

Behavioral effects of insect-resistant genetically modified crops on phytophagous and beneficial arthropods: a review

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Abstract Behavior is a main component of the survival and performance of arthropods. We have witnessed widespread adoption of insect-resistant genetically modified (IRGM) crops nowadays; however, no literature has reviewed the behavioral effects of IRGM crops on phytophagous and beneficial arthropods. In this review, we assessed the current information related to the effects of IRGM crops on arthropod behavior, mainly including locomotion (mobility, escape behavior and dispersal behavior), foraging (orientation, host plant selection/preference and feeding), mating, oviposition and other behaviors (associative learning). Almost all the studies have been conducted on Bt crops. The behavioral effects have been found in 54.2 %, 22 % and 33 % of the case studies on phytophagous arthropods, arthropod natural enemies and pollinators, respectively. Few behavioral studies have been documented on arthropod pollinators. The majority of cases reporting behavioral effects have derived from target phytophagous arthropods. Among them, locomotion and feeding behavior were the most frequently affected. For arthropod natural enemies, the cases using target prey/host in tri-trophic studies only accounted for a small proportion of behavioral effects observed on foraging behavior (host/

prey selection). Overall, the effects through tri-trophic pathways on behaviors of natural enemies are limited. To conclude, while attention needs to be paid to several behavioral effects that may undermine the efficacy of IRGM crops in sustainable pest management, the behavioral effects generally do not disrupt the role of IRGM crops in achieving the goal of integrated pest management and crop production.

Keywords Behavior · Parasitoids · Predators · Risk assessment · *Bacillus thuringiensis* (Bt) · IPM

Key message

- No literature has reviewed the behavioral effect of insect-resistant genetically modified (IRGM) crops on phytophagous or beneficial arthropods in agroecosystems.
- In this review, we found that behavioral effects have been mostly evident on phytophagous arthropods, less on natural enemies and arthropod pollinators.
- Behavioral effects of IRGM crops on arthropods may not disrupt the role of such a technology in integrated pest management and crop production.

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Introduction

Since the advent of genetically modified (GM) crops in the late 1970s, we have witnessed an unprecedented increase in the development and commercial use of this technology worldwide. The dominant GM traits nowadays include insect resistance, expressing *Bacillus thuringiensis* (Bt) and

digestive enzyme inhibitors, and herbicide tolerance, tolerating applications of particular herbicides (James 2014). IRGM crops that aim at controlling agricultural pests while reducing the use of insecticides have been extensively cultivated. They have been regarded as cost-efficient and environmentally sound (Ferry et al. 2006; Brookes and Barfoot 2006; Park et al. 2011). While IRGM crops are developed to act directly on the target phytophagous pests, the unintentional effects on non-target arthropods have been and continue to be a subject of much debate (Andow and Zwahlen 2006; Babendreier et al. 2006; Rose 2007; Romeis et al. 2006, 2008; Naranjo 2009; Desneux and Bernal 2010; Desneux et al. 2010; EFSA 2010; Romeis et al. 2011, 2012). Notably, arthropod natural enemies (the arthropod species from higher trophic levels) and arthropod pollinators have been the subject of risk assessment studies owing to their importance in agro-ecosystems (Duan et al. 2008; Lu et al. 2012).

Several review articles have discussed the effects of IRGM crops on non-target arthropods (O’Callaghan et al. 2005; Marvier et al. 2007; Romeis et al. 2008; Wolfenbarger et al. 2008; Duan et al. 2010), specifically on natural enemies (Lövei and Arpaia 2004; Romeis et al. 2006; Lövei et al. 2009; Lundgren et al. 2009) and arthropod pollinators (Duan et al. 2008). While these reviews have thoroughly discussed the potential effects of IRGM crops on non-target arthropods, they have not specifically addressed the behavioral effects of IRGM crops on either target or non-target arthropods. The importance of how IRGM crops affect arthropod behavior should not be underestimated for at least three reasons. First, like other animals, arthropod behaviors are susceptible to external (environmental variations) and internal factors (physiological requirements). Arthropods must behave in the right way to survive and develop (Wajnberg et al. 2007). Second, IRGM crops may interfere with behavioral patterns of phytophagous arthropods, natural enemies and arthropod pollinators, and a good knowledge of these effects may favor sustainable pest management (Lundgren et al. 2009). Taking phytophagous arthropods as examples, the behavior of caterpillars needs to be assessed when designing refuge strategies. Knowledge of the dispersal and movement behaviors of those caterpillars is required when designing so-called “refuge-in-the-bag” tactics that are valued to delay the development of pest resistance to IRGM crops (Mallet and Porter 1992; Goldstein et al. 2010; Ramalho et al. 2014). Lastly, from the perspective of behavioral ecology, identifying how IRGM crops influence arthropod behavior and consequently how these effects translate into population levels may help understanding the outcomes of species interactions in arthropod communities (DiRienzo et al. 2013). In summary, the sustainable use of IRGM crops within the framework of integrated pest management

(IPM) would be highly dependent on how these crops affect arthropod behaviors.

Interestingly, many studies have examined the sublethal behavioral effects of IRGM crops on arthropods, especially the behavioral traits that are highly ecologically relevant. For example, they have evaluated the feeding and oviposition behavior of phytophagous arthropods, foraging behavior of natural enemies, as well as foraging and flight activities of arthropod pollinators. Despite this, to our knowledge, no review article has been developed on this specific subject.

The scope of the current review is to systematically and critically survey the published, peer-reviewed literature regarding the behavioral effects of IRGM crops on phytophagous and beneficial arthropods (arthropod natural enemies and arthropod pollinators). The selection of literature for review not only includes the ones that involve solely the behavioral studies, but also the ones where the concomitant behavioral bioassays have been conducted with the measurements of other life-history traits (articles reviewed were selected using the ISI Web of Science database). Totally 115 case studies have been reviewed with 59 for phytophagous arthropods, 50 for arthropod natural enemies and 6 for arthropod pollinators. We point out two important aspects for the selection of the literature. First, we did not cover the studies using artificial diets contaminated with insecticidal proteins in our review. We only focused on the behavioral studies using whole plant or plant materials in field trials or laboratory bioassays, which are more ecologically relevant. Second, to enhance the quality appraisal of the covered studies in this review, the appropriateness of the non-IRGM plant material (i.e., negative control) used in the studies has been thoroughly investigated. The negative control should be as closely related to the IRGM plant as possible in order to obtain a robust comparison. To this end, we classified the negative control into three categories: “near isoline,” “experimental plant” or “not specified.” The negative control plant that was not clearly indicated as near the isoline or near-isogenic hybrid, but indicated as the conventional or nontransformed line, should be considered as the “experimental plants.” This is also the case for the studies using cultivars that genetically modified to produce lectin, protease inhibitor or other insect-resistant feature, which have not been fully characterized and yet commercialized (e.g., Beale et al. 2006; Chen et al. 2008; Loivamäki et al. 2008; Aasen and Hågvar 2012). These studies thus need to be taken with caution when behavioral effects have been observed. The reason is that the effects observed in the cases where genetic transformation was undergone using different cultivars (instead of using near isolines) are likely to be caused by other unknown

differences in the characteristics of the two cultivars and not due to the insecticidal proteins.

The goal of this review is to provide the state-of-the-art of current literature addressing behavioral effects of IRGM crops on phytophagous and beneficial arthropods, with the aim to enhance the understanding of the compatibility of IRGM crops in crop production.

Behavioral effects of IRGM crops on phytophagous arthropods

The high effectiveness of IRGM crops against major agricultural pests has made this technology extensively adopted by growers worldwide. However, the pest susceptibility could alter its behavior and in turn have considerable ecological consequences (Ramalho et al. 2014). Behavioral effects of IRGM crops have been extensively examined either on target or non-target phytophagous arthropods (summarized in Table 1). The behavioral traits most studied are feeding, oviposition and locomotion. These behaviors have been studied on target pests (e.g., *Helicoverpa armigera*, *Spodoptera frugiperda*, *Ostrinia nubilalis*) and non-target pests (e.g., *Aphis gossypii*, *Myzus persicae*, *Bemisia tabaci*, *Adelphocoris suturalis*).

Locomotion (spatial distribution, escape behavior and dispersal)

Movement and spatial distribution patterns of phytophagous insects across the plant may vary with plant quality. For phytophagous insects, aggregation in a given part of the plant indicates a preference toward this part or an avoidance of the other parts. In IRGM crops, this behavior may be linked to variations in expression levels of insecticidal proteins among those parts. For example, *H. armigera* larvae were mostly found on Bt cotton flowers and least on leaves, while on non-Bt cotton the larvae were equally found in flowers and leaves (Lu et al. 2011). In addition, this species has been found to move twice as far down on Bt cotton compared to non-Bt cotton (Gore et al. 2002a). Besides target phytophagous arthropods, the aggregation patterns of non-target arthropods are also affected by IRGM crops and the effects are case-dependent. For example, Bt cotton influenced the spatial distribution pattern of *A. gossypii*, but not for *B. tabaci* (Rojas et al. 2010). The aphid *A. gossypii* showed altered spatial distribution patterns on the crop with more alate and apterous aphids in the middle or bottom parts of Bt cotton, while the aphid population peaks took place on the nodes from the middle parts of non-Bt cotton (Fernandes et al. 2012).

There are many cases in which target arthropods tend to avoid the toxins present in IRGM crops and display an

escape behavior from IRGM crops (Ramachandran et al. 1998a; Stapel et al. 1998; Gore et al. 2002b; Zhang et al. 2004; Men et al. 2005; Goldstein et al. 2010; Razzi and Mason 2012). These findings suggest that a seed mixture strategy may not be an effective strategy to prevent or reduce the rate of resistance in these target pests. However, there are some exceptions that the target insects do not exhibit escape behaviors. For example, *H. zea* stayed in Bt cotton with minimal movement, which may be due to the fact that they lack the recognition of harmful substances present in the crop tissues (Jackson et al. 2010). Variations in this behavior could explain their various capabilities of developing resistance to Bt crops.

Dispersal capacity of phytophagous species reflect their colonization potential within a given habitat. Potato producing snowdrop lectin (*Galanthus nivalis agglutinin*, GNA) has been less likely to be colonized by alate aphid *M. persicae*, and the results may benefit controlling the aphids by altering the colonization behavior of alates (Aasen and Hågvær 2012). The presence of the Cry1Ac protein in Bt cotton and its probable detection by *Alabama argillacea* larvae increase the probability of dispersion from the plant where the larvae began (Ramalho et al. 2014). This study provided important information on how Bt cotton affects the dispersal behavior of target arthropods over time. Consequently, such information is helpful for predicting the long-term effectiveness of the “refuge-in-the-bag” tactic in management of resistance in target arthropods.

Foraging (orientation, host plant preference and feeding)

The first step of foraging is orientation, which is defined as a process through which organisms move to the sites with potential resources (Schone and Strausfeld 1984). In this process, some insects rely on visual and olfactory cues to determine their orientation (Han et al. 2010a). We could expect that orientation response in arthropods may vary with changes in host plant features. Indeed, IRGM crops may alter their chemical or physical features compared to their isogenic lines (Sun et al. 2013). However, so far, no study has been able to monitor how phytophagous arthropods locate their habitat and host plants because of the difficulties in measuring their orientation under field conditions. Still, how IRGM crops modify the orientation of phytophagous insects can be indirectly assessed by identifying where the insects perform their oviposition (see “Mating and oviposition” below).

After the orientation decision has been made, phytophagous arthropods must select host plants to feed. They are able to detect and confirm the suitability of hosts in terms of plant nutritional quality and defense (Schoonhoven et al. 2005) and then select the plants that represent

Table 1 A summary of behavioral effects of IRGM crops on phytophagous arthropods

References	Testing crop/gene	Negative control	Testing species	Target/non-target	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Aasen and Hågvar (2012)	Potato/GNA	Experimental plant	<i>Myzus persicae</i>	Target	Choice	Colonization behavior	Yes	Less likely to be colonized by potato producing GNA compared to near isoline
Alyokhin and Ferro (1999)	Potato/Cry3A	Not specified	<i>Leptinotarsa decemlineata</i>	Target	Non-choice	Flight behavior	Yes	Resistant beetles feeding on Bt potato took longer time to initiate flight
Arpaia et al. (2009)	Eggplant/Cry3Bb	Near isoline	<i>Leptinotarsa decemlineata</i>	Target	Choice	Oviposition behavior	No	The spatial distribution of egg masses were similar between IRGM and control plot
	Potato/Cry1Ab	Near isoline	<i>Leptinotarsa decemlineata</i>	Non-target	Choice	Oviposition behavior	No	As above
Beale et al. (2006)	Arabidopsis/ sesquiterpene- β -farnesene (E β f)	Experimental plant	<i>Myzus persicae</i>	Target	Choice and non-choice	Escape behavior	Yes	Repellent response in the aphids
Chen et al. (2008)	Rice/Cry1Ac, Cry2A, Cry9C	Experimental plant	<i>Chilo suppressalis</i>	Target	Choice and non-choice	Feeding behavior	Yes	Preferentially fed on non-Bt culm cuttings of rice
Clark et al. (2006)	Maize/Cry3Bb1	Near isoline	<i>Diabrotica virgifera</i>	Target	Non-choice	Feeding behavior	Yes	Larvae exposed to Bt maize roots consumed significantly less tissue than larvae on non-Bt maize
Cuong and Cohen (2003)	Rice/Bt	Experimental plant	<i>Scirpophaga incertulas</i> <i>Chilo suppressalis</i>	Target	Choice	Mating behavior	No	Mating occurred randomly among individuals emerging from Bt rice fields and nearby refuge fields
Fernandes et al. (2012)	Cotton/Cry1Ac	Near isoline	<i>Scirpophaga incertulas</i> <i>Chilo suppressalis</i> <i>Aphis gossypii</i>	Non-target	Non-choice	Spatial distribution	Yes	The distribution pattern of aphids on Bt cotton was different from those on non-Bt cotton
Goldstein et al. (2010)	Maize/Cry1Ab	Near isoline	<i>Ostrinia nubilalis</i>	Target	Non-choice	Movement/dispersal behavior	Yes	Neonates abandoned more frequently Bt maize compared to non-Bt maize

Table 1 continued

References	Testing crop/gene	Negative control	Testing species	Target/non-target	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Gore et al. (2002a)	Cotton/Cry1Ac	Near isoline	<i>Helicoverpa armigera</i>	Target	Choice	Movement	Yes	Movement twice as far down on Bt cotton compared to non-Bt cotton
Gore et al. (2002b)	Cotton/Cry1Ac	Near isoline	<i>Helicoverpa zea</i>	Target	Non-choice	Movement	Yes	More bollworms moved from the site of infestation on Bt cotton than on non-Bt cotton
Halcomb et al. (2000)	Cotton/Cry1Ac	Not specified	<i>Helicoverpa ten</i>	Target	Non-choice	Feeding behavior	No	Feeding indiscriminately on BTK and non-BTK cotton
Hardke et al. (2012)	Bt cotton/Cry1Ac, Cry2Ab, Cry1F	Not specified	<i>Heliothis virescens</i>	Target	Non-choice	Feeding behavior	No	As above
Jackson et al. (2010)	Cotton/Cry1Ac, Cry1F	Not specified	<i>Spodoptera frugiperda</i>	Target	Choice	Oviposition behavior	No	Random oviposition on Bt and non-Bt cotton
Kumar (2004)	Cabbage/Cry1Ab	Not specified	<i>Plutella xylostella</i>	Target	Choice	Oviposition/foraging behavior	No	
Lei et al. (2009)	Cotton/Cry1Ac, Cry1Ab, Cry2Ab, Cry1Fa	Near isoline	<i>Liriomyza trifolii</i>	Non-target	Choice and non-choice	Feeding/oviposition behavior	Yes	More eggs oviposited and more feeding on non-Bt cotton
Li et al. (2007)	Cotton/Cry1Ac, Cry2Ab	Near isoline	<i>Trichoplusia ni</i>	Target	Choice and non-choice	Foraging behavior	Yes	More first instars moved to non-Bt leaves, whereas the third and fifth instars did not show significant differences in the first 8 h, but eventually more moved to non-Bt leaves
Li et al. (2010)	Cotton/Cry1Ac + CpTI	Near isoline	<i>Adelphocoris suturalis</i>	Non-target	Choice and non-choice	Oviposition behavior	No	
Liu et al. (2005)	Cotton/Cry1Ac + CpTI	Near isoline	<i>Aphis gossypii</i>	Non-target	Non-choice	Feeding behavior	Yes	Feeding waveforms were lower; frequencies of moving and finding sites were higher on Cry1Ac + CpTI cotton compared to isogenic line
López et al. (2013)	Maize/Cry1Ab	Near isoline	<i>Sesamia nonagrioides</i>	Target	Choice and Non-choice	Dispersal behavior	Yes	Larvae that hatched on Bt plants tended to disperse more than those hatched on non-Bt plants

Table 1 continued

References	Testing crop/gene	Negative control	Testing species	Target/non-target	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Lu et al. (2011)	Cotton/Cry1Ac, Cry2Ab	Near isoline	<i>Helicoverpa armigera</i>	Target	Choice	Spatial distribution	No	No preference for laying eggs between Bt and non-Bt cotton
Luong et al. (2016)	Cotton/Cry1Ac	Near isoline	<i>Helicoverpa armigera</i>	Target	Choice	Oviposition behavior	No	No difference in the number of captured males from refuge and Bt crops; females do not move far away from the site of emergence
Marquardt and Krupke (2009)	Maize/Cry3Bb1	Not specified	<i>Diabrotica virgifera</i>	Target	Non-choice	Mating behavior/dispersal behavior	No	Feeding frequency decreased and movement frequency increased in larvae
Men et al. (2005)	Cotton/Cry1Ac	Not specified	<i>Helicoverpa armigera</i>	Target	Choice and non-choice	Feeding behavior/movement	Yes	
Obonyo et al. (2008)	Maize/CryAb	Near isoline	<i>Chilo partellus</i> <i>Sesamia calamistis</i>	Target	Choice and non-choice	Oviposition behavior	No	
Orr and Landis (1997)	Maize/Cry1Ab	Near isoline	<i>Ostrinia nubilalis</i>	Target	Choice	Oviposition	No	
Petzold-Maxwell et al. (2012)	Maize/Cry3Bb1	Near isoline	<i>Diabrotica virgifera</i> (Susceptible strain)	Target	Choice	Feeding behavior	No	
Rojas et al. (2010)	Cotton/Cry1Ac	Not specified	<i>Diabrotica virgifera</i> (Resistant strain) <i>Aphis gossypii</i>	Target Non-target	Choice Non-choice	Feeding behavior Spatial distribution	No Yes	Bt cotton altered the normal pattern of aphid distribution in the crop
Ramachandran et al. (1998a)	Canola/Cry1Ac	Near isoline	<i>Bemisia tabaci</i> <i>Plutella xylostella</i>	Non-target Target	Non-choice Choice	Spatial distribution Movement	No Yes	The larvae moved from Bt to non-Bt canola before acquiring lethal doses of insecticidal protein
Ramachandran et al. (1998b)	Canola/Cry1Ac	Near isoline	<i>Plutella xylostella</i>	Target	Choice	Oviposition behavior	No	
Ramalho et al. (2014)	Cotton/Cry1Ac	Near isoline	<i>Alabama argillacea</i>	Target	Non-choice	Feeding behavior/dispersal behavior	Yes	Low acceptance of Bt plant stimulated their dispersal
Rao and Rao (2008)	Cotton/Bt	Not specified	<i>Helicoverpa armigera</i>	Target	Non-choice	Orientation/feeding behavior	Yes	Restless and minimum feeding behavior on Bt cotton; No orientation to Bt cotton plants

Table 1 continued

References	Testing crop/gene	Negative control	Testing species	Target/non-target	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Rovenská et al. (2005)	Eggplant/Cry3Bb	Experimental plant	<i>Tetranychus urticae</i>	Non-target	Choice	Feeding behavior	Yes	The spider mite preferred feeding on Bt eggplants
Rovenská and Zemek (2006)	Potato/GNA	Experimental plant	<i>Aulacorthum solani</i> , <i>Thrips tabaco</i> and <i>Tetranychus urticae</i>	Non-target	Choice	Foraging behavior	Yes	GNA potato less preferred by the three species in a choice test
Razze and Mason (2012)	Maize/Cry1F, Cry1Ab	Near isoline	<i>Ostrinia nubilalis</i>	Target	Choice	Movement/Dispersal behavior	Yes	Movement and dispersal were higher on Bt maize
Spencer et al. (2003)	Maize/Cry3Bb1	Near isoline	<i>Diabrotica vigifera</i>	Target	Choice	Movement	Yes	Adults movement to adjacent soybean crops
Stapel et al. (1998)	Cotton/Bt	Experimental plant	<i>Spodoptera exigua</i>	Target	Non-choice	Feeding behavior	Yes	More larvae on non-Bt cotton and more damage observed on non-Bt cotton
Sun et al. (2013)	Rice/Cry2A	Experimental plant	<i>Chaphalacrocis medinalis</i>	Target	Choice	Oviposition behavior	No	
Swamy et al. (2008)	Pigeonpeas/Cry1Ab, SBTI	Experimental plant	<i>Helicoverpa armigera</i>	Target	Choice	Oviposition/feeding behavior	No	
Telléz-Rodríguez et al. (2014)	Maize/Cry1F	Near isoline	<i>Spodoptera frugiperda</i>	Target	Choice	Oviposition behavior	Yes	Oviposition preference for undamaged Bt maize over damaged conventional maize
Van den Berg and Van Wyk (2007)	Maize/Cry1Ab	Near isoline	<i>Sesamia calamistis</i>	Target	Choice	Oviposition behavior	No	
Whitehouse et al. (2007)	Cotton/Vegetative insecticidal protein (Vip)	Experimental plant	Mirid bugs pollen beetles	Non-target	Choice	Feeding behavior	Yes	Vip cotton attracted more bugs and beetles
Zhang et al. (2004)	Cotton/CpTI-Bt	Not specified	<i>Helicoverpa armigera</i>	Target	Choice and non-choice	Feeding behavior	Yes	Lepidoptera neonate larvae avoided transgenic plants
Zhao et al. (2009)	Cotton/Cry1Ac	Not specified	<i>Helicoverpa armigera</i>	Target	Non-choice	Calling behavior	Yes	Calling was reduced, and the age of calling was delayed in resistant strains

the suitable sites for population growth (Bernays and Chapman 1994). IRGM crops have been shown to disrupt the feeding behavior of target phytophagous arthropods in both choice and non-choice tests (Zhang et al. 2004; Men et al. 2005; Chen et al. 2008). Target species may avoid or feed less on Bt crops, even though several species have exhibited no feeding preference between Bt and non-Bt tissues in choice bioassays (Swamy et al. 2008; Petzold-Maxwell et al. 2012). The results often vary with the protocols adopted. For example, the study by Petzold-Maxwell et al. (2012) used a choice test, whereas a non-choice test was used in an earlier study by Clark et al. (2006). Notably, many studies have exhibited that the non-target species prefer feeding on Bt crops (Liu et al. 2005; Rovenská et al. 2005; Whitehouse et al. 2007). One mechanism that could explain such preferences is that IRGM crops (e.g., Bt crops) suffer significantly less damage by the target pests; as a result, they are often more healthy (e.g., lower levels of induced secondary metabolites that defend against the herbivorous insects) and thus could be more attractive and/or more suitable for feeding by non-target herbivores (Whitehouse et al. 2007; Hagenbucher et al. 2013).

Mating and oviposition

Mating behavior plays an important role in mediating the effectiveness of the refuge strategy, which was designed to mitigate the development of insect resistance to IRGM crops (Gould 1998). To obtain high efficacy of such a strategy, random mating is expected to occur between the pool of the homozygous susceptible individuals from non-Bt crops and the homozygous resistant individuals from Bt crop fields (Cuong and Cohen 2003; Zhao et al. 2008; Marquardt and Kruple 2009). Alteration in mating or other related behaviors (e.g., calling behavior) of phytophagous insects could occur in IRGM crops. However, few studies have examined this subject. Zhao et al. (2009) observed reduced time spent on calling behavior in Bt-resistant *H. armigera*, and it may reduce the mating frequency of the resistant strain. Such behavioral changes may reduce the likelihood of hybridization, which might compromise the effectiveness of the refuge strategy.

Theory predicts that there should be a strong selection on female moths to avoid oviposition on the IRGM crops (e.g., Bt crops), which has become a sink for the main target pest. However, most of the studies have shown that the insects did not show any oviposition preference between Bt and non-Bt crops (Ramachandran et al. 1998b; Kumar 2004; Van den Berg and Van Wik 2007; Obonyo et al. 2008; Li et al. 2010; Hardke et al. 2012; Zalucki et al. 2012; Sun et al. 2013). These results suggest that the adults are not able to perceive Bt proteins, or the potential

alterations in plant features due to genetic modification do not interfere with their oviposition. By contrast, few species (either target or non-target) have shown oviposition preference for non-Bt plants (Lei et al. 2009), or Bt plants (Telléz-Rodríguez et al. 2014), when they have opportunities to choose. Notably, the latter case has provided compelling evidence that a major pest of maize, *S. frugiperda*, had a strong oviposition preference for Bt maize. Such an oviposition preference may undermine the effectiveness of refuge strategy in delaying the evolution of resistance.

Other behaviors

Phytophagous arthropods exhibit many other sophisticated behaviors among which learning behavior is one of the most important aspects. Learning and memory, a process defined as the acquisition and retention of neuronal representations of new information, are ubiquitous among insects (Dukas 2008). Indeed, learning is essential for host plant searching and selection because the species must learn to adjust their host plant preference in order to have higher fitness. However, little is known about how IRGM crops influence the learning behavior of phytophagous arthropods, with only few studies documenting the effects of Bt proteins on arthropod pollinators (e.g., Ramirez-Romero et al. 2008a; Han et al. 2010a).

Behavioral effects of IRGM crops on arthropod natural enemies

Within the framework of IPM, the compatibility between IRGM crops and natural enemies has become a major subject (Lundgren et al. 2009). Natural enemies are expected to exert strong top-down control on major pest insects in IRGM crop agro-ecosystems (Han et al. 2014). However, natural enemy arthropods can be susceptible to IRGM crops. In terms of exposure pathways, IRGM crops can affect natural enemies (1) directly through exposure to insecticidal proteins via feeding on IRGM crops tissues (e.g., omnivorous predators) (Torres and Ruberson 2006), (2) indirectly because IRGM crops may induce changes in crop environment such as the quantity or nutritional quality of non-prey foods, as well as plant cues that natural enemies rely on searching for food or shelter (Lundgren et al. 2009) or (3) indirectly owing to changes in “plant-herbivore-parasitoid/predator” tri-trophic interactions in food webs (Hilbeck et al. 1998; Zwahlen et al. 2000; Couty et al. 2001; Prütz and Dettner 2004; Obrist et al. 2005; Torres et al. 2006; Walker et al. 2007; Ramirez-Romero et al. 2007; García et al. 2010). The importance of this latter pathway has been critically

reviewed (Romeis et al. 2006; Naranjo 2009; Lundgren et al. 2009). Predator and parasitoid behaviors are vital to their success in suppressing herbivorous insects (Wajnberg et al. 2007). Behavioral traits such as mobility, foraging (host/prey location, selection and suitability), mating/oviposition, orientation/associative learning and other behaviors related to specific species are susceptible to diverse biotic or abiotic constraints in realistic settings (Landis et al. 2000; Heimpel and Casas 2007). So far, numerous studies have addressed the behavioral effects of IRGM crops on natural enemies (summarized in Table 2), and the findings have been extensively discussed in the context of biological control.

Locomotion (mobility)

Locomotion behavior (or mobility) is characterized as a set of parameters including the total activity period, mean velocity, total distance moved or the duration of movement. Locomotion of natural enemies reflects somehow the degree of activeness during pursuit of prey/host. Taking the predatory beetle as an example, mobility is usually measured as walking speeds and the durations until the beetles twirled after being placed on their dorsum (i.e., flip time) (Lundgren and Wiedenmann 2002, 2005; Ferry et al. 2007). Several studies have examined the effects of IRGM crops on these behaviors. The spotted lady beetle *Coleomegilla maculata* exhibited a similar mobility when feeding on the aphids that had consumed Cry3Bb1 or non-Bt maize even though the Bt maize-fed aphids exhibited lower biomass and thus of lower prey quality (Lundgren and Wiedenmann 2005). Similarly, the potato expressing Cry3A did not affect the locomotion behavior of the ladybeetle *Harmonia axyridis* or the ground beetle *Nebria brevicollis* (Ferry et al. 2007). Furthermore, indirect evidence was found in a field study showing that three predator species exhibited no difference in abundances before, during and after pollen shed in both Bt maize and conventional maize (Pilcher et al. 1997). Overall, the trait of locomotion alone has not received much interest. Studies often prefer to measure this trait in a more ecological-relevant context such as “foraging” (the section below). In other words, the mobility has been measured when a given natural enemy has an objective to target or risk to avoid in the habitat. In contrast with predator mobility, no study has specifically assessed the effect of IRGM crops on locomotion of parasitoids. However, locomotion involves in the orientation behavior of parasitoids in response to semiochemicals [e.g., herbivore-induced plant volatiles (HIPVs)] (Kessler and Baldwin 2001), which is discussed in the following section.

Foraging

The foraging process of natural enemies involves mainly, but not exclusively, several distinct and consecutive processes: habitat location, host/prey location, host acceptance and suitability (for parasitoids), or prey handling and consumption activities (for predators) (Hågvar and Hofsvang 1991). Parasitoids and predators rely on plant-derived cues (e.g., HIPVs) as well as host/prey-derived cues (e.g., odor and frass) to locate host or prey (Dicke et al. 2000; Dicke 2009; Pareja et al. 2009; Desneux et al. 2010). After the location being made, they select the most suitable host or prey for parasitism and predation.

Parasitoids Numerous studies have documented the effect of IRGM crops on the foraging behavior of parasitoids. We firstly summarize the studies that have compared foraging between Bt and non-Bt crops. Due to the increasing evolution of pest resistance to Bt proteins (Carriere and Tabashnik 2001; Tabashnik et al. 2003; Gassmann et al. 2011; Zhang et al. 2011; Wan et al. 2012), we then compare the foraging preference between susceptible and resistant host genotypes.

There has been much evidence showing that parasitoids do not discriminate foraging on Bt or non-Bt crops (Orr and Landis 1997; Schuler et al. 2003; Turlings et al. 2005; Sanders et al. 2007; Himanen et al. 2009; Liu et al. 2011; Moraes et al. 2011; Dutra et al. 2012; Liu et al. 2015). Such an indiscrimination may be attributed to the fact that the volatile blend has not been altered in IRGM crops compared to the isogenic line (Moraes et al. 2011; Liu et al. 2015). The indiscrimination was even observed in the case where the blend of volatiles was actually altered in Bt crops (Turlings et al. 2005). However, discrimination in parasitoid foraging between Bt and non-Bt crops may still occur when the environmental condition has changed (Himanen et al. 2009). While IRGM crops themselves might not directly influence parasitoid foraging behavior, host insects feeding on these plants may experience physiological changes (e.g., modifying certain cues in frass), which may influence the attractiveness of parasitoids (Desneux et al. 2010). Such an effect may be linked to the detrimental effects of Bt protein on the bacterial community and the modification of odors that are attractive to the parasitoid. Besides the case study on Bt crops, other types of IRGM crops have exhibited strong effects on parasitoids. For instance, the parasitoid *Diaeretiella rapae* exhibited strong arrestment responses on the plants genetically modified to emit aphid alarm pheromone (Beale et al. 2006). In addition, no disruption in parasitoid foraging was found on crops producing GNA (Setamou et al. 2002).

Parasitoids are likely to be exposed to the co-existence of susceptible, heterozygous resistance or resistant hosts. In

Table 2 A summary of behavioral effects of IRGM crops on arthropod natural enemies

References	Testing crop/gene	Negative control	Testing species	Host/prey species	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Parasitoids								
Beale et al. (2006)	Arabidopsis/ sesquiterpene - β -farnesene (E β F)	Experimental plant	<i>Diaeretiella rapae</i>	<i>Myzus persicae</i> (NT)	Non-choice	Arrestant response	Yes	Stronger arresting response of parasitoids
Desneux et al. (2010)	Maize/Cry1Ab	Near isoline	<i>Cotesia marginiventris</i>	<i>Spodoptera frugiperda</i> (T)	Choice	Foraging behavior	Yes	The foraging behavior was disrupted by the frass derived from Bt maize-fed host
Himanen et al. (2009)	Oilseed rape/ Cry1Ac	Not specified	<i>Cotesia vestalis</i>	<i>Plutella xylostella</i> (T)	Choice	Foraging behavior/ orientation	Yes	Parasitoids orientated more to non-Bt than Bt oilseed rape under elevated O ₃ concentrations; Such an effect was not found under elevated CO ₂ concentrations
Liu et al. (2011)	Broccoli/Cry1Ac	Experimental plant	<i>Diadegma insulare</i>	<i>Plutella xylostella</i> (T)	Choice	Foraging behavior	No	Parasitoids did not discriminate between Bt and non-Bt Broccoli as foraging habitat
Liu et al. (2015)	Rice/CryAb	Experimental plant	<i>Cotesia chilonis</i>	<i>Chilo suppressalis</i> (T)	Choice	Foraging behavior	No	Parasitoids did not discriminate between caterpillar-infested Bt rice and non-Bt rice
Loivamäki et al. (2008)	Arabidopsis/ PciSPS (Isoprene-emitting)	Experimental plant	<i>Diadegma semiclausum</i>	Unknown	Choice	Foraging behavior/ orientation	Yes	A repellent effect of GM isoprene-emitting plants on <i>D. semiclausum</i>
Moraes et al. (2011)	Cotton/Cry1Ac	Near isoline	<i>Trichogramma pretiosum</i>	<i>Spodoptera frugiperda</i> (T)	Choice	Foraging behavior	No	The effect above was not found on <i>C. rubecula</i>
Orr and Landis (1997)	Maize/Cry1Ab	Near isoline	<i>Eriborus terebrans</i> <i>Macrocentrus grandii</i>	<i>Ostrinia nubilalis</i> (T)	Choice	Foraging behavior	No	
Sanders et al. (2007)	Maize/Cry1Ab	Near isoline	<i>Camponotus sonorensis</i>	<i>Spodoptera frugiperda</i> (T)	Choice	Foraging/host preference	No	
Schuler et al. (2003)	Oilseed rape/ Cry1Ac	Near isoline	<i>Cotesia Plutellae</i>	Unknown	Choice	Foraging behavior	No	Parasitoids did not discriminate between Bt and wild plants
			<i>Plutella xylostella</i> (T)		Choice	Foraging behavior	Yes	More attracted to Bt plants damaged by Bt (R) hosts than Bt (S) hosts

Table 2 continued

References	Testing crop/gene	Negative control	Testing species	Host/prey species	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Setamou et al. (2002)	Sugarcane/GNA	Experimental plant	<i>Cotesia flavipes</i>	<i>Diatraea saccharalis</i> (NT)	Choice and non-choice	Host preference/Location	No	
Turlings et al. (2005)	Maize/Cry1Ab	Near isoline	<i>Cotesia marginiventris</i> <i>Microplitis rufiventris</i>	Unknown	Choice	Foraging/Orientation	No No	
Predators								
Arpaia et al. (2009)	Potato/Cry1Ab	Near isoline	Unknown generalist predators	<i>Leptinotarsa decemlineata</i> (NT)	Choice	Predation behavior	No	No effect on predation in Bt-potato field
Dogan et al. (1996)	Potato / Bt	Not specified	<i>Hippodamia convergens</i>	<i>Leptinotarsa decemlineata</i> (T)	Non-choice	Predation behavior	No	Prey egg consumption was similar between Bt and non-Bt eggplant
Dutra et al. (2012)	Maize/Cry1Ab	Near isoline	<i>Harmonia axyridis</i>	<i>Spodoptera frugiperda</i> (T)	Choice	Predation behavior	No	
Esteves et al. (2010)	Cotton/Cry1Ac	Near isoline	<i>Phytoseiulus macropilis</i>	<i>Tetranychus urticae</i> (NT)	Non-choice	Predation behavior	No	
Ferry et al. (2006)	Oilseed rape/Cry1Ac	Near isoline	<i>Phytoseiulus macropilis</i>	<i>Tetranychus urticae</i> (NT)	Choice	Oviposition behavior	No	
Ferry et al. (2007)	Potato/Cry3A	Not specified	<i>Pterostichus madidus</i>	<i>Plutella xylostella</i> (T)	Choice	Predation behavior	Yes	Predators preferred selecting/consuming non-Bt fed prey or Bt (R) prey than Bt (S) prey
Li et al. (2011)	Rice/Cry1Ab	Near isoline	<i>Harmonia axyridis</i> <i>Nebria brevicollis</i> <i>Pirata subpiraticus</i> <i>Tetragnatha maxillosa</i>	<i>Acyrtosiphon pisum</i> (NT) <i>Lacanobia oleracea</i> (T)	Non-choice Non-choice Choice	Lotomotion Predation behavior Locomotion Predation behavior Predation behavior	No No No No No No	

Table 2 continued

References	Testing crop/gene	Negative control	Testing species	Host/prey species	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Ludy and Lang (2006b)	Maize/ Cry1Ab	Near isoline	<i>Araneus diadematus</i>	Unknown	Choice	Predation behavior	No	No effect on the predation activity of spider toward prey
Lundgren and Wiedenmann (2005)	Maize/ Cry3Bb1	Not specified	<i>Coleomegilla maculata</i>	<i>Rhopalosiphum maidis</i> (NT)	Non-choice	Mobility	No	No effect on the spider reaction time toward prey
Meissle et al. (2005)	Maize/ Cry1Ab	Near isoline	<i>Poecilus cupreus</i>	<i>Spodoptera littoralis</i> (T)	Choice	Predation behavior	No	No effect on the spider web-building behavior
Meier and Hilbeck (2001)	Maize/ Cry1Ab	Near isoline	<i>Chrysoperla carnea</i>	<i>Spodoptera littoralis</i> (T)	Choice	Predation behavior	Yes	Predators preferred consuming non-Bt maize fed prey than Bt maize-fed prey
Pilcher et al. (1997)	Maize/ Cry1Ab	Near isoline	<i>Coleomegilla maculat</i> <i>Orius insidiosus</i> <i>Chrysoperla carnea</i>	<i>Rhopalosiphum padi</i> (NT) Unknown	Non-choice	Mobility	No No No	
Prager et al. (2014)	Maize/ Cry3Bb1, Cry1Ab	Near isoline	<i>Phytoseiulus persimilis</i>	<i>Tetranychus cinnabarinus</i> (NT)	Choice	Predation behavior	Yes	Spent more time in the vicinity of non-Bt spider mites than near Bt spider mites
Riddick and Barbosa (1998)	Potato/ Cry3A	Not specified	<i>Coleomegilla maculate</i>	<i>Leptinotarsa decemlineata</i> (T)	Non-choice Choice	Predation behavior Predation behavior	Yes No	The predator consumed non-Bt spider mites at a faster rate than Bt spider mites
Rovenská et al. (2005)	Eggplant/ Cry3Bb	Experimental plant	<i>Phytoseiulus persimilis</i>	<i>Tetranychus urticae</i> (NT)	Choice	Predation behavior	Yes	Predators preferred consuming prey from non-Bt eggplant than Bt eggplant
Torres and Ruberson (2006)	Cotton/ Cry1Ac	Not specified	<i>Geocoris punctipes</i> <i>Chrysoperla rufilabris</i> <i>Micromus spec.</i>	Unknown	Non-choice	Oviposition behavior	No No No	

Table 2 continued

References	Testing crop/gene	Negative control	Testing species	Host/prey species	Choice/non-choice	Behavior types	Effect on behavior?	Outcome
Toschki et al. (2007)	Maize/Cry1ab	Near isoline	Spiders and carabid beetles	Unknown	Non-choice	Phenological behavior	No	
Zhang et al. (2006)	Cotton/Cry1Ac, Cry1Ab	Near isoline	<i>Propylaea japonica</i>	<i>Aphis gossypii</i> (NT)	Non-choice	Mating behavior	Yes	Predators preying on Bt-fed prey mated more frequently

T host/prey targeted by IRGM crops, NT host/prey not targeted by IRGM crops

this context, parasitoids have to make a choice among them when foraging. The decision made by parasitoids may influence how the pest population is structured, i.e., the relative abundance of the co-existing three genotypes. As a result, foraging behavior may have considerable effects on the evolution of resistance to IRGM crops in target pests (Lundgren et al. 2009), which has been demonstrated in a modeling study on *Plutella xylostella* (Onstad et al. 2013). Few empirical studies have addressed this specific issue. For example, the parasitoid *Cotesia plutellae* preferred to forage Bt-resistant diamondback moth than the Bt-susceptible host on Bt oil-seed rape (Schuler et al. 2003). This foraging preference may benefit the overall management of the diamondback moth as biocontrol service provided by the parasitoid can add up to the effect of the Bt crop. However, this was not always the case. For example, the parasitoid *Diadegma insulare* did not discriminate among different genotypes of *P. xylostella* feeding on Bt broccoli (Liu et al. 2011). In this case, the effects of parasitism on Bt-resistant host genotypes were diluted by the allocation of parasitism on Bt-susceptible hosts. In other words, the parasitism is actually considered redundant with the effects of Bt proteins. Furthermore, the non-discrimination in parasitoid foraging may not help reducing the selection of resistant pest populations in Bt crops.

Predators Predator foraging behavior is a set of activities that are closely associated with each other, including prey location and selection as well as the following prey handling and consumption activities. Paired-choice assays in the “Bt/non-Bt crop-prey-predator” tri-trophic systems have been largely used to test the effects of Bt crops on prey preference and consumption by predators. The effects of Bt crops on predators are discussed (1) when the predator itself belongs to the targeted insect order (e.g., Coleoptera) (direct effect via Bt protein toxicity), (2) when the prey species is targeted by Bt protein or (3) when the prey are non-target species but they can accumulate Bt proteins (e.g., spider mites).

Effects on predators may occur through direct ingestion of IRGM crop materials (e.g., pollen and tissues). Phytophagy is thought to sustain a certain group of predators (i.e., omnivorous predators) during the period of low prey availability. Thus, their fitness may be influenced via exposure to Bt protein (Lundgren et al. 2009). However, little evidence has been found for the effects of Bt crops on omnivorous predators even though feeding on Bt plants was directly observed (Moser et al. 2008). For example, the ladybird beetle *H. axyridis* and the carabid beetle *Nebria brevicollis* exhibited similar behaviors of prey selection and prey consumption on both Bt potato and conventional line (Ferry et al. 2007). The highly polyphagous predators from the Carabidae family appear to make the prey

selection decision mainly based on prey quality (see below), not based on whether the crop produces Bt protein.

In the case where prey is a target species, exposure to IRGM crops may cause lethal and sublethal effects on the prey species, which may in turn make them unsuitable for the predator. Predators have been documented to show behavioral avoidance of low-quality food (e.g., poisoned or sick prey), for example the Bt-fed susceptible (Bt (S)) prey, compared to the non-Bt fed prey (Riddick and Barbosa 1998; Meier and Hilbeck 2001; Ferry et al. 2006; but see Meissle et al. 2005) or the Bt-fed resistant (Bt (R)) prey (Ferry et al. 2006). Indeed, generalist predators are able to exhibit behavioral plasticity to cope with highly variable prey quality of numerous prey types (Symondson et al. 2002). Occasionally, they have to include the Bt (S) prey into their diet mixture to support their reproduction when the Bt (R) is scarce in the habitat (Ferry et al. 2006). The predation preference for Bt (R) prey can reduce the population size of this group and avoid delivering a redundant suppression force on Bt (S) prey. When the pest is consumed in the egg stage, however, prey quality is less likely to be affected by Bt crops. Then, it is readily understandable that generalist predators consumed the eggs of target pests from the Bt and their isogenic conventional lines equally (Orr and Landis 1997; Arpaia et al. 2009).

In the case where prey is a non-target species, we should stress the importance of Hemipteran pests even though Bt proteins exhibit negligible impact on sap-feeding insects (Chougule and Bonning 2012). Specifically, aphids, as one of the most important pest groups, do not ingest considerable amounts of insecticidal proteins when feeding on Bt crops (Ramirez-Romero et al. 2008b; Romeis and Meissle 2011). Thus, they generally do not represent a major route of exposure of Bt proteins to predators as well as other natural enemies. The lack of behavioral effects of Bt-fed aphid on predators has been documented (Dogan et al. 1996; Meissle et al. 2005). By contrast, spider mites are known to acquire and accumulate higher concentrations of Bt proteins than those present in Bt crops (Dutton et al. 2002; Obrist et al. 2006; Esteves et al. 2010; Torres and Ruberson 2008; Meissle and Romeis 2009; Li and Romeis 2010). Such an exposure pathway to Bt proteins via spider mite may put their predators at risk. However, most of the studies lack the behavioral assessment of the exposed predators, or the predator was found exhibiting a similar predation rate on the prey feeding on Bt and non-Bt crops (Esteves et al. 2010). Interestingly, predators have been shown to avoid foraging a given plant type that actually has attracted abundant prey. For example, the Cry3Bb eggplants attracted more spider mites, while this type of Bt-fed prey was less attractive to the predatory mite *Phytoseiulus persimilis*. Such an effect has been attributed to the fact that *Phytoseiulus persimilis* intended to avoid the Cry-

containing prey (Rovenská et al. 2005). A lower predation rate on Bt-fed spider mites by predatory mites has also been observed on Bt maize (Prager et al. 2014). Generally, predators often adopt active prey selection to compromise among maximizing energy intake, balancing the nutrient composition of the prey body and minimizing toxin consumption (Toft 1999). In the two cases described above, the disruption in predation behavior of the predatory mite, i.e., avoiding consumption of Bt-fed prey, may compromise the compatibility of Bt eggplants and predatory mites in managing spider mites.

Mating and oviposition

Few studies have assessed the effects of IRGM crops on mating and oviposition behavior of natural enemies. Zhang et al. (2006) observed a more frequent mating in the ladybeetle *Propylaea japonica* feeding on Bt cotton than on non-Bt cotton, whereas such an effect was not found in the Coccinellid, *H. axyridis* (Ferry et al. 2007). Although the transmission of Bt proteins through non-target prey to the ladybeetles may pose sublethal effects on their behavior, the mechanisms underlying such effects remain to be explored. After mating, predators should select a suitable plant species or plant part as oviposition site. It has been shown that predators rely upon physical traits such as substrate sickness, trichome density and shape when selecting an oviposition site (Shapiro and Ferkovich 2006; Lundgren et al. 2008; Seagraves et al. 2011). Despite the unintentional effects that may arise in the process of genetic modification in plants (Haslberger 2003; Cellini et al. 2004), these changes may not be able to disrupt the oviposition behavior of arthropod predators. Indeed, Torres and Ruberson (2006) showed that the spatial distribution pattern of predator eggs was similar between Bt and conventional cotton plots, indicating no difference in their site selection for oviposition. Similar results were found with the predator mite *Phytoseiulus macropilis* ovipositing on Bt and non-Bt cotton (Esteves et al. 2010).

In the case of parasitoids, mating behavior has been experimentally observed in the field studies (Antolin and Strand 1992; Fauvergue et al. 1999). However, no comparative study has been conducted to test the effects of IRGM crops on their mating behavior. The following oviposition behavior often refers to laying eggs inside the host bodies (larvae or eggs) or on the surface of the bodies, which is actually one part of the foraging process. For example, *Parallorhogas pyralophagus* females preferred to probe, drill and parasitize *Eoreuma loftini* larvae, the Mexican rice borer, fed on GNA-free sugarcane than those fed on GNA-containing sugarcane (Tomov et al. 2003). Such a parasitism preference may benefit the control of *E. loftini*. However, the ecological relevance needs to be

further assessed as GNA-containing sugarcane materials mixed in artificial diets was used in this study. Another case study has reported a neutral effect that the larval parasitoid *D. insulare* exhibited a similar parasitism rate between Bt broccoli-fed resistant and non-Bt broccoli fed *P. xylostella* larvae (Liu et al. 2011). Besides the direct observation of oviposition behavior, we can assess the oviposition behavior indirectly by examining the outcome of oviposition behavior (i.e., parasitism rate). However, this approach may be misleading since the parasitism rate can be influenced by host acceptance and suitability (Desneux et al. 2012).

Other behaviors

Orientation and foraging of natural enemies rely on an important activity, i.e., the associative learning of visual cues and oviposition/herbivory-induced plant volatiles (Lewis and Tumlinson 1988; Vet and Groenewold 1990; Meiners et al. 2003; De Boer and Dicke 2006; Schroder et al. 2008; Desouhant et al. 2010; Benelli and Canale 2012). There has been an increasing recognition of associative learning as an important capacity in foraging success, either for predators or parasitoid wasps (De Boer et al. 2005; Dukas 2008). For example, the parasitoid *Leptopilina heterotoma* can learn to respond to a novel odor of a given pest species that can be used in the subsequent host location. Such an association can be stronger when the parasitoid is rewarded with an oviposition experience (Vet and Groenewold 1990). Odor learning is of adaptive importance for this generalist parasitoid, since it helps enhance host location efficiency by reducing the time allocated to the decision on where to search for hosts (Canale et al. 2014). To our knowledge, however, no study so far has been conducted to assess the effects of IRGM crops on associative learning in arthropod natural enemies.

Other specific behaviors of concern are mainly exhibited by the species from the class Arachnida. Spiders exert strong predation pressures on a wide range of insect taxa and thus considerably contribute to the biocontrol services in the garden or cropping field (Peterson et al. 2011). Although spiders are exposed to Bt proteins by feeding pollen containing the proteins or infected prey (Ludy and Lang 2006a), such an exposure did not affect their fitness and predation activity on prey (Ludy and Lang 2006b; Meissle and Romeis 2009; also see review by Peterson et al. 2011). For example, the garden spider *Araneus diadematus* spent similar reaction times toward prey fed with Bt and conventional maize pollen. Moreover, orb-web geometry, the most direct parameter of the spider's web-building behavior, was not disrupted when they consumed Bt maize pollen (Ludy and Lang 2006b). A 3-year field study also demonstrated that the phenological behavior of

spiders and carabid beetles was not affected by the Bt maize (Toschki et al. 2007).

Behavioral effects of IRGM crops on arthropod pollinators

Since the debate over the potential risk of Bt plant pollen on the survival and feeding behavior of the monarch butterfly (Losey et al. 1999; Hansen Jesse and Obrycki 2000; Hellmich et al. 2001), concerns have been increasingly raised over the negative effects of IRGM crops on arthropod pollinators. Honeybees, bumblebees as well as other non-bee pollinators are the most known functional group of arthropod pollinators in nature (Rader et al. 2016). In Bt crops, for example, the cotton nectar or maize pollen attracts honeybee foragers (Babendreier et al. 2004; Duan et al. 2008) and thus becomes a potential route of exposure to the Bt proteins for honeybees (EFSA 2013). In certain cultivars, a relatively high expression level of Bt proteins has been reported (Han et al. 2010a, b). This scenario becomes even worse for the foraging bees if a given crop variety is extensively cultivated in an area where alternative nectar/pollen-producing plants are unavailable or out of season (Haydak 1970). Therefore, honeybee has been considered a key non-target arthropod surrogate in the framework of environmental risk assessments of IRGM crops (Romeis et al. 2008). Two review articles have concluded that Bt proteins did not induce lethal effects on honeybee larvae or adults (Duan et al. 2008; Malone and Burgess 2009), and the neutral effects have been documented in the more recent literature (Liu et al. 2009; Han et al. 2010a, b, 2012; Lima et al. 2011; Hendriksma et al. 2011; Dai et al. 2012a, b, 2015; Niu et al. 2013).

Several studies have examined the behavioral effects of Bt plant materials on feeding behavior (Han et al. 2010b), foraging behavior (Dai et al. 2012a) and olfactory/visual learning behavior (Han et al. 2010a; Dai et al. 2012a) in the honeybee *Apis mellifera* as well as larvae feeding behavior, movement (Prasifka et al. 2007) and oviposition behavior (Tschenn et al. 2001) in the monarch butterfly *Danaus plexippus* (summarized in Table 3). The deleterious effects of Bt pollen on honeybee feeding behavior may lead to malnutrition of the colony, though the mechanisms underneath such effects and the ecological consequences remain to be explored. The monarch butterfly was found to exhibit similar oviposition behavior on milkweed plant dusted pollen from Bt maize or the conventional maize (Tschenn et al. 2001). However, they behaved differently when exposed to Cry1Ab-expressing maize anthers in which they exhibited increased wandering and more movement under laboratory conditions (Prasifka et al. 2007). Still, whether such behavioral alterations could translate into population effects in the field remains to be

known. The results may be case dependent. In a larger scale experiment in greenhouses, however, the pollination activities of bumblebees were found to be compatible with Bt eggplant (Arpaia et al. 2011).

Other behavioral assays on honeybees or bumblebees have used artificial diets contaminated with insecticidal Cry protein or other toxic proteins (e.g., SBTI, BBI, CpTI) regarding feeding behavior (Malone and Pham-Delègue 2001; Ramirez-Romero et al. 2005, 2008a; Babendreier et al. 2008), flight activity (Malone et al. 2001), foraging (Picard-Nizou et al. 1995; Ramirez-Romero et al. 2005; Mommaerts et al. 2010) and olfactory learning behavior (Picard-Nizou et al. 1997; Pham-Delègue et al. 2000; Ramirez-Romero et al. 2008a). Most studies have performed the bioassays using artificial diets contaminated with high doses of those insecticidal proteins. Negative effects on olfactory learning and feeding behavior in honeybees have been reported (Picard-Nizou et al. 1997; Ramirez-Romero et al. 2005, 2008a). However, the ecological relevance of those behavioral effects needs to be further explored (Ramirez-Romero et al. 2008a).

The importance of behavioral aspects for sustainable use of IRGM crops

As part of the environmental risk assessment process that takes place before the commercial release of IRGM crops, the potential adverse effects of IRGM on non-target arthropods, notably the natural enemies and arthropod pollinators, have been considered an extremely important issue for the scientific community, public and regulatory agencies (Raybould 2006; Raybould et al. 2007; Rose 2007; Romeis et al. 2008, 2011; Hilbeck et al. 2012). A tiered approach has been internationally recognized, which focuses on problem formulation including policy goals, scope, assessment endpoints and methodology, testing of clearly defined risk hypotheses and progressing between testing tiers (i.e., laboratory, semi-field and open field conditions) (Romeis et al. 2008; Álvarez-Alfageme et al. 2011). To increase the robustness and confidence of data gathered under laboratory conditions, Romeis et al. (2011) provided recommendations on the experimental design concerning the selection of surrogate species and life-stages, test substance, measurement endpoints, test duration, control substances and statistical considerations under the defined standards of good laboratory practice. Currently, the primary measurement endpoints include mortality, fecundity, developmental duration of each life stage, growth, predation rate, parasitism rate and the percentage of testing individuals reaching a certain life stage. Behavioral aspects have been rarely considered in the legislation of IRGM crops. So far, no behavioral effect that later caused significant harm (e.g., failure of crop yield or pest

outbreaks) in the field has been missed in the pre-market risk assessment as it was conducted. However, we claim that special attention needs to be paid to several key behavioral traits either before or after the release of the IRGM crop line, such as locomotion/oviposition of the target Lepidopterans, olfactory/visual associate learning of honeybees and foraging behavior (e.g., prey/host selection) of arthropod natural enemies. Such an assertion is in line with the guidance document by the European Food Safety Authority (EFSA) regarding the risk assessment of IRGM crops on phytophagous arthropods and arthropod pollinators (EFSA 2011, 2013).

One major concern is that behavioral effects on phytophagous arthropods (especially the target species) might have important implications for management of resistance evolution. This issue becomes crucial as the resistance to Cry1F maize has been documented on *S. frugiperda* (Storer et al. 2010). One possible mechanism is that the isogenic conventional maize that was heavily damaged by *S. frugiperda* becomes less attractive to the ovipositing adults than Cry 1F maize. Such a behavioral change, i.e., the damage-avoiding oviposition as populations increase, may accelerate the resistance evolution and either lead to requirements for a larger refuge or undermine resistance management altogether (Telléz-Rodríguez et al. 2014). Besides oviposition, an increased larval dispersal rate with less exposure to Bt crops may also result in a lower efficiency for the refuge strategy (López et al. 2013). Indeed, physiologically mediated resistance is considered to develop more slowly when the species shows avoidance of food containing Bt proteins (Jallow and Hoy 2007; Onstad 2008). All these behavioral effects should be of major concern to the scientific community.

Pollinators such as honeybees exhibited many behavioral traits namely foraging, orientation, feeding, coordination, wagging dances, nestmate recognition and repellency, which are highly valued by apiculture and agriculture. Among them, foraging is a critical behavior for the nutritional status and health of the bee population (Malone and Pham-Delègue 2001; Chittka et al. 2003; Decourtye et al. 2010). When exposed to risky abiotic factors, the relevant traits, such as associate olfactory/visual learning capacities, are expected to be carefully assessed (Greggers and Menzel 1993; Ramirez-Romero et al. 2005, 2008a, b; Han et al. 2010a; Dai et al. 2012a). Furthermore, more realistic field studies on pollinators can follow laboratory evaluation procedures (Thompson 2003; Decourtye et al. 2004, 2013; Mommaerts et al. 2009; Gill et al. 2012; Rondeau et al. 2014; Dively et al. 2015). Once some behavioral effect has been observed, some procedures should be further tested, renewed and standardized. Numerous promising tools can be used and improved in future behavioral studies (summarized in Table 4).

Table 3 A summary of behavioral effects of IRGM crops on arthropod pollinators

References	Crop/gene	Control crop	Arthropod species	Behavior types	Effect on behavior?	Outcome
Dai et al. (2012a)	Maize/Cry 1Ah	Near isoline	<i>Apis mellifera</i>	Foraging behavior	No	
				Olfactory learning behavior	No	
Han et al. (2010a)	Cotton/Cry1Ac + CpTI	Near isoline	<i>Apis mellifera</i>	Olfactory learning/Visual learning behavior	No	
Han et al. (2010b)	Cotton/Cry1Ac + CpTI	Near isoline	<i>Apis mellifera</i>	Feeding behavior	Yes	Antifeedant effect on honeybees
Prasifka et al. (2007)	Maize/Cry1Ab	Near isoline	<i>Danaus plexippus</i>	Movement/feeding behavior	Yes	Larvae exposed to Bt anthers spent more time moving and less time for feeding on anthers
Tschenn et al. (2001)	Maize/Cry1Ab	Near isoline	<i>Danaus plexippus</i>	Oviposition behavior	No	

While behavioral effects on arthropod natural enemies are less advocated by researchers and regulators, we do advocate that understanding natural enemy foraging preferences among various genotypes of pest insects (susceptible, resistance or heterozygous resistance) is vital to increase the synergy between IRGM crops and the bio-control agents in pest management. For instance, we could improve IPM if natural enemies prefer to attack resistant pest genotypes (Riddick and Barbosa 1998; Meier and Hilbeck 2001; Schuler et al. 2003; Ferry et al. 2006). Moreover, contrast, the unexpected foraging preferences may undermine the goal of IPM when predators do not prefer to locate on Bt crops where pests have been attracted (Rovenská et al. 2005). Other important behavioral traits in natural enemies such as mating and oviposition should also be investigated for the potential risks of IRGM crops, following the experience of studying sublethal effects of insecticides on arthropod natural enemies (Desneux et al. 2007; Biondi et al. 2012).

Furthermore, the behavioral aspects need to be carefully assessed for the following reasons. First, the process of behavioral effects assessment is likely to offer new insights into examining associated physiological aspects that have not been considered before. Behavioral effects often coincide with physiological change in arthropods (Desneux et al. 2007), and any evidence of behavioral disruption may trigger additional tests on physiological changes. For example, the antifeedant effect observed in honeybees during an oral exposure to cotton pollen containing Cry1Ac (Han et al. 2010b) has triggered further investigations into the possible effects of antifeedant behavior on hypopharyngeal gland development and into the mechanisms underlying such an antifeedant effect (Han et al. 2012). Sublethal behavioral effects are often recorded by detailed

observation; once verified, the mechanisms underlying the effect are expected to be explored. The data from the following in-depth studies can not only enhance the reliability of the observed behavior effect, but also propose new questions. Second, rapid advances in insect behavioral ecology from theoretical approaches to field applications have been achieved with a vision of multi-trophic interactions (Wajnberg et al. 2007). One of the longstanding goals of behavioral ecology is to understand how individual behavioral changes translate into population processes and to unravel the role of these traits in shaping community structure (Werner and Peacor 2003; Vet and Godfray 2007). Based on this point, with the increasing cultivation of IRGM crops worldwide, the agro-ecosystem landscapes are undergoing tremendous changes in community structure and functioning of biological interactions. If the assumptions above are true, more attention needs to be paid to the responses of insect behaviors (mainly major pest species, key natural enemies and arthropod pollinators) in future studies.

Conclusions

The widespread cultivation of IRGM crops creates an agricultural environment conserving the ecological services of resident and immigrant natural enemies (Lundgren et al. 2009; Lu et al. 2012) and arthropod pollinators (Johnson et al. 2010). The concurrent benefit is that the reduction in insecticide applications, may favor the fitness of beneficial arthropods (Thompson 2003; Desneux et al. 2007). However, behavioral effects of IRGM crops on phytophagous arthropods (mainly major agricultural pest), natural enemies and arthropod pollinators need to be

Table 4 An overview of promising tools/procedures for assessing behavioral effects of IRGM crops on arthropod pollinators and natural enemies

Arthropod group	Behavioral trait	Evaluation tools/procedures	References	
Pollinators	Olfactory learning	Conditioned-PER (proboscis extension response)	Picard-Nizou et al. (1997) Pham-Delègue et al. (2000) Ramirez-Romero et al. (2005, 2008a) Han et al. (2010a)	
	Visual learning	T-maze	Han et al. (2010a)	
	Foraging behavior/ Pollination	Artificial flower feeder Field parallel strips observation Evaluation of foraging bees returning to hives	Pierre et al. (2003) Decourtye et al. (2004) Ramirez-Romero et al. (2005) Dai et al. (2012a)	
	Flight activity	Evaluation of tagged bees	Malone et al. (2001)	
	Parasitoids	Foraging behavior	“Y-tube” dual-choice olfactometer Four-arm olfactometer Wind tunnel Six-arm olfactometer	Moraes et al. (2011) Vet and Groenewold (1990) Setamou et al. (2002) Desneux et al. (2010) Schuler et al. (1999, 2003) Turlings et al. (2005)
Predators		Olfactory learning	Conditioning using host frass/odor and subsequent testing	Meiners et al. (2003)
		Locomotion/foraging behavior	Visual-observation or video-recording in arena	Meier and Hilbeck (2001) Meissle et al. (2005) Ferry et al. (2006, 2007) Dutra et al. (2012)
		Predation behavior	DNA-based gut-content analysis	Harwood et al. (2007)
	Predation behavior	PCR-ligase detection reaction (LDR)	Li et al. (2011)	
Predators	Predation behavior	Modified Mungler cell	Rovenská et al. (2005)	
	Predation/ mobility/web building	Wood frames with spider web exposure to IRGM crop pollen in the field and feeding by spiders	Ludy and Lang (2006b)	

carefully assessed in order to maintain the potential benefits of IRGM crops in agriculture. Key results of this review are outlined:

1. Among the three groups, phytophagous arthropods are the most affected by the IRGM crops (54.2 % out of total cases) (Table 5). Locomotion and foraging behaviors are frequently affected by IRGM crops, while mating and oviposition behaviors are less affected. Target species are more likely to experience behavioral changes (e.g., locomotion and feeding), and the implications of these behavioral effects relevant to insect resistance evolution need to be considered with caution. The altered behavior in non-target arthropods (preference to Bt crops) may contribute to higher damage to Bt crops.
2. The minority of the studies (22 %) exhibited behavioral effects on arthropod natural enemies (Table 5). The effects mainly refer to the behavioral preference

when they select their host or prey. Generally, they avoid the host or prey of lower quality because of the lethal and/or sublethal effects of IRGM crops. However, we should notice that these behavioral effects may be unnecessarily due to the presence of plant insect-resistant traits. In around 30% of the total case studies reporting behavioral effects, the genetic background of negative control plants has not been fully characterized, and the plant counterparts are likely to differ in many other unknown characteristics as discussed above. Thus, caution needs to be taken when referring to these studies. Overall, we conclude that behavioral effects of IRGM crops on arthropod natural enemies via tri-trophic links are limited. However, we should not underestimate the unintentional behavioral effects that may undermine their biocontrol services in agro-ecosystems (e.g., predation behaviors, Rovenská et al. 2005; Prager et al. 2014).

Table 5 A summary of existing case studies on behavioral effects of IRGM crops on phytophagous arthropods, arthropod natural enemies and arthropod pollinators

	Effect (yes)			Effect (no)			Total
	Target	Non-target	Unknown	Target	Non-target	Unknown	
Phytophagous arthropods							
Number of studies	22	10		25	2		59
Percentage	54.2% (yes)			45.8% (no)			
Arthropod natural enemies	Target prey/host	Non-target prey/host	Unknown	Target prey/host	Non-target prey/host	Unknown	
Number of studies	5	5	1	15	8	16	50
Percentage	22% (yes)			78% (no)			
Arthropod pollinators							
Number of studies		2			4		6
Percentage		33% (yes)			67% (no)		

Effect (yes) or effect (no) indicates the presence or absence of behavioral effects. The effects on phytophagous arthropods have been separated as the species is targeted (or not) by the genetically modified insect resistance. The effects on natural enemies have been separated as the prey/host species is targeted (or not) by the genetically modified insect resistance or unknown. The proportions of observations of behavioral effects for each arthropod group were calculated based on the number of case studies

3. Behavioral effects of IRGM crops on arthropod pollinators are relatively limited (Table 5). Negative effects on honeybee foraging behavior have been found in several studies using artificial diets containing transgenic plant materials. More realistic bioassays are required to better understand the ecological relevance.

Understanding the behavioral effects of IRGM crops on phytophagous and beneficial arthropods is critical for the compatibility among genetically modified insect resistance, biological control and beneficial pollinators in securing crop production. In general, behavioral alterations in arthropods due to IRGM crops seem not deleterious to the goal of IPM. However, the current knowledge is far from telling us how those arthropods are actually influenced and what the real ecological consequences are. We face various constraints in enhancing our understanding on this subject. For example, current studies have been mostly carried out in laboratory settings with semi-field and field tests largely lagging behind, which is especially the case for parasitoids (Heimpel and Casas 2007). The techniques available for behavioral tests have been well developed but are still limited (Table 4). Future efforts can be made to design more reliable tools for behavioral studies under field conditions. Furthermore, it provides valuable insights about the effects of behavioral changes on the community dynamics of interacting species (Vet and Godfray 2007). It is important to understand the indirect interactions

triggered by behavioral traits, for example, the trait-mediated indirect interactions among the natural enemies and other organisms from different trophic levels within the arthropod community (Werner and Peacor 2003; Schmitz et al. 2004). As IRGM crops become increasingly widespread worldwide, we believe that more in-depth behavioral studies on plant-inhabiting arthropods are going to considerably improve the sustainability of agriculture using IRGM crops.

Author contribution statement

RRR and ND conceptualized the review article. PH, MCVH, RRR and ND wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Glossary

Associative learning behavior	The behavior involves the establishment, through experience, of an association between two stimuli or between a stimulus and a response.
Sublethal behavioral effects	The behavioral alteration in an arthropod individual that survives an exposure to plant materials containing genetically modified insect-resistant proteins or other toxic compounds.
Calling behavior	Acoustic signals displayed by males for the purpose of attracting mates and repelling rivals.
Dispersal behavior	The capacity of an arthropod in moving/flight and the potential for its spatial distribution.
Foraging behavior	The behavior of an arthropod searching for food, host or prey.
Refuge-in-the-bag	A tactic that planting of mixed Bt and non-Bt crops for preventing or delaying resistance evolution in target arthropod species.

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