



## Sublethal effects of beta-cypermethrin modulate interspecific interactions between specialist and generalist aphid species on soybean

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### ABSTRACT

In agroecosystems, plant-pest interactions are at the basis of complex food webs, which can be affected by both biotic and abiotic factors. In the present study, we evaluated the impact of the insecticide beta-cypermethrin on interspecific interactions between the specialist aphid *Aphis glycines* and the generalist aphid *Aulacorthum solani* on soybean. *Aphis glycines* showed higher fecundity than *A. solani* on soybean and the aphids caused unbalanced reduction in population growth on each other. A sublethal concentration of beta-cypermethrin (LC<sub>5</sub> for *A. glycines*) stimulated the reproduction of *A. glycines* but it did not impact the fecundity of *A. solani*. However, the LC<sub>5</sub> of beta-cypermethrin enhanced the interspecific inhibition of fecundity between the two aphid species. Moreover, the two species showed different spatial distribution on soybean seedlings. *Aphis glycines* mainly aggregated on the stem of soybean plant while *A. solani* colonized soybean leaves. The LC<sub>5</sub> of beta-cypermethrin drove *A. solani* migrating from soybean leaves to stems independently of interspecific competition. *Aphis glycines* facilitated *A. solani* colonization on soybean plant through impacting host susceptibility, and vice versa. Nevertheless, such facilitated colonization-induced susceptibility could be modulated through exposure to the LC<sub>5</sub> of beta-cypermethrin. These findings hinted that the pyrethroid insecticide beta-cypermethrin has the potential to mediate the interspecific competition between specialist and generalist aphids (at the sublethal concentration of LC<sub>5</sub>), and that it could influence aphid population growth and community structure in soybean crops. This knowledge could contribute to rationalize application of insecticides and to optimize Integrated Pest Management in soybean.

### 1. Introduction

Aphids (Hemiptera: Aphididae) specialize in feeding on plant sap, and are among the most destructive pests on soybean *Glycine max* [L.] (Giordanengo et al., 2010; Hohenstein et al., 2019). High aphid population densities are achieved through parthenogenesis reproduction and short generation time. Aphids can pullulate, weakening infested soybean plants (Hullé et al., 2020), and they could be also vectors of various plant viruses, causing drastic quality decline and yield loss (Giordanengo et al., 2010; Nalam et al., 2019; Powell et al., 2006; Ullah et al., 2019c). Soybean aphid, *Aphis glycines* Matsumura, one of the specialist pests on soybean, has become a key pest in the last two decades (Ragsdale et al.,

2011). *Aphis glycines* can reduce soybean yield by up 58% via reduced quantity of soybean pots, smaller seed size, transmission of viruses such as *Soybean mosaic virus*, and *Alfalfa mosaic virus*, and potential facilitation to infestation by soybean cyst nematodes in roots (Hill et al., 2001; Qu et al., 2017; Ragsdale et al., 2007, 2011). Foxglove aphid, *Aulacorthum (Acyrthosiphon) solani* Kaltentbach, native to Europe, is a cosmopolitan pest on a wide range of host plants (approximately 95 different plant species from 25 families), such as pepper, potato, lettuce and soybean (Down et al., 1996; Jandricic et al., 2010, 2014; Sanchez et al., 2007). *Aulacorthum solani* could cause leaf necrosis, deformation of soybean grains, and also defoliation of the entire plants at high density (Sanchez et al., 2007). It is as well a vector for various plant viruses and

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its honeydew benefits the fungal growth on leaves and thereby disturbing plant photosynthesis (Sato et al., 2013, 2014). Taken together these negative effects may induce up to 80% yield loss in soybean (Nagano et al., 2001; Sato et al., 2013).

To date, a variety of sustainable approaches have been used to control the two aphid species, including introduction of natural enemies (Costamagna et al., 2008; Desneux and O'Neil, 2008; Desneux et al., 2006a, 2009) and selection of aphid-resistance soybean strains (Lee et al., 2015; Ragsdale et al., 2011), still, insecticide applications are at the forefront of management methods owing to rapid reduction of aphid populations (Desneux et al., 2007; Koch et al., 2018; Mohammed et al., 2018; Ullah et al., 2019a). Beta-cypermethrin is a pyrethroid insecticide with a broad of insecticide spectrum; it has been widely used to control aphids in soybean fields (Hodgson et al., 2012; Ragsdale et al., 2011; Qu et al., 2017). Although field application rates cause rapid death of pests (i.e. being used at lethal rates as aiming at controlling targeted organisms), insecticides degrade over time in the environment following initial application and lead to residues on plants and in soil (e.g. Desneux et al., 2005); these residues could induce sublethal exposures in organisms which escaped initial treatments or those recolonizing treated areas (Desneux et al., 2006b). Furthermore, various sublethal effects (Desneux et al., 2007; Jam and Saber, 2018; Passos et al., 2018) of beta-cypermethrin involving physiological and behavioral alterations in the individuals that survived post-exposure to sublethal concentrations have been documented on some aphids (Gao et al., 2008; Wang et al., 2014; Zuo et al., 2016). In a previous study, a series of beta-cypermethrin concentrations (including LC<sub>15</sub>, LC<sub>5</sub>, and three other concentrations that are less than LC<sub>5</sub>) were tested for their sublethal effects on the development and reproduction of soybean aphid. We demonstrated that all the five concentrations shortened adult longevity and oviposition period. However, only LC<sub>5</sub> significantly increased the values of key demographic parameters, including net reproduction rate ( $R_0$ ), intrinsic rate of increase ( $r_m$ ), and finite rate of increase ( $\lambda$ ), which may be linked to pest resurgences in the field (Qu et al., 2017). The stimulatory reproduction of soybean aphids exposed to the LC<sub>5</sub> of beta-cypermethrin could be due to the endocrine-disrupting effects of pyrethroids (Brander et al., 2016). They have been demonstrated to act as endocrine disruptors at low concentrations in some vertebrate and invertebrate organisms, and therefore affect their reproduction via interference with the endocrine signaling (e.g. hormones) of organisms (Brander et al., 2016; Hu et al., 2013; Lüring and Scheffer, 2007; Wei and Du, 2004).

Plants are commonly attacked by various pests (simultaneously or successively) with different feeding habits (Bompard et al., 2013; Jaworski et al., 2015; Mohammed et al., 2019; Desneux et al., 2019). Induced defenses mainly depending on phytohormonal signaling pathways including salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) could be activated locally and systemically after insects feeding on the plants and thereby result in the downstream defenses with production of a variety of plant secondary metabolites (Biere and Goverse, 2016; Han et al., 2020; Kersch-Becker and Thaler, 2019; Nalam et al., 2019; War et al., 2018). Such physiological or chemical alterations induced by early arriving pests in plants may impact individual performance, preference and even population dynamics of subsequent pests on the same host plants (Kroes et al., 2016; Mouttet et al., 2011, 2013; Rechner et al., 2017; Stout et al., 2006; Wondafrash et al., 2013). In addition to the interactions between signaling pathways which are specifically induced by different feeding guilds of pests (Caarls et al., 2015; Stout et al., 2006; Wondafrash et al., 2013), resource reallocation, modulation of source-sink relationships in plants, and host specificity of herbivores could as well shape the outcome of such plant-mediated interspecific interactions between diverse herbivores sharing host plants (Biere and Goverse, 2016; Caarls et al., 2015; Hohenstein et al., 2019; Lemoine et al., 2013; Studham and Macintosh, 2013). Moreover, there has been a long-standing hypothesis that specialist and generalist insect herbivores interact with plants in different ways, including regarding plant defenses

(Dussourd and Denno, 1994; Poelman et al., 2008). Therefore, the distinct induction of plant defenses triggered by specialist and generalist aphids may contribute to their interactions on soybean. However, in order to cope with plant defenses, constitutive and induced adaptation (s) have been respectively developed by oligophagous and polyphagous insects (Gatehouse, 2002). Along with the co-evolution during the compatible interactions between aphids and their hosts, plant defenses may be overcome due to aphid adaptation(s), resulting in facilitation to their colonization on the host plant (Giordanengo et al., 2010; Hogenhout and Bos, 2011; Yates and Michel, 2018).

Plants could be exposed to various biotic (herbivores, viruses, bacteria, fungi, and nematodes) and abiotic factors (water, nitrogen, temperature and pesticide) in agroecosystems. Moreover, multiple abiotic factors, e.g. water, nitrogen, temperature, have been reported to impact phytophagous insects performance, plant-mediated interactions between pests, and even performance of natural enemies (Blazhewski et al., 2018; Dong et al., 2018; Han et al., 2014, 2016, 2019; Kutyniok and Müller, 2013). However, the influence of chemical pesticides on the interspecific interactions between two pest species (showing different specialization degree) has been scarcely documented. An hormesis effect of beta-cypermethrin (at LC<sub>5</sub>) on soybean aphid reproduction was reported (Qu et al., 2017). Improving the knowledge on long-term effects of beta-cypermethrin on pest communities in soybean fields (e.g. by studying interspecific interactions between the specialist aphid *A. glycines* and the generalist aphid *A. solani* when exposed to sublethal concentrations) may help to optimize Integrated Pest Management. In the present study, we assessed how sublethal effects of beta-cypermethrin may shape interspecific interactions between the two predominant aphids on soybean. This may contribute to comprehensively understanding soybean-aphid-pesticide interactions and optimizing the management of aphids in soybean.

## 2. Materials and methods

### 2.1. Study insects

The laboratory colonies of *A. glycines* and *A. solani* were established from apterous individuals that were collected from soybean fields in Langfang (Hebei province, China) June 2007 and in Harbin (Heilongjiang province, China) June 2014, respectively. The two colonies were maintained by continuous supply of insecticide-free soybean seedlings in climate chambers, at 25 ± 2 °C, 60 ± 10% RH (relative humidity), L17: D7 photoperiod (Qu et al., 2015, 2017).

### 2.2. Insecticide and acute toxicity assessment

Analytical grade beta-cypermethrin (95%) was purchased from Jiangsu Pesticide Research Institute Co., Ltd (China) and a 2000 mg/L stock solution was obtained with acetone solvent. Both insect-dipping (NY/T 1154.6–2008) and leaf-dipping methods (NY/T 1154.14–2008) were applied in bioassays to evaluate the toxicity of beta-cypermethrin on *A. glycines* and *A. solani* depending on the Agricultural Industry Standard of the People's Republic of China. Two concentration gradients of beta-cypermethrin (obtained from pretests as well as our previous study) from the stock solution diluted by 0.005% (v/v) Triton X-100 (a non-ionic surfactant) were used in the bioassays on *A. glycines* (1, 10, 25, 50 and 100 µg/L) and *A. solani* (10, 100, 250, 500 and 1000 µg/L), respectively (Qu et al., 2017). Leaf discs (20 mm diameter) from insecticide-free soybean leaves and the 3rd instar apterous nymphs were dipped into the corresponding concentrations of beta-cypermethrin solution for 10 s, and then placed in shadow to air dry for 1 h. One leaf disc and twenty aphids per replicate exposed to the same concentration of beta-cypermethrin were transferred into one well of a 12-well tissue-culture plate which contained 2% agar on the bottom and then covered with a filter paper strip (Hangzhou, China). Control solution for *A. glycines* and *A. solani* contained 0.005% (v/v) Triton X-100 (a

**Table 1**

List of treatments used to assess the impact of the sublethal concentration of beta-cypermethrin and interspecific interaction on aphids on soybean seedlings (using a 2 by 2 factorial experimental design: [i] with and without 1st attacker, and [ii] with and without Beta-cypermethrin).

Treatment	The 1st attacker	Beta-cypermethrin	The 2nd attacker
A1	No	No	<i>A. solani</i>
A2	No	Yes	<i>A. solani</i>
A3	<i>A. glycines</i>	No	<i>A. solani</i>
A4	<i>A. glycines</i>	Yes	<i>A. solani</i>
B1	No	No	<i>A. glycines</i>
B2	No	Yes	<i>A. glycines</i>
B3	<i>A. solani</i>	No	<i>A. glycines</i>
B4	<i>A. solani</i>	Yes	<i>A. glycines</i>

Both soybean seedlings and the 1st attackers were treated by the LC<sub>5</sub> of beta-cypermethrin in this study.

non-ionic surfactant) and 0.005% or 0.05% acetone, respectively, which was equal to the concentration of acetone in the highest treatment solution. There were four replicates for each concentration of beta-cypermethrin and control and the mortality of aphids was assessed after 24 h exposed to each solution. Aphids were presumed dead when there was no reflex movement, i.e. no leg moved when they were touched with a fine brush (Moores et al., 1996). All the experimental setups were maintained in the climate chambers as the same condition described above. The concentration-mortality regression equation (Abbott, 1925) and LC<sub>5</sub>, LC<sub>50</sub>, LC<sub>90</sub> values of beta-cypermethrin on *A. glycines* and *A. solani*, were calculated for the further experiments.

### 2.3. Sublethal concentration assessment

The sublethal concentration of beta-cypermethrin to be tested was selected according to the definition provided by Desneux et al. (2007) who defined sublethal concentrations as those not inducing statistically significant mortality when compared to a control group. We selected the LC<sub>5</sub> as sublethal concentration following the same paradigm than previous studies which assessed sublethal effects of pesticides on arthropods (e.g. Qu et al., 2015, 2017). The insecticide exposure was carried out using insect-dipping and leaf-dipping methods as described above (section *Insecticide and acute toxicity assessment*) and the sublethal concentration of beta-cypermethrin tested was selected as 7 µg/L (the LC<sub>5</sub> for *A. glycines*, see section 3.1, below). Leaf discs (20 mm diameter) and 3rd instar nymphs of each species were separately dipped into 7 µg/L beta-cypermethrin for 10 s and then they were placed in shadow to air dry for 1 h. One leaf disc and twenty aphids treated by this sublethal concentration of beta-cypermethrin (7 µg/L) or control solution (0.005% Triton X-100) were introduced into one well of the tissue-culture plate. Two percent of the agar was pre-placed at the bottom of the well and then it was covered with a filter paper strip (Hangzhou, China). Twenty-four-hour post-exposure to 7 µg/L beta-cypermethrin, mortality of the aphids was measured (as well as in control group). The treatments and control were replicated four times for both aphid species.

### 2.4. Effects of sublethal beta-cypermethrin concentration and interspecific interaction on aphid fecundity and spatial distribution on the soybean plants

The impact of the sublethal concentration of beta-cypermethrin and interspecific interaction on aphids was studied using a 2 by 2 factorial experimental design (Table 1). The impact of interspecific constraint on aphids was assessed with cross-infestation on the soybean plant, i.e. pre-infestation by a first attacker affects performance of the second attacker. The impact of sublethal effects on aphids was evaluated using insecticide-treated plants (with/without the first attacker) and control plants (i.e. no insecticide, with/without the first attacker).

When the soybean plant was only attacked by one aphid species (the “second” attacker), the 15-day-old soybean seedling was dipped into the LC<sub>5</sub> beta-cypermethrin solution (7 µg/L) for 10 s, and then placed in shadow to air dry for 1 h. Five days later, five apterous adults of *A. solani* (in treatment A2) or *A. glycines* (in treatment B2) were settled on the top leaf (the first trifoliate leaf) of the soybean seedling. After four days, the number of aphids (*A. solani* or *A. glycines*) on leaves and stems was recorded. Treatments A1 and B1 (where the same-age soybean seedlings were exposed to 0.005% Triton X-100) were considered as the control for each aphid species, i.e. no insecticide exposure nor pre-infestation by aphids.

When the soybean was infested by two different attackers, the two species of aphids were placed on the soybean plant in sequence. When *A. glycines* was the first attacker (in treatment A4) on soybean plant, both 15-day-old soybean seedlings and 3rd instar *A. glycines* apterous nymphs were exposed to the LC<sub>5</sub> (7 µg/L) of beta-cypermethrin. Five survived *A. glycines* nymphs were introduced on the unifoliate leaf for five days, and then five *A. solani* apterous adults were settled on the top leaf (the first trifoliate leaf) of the soybean plants. After four days, the numbers of *A. solani* on leaves and stems were measured, respectively. Experiments followed the same scenario as described above when *A. solani* was the first attacker (in treatment B4) on soybean plant. The same-age soybean seedlings and the first attacker (*A. glycines* or *A. solani*) were exposed to the Triton X-100 in treatments A3 and B3, respectively. Thereafter, the same procedure as that in treatments A4 and B4 was conducted for both infestation and measurement of the second attacker in treatments A3 and B3.

One soybean seedling represented one replicate, which was separately caged and maintained in climate chambers, at 25 ± 2 °C, 60 ± 10% RH (relative humidity), L17: D7 photoperiod. Each treatment was replicated 20 times.

### 2.5. Effects of sublethal beta-cypermethrin concentration and interspecific interaction on susceptibility of soybean plants to aphids

Four types of 15-day-old soybean plants, i.e. (1) plants without insecticide application and pre-infestation by aphids, (2) plants exposed to sublethal concentration of beta-cypermethrin for 10 s, (3) plants infested by the first attackers (five 3rd instar nymph aphids), (4) plants with infestation by the first attackers (five 3rd instar nymphs) exposed to sublethal concentration of beta-cypermethrin for 10 s, were prepared to place in the climate chambers for 5 days. Thereafter, one leaflet from each treatment was harvested for preparation of leaf discs to assess the plant susceptibility to aphids. Sixty individuals of the second attackers (apterous adult aphids after a starvation period of 3 h) were introduced to the center of Petri dish surrounded with four leaf discs (one of each type). The number of aphids on each leaf disc was recorded after they moved, fed and settled on each leaf for 1 h (15 replicates were carried out per group tested).

### 2.6. Statistical analysis

The concentration-mortality regression equations and values of LC<sub>90</sub>, LC<sub>50</sub> and LC<sub>5</sub> were calculated using a log-probit analysis. Mortality of aphids exposed to low concentrations of beta-cypermethrin and control solution was analyzed using *t*-test to ensure that we effectively selected a sublethal concentration of beta-cypermethrin (LC<sub>5</sub>). The effects of sublethal beta-cypermethrin concentration and interspecific constraint on fecundity, spatial distribution on soybeans and plant susceptibility to the second attackers were analyzed using a two-way ANOVA (analysis of variance), followed by a Tukey's HSD post hoc test for multiple comparisons (to compare aphid fecundity, spatial distribution and plant susceptibility among different treatments). All the analyses were performed with the SPSS 25.0 software. Datasets were tested for homogeneity of variance and normality using Cochran's test and Kolmogorov-Smirnov D test respectively, and transformed if necessary before

**Table 2**  
Toxicity of beta-cypermethrin on the 3rd instar nymphs of *A. solani* and *A. glycines*.

Aphid	concentration-response regression equation	$\chi^2$	df	P	LC <sub>5</sub> /μg/L (95% CI)	LC <sub>50</sub> /μg/L (95%CI)	LC <sub>90</sub> /μg/L (95%CI)
<i>A. glycines</i>	Y = 3.212 X+5.268	7.387	18	0.986	7 (5–9)	23 (20–26)	57 (48–73)
<i>A. solani</i>	Y = 3.013 X+2.099	23.561	18	0.170	57 (38–76)	201 (171–232)	536 (446–686)

95% CI indicates 95% confidence interval; the variable X is transformed using a log base of 10.

**Table 3**  
Statistics from the two-way ANOVA used to analyze aphid fecundity, aphid spatial distribution on soybean plants, and the plant susceptibility to *A. glycines* and *A. solani*.

Effects	Factors	Effects on <i>A. solani</i>		Effects on <i>A. glycines</i>	
		F	P	F	P
Fecundity	Interspecific constraint	8.724	0.004*	76.393	<0.001*
	Insecticide	0.252	0.617	0.068	0.795
	Interspecific constraint × insecticide	1.190	0.279	9.861	0.002*
Spatial distribution of aphids	Interspecific constraint	0.153	0.697	19.703	<0.001*
	Insecticide	13.678	<0.001*	13.039	0.001*
	Interspecific constraint × insecticide	0.014	0.907	24.705	<0.001*
Plant susceptibility	Interspecific constraint	72.475	<0.001*	63.603	<0.001*
	Insecticide	4.971	0.03*	7.826	0.007*
	Interspecific constraint × insecticide	18.992	<0.001*	18.496	<0.001*

P value followed by asterisk (\*) indicates that the factor (or interactions of factors) has a significant effect on aphid fecundity, spatial distribution or plant susceptibility.

statistical analyses.

### 3. Results

#### 3.1. Acute toxicity of beta-cypermethrin on *A. glycines* and *A. solani*

The results of the log-probit regression analyses between the beta-cypermethrin concentrations tested and the mortality recorded in *A. glycines* and *A. solani* individuals are reported in Table 2. The beta-cypermethrin was more toxic to *A. glycines* than to *A. solani* as the

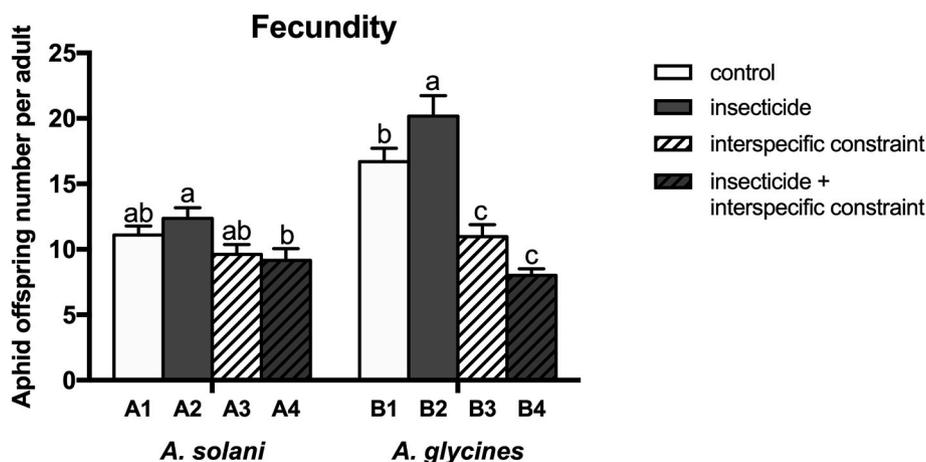
LC<sub>5</sub>, LC<sub>50</sub> and LC<sub>90</sub> values of beta-cypermethrin on *A. glycines* (7, 23 and 57 μg/L) were nearly 10 times lower than those on *A. solani* (57, 201 and 536 μg/L), respectively. Therefore, the lowest LC<sub>5</sub> value (7 μg/L), i.e. the one causing 5% in mortality in *A. glycines*, was selected as the tested sublethal concentration for the following assessments which implied exposing both species to a single sublethal concentration on a shared plant. This enabled to expose both aphid species simultaneously to a concentration not inducing significant mortality in exposed individuals when compared to a control (i.e. sublethal concentration according to Desneux et al., 2007).

#### 3.2. Effect of sublethal beta-cypermethrin concentration on *A. glycines* and *A. solani*

The exposure to 7 μg/L beta-cypermethrin induced 7 ± 1.22% and 2 ± 1.22% mortality in *A. glycines* and *A. solani*, respectively. As expected, these mortality values were not significantly different than the mortality values recorded in respective controls (*A. glycines*: 5 ± 1.58%,  $P = 0.347$ ; *A. solani*: 1 ± 1%,  $P = 0.545$ ), and it confirmed that 7 μg/L (i.e. the LC<sub>5</sub> in the following context) could be considered as a sublethal concentration of beta-cypermethrin on these two aphids.

#### 3.3. Effects on aphid fecundity

Statistical results are reported in Table 3. Interspecific constraint (interactions) had significant influence on the fecundity of both *A. solani* ( $F_{1,76} = 8.724$ ;  $P = 0.004$ ) and *A. glycines* ( $F_{1,72} = 76.393$ ;  $P < 0.001$ ), whose fecundity was as well affected by the interaction of interspecific constraint and insecticide ( $F_{1,72} = 9.861$ ;  $P = 0.002$ ). Interspecific constraint didn't change *A. solani* fecundity without exposure to the LC<sub>5</sub> of beta-cypermethrin while it decreased *A. solani* fecundity on the soybean plant previously treated with the insecticide ( $F_{3,76} = 3.389$ ;  $P = 0.022$ ; Fig. 1). However, the fecundity of *A. glycines* was significantly reduced by the interspecific constraint on both insecticide-treated and insecticide-free soybean plants. The LC<sub>5</sub> of beta-cypermethrin significantly increased *A. glycines* fecundity on the soybean plants that were not pre-infested by *A. solani*, but it didn't change the reproduction of *A.*



**Fig. 1.** Offspring (mean number ± SEM) produced by each *A. solani* (group A) and *A. glycines* (group B) adult in the different treatments (see Table 1). Different letters for each aphid species indicate significant difference (at  $P < 0.05$ ).

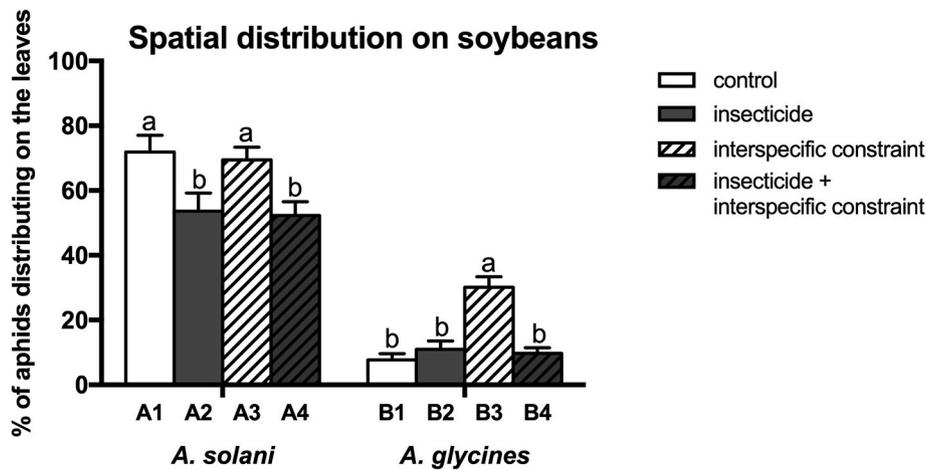


Fig. 2. Distribution (mean percentage  $\pm$  SEM) of *A. solani* (group A) and *A. glycines* (group B) on the leaves of soybean plants in the different treatments (see Table 1). Different letters for each aphid species indicate significant difference (at  $P < 0.05$ ).

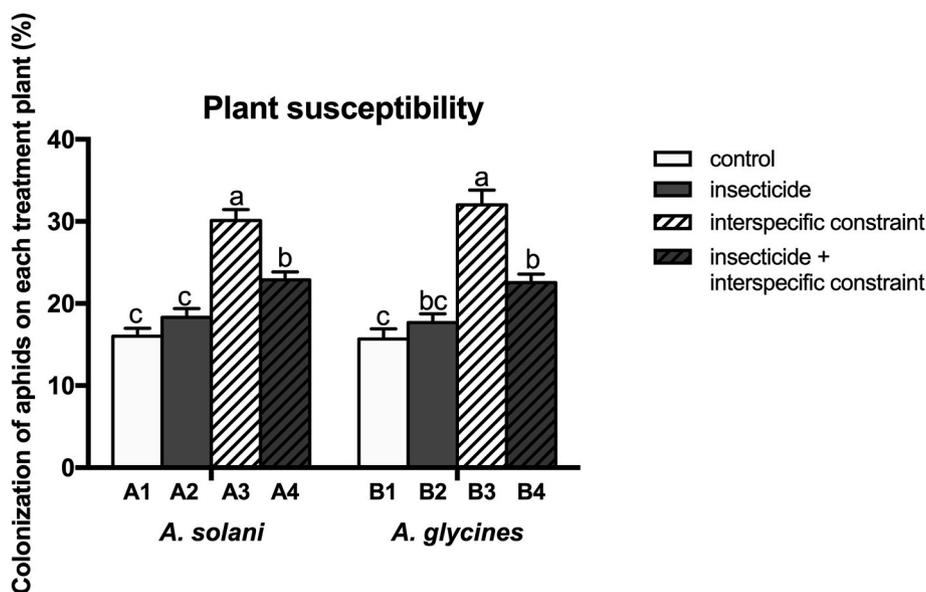


Fig. 3. Colonization (mean percentage  $\pm$  SEM) of *A. solani* (group A) and *A. glycines* (group B) on soybean leaves in the different treatments (see Table 1). Different letters for each aphid species indicate significant difference (at  $P < 0.05$ ).

*glycines* on the soybean plants that were pre-infested by *A. solani* ( $F_{3,72} = 28.247$ ;  $P < 0.001$ ; Fig. 1).

### 3.4. Effects on aphid spatial distribution on soybean plants

The percentage of *A. solani* individuals settling on soybean leaf was significantly impacted by the sublethal concentration of insecticide ( $F_{1,76} = 13.678$ ;  $P < 0.001$ ; Table 3) while *A. glycines* distribution on the soybean plant was distinctly affected by both interspecific constraint ( $F_{1,70} = 19.703$ ;  $P < 0.001$ ; Table 3), insecticide ( $F_{1,70} = 13.039$ ;  $P = 0.001$ ; Table 3) and their interactions, i.e. 'interspecific constraint  $\times$  insecticide' ( $F_{1,70} = 24.705$ ;  $P < 0.001$ ; Table 3). Exposure to LC<sub>5</sub> of beta-cypermethrin significantly decreased the proportion of *A. solani* colonizing on the soybean leaves no matter whether *A. solani* was under the stress of interspecific interactions or not ( $F_{3,76} = 4.615$ ;  $P = 0.005$ ; Fig. 2). However, the percentage of *A. glycines* settling on insecticide-free soybean leaves was increased during interspecific constraint. Although LC<sub>5</sub> treatment did not change the proportion of *A. glycines* on leaves which were not pre-infested by *A. solani*, it significantly reduced the ratio of soybean aphids colonizing on leaves with the

foxglove aphid pre-infestation ( $F_{3,70} = 18.957$ ;  $P < 0.001$ ; Fig. 2).

### 3.5. Effects on the plant susceptibility to aphids

Both factors, i.e. interspecific constraint ( $F_{1,56} = 72.475$ ;  $P < 0.001$  for *A. solani*;  $F_{1,56} = 63.603$ ;  $P < 0.001$  for *A. glycines*) and insecticide ( $F_{1,56} = 4.971$ ;  $P = 0.03$  for *A. solani*;  $F_{1,56} = 7.826$ ;  $P = 0.007$  for *A. glycines*), and their interactions 'interspecific constraint  $\times$  insecticide' ( $F_{1,56} = 18.992$ ;  $P < 0.001$  for *A. solani*;  $F_{1,56} = 18.496$ ;  $P < 0.001$  for *A. glycines*) had significant influence on the susceptibility of soybean plants to aphids (Table 3). Susceptibility to *A. solani* and *A. glycines* was increased by the interspecific constraint whatever aphids were exposed to LC<sub>5</sub> of beta-cypermethrin or not. LC<sub>5</sub> treatment did not affect plant's susceptibility to *A. solani* and *A. glycines* when aphids were not subjected to interspecific constraint, still, the insecticide reduced this susceptibility when the aphids were subjected to interspecific constraint ( $F_{3,56} = 32.146$ ;  $P < 0.001$  for *A. solani*;  $F_{3,56} = 29.975$ ;  $P < 0.001$  for *A. glycines*; Fig. 3).

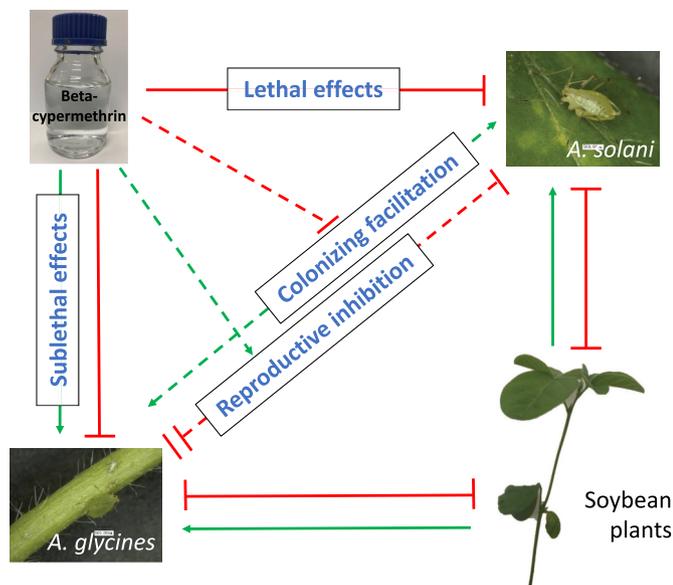
#### 4. Discussion

We investigated the effects of both the LC<sub>5</sub> of beta-cypermethrin (abiotic stress) and interspecific constraint (biotic stress) on *A. glycines* and *A. solani* fecundity, spatial distribution on soybean and on plant susceptibility to the two aphid species. A mutual negative effect on fecundity of aphids was detected in the interspecific interactions between *A. glycines* and *A. solani*, which may be due to the induced plant defenses against the aphids (Hohenstein et al., 2019; Sato et al., 2014; Studham and Macintosh, 2013). Induced plant responses triggered by *A. glycines* were mainly attributed to the JA signaling pathway which may cause the accumulation of isoflavonoids that act as toxins against the subsequent aphids on the soybean (Hohenstein et al., 2019). Moreover, after inoculation of *A. solani* on soybean leaves, there were yellow blotches surrounding the feeding location, which may be accompanied by a decrease in concentrations of citrate and amino acids, leading to the reduction of plant quality for the subsequent aphids (Sato et al., 2013, 2014). The LC<sub>5</sub> of beta-cypermethrin increased the interspecific interaction-related inhibition on *A. solani* fecundity (from 13.4% to 26%, calculated using the offspring numbers produced per *A. solani* adult;  $[A2 - A4]/A2$ ) (Table 1; Fig. 1). Moreover, the reduction of *A. glycines* reproduction rate caused by the interspecific interaction was enhanced from 34.4% to 60.3% by the exposure to the LC<sub>5</sub> of beta-cypermethrin. It hints that the LC<sub>5</sub> of beta-cypermethrin could magnify the inhibition of aphid growth resulting from interspecific interactions. The mechanism(s) underneath insecticide-accelerated interspecific competitions between the two aphid species could result from increased energy spent to detoxify insecticide and/or to migrate within plants (Jager et al., 2013; Qu et al., 2017). In addition, the reduction of *A. glycines* fecundity caused by the interspecific constraint was twice more than that on *A. solani* fecundity, which may be linked to the bigger biomass and body size of *A. solani* as well as its wider spatial niches on the plant. *Aulacorthum solani* mainly stays on soybean leaves (these are the most valuable source tissues to synthesize photosynthates). Moreover, infestation by aphids may alter the source-sink dynamics of phloem transport via the resource sequestration to secure the local resources for *A. solani* on leaves, thereby reducing the carbohydrate supply to *A. glycines* that mainly settles on stems (Biere and Goverse, 2016; Lemoine et al., 2013). In addition, the lower ability of *A. glycines* to cope with the interspecific interactions with *A. solani* may be also linked to the maladaptation of the specialist aphid to some insecticidal compounds induced by the generalist aphid (as the later can successfully colonize a wide range of host plants, Gatehouse, 2002). However, compared to the generalist aphid *A. solani* on soybean, *A. glycines* as specialist consumer has evolved more physiological adaptations to cope with the plant constitutive defenses, e.g. the detoxification or the sequestration of toxins (Ali and Agrawal, 2012; Barrett and Heil, 2012; Florent, 2013). This may be responsible for the higher *A. glycines* fecundity on infestation-free soybean plants. The LC<sub>5</sub> of beta-cypermethrin significantly facilitated the reproduction of *A. glycines* on clean soybean plants (soybeans were only infested by one attacker, i.e. the second attacker, in treatments B1 and B2), which was consistent with the hormesis effect observed on soybean aphid fecundity in our previous study (Qu et al., 2017). This stimulation effect on aphid fecundity may result from pesticide-induced production of vitellogenin (yolk protein precursor) and ovarian development at the low concentration of beta-cypermethrin (Chinzei et al., 1989; Ullah et al., 2019b). However, the reversed/suppressed impact caused by LC<sub>5</sub> of beta-cypermethrin on soybean aphid fecundity on the hosts pre-infested by *A. solani* may be associated with the movement of *A. solani*; they transferred from leaves to stems post-exposure to the insecticide. Nevertheless, no influence was detected on the fecundity of *A. solani* post-exposure to beta-cypermethrin. It may be due to the higher resistance of *A. solani* to this insecticide and the concentration used in the test (7 µg/L is approximately LC<sub>1</sub> on *A. solani*) may be too low to alter *A. solani* reproduction (Qu et al., 2017; Ullah et al., 2019b; Wang et al., 2014).

Niche complementarity is a strategy to maintain compatible interactions when diverse herbivore species consume the same plant host (Gable et al., 2012; Northfield et al., 2010). As stressed in our study (Fig. 2), *A. solani* and *A. glycines* populations had different spatial distribution on soybean plant, where the generalist aphid, *A. solani*, mainly colonizes the leaves and the specialist aphid, *A. glycines*, preferred settling on stems. The different composition of phloem sap within the plant may drive the different spatial distribution of aphids on the host plant (Jakobs and Müller, 2019; Jakobs et al., 2019). In addition, aphids are considered as a key model insect to research species differentiation and speciation, and they may have a predisposition to sympatric speciation (Berlocher and Feder, 2002; Dixon, 1998; Powell et al., 2006). In the present study, soybean aphids were observed to largely moved from the stem to soybean leaves when they were under the stress of interspecific interaction (Fig. 2). Because pesticides are more accessible to *A. solani* on soybean leaves (larger surface), alarm pheromones could be released by *A. solani* to warn conspecific individuals to evade and to move to stems. Moreover, irritated by pesticides (including pyrethroids), chemoreceptors located on the surface of insect body may also cause a reflex action, leading to the movement of insects away from the pesticide-treated areas (Alzogaray and Zerba, 2001; Desneux et al., 2007). Finally, altered aphid spatial distribution on the soybean plants might increase foraging time in specialist natural enemies as they search specific prey; this may reduce the biocontrol services they provide as well as affect their population dynamics (Desneux et al., 2007; Guedes et al., 2016).

Pest-induced plant responses are not always detrimental to pests and they may be actually manipulated by pests to increase host plant susceptibility (Gatehouse, 2002; Inbar et al., 1999; Studham and Macintosh, 2013). It has been documented that soybean aphids can increase the suitability of their host to conspecifics depending on feeding facilitation (Varenhorst et al., 2015; Yates and Michel, 2018). The induced susceptibility of host plants to interspecific aphids may be linked also to the ability of aphids to block effective defenses (in case of compatible interactions) via secreting salivary effectors that can overcome host plant defenses and thus increase plant susceptibility (Hohenstein et al., 2019; Yates and Michel, 2018). Consequently, the leaves from soybean plants pre-infested by one species of aphids were easier to be colonized by the other species of aphids but they were abandoned by aphids when treated by the LC<sub>5</sub> of beta-cypermethrin. Aphids circumvented the leaves exposed to beta-cypermethrin, which may be associated with the repellent and antifeedant effects of pyrethroids, e.g. on *Apis mellifera* and *Aedes aegypti* (Bandason, 2018; Bowman et al., 2018; Rieth and Levin, 1988). The survival of infestation-free leaves in face of aphid colonization implies that constitutive defense strategies are as well employed by soybean plants in addition to the induced defenses. The constitutive defenses could act as a barrier by lignification and production of feeding or egg deposition deterrents to protect plants from being heavily colonized by insects (Bixenmann et al., 2016; Gatehouse, 2002; Mithöfer and Maffei, 2017).

Our results stressed that although the LC<sub>5</sub> of beta-cypermethrin stimulated reproduction of the soybean aphid, its population may not increase dramatically if the foxglove aphid attacked the plant at the same time. This could be due to the enhanced interspecific competition and/or the lower feeding preference of aphids on the soybean caused by the LC<sub>5</sub> of beta-cypermethrin. In this case, population growth of both aphids on soybean may slow down few days following beta-cypermethrin field application. In addition, as reported previously, LC<sub>5</sub> of beta-cypermethrin (3.158 mg/L) could increase the fecundity of *Harmonia axyridis* both in *F*<sub>1</sub> and *F*<sub>2</sub> generations (Xiao et al., 2016). Therefore, some generalist natural enemies of aphids may not be negatively affected by beta-cypermethrin residues and they may be useful to prevent or delay repeated chemical application(s) against these aphids in soybean crops.



**Fig. 4.** A network of soybean plant-specialist aphid-generalist aphid-insecticide interactions. *Aulacorthum solani*, the generalist aphid primarily settling on soybean leaves, had a bigger spatial niche than *A. glycines*, the specialist aphid that mainly colonizes on soybean stems. Aphids as consumers of phloem sap were supported by the soybean plants for food resource, but on the other hand, aphids are negatively affected by plant defensive compounds. When *A. glycines* and *A. solani* attack soybean plants in sequence, the fecundity of the second attacker was inhibited by the interspecific interaction. Moreover, interspecific constraint caused stronger suppression on the reproduction of soybean aphids, compared to foxglove aphids. However, pre-infestation by one species facilitated subsequent aphids' colonization on the host by increased plant susceptibility to aphids. Beta-cypermethrin (as a commonly used insecticide to control aphids) stimulated the reproduction of *A. glycines* at the sublethal concentration of  $LC_5$ , but it did not alter the fecundity of *A. solani* at this concentration. In addition, exposure to the  $LC_5$  of beta-cypermethrin caused a stronger interspecific negative effect on the fecundity of the two aphid species. Positive effects are indicated by green arrows, while negative effects are indicated by red lines ending by a block. Two blocks indicate a stronger inhibiting impact on fecundity of *A. glycines* in the interspecific competition, compared to *A. solani*. Solid lines with block/arrow at the end indicate direct effects on plants/aphids and dashed lines indicate interspecific interactions and indirect modulation on interactions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

## 5. Conclusions

Interspecific interactions decreased fecundity of both *A. solani* and *A. glycines*, but  $LC_5$  of beta-cypermethrin had stimulatory effects on the fecundity of *A. glycines* when soybean plants were not pre-infested by *A. solani*. Exposure to the  $LC_5$  of beta-cypermethrin distinctly drove *A. solani* migrating from leaves to stems and also caused *A. glycines* to aggregate on soybean plant stems (when plants were pre-infested by *A. solani*) (Fig. 4). The reproduction of the two aphid species was inhibited through interspecific constraint while their colonization on the host plant was facilitated by each other. The  $LC_5$  of beta-cypermethrin caused the acceleration of interspecific competition and the reduction of aphid-induced susceptibility of hosts. All these results may contribute to fully understanding the plant-aphid-pesticide interactions and expanding our knowledge on side-effects of pesticides used in the agro-system. This knowledge could contribute to rationalizing application of insecticides and optimizing Integrated Pest Management in soybean.

## Credit author statement

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Visualization; Writing - original draft; Writing - review & editing. Farman Ullah: Investigation; Methodology; Writing - review & editing. Chen Luo: Formal analysis; Visualization. Lucie S. Monticelli: Formal analysis. Anne-Violette Lavoit: Conceptualization; Writing - review & editing. Xiwu Gao: Resources. Dunlun Song: Funding acquisition; Methodology; Resources; Supervision; Writing - review & editing. Nicolas Desneux: Conceptualization; Funding acquisition; Methodology; Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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