ANTIPREDATOR RESPONSE OF APHIDS TO LADYBEETLES: EFFECT OF INTERCROPPING ON APHID DISPERSAL

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SUMMARY

Dispersal of viruses is intimately tied to their vectors. Aphids are known to invest in costly antipredator behavior when perceiving cues of predators. It is hypothesized that the absconding behavior of aphids in the presence of predators can increase virus spread in fields. Whereas most of the studies investigating this hypothesis were conducted in monoculture, we studied aphid antipredator behavior in intercropping with wheat (*Triticum aestivum* L.)-broad bean (*Vicia faba* L.) as a model. The bird cherry-oat aphid, *Rhopalosiphum padi* Linnaeus (Hemiptera: Aphididae), is an important vector of the barley yellow dwarf virus. The effects of two natural aphid enemies, adults and larvae of the seven-spot ladybeetle, *Coccinella septempunctata* Linneaus (Coleoptera: Coccinellidae), on *R. padi* dispersion was studied under laboratory conditions. Trays composed of 7 × 8 lines of plants were considered. In intercropping, one line of broad-bean succeeded one line of wheat. Six treatments were compared: in both wheat monoculture and intercropping, aphids were introduced alone, with ladybeetle larvae or with ladybeetle adults. Aphids and predators were introduced on wheat tillers in the middle of the system (source line) and aphids were counted on every plant after two and 24 hours. Results show that the total number of aphids was higher in intercropping than monoculture in treatments without ladybeetles, while the contrary was observed in the presence of ladybeetle larvae. But after 24 hours, such differences were not observed anymore. However, in receptor lines (other lines than the source one), two hours after the experiment started, aphids were more abundant in monoculture than intercropping in the presence of ladybeetle adults and larvae and after 24 hours, it was still the case in the presence of predatory larvae. These results might be explained by the non-host plant chemical cues and the physical barrier that was broad-bean plants confusing *R. padi* when searching for their host plants after being dropped from wheat by predators (i.e. associational resistance). This study shows that intercropping can reduce the dispersal of aphids in the presence of predators, *in fine* potentially limiting virus dispersal, especially shortly after aphids colonize plants.

Key words: Vectors, Predators, *Rhopalosiphum padi*, *Coccinella septempunctata*, Intercropping, Associational resistance

INTRODUCTION

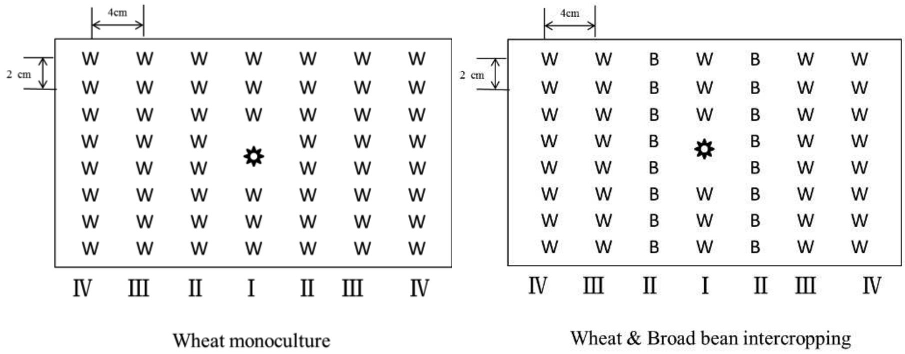
Aphids (Hemiptera: Aphididae) damage crops by feeding on phloem sap, while some species are efficient vectors of viruses (Goggin, 2007). Chemical insecticides, used to control them, constitute a danger for the environment (Wu and Guo, 2003). Moreover, because of their recurrent applications overtime, aphids develop resistances, rendering insecticides less effective (Bass *et al*., 2014; Foster *et al*., 2014; Lu and Gao, 2009). Hence, there is a need of exploring alternative strategies for managing pest populations. A substantial body of literature has

illustrated that insect pests are less problematic in areas with an increased plant species diversity (Letourneau *et al*., 2011; Malézieux *et al*., 2009). Intercropping systems for instance, which consist in cultivating at least two plant species simultaneously in the same field without necessarily being sown or harvested at the same time (Lithourgidis *et al*., 2011; Xie *et al*., 2012), can be less sensitive to aphid populations compared with monocultures (Labrie *et al*., 2016; Lopes *et al*., 2016; Wang *et al*., 2009). Additionally, intercropping cereal with leguminous crops, e.g. wheat (*Triticum aestivum* L.) with broad bean bean (*Vicia faba* L.), allows reducing nitrogen inputs, favoring the adoption of such a practice by farmers (Gooding *et al*., 2007; Li *et al*., 2009; Tosti and Guiducci, 2010; Xiao *et al*., 2004; Yang *et al*., 2009).
Aphids are vectors of viruses and their population dynamics play a key role in the dispersal of vector-borne plant viruses. Natural enemies affect vectors by causing direct mortality, but can also promote their dispersion because of their prey's induced antipredator behavior (Dill *et al*., 1990; Villagra *et al*., 2002). Aphids can respond directly to predator attacks by escaping, defending themselves or counterattacking. They can perceive predators in advance through cues associated with the presence of natural enemies and subsequently change their behavior to reduce predation risk. For instance, aphids emit an alarm pheromone in response to predator attacks that induces a dropping off behavior, and in case of prolonged exposure can enhance the production of winged offspring (Kunert *et al*., 2005; Minoretti and Weisser, 2000).
The oat-bird cherry aphid *Rhopalosiphum padi* L. is a key pest of cereals such as barley (*Hordeum vulgare* L.), wheat and maize (*Zea mays* L.), being an important vector of the barley yellow dwarf virus (BYDV). It is also a frequent prey for the seven-spotted ladybeetle *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). The antipredator behavior in wheat monoculture system of *R. padi* to coccinellids is one of the beat understand (Bailey *et al*., 1995; Smyrnioudis *et al*., 2001). To address this question on the effect of antipredator behavior on aphids spread in an intercropping system, we used wheat as host plant, intercropped with broad bean, as non-host plants, the aphid *R. padi* and one of its main predators: larvae and adults of the *C. septempunctata*. Physical and chemical stimuli are used by aphids to locate their host from non-host plants (Döring, 2014) and intercropping, by potentially associating host with non-host plants, is known to complicate the search of host plants for aphids (Poveda *et al*., 2008). Hence, how does intercropping affect anti-predator behavior of aphids in the presence of ladybeetles? We hypothesize that whereas ladybeetles can increase aphid - and thus virus vector - dispersion in monoculture because of prey anti-predator behavior, this dispersion in the presence of predators is reduced in intercropping systems.

MATERIALS AND METHODS

Plant material

Wheat and broad bean were grown from seed in a climate room chamber (T=25°C±1°C, RH= 60%±10%, photoperiod= 16:8h L: D) in plastic boxes (35 × 20 × 10 cm), and the soil was organic matter mixed with sand with a proportion of 3:1. Each box consisted in seven lines (5 cm between them) of eight plants (2 cm between them). The monoculture treatment consisted in only wheat tillers, while for intercropping, two lines of broad bean were sown besides the central line of wheat (Figure 1). Each experimental unit was a 45 × 45 × 45 cm bug dorm insect cage maintained in the climate room containing the plastic box with plants. Plants were 10 day old (~18 cm tall) when insects were introduced.



W: Wheat
B: Broad bean
✲ : Introduction point of aphids and ladybeetles

Figure 1 Design of boxes for wheat monoculture and wheat-broad bean intercropping (source line: Ⅰ, receptor lines: Ⅱ, Ⅲ, Ⅳ. Aphids and ladybeetles were introduced in the middle of the source line.

Insects

Multi-clonal populations of *R. padi* were reared on wheat plants in plastic boxes (8 × 8 × 8 cm). They were kept in a controlled environment chamber (18-22ºC, 16:8h L:D) and no efforts were made to control humidity. As for ladybeetles, *C. septempunctata* were reared in cages (40 x 40 x 80 cm) placed in a controlled environment chamber (18-22°C, 16:8h L:D, 80% relative humidity) and fed with pea aphids (*Acyrthosiphon pisum* Harris) on broad bean plants. The sex of ladybeetle adults was determined according to Baungaard (1980).

Aphid dispersal

Six treatments, with four repetitions each, were conducted: wheat monoculture without ladybeetles (WW_Aphids), wheat monoculture with ladybeetle adults (WW_Aphids+LB), wheat monoculture with ladybeetle larvae (WW_Aphids+LBL), wheat-broad bean intercropping without ladybeetles (WW_BB_Aphids), wheat-broad bean intercropping with ladybeetle adults (WW_BB_Aphids+LB), wheat-broad bean intercropping with ladybeetle larvae (WW_BB_Aphids+LBL). One hundred aphids (starved one hour before starting the experiment) were placed on the wheat tillers of line I (source line, Figure 1) in each box. As for predators, two ladybeetle larvae (3rd instar) or two ladybeetle adults (one male and one female) were also placed on the source line plants five minutes after the introduction of aphids. The experimental boxes were maintained in a climate-controlled room under the conditions explained in 'Plant material'. The number of aphids was recorded on the source line and on the receptor lines 0.25h, 0.5h, 1h, 2h, 4h, 6h and 24h after the introduction of aphids.

Statistical analyses

First, time (i.e. two hours, 24 hours) and crop design (i.e. monoculture, intercropping) were considered separately. For each time and crop design, generalised linear models (GLM) were

fitted to assess the effect of ladybeetle treatments (i.e. aphids, aphids+LB, aphids+LBL) on aphid abundance found on (i) the source line and (ii) receptor lines. GLM were tested using independent-test, and ladybeetle treatments were compared by using Duncan post-hoc test. Second, time (two hours, 24 hours) and ladybeetle treatments (i.e. aphids, aphids+LB, aphids+LBL) were considered separately. For each time and ladybeetle treatments, GLM were fitted to assess the effect of crop design (i.e. monoculture vs. intercropping) on aphid abundance on (i) all crop lines merged, (ii) the source line only, (iii) receptor lines only. GLM were tested using independent-test.
To meet assumptions of normality and homogeneity of variances, data on the number of aphids was transformed by $\log_{10}(n+1)$, but for presentation untransformed arithmetic means and standard deviation were used. GLM and independent-tests were applied by SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Effect of ladybeetle adults and larvae

In wheat monoculture, aphid density on the source line was not significantly different between the treatments after two hours, and it was significantly lower in the presence of ladybeetle larvae than in other treatments after 24 hours. Dispersal of aphids towards receptor plants in the treatments with ladybeetle adults and larvae was higher than in the treatment without ladybeetles two hours after the experiment started. No differences between the three treatments were observed on the receptor lines 24 hours after the experiment started. In wheat-broad bean intercropping, after two and 24 hours, aphid density on the source line was significantly different between each treatment, being the lowest in the presence of ladybeetle larvae and the highest without predators. However, the dispersal of aphids towards receptor plants was not significantly different between the treatments after two and 24 hours (Table 1).

Table 1. Mean number of aphids (± SE) on plants (source line and receptor lines) found 2h and 24h after the aphid dispersal experiment started. Letters indicate significant differences based on post-hoc tests of Duncan performed on GLM (p<0.05).

		Source line		Receptor lines	
		2 h	24 h	2 h	24 h
WW	Aphids	36.75±1.89a	32.75±2.78a	15.25±1.79a	25.50±3.75a
	Aphids+LB	35.25±5.11a	28.50±3.84a	22.00±2.19b	25.00±3.98a
	Aphids+LBL	29.50±0.29a	4.50±0.29b	27.50±2.33b	20.00±3.62a
WW_BB	Aphids	55.25+3.82a	49.25±4.11a	13.75±1.93a	18.50±1.32a
	Aphids+LB	40.25±4.57b	30.25±2.56b	10.25±2.02a	15.50±1.19a
	Aphids+LBL	28.00±2.89c	19.50±0.29c	12.75±1.03a	16.75±1.89a

Effect of intercropping vs. monoculture

Two hours after the experiment started, the total number of aphids in all lines on the treatment without predators and with ladybeetle larvae were significantly different between monoculture and intercropping (**Figure 2**a, $t_6=-2.94$, $p=0.026$; $t_6=4.72$, $p=0.003$, respectively). Nevertheless, after 24 hours no differences were observed anymore (**Figure** 2b).

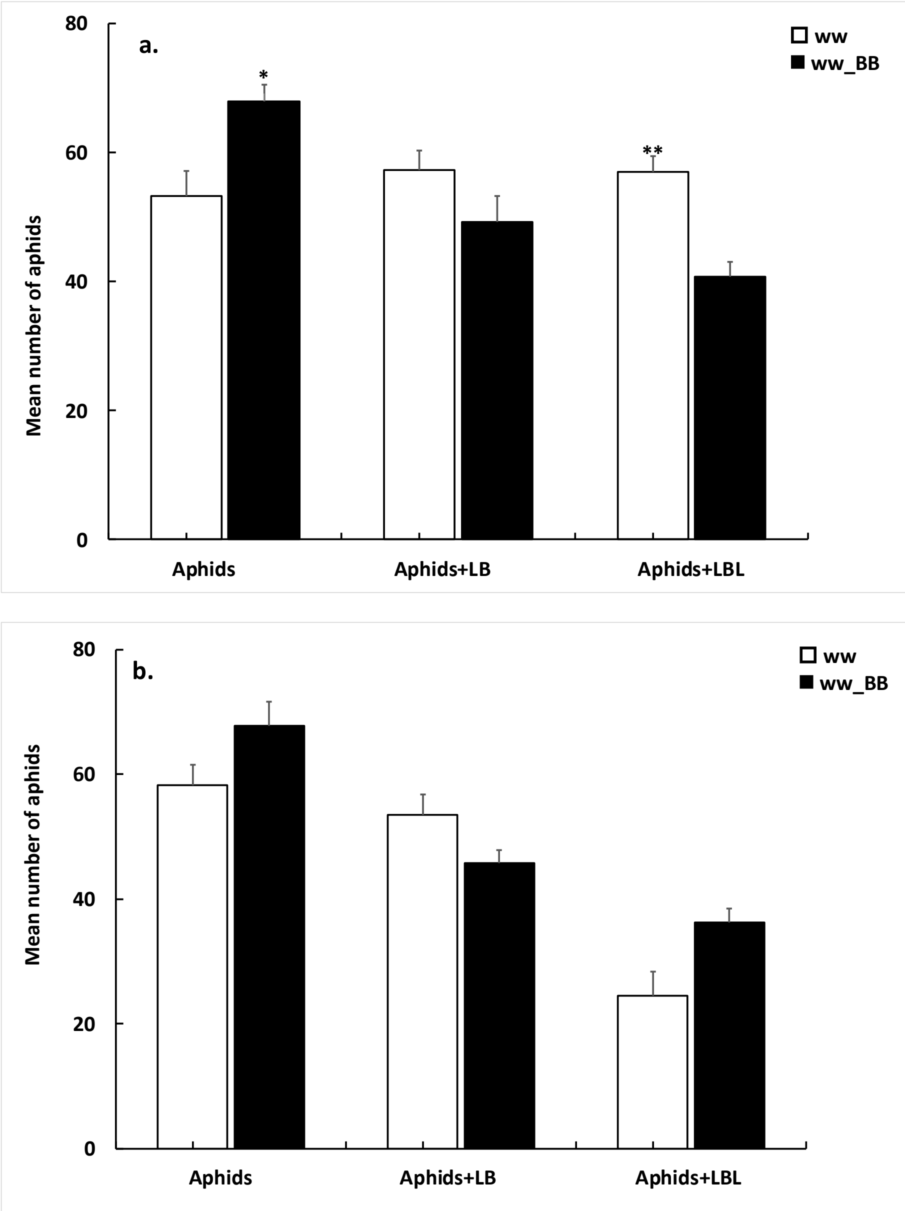


Figure 2 Mean number of aphids (± SE) on all lines (source and receptor lines) found (a) two hours and (b) 24 hours after the experiment started. (Independent-test, * P<0.05, ** P<0.01).

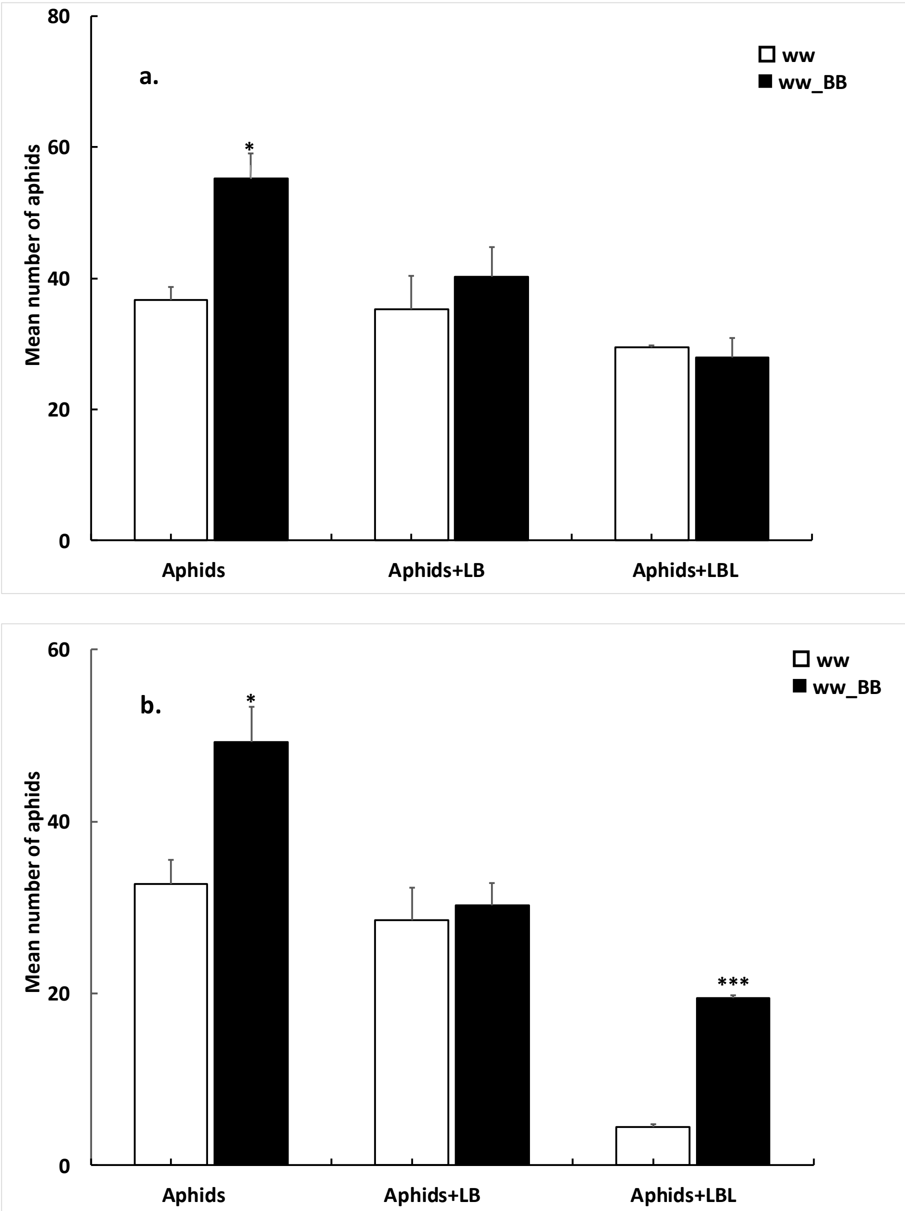


Figure 3 Mean number of aphids (± SE) on the source line found (a) two hours and (b) 24 hours after the experiment started. (Independent-test, * P<0.05, *** P<0.001)

On the source line, the number of aphids without ladybeetles was significantly lower in monoculture than in intercropping after two and 24 hours (**Figure 3**a, t_6=-4.62, p=0.003; Figure 3b, t6=-3.30, p=0.016). In the presence of predators, it is only at 24 hours that aphids were significantly less abundant in monoculture than in intercropping (**Figure 3**b, t6=-24.22, p<0.001). For the other cases, no significant differences were observed.

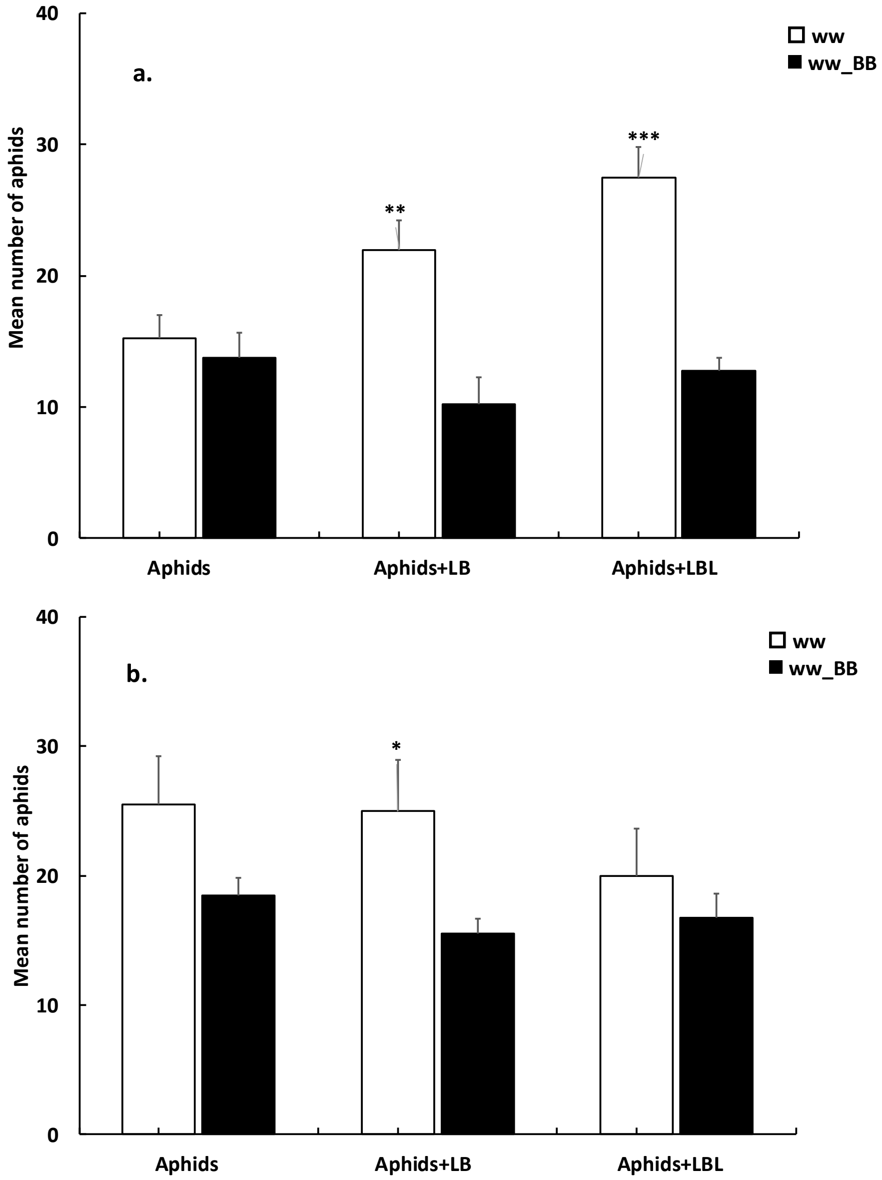


Figure 4 Mean number of aphids (± SE) on the receptor lines found (a) two hours and (b) 24 hours after the experiment started. (Independent-test, * P<0.05, ** P<0.01, *** P<0.001)

On receptor lines after two hours, the number of aphids was significantly reduced in intercropping compared to monoculture, with ladybeetle adults and larvae (**Figure 4**a, t6=3.60, p=0.011; t6=6.69, p<0.001, respectively). After 24 hours, only in the treatment with ladybeetle adults, aphids were less abundant in intercropping than monoculture (**Figure 4**b, t6=2.63, p=0.039).

DISCUSSION

The present study shows that in wheat monoculture, both ladybeetle adults and larvae promoted the dispersal of *R. padi* towards the initially uninfected plants nearby, especially shortly after the introduction of predators (i.e. two hours after the experiment started). Moreover, it shows that this dispersion was limited in intercropping systems, confirming our hypothesis.

Previously, Smyrnioudis (2001) also observed an increased dispersion of aphids in the presence of natural enemies (parasitoids in their case) in monocultures. However in our experiment, no significant differences were observed on receptor lines after 24 hours between treatments with and without ladybeetles. It indicates that in this time-frame, aphids independently from predators, were able to colonize the whole tray. Nevertheless, a reduced abundance of aphids on the source line in the presence of ladybeetle larvae was observed, which may be due to the feeding behavior of the predators, or the aphids dropping from plants (Belliure *et al.*, 2011). As for wheat-broad bean intercropping, the absence of differences on the receptor lines between the treatments with and without ladybeetles during the whole experiment indicates that, despite the presence of predators, *R. padi* dispersal was limited.

Without predators, the number of aphids was not significantly different on the receptor lines between monoculture and intercropping. But in the presence of predators, there were significantly more aphids on the receptor lines in monoculture than in intercropping, except on the receptor lines after 24 hours with ladybeetle larvae. However with predators, there were no significant differences on the source line between monoculture and intercropping, except in the presence of ladybeetle larvae at 24 hours. It shows that intercropping limits the ability of aphids to disperse, even in the presence of predators, which may favor an increased efficiency of predation. In intercropping systems, non-host plants can represent chemical and physical barriers limiting the ability aphids to find their host plants after being dropped from wheat (Lopes *et al*., 2015). Predator size and foraging speed have been noticed as factors used by aphids to assess predation risks, also, the consumption rate of *C. septempunctata* larvae was much higher than the adult one (Brodsky and Barlow, 1986).

In agroecosystems, dispersal has important consequences not only in impacting the regional population dynamics, but also in impacting the epidemiology (Ward *et al*., 1998). The dispersal of viruses and other pathogens transmitted by arthropods is intimately tied to the dispersal of their vectors (Jeger *et al*., 2009). Hence, the effects of predators on vectors might affect virus spread. Understanding how intercropping affects vector populations and behavior spread would participate in assessing how such a practice may affect pathogen spread. Several studies evaluated the impact of intercropping on disease spread for vector-borne viruses. Fargette and Fauquet (1988) suggested that mixed cropping including cassava (*Manihot esculenta* Crantz) may allow decreasing whitefly (Hemiptera: Aleyrodidae) vector populations, hence the spread of cassava mosaic disease. Moreover, Fondong *et al*. (2002) observed that cassava intercropped with maize or cowpea (*Vigna unguiculata* L.) allows decreasing adult whitefly populations on cassava by 50% and cassava mosaic disease incidence by 20%. Therefore, we can hypothesize that intercropping can reduce the transmission of BYDV by *R. padi*. Nevertheless, such a hypothesis remains to be tested.

After dropping to the ground, aphids can incur significant mortality from desiccation (Roitberg and Myers, 1978, 1979). In the present experiment, aphids that were dislodged from the plants were able to search and find another plant in intercropping system. Nevertheless, in the field, aphids on soil could encounter many dangers, such as ground predators or infection by entomopathogenic fungi (Ramezani *et al*., 2013). Thus, the survival of aphids disturbed by natural enemies may be lower than in this experiment. Moreover, due to the small size of boxes and short distance between plants, predatory larvae could easily move from one plant to another. However, this moving may be reduced in field conditions.
In summary, our results show that a higher dispersal of aphids occurs in the presence of lady-beetle adults and larvae in wheat monoculture than in wheat-broad bean intercropping, and that this might be due to the non-host plant chemical and physical cues confusing *R. padi* when searching for their host plants after being dropped from wheat. This is the first time that the effect of predators on aphid spread was studied in an intercropping system. Future research will need to assess whether the anti-predator behavior of *R. padi* indeed affects the spread of BYDV in intercropping systems compared to monocultures.

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