration was replicated three times. For each replicate, 25 – 30 females were transferred to the experimental units consisting of a 50-mm-diameter bean leaf disc placed on wet cotton laying in a 90-mm-diameter Petri dish and maintained for up to 4 h before the commencement of the experiment. A Potter spray tower (Burkard, Uxbridge, UK) that produces a deposit of 9.4 mg/cm^2 of pesticide at 25 ± 0.5 °C was used to spray the leaf discs. The mortality of mites was assessed after 24 h, and appendage movements were used to determine their survival.

Body size measurement

Body size was measured every month, from January to November 2018. Following the method in Danielson-Francois et al. (2002), each month, three replicates of 50 females were randomly selected from the population under each photoperiod regime and fixed on glass slides using double-sided tape. Sampled mites were placed under the light microscope (GL-99TI, Guiguang Instrument Co., Ltd. Guangxi, China). Body length and width were measured using the micromorphology instrument (Dongfang Agricultural Biotechnology Co., Ltd., Beijing, China). The size index (= body length × body width) was used to determine body size and used for statistical analyses (Jakob et al. 1996).

Glutathione S-transferases (GSTs) activity assay

To determine whether GSTs could alter the response of different populations of *T. urticae* to pesticide, and whether it also interferes with the seasonal changes of these responses, three replicates of 50 female *T. urticae* were randomly sampled from each population every month. For each replicate, mites were homogenized in a 1 L ice-cold sodium phosphate buffer (0.04 M, pH 6.5). The homogenate was centrifuged at 10,000 × g for 10 min at 4 °C and the supernatant that contained the GST enzymes was transferred into a clean micro-centrifuge tube. GSTs activity was monitored using a Glutathione S-transferase (GSTs) activity test kit (Micro method kit, Solarbio, Beijing, China) following the manufacturer's instruction. The GSTs activity was measured as the absorbance at 340 nm using a spectrophotometer (xMarkTM Microplate Reader, BIO-RAD, USA) at 15 s intervals during a five-min reaction period at 37 °C.

Statistical analyses

To determine the effects of photoperiodism and seasonality on the toxicity of propargite and diafenthiuron on *T. urticae* populations, mortality rates were subjected to probit analysis (PROC PROBIT, SAS v9.4, SAS Institute Inc., Cary, NC, USA), with the dose, photoperiod, month, and the interaction between photoperiod and month being the fixed terms (= Dose + Photoperiod + Month + Photoperiod × Month). The 50% lethal concentration (LC$_{50}$) with a 95% confidence interval was used to represent the toxicity of each pesticide for each month. The seasonality in changes of the toxicity of both pesticide to *T. urticae* was deduced from the annually changing patterns from 2017 to 2018. Data on body size and GSTs activity were compared among photoperiod regimes or seasons using the linear mixed effects model (PROC MIXED, SAS v9.4, SAS Institute Inc., Cary, NC, USA) and Tukey's HSD method was for post hoc comparison. In addition, the relationship between the body size and the GSTs activity was examined with the aid of the Pearson's correlation model.

Results

Seasonality but not photoperiodism affects the toxicity of diafenthiuron and propargite on *T. urticae*

In 2017, only the Month term showed a significant effect on the toxicity of both diafenthiuron ($\chi_{(8)} = 172.3$, $P < 0.0001$, Fig. 1a) and propargite ($\chi_{(8)} = 81.5$, $P < 0.0001$, Fig. 1b). Similar effects from the Month term were observed in 2018 (diafenthiuron: $\chi_{(10)} = 59.4$, $P < 0.0001$, Fig. 1c, propargite: $\chi_{(10)} = 58.6$, $P < 0.0001$, Fig. 1d). However, none of the Photoperiod and the interaction terms of Month and Photoperiod had any effects on the toxicity of both pesticides (Fig. 1a-d). In 2017, the toxicity of both pesticides had the same levels from March to September, but started decreasing from October, and reached their minimum in December (Fig. 1). For example, the LC$_{50}$ of diafenthiuron on *T. urticae* at Photoperiod 12L:12D increased from 7.5 (95%CI: 5.0 – 11.5) mg/L on March to 17.1 (95%CI: 14.5 – 20.2)

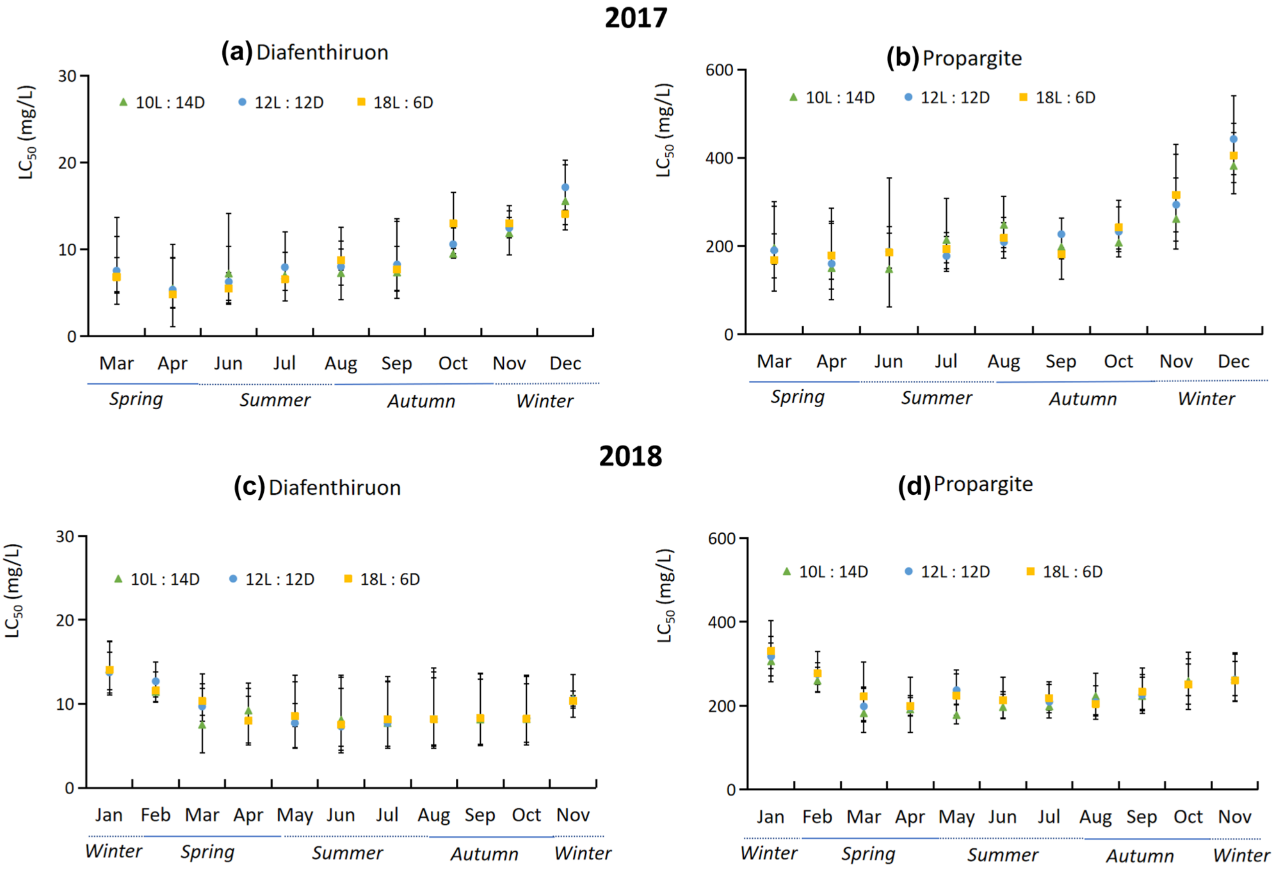

Fig. 1 Susceptibility of *T. urticae* to diafenthiruon and propargite increased in the winter and decreased in the summer. Represented by LC_{50} (mg/L), mortalities of three *T. urticae* populations that reared under three different photoperiod regimes, including 10L:14D, 12L:12D, and 18L:6D were measured every month from March 2017 to November 2018. The error bars represent 95% confidence interval

mg/L on December (Fig. 1a), and the LC_{50} of propargite at Photoperiod 12L:12D increased from 190.1 (95%CI: 159.3 – 227.1) mg/L on March to 442.4 (95% CI: 362.1 – 540.5) mg/L on December in 2017 (Fig. 1b). Similar changing trends across-months were observed in 2018 where mite mortality, at constant temperature and relative humidity, started decreasing from January to March, and remained at similar levels for the following eight months. Results in both years suggested that pesticide toxicity on *T. urticae* were affected by seasonality but not by photoperiodism.

Fig. 2 The body size index of female *T. urticae* reared under three photoperiod regimes. The error bars represent the standard error

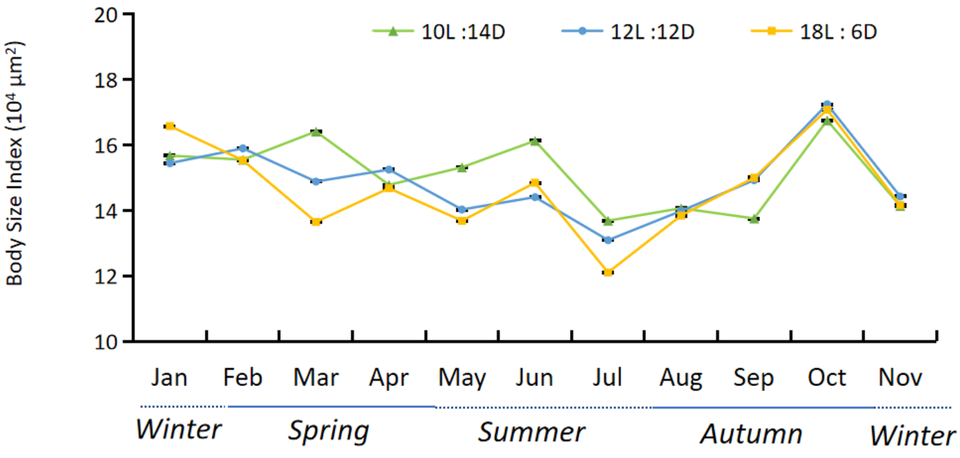

Table 1 Pearson's correlation coefficients with 95% confidence intervals (CI) between body size and pesticide toxicity, and between the total GST activities and pesticide toxicity

Variable	Pesticide	Pearson's *r* (95% CI)		
		10L:14D	12L:12D	18L:6D
Body size	Diafenthiruon	0.04 (-0.04 – 0.12)	0.20 (0.12 – 0.28)	0.25 (0.17 – 0.33)
	Propargite	0.05 (-0.04 – 0.13)	0.24 (0.16 – 0.32)	0.39 (0.32 – 0.46)
GSTs activity	Diafenthiruon	-0.25 (-0.43 – 0.05)	0.12 (-0.09 – 0.32)	0.07 (-0.14 – 0.27)
	Propargite	-0.23 (-0.42 – 0.04)	-0.19 (-0.38 – 0.02)	-0.21 (-0.39 – 0.004)

Body size correlates with susceptibility to pesticide

The body size of *T. urticae* was significantly affected by Month ($F_{(10,\ 1616)} = 67.6$, $P < 0.0001$), Photoperiod ($F_{(2,\ 1616)} = 11.3$, $P < 0.0001$), and the interaction term of Month and Photoperiod ($F_{(2,\ 1616)} = 8.9$, $P < 0.0001$) (Fig. 2). Spider mites reared at 10L:14D had their body size larger than those reared at 12L:12D and 18L:6D (results of post hoc comparisons reported in Table S1). Pearson's correlation analyses showed a weak negative correlation between the body size index and toxicity of both pesticides (Table 1), suggesting smaller *T. urticae* may be the most susceptible to pesticides.

The GSTs activity in *T. urticae* did not correlate with pesticide toxicity

The GSTs activity of *T. urticae* was affected by the Month ($F_{(10,\ 246)} = 171.9$, $P < 0.0001$), Photoperiod ($F_{(2,\ 246)} = 9.9$, $P < 0.0001$), and the interaction term of Month and Photoperiod ($F_{(2,\ 246)} = 8.6$, $P < 0.0001$) (Fig. 3). The spider mites reared at 18L:6D had the highest GSTs activity. However, the GST activities of the mites reared on 12L:12D and 14L:10D were not significantly different (Table S2). There was a peak of the GSTs activity in March 2018 for mites reared at 18L:6D and 12L:12D, and for those reared at 14L:10D, the GSTs activity reached the maximum in both March and June 2018 (Fig. 3 and Table S2). Pearson's correlation analyses showed all coefficients have 95% confidence limits that overlapped with 0 (Table 1), suggesting no correlation between the GSTs activity and toxicity of both pesticides.

Discussion

This study has the merit of investigating the effects of seasonality and photoperiodism on the toxicity of two commonly used pesticides, diafenthiruon, and propargite, against the two-spotted spider mite, *T. urticae* in the laboratory. The results showed that the toxicity of diafenthiruon and propargite on *T. urticae* did not significantly differ among the three photoperiod regimes (10L:14D, 12L:12D, and 18L:6D) but changed consistently across the seasons, even when other abiotic factors including photoperiod, temperature, and relative humidity were controlled. Pesticide toxicity to *T. urticae* increased in spring and summer (i.e., from March to September), and decreased in winter (i.e., from October to February in the next year) under all photoperiod regimes. Even though mite body size and GSTs activity were found to be affected by both photoperiod and seasonality, only a weak correlation was observed between body size and mite mortality caused by pesticide applications. In contrast, changes in GSTs activities were not associated with toxicity for both pesticides.

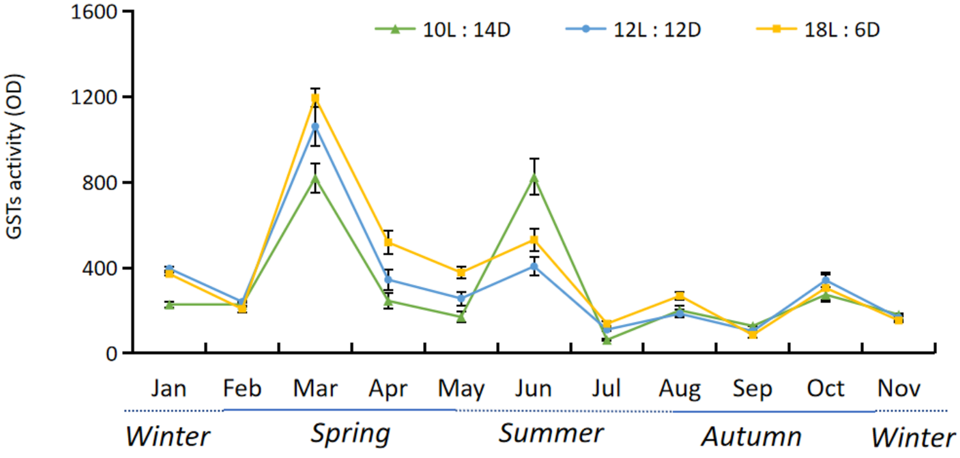

Fig. 3 The total GSTs activity of female *T. urticae* reared under three photoperiod regimes. The error bars represent the standard error

These results are consistent with the findings in our previous study which only examined the susceptibility of *T. urticae* to diafenthiuron and propargite at a single time point in the summer of 2016 (Yang et al. 2020). Photoperiodism, reflecting the daily variation of day length, is acknowledged to play a crucial role in modulating physiological changes in different arthropod species (Goto 2016; Khyati and Seth 2017). The current results are, at least, partially consistent with this, thereby showing that photoperiodism did affect body size and GSTs activities of *T. urticae*. Although we hypothesized that physiological changes such as diapause or induction of seasonal morphs due to different photoperiod regimes could affect pesticide toxicity, such effects have not been observed in our study. One possible explanation to this finding might be that the majority of cases with photoperiod-induced changes in pesticide toxicity are linked with diapause induction or growth inhibition in arthropods (Bouvier et al. 1998; Boivin et al. 2004; Bryon et al. 2013). However, our experimental setup did not allow induction of diapause in the *T. urticae* populations. Physiological changes during diapause could, indeed, increase tolerance to environmental stresses (King and MacRae 2015; Koštál et al. 2017; Anduaga et al. 2018) and toxins (Balmert et al. 2014; Onstad 2014), which may be a mechanism contributing to increased insecticide resistance in arthropods. However, since this study did not aim at testing the effects of diapause, spider mites were maintained outside the range of photoperiods that may induce diapause in their populations (Bryon et al. 2017). It appears, therefore, that without diapause induction, physiological differences in *T. urticae* populations that lived under photoperiod regimes from 6- to 14 h daytime may not alter their susceptibility to diafenthiuron or propargite.

The most remarkale achievement of this study is that, instead of measuring pesticide toxicity at a specific time point, we extended the understanding of the effects of photoperiodism on pesticide toxicity of *T. urticae* over a continuous period of two consecutive years. The results showed that, contrary to the effects of photoperiod, pesticide toxicity to *T. urticae* was reduced in the winter. Seasonality can, indeed, alter different aspects of arthropod physiology which may influence their susceptibility to pesticides. This has been observed in field-collected populations of bees (Piechowicz et al. 2013, 2016), moths (Kranthi et al. 2002), and mosquitoes (Gressel 2011). However, measurements on field-collected arthropods are associated with seasonally changing abiotic factors (Boivin et al. 2003; Cousens and Fournier-Level 2018), which did not allow to determine if seasonality has an endogenous effect on pesticide resistance in this spider mite species. In our study, *T. urticae* were reared in environmentally controlled incubators with a constant level of temperature, relative humidity, and light intensity. In such environment, our results over the two consecutive years showed lower mortalities in winter and higher ones in summer; thereby suggesting that seasonality does affect survival of arthropods when applying pesticides, even in absence of changes in abiotic factors.

In this two-year study, susceptibility of *T. urticae* to diafenthiuron and propargite appeared to be modulated by seasonality but was not affected by photoperiodism. Therefore, under field conditions, except for considering the varying effects of abiotic factors in different seasons, timing and dosage of pesticide applications should be adjusted to coordinate with the endogenously changing susceptibility of the spider mites to pesticide toxicity. Such strategies might hopefully be efficient by preventing the development of pesticide resistance in *T. urticae* populationsduring the following season (Kranthi et al. 2002; Hooven et al. 2009; Khyati and Seth 2017; Helps et al. 2017; Lee et al. 2020). These considerations in pest management strategies can improve the efficacy of chemical controls, thereby, contributing to a safer agricultural environment.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42690-022-00920-5.

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Declarations

Conflicts of interest The authors declare no conflict of interest.

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