Three-way interactions between crop plants, phytopathogenic fungi, and mirid bugs. A review

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REVIEW ARTICLE

Three-way interactions between crop plants, phytopathogenic fungi, and mirid bugs. A review

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Abstract

Miridae is the largest Heteroptera family, with a tremendous worldwide economic impact, both as pests and natural enemies. Unlike most Hemiptera, herbivorous and omnivorous mirid bugs are lacerate/macerate and flush feeders, not phloem feeders. Plant responses to damage by arthropods of this feeding guild therefore occur via jasmonic acid or ethylene signaling pathways rather than the salicylic acid pathway. Moreover, unlike most other Heteroptera that lay eggs on the plant surface, mirids insert their eggs in plant tissues, resulting in oviposition injury. Similarly, regarding phytopathogenic fungi and oomycetes, a distinction should be made between biotrophic fungi (triggering the salicylic acid pathway plant response), and necrotrophic and/or hemibiotrophic fungi or oomycetes (triggering jasmonic acid or ethylene pathway plant responses). In that respect, phytopathogenic fungi or oomycetes (PFO) differ from phytopathogenic viruses and bacteria, the former being all biotrophic while the latter are theoretically hemibiotrophic. Here, for the first time, we review tripartite interactions between mirids, PFO, and crop plants. The major deliverables are as follows: Five major interaction frameworks are identified: (i) crop plant infection by PFO mechanically facilitated by prior mirid infestation; (ii) crop plant infection by PFO hampered by prior mirid infestation via crop plant signaling; (iii) crop plant infestation by mirids facilitated by prior PFO infection via crop plant signaling; (iv) crop plant infestation by mirids hampered by prior PFO infection via crop plant signaling; (v) crop plant infestation by mirids and/or infection by PFO hampered by prior mirid infestation and/or PFO infection via crop plant resource quality alteration. PFO and mirids may also occur concomitantly, favored by the same conditions, i.e., climatic or linked to endogeneous factors (e.g., redox status) in crop plant. Instances from each framework are described, and highlighted interactions are examined in view of managing mirid–PFO complexes on crop plants.

Keywords Biotrophic · Grain mold · Herbivorous · Heteroptera · Mango · Miridae · Necrotrophic · Omnivorous · Powdery mildew · Sorghum

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1 Introduction

Plant pathogens and arthropod pests individually or cumulatively have an adverse impact on crop plant health, generally leading to crop damage and loss, and sometimes plant mortality (Oerke 2006). Plant pathogens (Savary et al. 2012), particularly phytopathogenic fungi and oomycetes (Meng et al. 2009), cause many highly destructive plant diseases, often with severe economic consequences for farmers.

For instance, in the European Union alone, late blight caused by the oomycete *Phytophthora infestans* (responsible for the disastrous Irish famine in the mid-nineteenth century; Wheeler Jr 1981) still causes annual losses (control and damage costs) estimated at more than €1.0 billion (Haverkort et al. 2008). Otherwise, insect pests were estimated to cause an average annual loss of 7.7% in crop production in Brazil alone, corresponding to a total annual economic loss of approximately US$17.7 billion (Oliveira et al. 2014). In China, the plant bug *Apolygus lucorum* alone is held responsible for cotton yield losses of up to 20–30% every year (Zhang et al. 2017).

Stout et al. (2006) assessed plant-mediated interactions between pathogenic microorganisms and herbivorous arthropods. Hatcher (1995) and Rostas et al. (2003) reviewed three-way interactions between plant pathogenic (or phytopathogenic) fungi or oomycetes (hereafter referred to as PFO), herbivorous insects (of all types), and their host plants. In addition, Mitchell (2004) investigated the vectorial status of Heteroptera regarding plant pathogens of all types, and Hauser et al. (2013) conducted a meta-analysis on the combined (synergistic or antagonistic) effects of herbivorous arthropods and phytopathogens on plant performance.

However, specific three-way (or tripartite) interactions between PFO and plant bugs belonging to the Miridae family (the largest family in the Heteroptera sub-order), hereafter referred to as mirid bugs (MB), have to our knowledge never been reviewed. Here, we specifically review such interactions for this Heteroptera group, which is relevant for two major reasons.

Firstly, the Miridae family is of tremendous economic importance since it encompasses both major crop pests (the incidence of some increasing as emerging pests on crops genetically modified with *Bacillus thuringiensis* (*Bt*) genes; e.g., Lu et al. 2010; Sequeira 2019) and major natural enemies of pests (e.g., Pérez-Hedo and Urbaneja 2015), and to a lesser extent of weeds/invasive plants (e.g., Ray and Hill 2016). Regarding the former (MB as crop pests), all possible ways to manage them without synthetic pesticides (due to their adverse environmental and sanitary impacts) have to be sought, particularly by taking advantage of biological interactions within agroecosystems. Similarly, regarding the latter two (MB as natural enemies), all possible ways to increase their efficiency should be investigated (including reduction/suppression of synthetic pesticide use).

Secondly, although true bugs, particularly MB, are generally perceived as ineffective in disseminating plant pathogens, particularly PFO (Wheeler Jr 2001), their interactions with the latter deserves further attention and investigation because MB differ from other insect groups in their relation to plant pathogens, particularly due to:

- the feeding styles of herbivorous and omnivorous MB (Fig. 1a);
- the extent of omnivory (zoophytophagy) in this group;
- their oviposition behavior, with egg insertion in plant tissues (Fig. 1b).

Indeed, among Heteroptera, there is a clearcut difference in feeding styles between herbivorous/omnivorous Cimicomorpha (Miridae, Tingidae, and Anthocoridae) on the one hand, and Pentatomorpha (e.g., Coreidae, Geocoridae, Lygaeidae, Pentatomidae, and Pyrrhocoridae) on the other (Gopalan and Subramaniam 1978; Hori 1974; Miles 1978; Wheeler Jr 2001). Contrary to the generally accepted view, herbivorous and omnivorous mirid bugs are not phloem

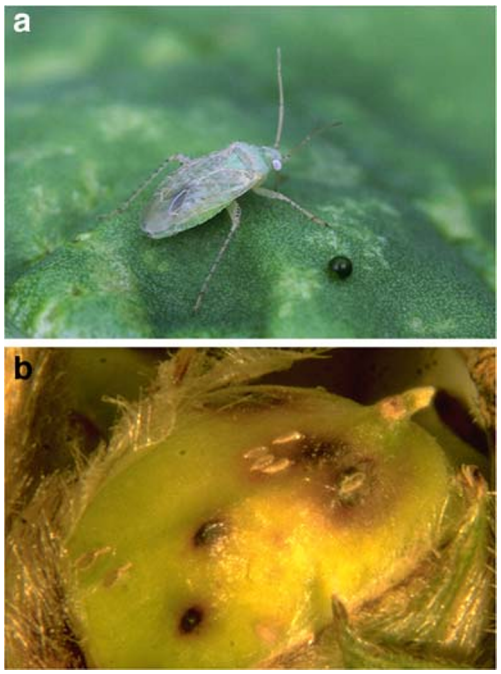

Fig. 1 **a** Adult *Moissonia importunitas* mirid bug on a rattlebox (*Crotalaria spectabilis*) leaf in Réunion. Yellow/light green stains are symptoms of feeding damage. Both of these symptoms and black feces are evidence of "lacerate/macerate and flush" mesophyll feeding (© F. Le Bellec – CIRAD). **b** Egg-laying punctures of *Eurystylus oldi* and *Creontiades pallidus* mirid bugs on a developing sorghum kernel. Egg tips (opercula) protrude from the kernel surface. These punctures may serve as entry points for grain mold phytopathogenic fungi (© A. Ratnadass – CIRAD)

feeders, unlike most phytophagous Heteroptera, and more generally Hemiptera, but rather either lacerate and flush (L&F) or macerate and flush (M&F) feeders (Cobben 1978; Hori 2000; Sharma et al. 2014; Wheeler Jr 2001). Plant responses to their damage are therefore generally via jasmonic acid (JA) or ethylene (ET) signaling pathways rather than via the salicylic acid (SA) pathway (Al-Naemi and Hatcher 2013; Karban and Chen 2007; Koornneef and Pieterse 2008; Pappas et al. 2015; Pappas et al. 2016; Wielgoss et al. 2012). However, in their review of the effects of plant fungal infection on herbivorous insects, according to both insect and pathogen lifestyles, Fernandez-Conradi et al. (2018) overlooked the difference between phloem feeders and L&F and M&F feeders.

Similarly, regarding PFO, a distinction should be made between biotrophic fungi (which trigger the SA pathway plant response) and necrotrophic and/or hemibiotrophic fungi/oomycetes (which trigger JA/ET pathway plant responses) (De Vos et al. 2005; Heidel and Baldwin 2004; Ponzio et al. 2013; Thaler et al. 2012; Walling 2000). In that respect, PFO differ from phytopathogenic viruses and bacteria, the former being all biotrophic since they need living tissue for their multiplication (Pallas and Garcia 2011), while the latter should all be considered as hemibiotrophic (Kraepiel and Barny 2016).

One typical tripartite association that is never found with MB is the development of sooty mold, a fungus-pest association/interaction common in other Hemiptera groups since L&F/M&F feeders do not exploit phloem sap, resulting in the absence of honeydew production.

Otherwise, MB, along with most other Cimicomorpha and unlike other Heteroptera, cause oviposition injury resulting from egg insertion, because the females have a robust ovipositor which they use to drill into the host plant in order to release the egg inside the vegetative tissues (Romani et al. 2005), while Pentatomorpha lay eggs on the plant surface (Wheeler Jr 2001). Furthermore, oviposition is preceded by rostrum probing of the substrate, a process during which plant bug stylets are inserted in plant tissues (Constant et al. 1996; Ferran et al. 1996; Gopalan and Basheer 1966; Wheeler Jr 2001).

Our review does not encompass entomopathogenic fungi, non-pathogenic endophytic fungi, mycorrhizae, nor specifically mycetophagous MB (for these aspects, refer to Vega and Blackwell (2005)). Note however that L&F/M&F feeders are more likely, just like chewing herbivorous arthropods, to indiscriminately consume plant and fungus tissue, unlike sap feeders (Fernandez-Conradi et al. 2018; Mondy and Corio-Costet 2004; Moran 1998; Rostas et al. 2003).

Moreover, although we focused on crop plants, when evidence from such plants was lacking in the literature, we took examples concerning weeds or invasive plants, especially when we felt that generic lessons could be drawn and applicable to crop plants. Similarly, some examples were taken from other herbivorous or omnivorous Cimicomorpha (viz. lacebugs (Tingidae) and pirate bugs (Anthocoridae)), and even other arthropod groups (viz. some herbivorous thrips (Thysanoptera) and mites (Acari)) with the same life/feeding style as herbivorous MB.

Direct and indirect interactions were defined by Willsey et al. (2017). The potential mechanisms through which crop plants, PFO, and MB interact fall within five major frameworks (Fig. 2), namely (i) CP infection by PFO mechanically facilitated by prior MB infestation; (ii) CP infection by PFO hampered by prior MB infestation via CP signaling; (iii) CP infestation by MB facilitated by prior PFO infection via CP signaling; (iv) CP infestation by MB hampered by prior PFO infection via CP signaling; and (v) CP infestation by MB and/or infection by PFO hampered by prior MB infestation and/or PFO infection via CP resource quality alteration.

Otherwise, PFO and MB may also merely occur concomitantly, namely favored by the same conditions, i.e., climatic or linked to endogeneous crop plant factors (e.g., redox status; Husson 2013), triggered or not by abiotic factors. Our review focuses on the first four interaction frameworks, since the fifth one (dealing with resource quality alteration) is quite trivial and has been well described elsewhere (e.g., Fernandez-Conradi et al. 2018). Our review does not encompass either phytotoxaemia, i.e., the case when MB feeding symptoms can be confused with those caused by chewing insects, drought, hail, high temperatures, insufficient pollination, mechanical injury, nutrient deficiency or toxicity, and pollution, but especially with plant disease symptoms (Wheeler Jr 2001), including those resulting from infection by PFO (Hori 2000; Gopalan and Subramaniam 1978). Interestingly, even the potato late blight disease was mistakenly proposed to be caused by the plant bug *Lygus lineolaris* (Wheeler Jr 1981).

2 Crop plant infection by phytopathogenic fungi is facilitated by prior mirid bug infestation

This specific aspect (dissemination of fungal pathogens) was partially reviewed by Wheeler Jr (2001). There are several examples whereby MB infestation facilitates mechanical transmission of PFO to crop plants (annual or perennial). For instance, *Calonectria rigidiscula*, which causes cocoa dieback, infects trees through MB (*Sahlbergella singularis* (Fig. 3) and *Distantiella theobroma*) lesions on stems (Crowdy 1947). Actually, it was reported that neither the insects nor the fungus alone normally causes serious damage to the tree, but their combined damage has a major impact on the cocoa industry in West Africa (Crowdy 1947). On cashew trees in India, the MB *Helopeltis antonii* was reported to be the primary causal agent of inflorescence blight, with *Gloesporum mangifera*, *Phomopsis anacardiae*, *Pestaliopsis* spp., and *Botrydiplodia* spp. associated with it as secondary saprophytic

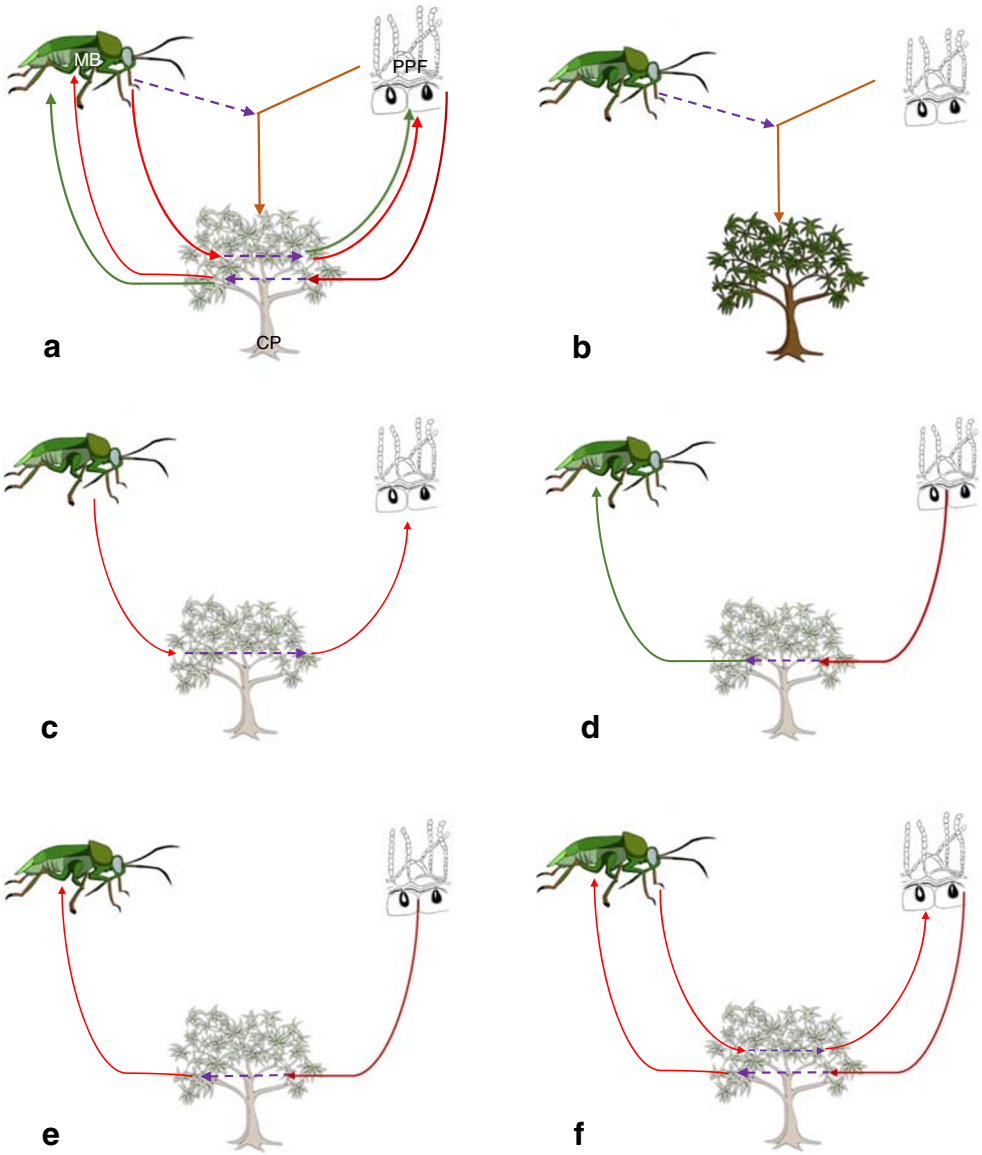

Fig. 2 **a** Main 3-way interactions between herbivorous mirid bugs (MB), phytopathogenic fungi/oomycetes (PFO), and crop plants (CP). Solid green arrows, positive (on target organism) direct effects; solid red arrows, negative (on target organism) direct effects; dotted purple arrows, indirect effects (either positive or negative). **b** CP infection by PFO mechanically facilitated by prior MB infestation. **c** CP infection by PFO hampered by prior MB infestation via CP signaling. **d** CP infestation by MB facilitated by prior PFO infection via CP signaling. **e** CP infestation by MB hampered by prior PFO infection via CP signaling. **f** CP infestation by MB and/or infection by PFO hampered by prior MB infestation and/or PFO infection via CP resource quality alteration. Illustrations by Simon Ratnadass

colonizers (Wijetunge et al. 2003). In addition to these quite well-documented cases, Cech (1989) suspected that MB egg-laying injuries facilitate the entry of fungal pathogens of oak. In Dominica, Whitwell (1993) reported evidence of egg-laying scars by MB *Dagbertus* sp. and *Rhinacloa antennalis* as sites of pathogen entry and subsequent infection in mango. This was also reported for the same MB species in avocado (Peña et al. 2003).

Besides perennial plants, several cases have been reported in annual crops, e.g., *Orthops campestris* as vector of the carrot phytopathogenic fungus *Stemphylium radicinum* (Bech 1967). In the USA, the cotton fleahopper *Pseudatomoscelis serratus* was suspected to contaminate cotton flower buds with various micro-organisms, particularly fungi of the genera *Penicillium*, *Fusarium*, and *Alternaria* (Cadou 1994; Martin Jr et al. 1987). This was also observed in the Congo with *Helopeltis* spp. and *Colletotrichum gossypii* causing cotton anthracnose (Cadou 1994; Steyaert and Vrydagh 1933; Vrydagh 1936). *Lygus hesperus* was also reported to be a vector of *Aspergillus flavus* in cotton (Stephenson and Russell 1974). However, the best documented example concerns sorghum panicle-feeding MB (mainly *Eurystylus oldi*)/grain mold (Figs. 1b and 4a and b) in West and Central Africa (Aheto et al. 2017; Marley and Malgwi 1999; Ratnadass et al. 1995; Ratnadass et al. 2003a).

Feeding/egg-laying puncture symptoms induced by panicle-feeding MB (also referred to as "head bugs") may be confused with those of grain mold infection due to phytotoxaemia (Fig. 4a and b). While grain mold fungi may penetrate sorghum grains directly under high humidity conditions, infection by these fungi can also be facilitated by biotic

Fig. 3 Cocoa mirid bugs (*Sahlbergella singularis*) in Cameroon. An adult in the foreground and nymphs in the background. Brown stains are symptoms of leaf feeding damage (© R. Babin – CIRAD)

factors, especially insects (Bandyopadhyay et al. 2000). As reviewed by Marley and Ajayi (1999), the first clear evidence of this relationship in the West and Central Africa sub-region was obtained in experiments carried out by the *Institut d'économie rurale* (IER) at Sotuba (Mali) in 1990 and 1991, which demonstrated a close relationship between panicle-feeding MB and grain mold (Ratnadass et al. 1995). Fungicide application only slightly affected MB damage, but grain mold damage was greater on unprotected than on fungicide-protected panicles. Yet, panicles protected from MB only with plastic bags had no more mold severity than those protected by fungicide treatment alone, or jointly by fungicide treatment and plastic bags (Ratnadass et al. 1995). This was confirmed in experiments conducted by the Institute for Agricultural Research (IAR) at Samaru (Nigeria) in 1995 and 1996 (Marley and Malgwi 1999).

The relationship between panicle-feeding MB infestation and mold infection was confirmed in the Regional Sorghum Head Bug and Grain Mold Trial conducted in 1996 and 1997 under the West and Central African Sorghum Research Network (WCASRN) in 15 research stations across 10 countries participating in the network. Insecticidal treatment had a significant impact on the grain mold incidence respectively in five and four out of 11 localities where this parameter was measured in 1996 and 1997, thus partially confirming the critical role played by panicle-feeding MB as factors aggravating mold infection (Ratnadass et al. 2003a). PFO involved in all of these cases were necrotrophic or hemibiotrophic.

3 Crop plant infection by phytopathogenic fungi is hampered by prior mirid bug infestation

Herbivorous or omnivorous MB may induce plant resistance to other more damaging L&F arthropod pests, e.g.:

- *Macrolophus pygmaeus* vs spider mites (Pappas et al. 2015; Zhang et al. 2018) and thrips (Zhang et al. 2018) on cultivated Solanaceae;
- *Tupiocoris notatus* vs chewing caterpillars (*Manduca sexta*) on wild tobacco (*Nicotiana atenuata*) (Halitschke et al. 2011; Kessler and Baldwin 2004; Voelckel and Baldwin 2004);
- *Helopeltis sulawesi* vs the major pest/pod-boring moth *Conopomorpha cramerella* on cocoa in Southeast Asia (Wielgoss et al. 2012).

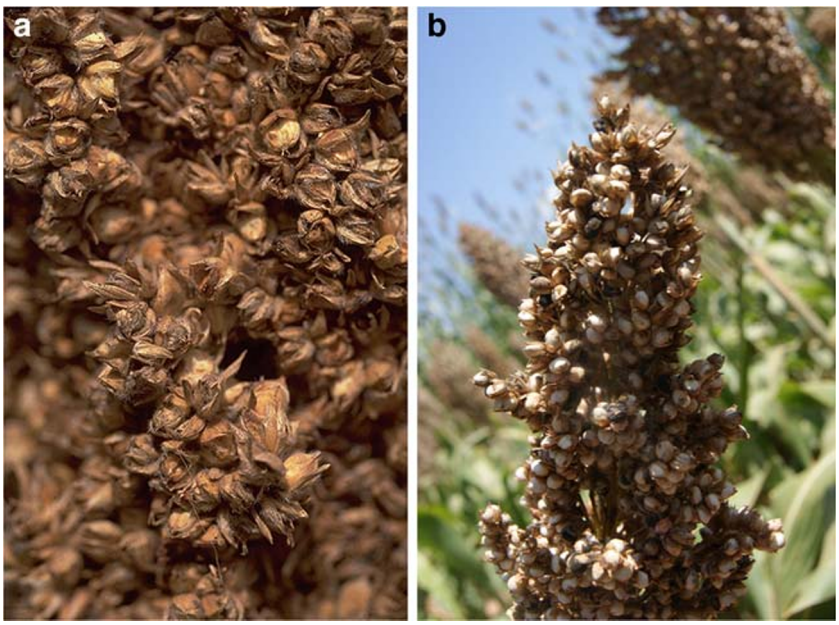

Fig. 4 **a** *Eurystylus oldi* induced damage on a sorghum panicle in Mali. This is a case of mere phytotoxaemia due to extensive adult feeding at the milk stage. Mirid bug punctures at a later stage may facilitate grain mold infection (© A. Ratnadass – CIRAD). **b** Grain mold damage on a sorghum panicle in Mali. This may or not have been facilitated by prior mirid bug punctures. Molded grains may be pink, white, or black (depending on the pathogen) (© K. Vom Brocke – CIRAD)

Prior infestation by some MB may also induce systemic resistance in plants against subsequent PFO infection (Karban and Chen 2007). For instance, studies on interactions between the MB *Eccritotarsus catarinensis* and the necrotrophic PFO *Acremonium zonatum*, a biocontrol agent of water hyacinth, *Eichhornia crassipes*, suggested an initial development of a plant defense response to MB feeding, thus delaying infection by PFO (Ray and Hill 2016).

Studies by Frati et al. (2006) showed that MB produced endo-polygalacturonase (PGs) hydrolytic enzymes that are involved in the degradation of pectin, a major plant cell wall component. Several plants are known to produce extracellular plant proteins like polygalacturonase-inhibiting proteins (PGIPs), which are known for their ability to inhibit fungal PGs and restrict fungal colonization (Frati et al. 2006). PGIPs of bean (*Phaseolus vulgaris*) also inhibited PGs of two MB species (*Lygus rugulipennis* and *Adelphocoris lineolatus*) and two necrotrophic PFO, i.e., *Colletotrichum acutatum* and *Botrytis cinerea* (d'Ovidio et al. 2004). PGs are also produced by *A. lucorum* (Zhang et al. 2015), yet prior infestation of garden balsam (*Impatiens balsima*) by this MB did not have any effect on powdery mildew infection (Pan et al. 2013). This absence of effect was also observed with *Helopeltis* spp. infestation in cashew, and *Oidium anacardii* infection (Agboton et al. 2013). Both of these cases involved biotrophic fungi.

Lastly, MB could potentially adversely affect fungal growth via the antifungal function of scent gland secretions. For instance, trans-2-hexenal, a volatile aldehyde which is a major compound secreted by rice stink bugs (Blum et al. 1960), was found to inhibit *Aspergillus flavus* growth and aflatoxin production in corn (De Lucca et al. 2011). However, this was not confirmed with regard to MB *Adelphocoris suturalis* (Zhang et al. 2014).

4 Crop plant infestation by mirid bugs is facilitated by prior phytopathogenic fungus infection

There are no documented examples of MB infestation of crop plants being facilitated by PFO infection, while there are many documented examples of L&F/M&F feeding arthropod (other than MB) infestation of CP facilitated by PFO infection (Table 1). In those cases, three fungi out of four are biotrophic (which is consistent with the CP signaling assumption), while in the case of cotton lint rot, the use of the fungus for food by the mite seems to overcome this signaling.

In the case of *Orthops palus* and the powdery mildew *Pseudoidium anacardii* (formerly *Oidium mangiferae*) fungus in mango, such facilitation is highly suspected in Réunion, although its pathway remains unknown (Atiama 2016; Deguine et al. 2018). *O. palus* and *P. anacardii* were found to have simultaneously caused damage. *O. palus* was also absent in 80% of cases when powdery mildew was absent (2387 observations over 3 years; Deguine et al. 2018). In addition, a preliminary experiment conducted in a mango orchard showed that sulfur application against powdery mildew slightly adversely affected *O. palus*, whereas powdery mildew infection was not at all affected by insecticide (Lambda-cyhalothrin) treatment (Ratnadass, unpublished).

Turner et al. (2018) also reported the co-occurrence of a biotrophic PFO and a MB, i.e., *Puccinia silphii* and *Lygus lineoralis*, respectively, on the perennial oilseed crop *Silphium integrifolium*, although these authors did not highlight a facilitation phenomenon in that case.

5 Crop plant infestation by mirid bugs is hampered by prior phytopathogenic fungus infection

Some PFO, particularly *Fusarium* spp., produce beauvericin (Logrieco et al. 2002), which has insecticidal activity. Although this may mainly be harmful to chewing herbivores that indiscriminately consume plant and fungus tissues, and less so to piercing-sucking herbivores that only consume sap (Fernandez-Conradi et al. 2018), beauvericin may also affect L&F/M&F feeders, including MB, e.g., *Lygus* spp. (Leland et al. 2005).

A particular case concerns the natural enemy *Nesidiocoris volucer* on tobacco plants infested with tobacco powdery mildew caused by *Golovinomyces cichoracearum* in Réunion (Fontaine and Atiama, La Coccinelle®, pers. com., 2019). It was assumed that mycelium hampered egg-laying, hatching, and movement of MB nymphs (Fig. 5).

6 Other potential pathways

The co-occurrence of MB and PFO may be due to microclimatic conditions that favor both attackers, which is (along with facilitation) a partial explanation in the case of sorghum panicle-feeding MB and grain mold (Ratnadass et al. 2003b). This hypothesis should be tested and possibly ruled out in the case of mango MB/powdery mildew (Atiama 2016; Deguine et al. 2018; Ratnadass et al. 2019). No general rule can be put forward in this respect since the relationship depends on the MB species (e.g., Ratnadass and Butler 2003), and PFO species (e.g., powdery mildew pathogens being favored by cooler and dryer conditions than those conducive to the development of pathogens responsible for grain mold; Nasir et al. 2014; Tonapi et al. 2007).

Another case of co-occurrence of MB and PFO concerns the cultivation of transgenic insect-resistant (*Bt*) cotton lines, which significantly reduced insecticide usage against Lepidopteron pests, resulting in an outbreak of pests that were

Table 1 Documented examples of arthropod infestation of crop plants facilitated by phytopathogenic fungus infection

Arthropod	Fungus/disease	Fungus trophic strategy	Plant	Process	References
Thrips tabaci	*Sphaerotheca pannosa*/powdery mildew	Biotroph	Vine, rose, strawberry, cantaloupe, clove	Fungus required as food for thrips	Yarwood (1943); Coyier (1983)
Tetranychus urticae	*Sphaerotheca pannosa*/powdery mildew	Biotroph	Rose	Fungus required as food for mites	Poncet et al. (2008); Bout et al. (2011)
Tetranychus spp.	*Podosphaera* spp./powdery mildews	Biotroph	Apple & cherry	Unknown	Reding et al. (2001)
Siteroptes reniformis	*Nigrospora oryzae*/lint rot	Necrotroph	Cotton	Fungus required as food for mites	Laemmlen and Hall (1973)

considered secondary, particularly MB (Lu et al. 2010). On the other hand, *Bt* cotton lines also exhibited reduced disease resistance in comparison to conventional lines, especially for *Fusarium* wilt in China (Li et al. 2009); *Bt* cotton cultivation in India was also associated with an increase of damage by many PFO/diseases, e.g., *R. solani* and *Macrophomina phaseolina* root rot, *Alternaria macrospora* and *Myrothecium* leaf blight, and *Ramularia areola* grey mildew (Saravanan et al. 2015).

Recent research has also highlighted the role of endogenous plant factors, such as the crop plant reduction/oxidation and acidification/alkalinization (redox/pH) status in relation with soil, favoring/hampering specific types of pests/pathogens (Bousset et al. 2019; Husson 2013), which should therefore also be considered. For instance, biotrophic fungi are associated with more alkaline media than necrotrophic fungi (e.g., those whose infection is facilitated by MB puncture). This redox/pH framework also helps explain why MB, unlike phloem-feeding Hemiptera, are poor virus and biotrophic fungi transmitters, but better at transmitting bacteria or necrotrophic fungi (Wheeler Jr 2001).

Fig. 5 Newly hatched nymph of the mirid bug *Nesidiocoris volucer* on a tobacco leaf in Réunion. This shows that tobacco powdery mildew mycelium hampers bug movements, while also probably deterring egg-laying (© La Coccinelle)

7 Implications in terms of management measures

Many action levers could eventually be mobilized based on the evidence from various crops culled in the literature, as detailed hereafter (§7.1 to 7.6).

7.1 Chemical and mineral control

Synthetic insecticides (cypermethrin and deltamethrin) used in the WCASRN regional trial (Ratnadass et al. 2003a) were found to be effective against both head bugs and grain mold (although to a lesser extent for the latter). Zhang et al. (2017) reported that neonicotinoid seed treatments, particularly with nitenpyram, could provide effective protection and play an important role in the management of early season *A. lucorum* in *Bt* cotton fields in China. Moreover, seed treatments combining nitenpyram with fungicides could be a suitable choice for controlling both MB and PFO (e.g., *Rhizoctonia solani* and *Verticillium dahliae*) during the cotton seedling stage (Zhang et al. 2017).

Some mineral pesticides (like sulfur) may have a dual effect on powdery mildew and MB. This is the case in tomato regarding *Oidium neolycopersici* and the natural enemies *Nesidiocoris tenuis* and *Deraeocoris brevis* (potentially), which are omnivorous MB (Amarasekare and Shearer 2013; Zappalà et al. 2011). *N. tenuis* is presently released as natural enemy in tomato fields, yet it may turn out to be a crop pest (Arno et al. 2010). However, there are no reported instances of mainly herbivorous MB being directly controlled by powdery mildew-targeted sulfur applications. On the other hand, Fernandez et al. (2006) also found that apple fruit damage by the mullein MB *Campylomma verbasci* was reduced by mineral oil sprays targeting apple powdery mildew (*Podosphaera leucotricha*).

The use of elicitors of plant defenses, or so-called plant activators, has been proposed as an alternative approach to chemical crop protection (Bruce 2010; Sobhy et al. 2014; Thaler et al. 2001; Vallad and Goodman 2004; Worrall et al.

2012). However, to our knowledge, no cases jointly involving MB and PFO have been reported.

7.2 Physical methods

One particular case pertains to mechanical control with a bug vac that was developed to suck *L. hesperus* MB out of strawberry fields (Dietrick 1961), but which at the same time spreads diseases like powdery mildew and gray mold (Kuepper and Thomas 2002). With such conflicting effects, tradeoffs should be sought.

On the other hand, the potential of powdery mildew inoculum removal in mango (as suggested by Misra 2001; Misra et al. 1998; Nasir et al. 2014) could be tested in Réunion, including for its effect on mango MB infestation.

7.3 Host plant resistance

Regarding head bugs and grain mold, sorghum varietal resistance to the former contributed to resistance to the latter, which was also the case with phenotypic plant characteristics negatively affecting both attackers in relation to microclimatic conditions (i.e., panicle laxity/openness) (Ratnadass et al. 2003a). Similarly, genetic resistance of cotton to MB pests, e.g., that due to leaf pubescence (trichome density; McLoud et al. 2015; Wood et al. 2017), is expected to reduce flower bud infection by PFO.

7.4 Biological control

On cotton, the fungal natural enemy *Beauveria bassiana* has synergistic control potential due to its dual effect on *Lygus* spp., as well as *R. solani* and *Pythium myriotylum* (Leland et al. 2005; Ownley et al. 2008). However, *B. bassiana* application as an augmentative biological control measure against *Lygus* bugs in strawberry overcomes the need for powdery mildew-specific fungicide treatments (Dara 2017).

Otherwise, regarding conservation biological control, conflicting effects were highlighted in cocoa orchards in tropical Africa. Namely, measures to encourage weaver ants (*Oecophylla longinoda*) and other ant species as predators of MB (Bagny-Beilhe et al. 2018) (which could reduce cocoa dieback incidence: Crowdy 1947) may result in increased incidence of black pod rot, since ants are disseminators of *Phytophthora megakarya*, the oomycete causative agent of the disease (Bisseleua et al. 2017).

7.5 Plant species diversity deployment

This refers to a set of agroecological management strategies implemented at various scales (Ratnadass et al. 2012). For instance, through the use of cover crops in conservation agriculture strategies, the redox conditions of soil and crop plants could be altered to make them unfit for both types of attackers (Husson et al. 2016, 2018).

Fig. 6 *Orthops palus* punctures on a mango inflorescence in Réunion. Adult and nymph feeding mainly affects mature inflorescences. This results in their drying up and causes flower and young fruit drop (© A. Franck – CIRAD)

At the scale of the field and its margins, it was found in China that mungbean (*Vigna radiatus*) had considerable potential as a trap crop for *A. lucorum* in *Bt* cotton fields (Lu et al. 2009). Maize (*Zea mays*) fields were also proposed as potential sinks for these pests (Jiao et al. 2019). In addition, buckwheat (*Fagopyrum esculentum*) strip crops were found to increase *A. lucorum* regulation in cotton by a Braconid parasitoid species (Li et al. 2019). Although no direct interactions with PFO have been highlighted for this MB species, such principles could be applied for other MB that are known for their facilitating effects for infection by PFO, for instance, the use of sorghum as a trap crop for MB management on cotton (Ratnadass et al. 2009), or trap cropping with castor bean (*Ricinus communis*) to reduce sorghum infestation by *Eurystylus oldi* (Ratnadass et al. 2001).

Moreover, in agroforestry (AF) strategies, shade generated by AF trees in cocoa orchards was found to both facilitate black pod rot infection and negatively affect MB infestation (Babin et al. 2010; Gidoin et al. 2014), and hence potentially dieback incidence. With such conflicting effects, tradeoffs should be sought.

Fig. 7 Powdery mildew (*Pseudoidium anacardii*) on mango inflorescences in Réunion. Some inflorescences are completely covered with mycelium. This will eventually result in their browning and drying up (© A. Ratnadass – CIRAD)

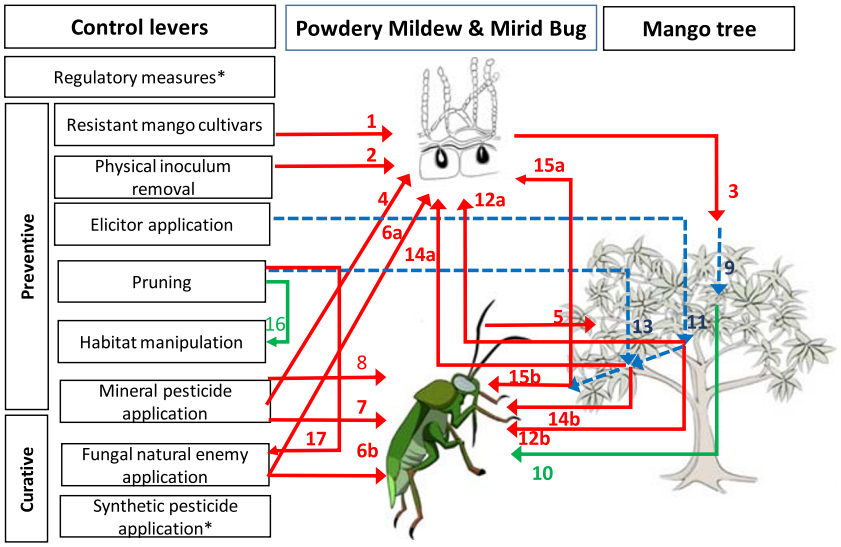

Fig. 8 Proposed strategy for agroecological protection of mango against *P. anacardii* and *O. palus* in Réunion with action levers that could be mobilized (partially adapted from Deguine et al. 2018 and Ratnadass et al. 2019). Solid green (resp. red) arrows, positive (resp. negative) direct effect on target organism or lever; dotted blue arrows, indirect effects via the crop plant. *Not applicable (no regulatory measures nor synthetic pesticide for curative control). **1.** Powdery mildew-resistant mango cultivars (e.g., Joubert et al. 1993; Vincenot and Normand 2009); **2.** Effectiveness of powdery mildew inoculum removal (e.g., Misra 2001; Misra et al. 1998; Nasir et al. 2014); **3.** Damage caused by powdery mildew to mango inflorescences (e.g., Nasir et al. 2014); **4.** Effectiveness of sulfur application against mango powdery mildew (e.g., Nasir et al. 2014); **5.** Damage caused by mango MB to mango inflorescences (e.g., Atiama 2016); **6a and 6b.** Potential effect of *Lecanicillium lecanii* as a pathogen of some powdery mildews and some MB species (e.g., Romero et al. 2003; Pasaru et al. 2014); **7.** Effectiveness of sulfur application against omnivorous MB (e.g., Amarasekare and Shearer 2013; Zappalà et al. 2011); **8.** Potential effect of natural enemies on *O. palus* e.g predatory *Campylomma leucochila* enhanced via habitat manipulation (e.g., Atiama 2016; Deguine et al. 2018; Jacquot 2016; Ratnadass et al. 2018); **9.** Inhibition of JA plant response following biotrophic attack (e.g., Ponzio et al. 2013); **10.** Attractiveness for *O. palus* as a necrotrophic attacker (e.g., Deguine et al. 2018); **11.** Effect of elicitor application on mango flowering synchronization (e.g., Singh et al. 2001; Mohammadi et al. 2015); **12a and 12b.** Potential of SA and JA plant signaling pathways against resp. *P. anacardii* and *O. palus*; **13.** Effect of pruning on mango flowering synchronization (e.g., Oosthuyse and Jacobs 1997); **14a and 14b.** Potential of reduced duration of pest-susceptible stage against resp. *P. anacardii* and *O. palus*; **15a and 15b.** Potential of microclimate alteration on suppression of resp. *P. anacardii* and *O. palus* (Ratnadass et al. 2019); **16.** Potential effect of pruning on light penetration in the orchard and floor vegetation growth (including habitats for conservation biological control; e.g., Rothe et al. 2019). **17.** Potential effect of pruning on fungal natural enemies via microclimate alteration (Mahot et al. 2019; Ratnadass et al. 2019). Artwork by Simon Ratnadass

7.6 Agroecological crop protection

As illustrated above, many control techniques may be used for managing MB and/or PFO, either individually or in combination, as part of IPM strategies (Barzman et al. 2015). However, those levers may also be combined within the more relevant agroecological crop protection (ACP) framework, as described by Deguine et al. (2017). Indeed, controlling crop pests and pathogens using synthetic pesticides with direct toxic activity is increasingly discouraged, while the use of more environment-friendly approaches such as ACP is essential for a more sustainable future.

While the most documented example of facilitation of fungus infection following MB infestation concerned panicle-feeding MB/grain mold in sorghum, a challenging case where the reverse was observed concerned mango MB and powdery mildew (Figs. 6 and 7). Although this case is still pending confirmation, it is supported by other evidence regarding herbivorous arthropods with the same feeding style as MB (see part 4). On this basis and that of confirmed or potential action levers, in Fig. 8, we propose a framework for management of *O. palus* and *P. anacardii* in mango orchards in Réunion according to ACP principles (including the strict order according to which these levers should be implemented).

For this mango, MB/powdery mildew case study neither the first nor the last step is applicable since, as both attackers are well established on the island, there are no regulatory measures for their control, and also synthetic pesticide treatments are likely to be banned soon for curative control.

With respect to preventive methods, there are no reports of varietal differences in resistance to MB. Regarding host plant resistance to powdery mildew among mango cultivars that have been evaluated in Réunion, Sensation was found to be less susceptible to *P. anacardii* (Joubert et al. 1993), contrary to Kent and Cogshall, both of which are highly susceptible (Vincenot and Normand 2009), with Tommy Atkins being intermediate. Regarding physical control for powdery mildew, the methods reported by Misra (2001), Misra et al.

(1998), and Nasir et al. (2014) have not been tested in Réunion. Pruning might also have a direct effect on mango bug/powdery mildew through microclimatic effects, but also indirect effects via changes in tree phenology (particularly flowering dynamics), and effects on vegetation soil cover growth (increased available light), resulting in potential indirect effects on mango bugs through natural enemies, e.g., predatory *Campylomma leucochila* and potential parasitoid *Leiophron* sp. (Atiama 2016; Jacquot 2016; Ratnadass et al. 2018; Williams et al. 2003 ; Demirel et al. 2005). As for elicitors, a literature review suggests that JA sprays could balance endogenic SA production triggered by powdery mildew infection, without affecting flowering synchronization (Singh et al. 2001; Mohammadi et al. 2015), which is another indirect way of minimizing MB damage by reducing the duration of the susceptible stage.

With respect to curative measures, application of sulfur as a mineral fungicide could actually also be considered as preventive against MB, since it does not seem to have a direct effect on MB. Sulfur may also have an indirect effect by hampering powdery mildew and therefore not triggering the SA pathway in host plants, resulting in non-inhibition of JA signaling, while having a negative effect on pests with necrotrophic lifestyles like MB. Augmentative biological control concerns biopesticides, e.g., *Lecanicillium* as a pathogen of powdery mildews and some MB species (Pasaru et al. 2014), or in combination with *Beauveria* (Portilla et al. 2014).

8 Conclusion

A wealth of examples may be found in the literature regarding the co-occurrence of L&F/M&F feeding arthropods and biotrophic PFO, namely two-way interactions, but without reference to a three-way interaction with the plant (e.g., Rur 2016). In many cases, associations and causal effects are only suspected, while in others, an absence of effect has been put forward, supported or not by experimental findings.

All of the interaction pathways we reviewed (including pre-disposition, namely induced higher susceptibility or resistance resulting in cross-resistance/susceptibility, or a decrease/increase in host plant resource quality for insects or pathogens), may overlap, while being synergistic or antagonistic, sometimes resulting in an absence of effect.

This review highlights new outlooks that could give rise to agroecological options for the management of both types of biotic aggressors.

Our recommendations on ACP against mango MB and powdery mildew could serve as a basis for ACP against other MB and PFO of the same guilds/lifestyles that damage other crops. Beyond the mere pest and pathogen regulation service, the ACP strategy contributes to other key ecosystem services, thus enhancing agroecosystem functioning.

Further research should also be focused on such biological models (= "pathosystems") on mango and other plants in order to obtain experimental findings on the suspected interactions (as already achieved for MB/grain mold on sorghum, also regarding potential interactions with climatic parameters), while also considering plant hormones and redox/pH aspects (e.g., in the case of elemental sulfur application; Williams and Cooper 2004).

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Compliance with ethical standards

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