

Chapter 8

Biological Control of Spotted-Wing *Drosophila*: An Update on Promising Agents



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Abstract Following the global invasion of *Drosophila suzukii* (spotted-wing drosophila or SWD), nearly 100 studies have explored biological control of this pest. In 2019, a review summarized 75+ papers covering 57 species of SWD parasitoids, predators, competitors, and pathogens and identified the most promising ones. This review provides an update with recent studies. Since parasitoids are promising natural enemies that can be host-specific and self-disperse, this chapter focuses on SWD parasitoids in its invaded and native ranges, and prospects for classical biological control. To date, six species have been confirmed to attack SWD in the invaded regions including three widely studied generalist pupal parasitoids, *Pachycrepoideus vindemiae*, *Trichopria drosophilae*, and *T. anastrephae*. No locally occurring larval drosophila parasitoids can develop from SWD. In contrast, foreign explorations in China, Japan, and South Korea have revealed 19 species of SWD larval parasitoids. *Asobara japonica*, *Ganaspis brasiliensis*, and *Leptopilina japonica* spp. *japonica* have been evaluated. *Ganaspis brasiliensis* is a complex of cryptic species/strains with varying host specificity, some which also occur in regions outside of Asia, but one East Asian strain was found to be the most host-specific to SWD and is currently being petitioned for introduction into North America and Europe.

Keywords *Asobara* · *Drosophila* · *Ganaspis* · *Leptopilina* · *Pachycrepoideus* · *Trichopria*

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Drosophila suzukii Matsumura (Diptera: Drosophilidae) (spotted-wing drosophila or SWD) is an invasive pest in North and South America and Europe that threatens the small fruit and cherry industry (Asplen et al. 2015). Although chemical insecticides are effective, this has increased management costs (Farnsworth et al. 2017), led to resistance development (Gress and Zalom 2019), loss of markets (Haviland and Beers 2012), and impacted natural enemies (Whitehouse et al. 2018). Long-term sustainable management relies on effective biological control as well as cultural and behavioral controls. To develop biological control of invasive pests, the classical approach is to use natural enemies that are native to their countries of origin. Introduction of these specialist parasitoids has historically been preferred for controlling exotic pests because these parasitoids are generally more efficient in targeting hosts due to their long-shared history of co-adaptation. However, some indigenous generalist parasitoids can adapt to exotic hosts, and such novel interactions may also play an important role in regulating the exotic pests. It is therefore important to evaluate the impacts of indigenous natural enemies while considering imported specialist parasitoids for the management of invasive pests. This chapter review will primarily focus on parasitoids since they are generally more host-specific than predators and entomopathogens, but will also summarize recent work on predators, competitors, and pathogens of SWD since the last review of SWD biological control (Lee et al. 2019). Predators and competitors of SWD are already common in crops and can be further conserved to suppress SWD populations. Pathogens are often commercially available, and if delivered effectively, provide growers additional control options.

8.1 Parasitoids of *Drosophila*

Parasitoids clearly play an important role in regulating some *Drosophila* populations, with reported levels of parasitism as high as 80–100% in Europe (e.g., Fleury et al. 2009; Janssen et al. 1988). Over 50 hymenopteran species have been reported to attack frugivorous drosophilids worldwide, including members of Braconidae (*Asobara*, *Aphaereta*, *Phaenocarpa*, *Tanycarpa*, *Aspilota*, and *Opius*), Figitidae (*Leptopilina*, *Ganaspis*, *Kleidotoma*, and *Dicerataspis*), Diapriidae (*Trichopria* and *Spilomicrus*), and Pteromalidae (*Pachycrepoideus*, *Spalangia*, *Trichomalopsis*, and *Toxomorpha*) (Carton et al. 1986). So far, no drosophilid egg or adult parasitoids have been discovered. All known *Drosophila* parasitoids are solitary koinobiont larval endoparasitoids in the families of Braconidae and Figitidae (subfamily Eucoilinae), and solitary pupal parasitoids in the families of Pteromalidae and Diapriidae. Larval *Drosophila* parasitoids attack host larvae, but all emerge from the host puparium formed from the hardened exoskeleton of the fly's last larval stage. Most known larval parasitoids belong to the genera *Asobara*, *Leptopilina*, and *Ganaspis*. Among them, *Asobara tabida* (Nees), *Leptopilina boulardi* Barbotin et al., and *L. heterotoma* (Thompson) are the three most extensively studied parasitoids attacking common drosophilids such as *Drosophila melanogaster* (Meigen)

breeding in rotting fruit (reviewed in Prévost 2009). The pteromalids are ectoparasitoids that lay their eggs between the host's puparium case and the pupa, while the diapiiids are endoparasitoids. *Pachycrepoideus vindemiae* (Rondani) and *Trichopria drosophilae* Perkins are two of the most common and cosmopolitan pupal drosophila parasitoids (Wang et al. 2016a, b).

The parasitoid fauna associated with SWD was poorly understood prior to its worldwide invasion. Since then, a number of studies have discovered and identified effective parasitoids both in Asia and around the world (Daane et al. 2016; Giorgini et al. 2019; Girod et al. 2018b). An earlier review article discussed the practical application potential of parasitoids for a broader audience (Lee et al. 2019). Here, we present a comprehensive review on the complexes of parasitoid species attacking SWD worldwide. We summarize the evaluations for promising parasitoids, and the diversity, dominance, and host specificity of parasitoids native to Asia. Finally, we propose future research directions for promoting parasitoids for the control of SWD by classical, augmentative, or conservation biological control.

8.2 Impact of Parasitoids in the Invaded Ranges

Surveys of locally occurring parasitoids on SWD and closely related frugivorous *Drosophila* species have been conducted in the USA (Kamiyama et al. 2019; Miller et al. 2015), Mexico (Cancino et al. 2015), Brazil (Wollmann et al. 2016), Spain (Gabarra et al. 2015), France (Kremmer et al. 2017), Switzerland (Knoll et al. 2017), Italy (Mazzetto et al. 2016; Rossi Stacconi et al. 2013), Slovenia (Modic et al. 2019), and Turkey (Zengin and Karaca 2019). These surveys used sentinel traps baited with larval or pupal SWD or *D. melanogaster* in fruit or artificial diet, and occasionally with collections of infested fruits. Exposed materials in the traps were often inevitably contaminated by other drosophilid species. Thus, some reported parasitoid species, especially *L. bouleardi*, may need verification in laboratory tests to confirm the host-parasitoid association (e.g., Garcia-Cancino et al. 2015; Wollmann et al. 2016; Garrido et al. 2018). The three larval parasitoids (*A. tabida*, *L. bouleardi*, and *L. heterotoma*) and two pupal parasitoids (*P. vindemiae* and *T. drosophilae*) were commonly collected in North America and Europe. These larval parasitoids were, however, exclusively reared from drosophilids other than SWD, whereas the pupal parasitoids were collected from both SWD and other drosophilid species (Table 8.1). In the literature, *P. vindemiae* is sometime mentioned as *P. vindemmiae* (e.g., Wollmann et al. 2016). According to Rossi Stacconi et al. (2013), this species was originally described as *P. vindemiae* by Rondani in 1875, and the latter name should be used thereafter. In several European reports, the *Trichopria* species was reported as *T. cf. drosophilae* (e.g., Chabert et al. 2012; Gabarra et al. 2015; Mazzetto et al. 2016). These specimens are likely conspecific to *T. drosophilae* as reported in other studies. Other pupal parasitoids that were collected from SWD-baited sentinel traps include the pteromalid *Spalangia simplex* Perkins in Mexico, and the diapiiid *Trichopria anastrephae* Lima in Brazil (Table 8.1).

Table 8.1 Parasitoid complexes and their observed parasitism on *Drosophila suzukii* (SWD) in different regions of its native and introduced ranges

Parasitoid species	Countries	Host species ²	Parasitism (%)	References
Larval parasitoids				
Braconidae				
<i>Asobara tabida</i>	Japan	SWD/ Others	–	Mitsui et al. (2007)
<i>A. brevicauda</i>	South Korea	SWD	< 1	Daane et al. (2016)
<i>A. japonica</i>	Japan, South Korea	SWD/ Others	0–16.7	Mitsui et al. (2007), Daane et al. (2016)
<i>A. leverii</i>	China, South Korea	SWD/ DP/ Others	<1	Daane et al. (2016), Giorgini et al. (2019)
<i>A. mesocauda</i>	China, South Korea	SWD/ DP/DSP	–	Girod et al. (2018a), Giorgini et al. (2019)
<i>A. pleuralis</i>	China	SWD/ DP	–	Girod et al. (2018a)
<i>A. sp.</i>	Japan	SWD	<7	Kasuya et al. (2013)
<i>A. sp. TS1</i>	Japan	SWD	1.2	Ideo et al. (2008)
<i>A. triangulata</i>	South Korea	SWD	<1	Daane et al. unpub. data
<i>A. unicolorata</i>	China	SWD/ DP	<1	Giorgini et al. (2019)
<i>Areotetes striatififerus</i>	China	SWD/ DP	0.6–6.9	Girod et al. (2018a)
<i>Tanycarpa chors</i>	China	SWD/ DP	2.1	Girod et al. (2018a)
Figitidae				
<i>Ganaspis brasiliensis</i>	China, Japan, South Korea	SWD/ DP	0–47.8	Kasuya et al. (2013), Daane et al. (2016), Giorgini et al. (2019)
<i>G. cf. brasiliensis</i>	China, Japan, South Korea	SWD/ DP/DSP	0.2–75.6	Girod et al. (2018a), Daane et al. unpubl. Data
<i>G. xanthopoda</i> ^a	Japan	SWD/ Others	–	Mitsui et al. (2007)
<i>Leptopilina bouhardi</i>	Argentina, Brazil, Mexico	SWD/ Others	–	Cancino et al. (2015), Wollmann et al. (2016), Garrido et al. (2018)
<i>L. heterotoma</i>	Italy	SWD/ Others	< 1	Miller et al. (2015)
<i>L. j. formosana</i>	South Korea, Japan	SWD/ Others	< 1	Novkovic et al. (2011), Daane et al. (2016)
<i>L. j. japonica</i>	China, Japan, South Korea	SWD/ DP	0–34.5	Novkovic et al. (2011), Kasuya et al. (2013), Daane et al. (2016), Girod et al. (2018a), Giorgini et al. (2019)

(continued)

Table 8.1 (continued)

Parasitoid species	Countries	Host species ²	Parasitism (%)	References
<i>L. sp.</i>	China	SWD/ DP	7.2–35.9	Girod et al. (2018a)
Pupal parasitoids				
Diapriidae				
<i>Trichopria cf. drosophilae</i>	Italy, Spain	SWD/ Others	0–10.7	Gabarra et al. (2015), Mazzetto et al. (2016), Kremmer et al. (2017)
<i>T. drosophilae</i>	China, France, Italy, Mexico, Slovenia, South Korea, Switzerland, USA	SWD/ Others	0–11.1	Cancino et al. (2015), Miller et al. (2015), Rossi-Stacconi et al. (2015), Daane et al. (2016), Knoll et al. (2017), Giorgini et al. (2019), Modic et al. (2019)
<i>T. anastrephae</i>	Brazil	SWD	–	Wollmann et al. (2016)
Pteromalidae				
<i>Pachycrepoideus vindemiae</i>	China, France, Italy, Mexico, the Netherlands, South Korea, Spain, Switzerland, Turkey, USA	SWD/ Others	0–31.0	Rossi Stacconi et al. (2013), Cancino et al. (2015), Miller et al. (2015), Daane et al. (2016), Mazzetto et al. (2016), Knoll et al. (2017), Kremmer et al. (2017), Haro-Barchin et al. (2018), Zengin and Karaca (2019)
<i>Spalangia erythromera</i>	Italy	SWD/ Others	–	Mazzetto et al. (2016)
<i>S. simplex</i>	Mexico	SWD	–	Cancino et al. (2015)

^aThis species was later reassigned as *Ganaspis brasiliensis* (Nomano et al. 2017)

^bSWD = *Drosophila suzukii*, DP = *D. pulchrella*, DSP = *D. subpulchrella*, and Others = other drosophilids when the species was either not known, not provided or not one of the above species

Various populations of *A. tabida*, *L. boulandi*, and *L. heterotoma* have been tested for their ability to attack and then develop from SWD under laboratory conditions (Table 8.2). To date, none of these larval parasitoids were able to complete development, except for a low percentage of development of *L. heterotoma*, using populations from northern Italy (Rossi-Stacconi et al. 2015) and France (Iacovone et al. 2018) (Table 8.2). The same larval parasitoid, however, successively parasitized *D. melanogaster* and other closely related drosophilids in parallel tests. The larval parasitoids' immature stages failed to develop due to a strong cellular immune response by SWD, causing the fly larvae to increase hemocyte production to encapsulate the immature parasitoids inside the host (Chabert et al. 2012; Iacovone et al. 2018; Kacsoh and Schlenke 2012; Poyet et al. 2013). Nevertheless, this species would still oviposit in SWD larvae which significantly reduced survival of SWD by up to 90%. Variation in mortality was likely due to different experimental procedures with host-parasitoid ratios and exposure times, or geographic variations of

Table 8.2 Frugivorous *Drosophila* parasitoids species evaluated for their efficiency on *Drosophila suzukii* (SWD) in laboratory or field trials

Parasitoid	Parasitoid origin	Rate of parasitism ^a	Emergence ^a	References
Larval parasitoids				
Braconidae				
<i>Aphaereta</i> sp.	USA	Low	None	Kacsoh and Schlenke (2012)
<i>Asobara citri</i>	Ivory Coast	Low	None	Kacsoh and Schlenke (2012)
<i>A. japonica</i>	Japan, South Korea	High	High	Ideo et al. (2008), Chabert et al. (2012), Kacsoh and Schlenke (2012), Daane et al. (2016), Girod et al. (2018b, c), Wang et al. (2018a, 2019, 2020)
<i>A. pleuralis</i>	Indonesia	Low	None	Kacsoh and Schlenke (2012)
<i>A. tabida</i>	France, Switzerland	Low	None	Chabert et al. (2012), Kacsoh and Schlenke (2012), Knoll et al. (2017)
Figitidae				
<i>Ganaspis brasiliensis</i>	China, South Korea	High	High	Wang et al. (2018a, 2019, 2020), Giorgini et al. (2019)
<i>Ganaspis</i> cf. <i>brasiliensis</i>	China, Japan	High	High	Girod et al. (2018b, c)
<i>Ganaspis</i> sp.	USA	Low	Low	Kacsoh and Schlenke (2012)
<i>G. xanthopoda</i> ^b	Japan, Uganda, USA	Low	Low	Mitsui and Kimura (2010), Kacsoh and Schlenke (2012)
<i>Leptopilina bouhardi</i>	Congo, France, Italy, Kenya, Mexico ^c , Switzerland, USA	Low	None	Chabert et al. (2012), Kacsoh and Schlenke (2012), Mazzetto et al. (2016), Gonzalez-Cabrera et al. (2020)
<i>L. clavipes</i>	The Netherlands	Low	None	Kacsoh and Schlenke (2012)
<i>L. guineaensis</i>	Cameron, South Africa	Low	None	Kacsoh and Schlenke (2012)
<i>L. heterotoma</i>	France, Italy, Switzerland, USA	Low	Low	Chabert et al. (2012), Kacsoh and Schlenke (2012), Rossi-Stacconi et al. (2015), Mazzetto et al. (2016), Knoll et al. (2017), Iacovone et al. (2018), Girod et al. (2018b)
<i>L. j. japonica</i>	China, South Korea	High	High	Girod et al. (2018b, c), Wang et al. (2018a, 2019, 2020)
<i>L. victoriae</i>	Philippines, USA	Low	None	Kacsoh and Schlenke (2012)
Pupal parasitoids				
Diapriidae				
<i>Trichopria</i> cf. <i>drosophilae</i>	France, Italy, Spain	High	High	Chabert et al. (2012), Gabarra et al. (2015), Mazzetto et al. (2016)

(continued)

Table 8.2 (continued)

Parasitoid	Parasitoid origin	Rate of parasitism ^a	Emergence ^a	References
<i>T. drosophilae</i>	China, Italy ^c , Mexico ^c , South Korea, Switzerland, USA	High	High	Rossi Stacconi et al. (Rossi-Stacconi et al. 2015, Rossi Stacconi et al. 2017, Rossi-Stacconi et al. 2018, Rossi Stacconi et al. 2019), Wang et al. (2016a, b, 2018b), Kaçar et al. (2017), Knoll et al. (2017), Gonzalez-Cabrera et al. (2019, 2020), Wolf et al. (2019), Yi et al. (2020)
<i>T. sp.</i>	France, USA	High	High	Kacsoh and Schlenke (2012)
<i>T. anastrephae</i>	Brazil	High	High	Kruger et al. (2019), Vieira et al. (2020)
Pteromalidae				
<i>Muscidifurax raptorellus</i>	Canada	High	High	Bonneau et al. (2019)
<i>Pachycrepoideus sp.</i>	USA	High	High	Kacsoh and Schlenke (2012)
<i>P. vindemiae</i>	Canada, China, France, Italy, South Korea, Spain, Switzerland, USA	High	High	Chabert et al. (2012), Gabarra et al. (2015), Rossi-Stacconi et al. (2015), Dancau et al. (2017), Kaçar et al. (2017), Wang et al. (2016a, b, 2018b), Knoll et al. (2017), Zhu et al. (2017), Bonneau et al. (2019), Bezerra da Silva et al. 2019a, b
<i>Spalangia erythromera</i>	Switzerland	High	High	Knoll et al. (2017)
<i>Vrestovia fidenas</i>	Switzerland	High	High	Knoll et al. (2017), Wolf et al. (2019)

^aStudies were conducted with SWD larvae or pupae presented either in artificial diet or in contained fruit

^bThis species was later reassigned as *Ganaspis brasiliensis* (Nomano et al. 2017)

^cOpen field release

resistance and virulence among populations (Kacsoh and Schlenke 2012). Within the SWD's native range, *L. heterotoma* and *L. bouhardi* have never been recorded from SWD (Daane et al. 2016; Giorgini et al. 2019; Ideo et al. 2008; Mitsui et al. 2007; Novkovic et al. 2011), while *A. tabida* has been collected from SWD in Japan possibly from a misidentification (Mitsui et al. 2007). Alternatively, some *A. tabida* populations in Japan and some *L. heterotoma* populations in Europe have locally adapted to SWD, explaining the reported parasitism by these species in those areas.

Pachycrepoideus vindemiae and *T. drosophilae* are the two most studied pupal SWD parasitoids. Although both species are cosmopolitan and sympatric in many regions, *P. vindemiae* is more widely distributed than *T. drosophilae* (Knoll et al.

2017; Miller et al. 2015; Wang et al. 2018b). *Pachycrepoideus vindemiae* is more of a generalist than *T. drosophilae*, as the former species also attacks hosts in other families of cyclorrhaphous Diptera (Wang and Messing 2004), while *T. drosophilae* attacks only Drosophilidae (Carton et al. 1986). A lack of pupal immunity against parasitoids may explain why these pupal parasitoids have broader host ranges than larval parasitoid wasps (Kacsoh and Schlenke 2012). These two pupal parasitoids have been evaluated for their efficiency, host specificity, thermal tolerance, and interspecific interactions (Kaçar et al. 2017; Rossi-Stacconi et al. 2015; Rossi Stacconi et al. 2017; Wang et al. 2016a, b, 2018b; Zhu et al. 2017; Bezerra da Silva et al. 2019a, b). Both species can locate SWD pupae in fruit or soil, but *T. drosophilae* was more efficient than *P. vindemiae* at some temperatures (Garcia-Cancino et al. 2020; Kaçar et al. 2017; Wang et al. 2018b). At 23 °C, *T. drosophilae* females from California and South Korea populations survived 27.5 and 20.2 days, respectively, and produced a total of 63.8 and 52.0 offspring, whereas *P. vindemiae* females from a California population survived 21.5 days and produced 70.0 offspring (Rossi-Stacconi et al. 2015; Wang et al. 2016a). *Pachycrepoideus vindemiae* has a wider temperature range than *T. drosophilae*, which may explain the current distribution of these species in North America (Wang et al. 2018b). Interspecific competition between these two parasitoids may reduce the overall impact on the host population. *Trichopria drosophilae* seems to have an advantage over *P. vindemiae* in laboratory tests (Wang et al. 2016b). All other tested pupal parasitoids also readily developed from SWD in laboratory tests (Table 8.2). These include the pteromalids *Vrestovia fidenas* (Walker) and *Spalangia erythromera* Förster in Europe (Knoll et al. 2017; Mazzetto et al. 2016; Wolf et al. 2019), *Muscidifurax raptorellus* Girault & Sanders in Canada (Bonneau et al. 2019), and *T. anastrephae* in Brazil (Kruger et al. 2019; Vieira et al. 2020). All four parasitoids appear to have the potential to help in the control of SWD. Naturally occurring parasitism of SWD populations by pupal parasitoids is generally low (Table 8.1), but augmentative releases may allow them to be useful. In Italy, *T. drosophilae* was commercially available, and evaluated for its host location, dispersal, and host suppression capabilities in an augmentative release in netted raspberry fields (Rossi-Stacconi et al. 2018). The parasitoid was able to locate SWD in traps up to 40 m away from the release site, and SWD emergence was significantly reduced within a radius of 10 m of the release within netting environment. Recently, the effectiveness of this parasitoid has been evaluated in releases in unmanaged vegetation surrounding cherry orchards in Italy (Rossi Stacconi et al. 2019) and in commercial berry (*Rubus fruticosus* L.) crops in Mexico (Gonzalez-Cabrera et al. 2019). In Italy, weekly release of the parasitoid at a rate of 0.33 specimens/m² for 7 weeks resulted in a 34% reduction in fruit infestation in the unmanaged vegetation surrounding orchards. In Mexico, semi-weekly release of the parasitoid at a rate of 4.5 wasps/m² for 50 weeks resulted a fourfold increase in parasitism and a 50% reduction of SWD in the field. Results from these studies suggest that augmentative release of *T. drosophilae* can suppress SWD populations in the unmanaged areas surrounding crops, thus lowering the severity of pest outbreaks in the crop (Rossi Stacconi et al. 2019). While no augmentative trials have been made with *M. raptorellus*, this pupal parasitoid is

commonly sold for release in livestock operations, making releases in crops potentially feasible.

A population model predicts the optimal timing for releasing *T. drosophilae* against SWD would be between late spring and early summer when the host population begins to increase (Pfab et al. 2018). Early releases would help reduce fly populations that would likely move from overwintering unmanaged vegetation into early susceptible fruit crops, and at the same time, those released parasitoids would increase their population (Pfab et al. 2018). However, the timing of release will depend on geographical region. For example, in a warm temperate climate such as Mexico, SWD populations are active year-around, and sufficient pest suppression would require repeated augmentative releases (Gonzalez-Cabrera et al. 2019).

8.3 Exploration for Parasitoids in Asia

Exploration for parasitoids native to South Korea, China, and Japan have discovered at least 19 larval parasitoids associated with SWD, including 12 *Asobara* and 7 figitids (Table 8.1). In South Korea, eight species, *Asobara japonica* Belokobylskij, *A. leverii* (Nixon), *A. brevicauda* Guerrieri & van Achterberg, *A. triangulata* van Achterberg and Guerrieri, *A. mesocauda* van Achterberg and Guerrieri, *Ganaspis brasiliensis* Ihering, *Leptopilina japonica* Novković & Kimura, and *L. j. formosana* Novković & Kimura, and the pupal parasitoid *T. drosophilae* were collected from SWD and other Drosophilidae (Daane et al. 2016). *Leptopilina japonica* is further divided into the temperate subspecies (*L. j. japonica*, thereafter, referred to *L. japonica*) and the subtropical subspecies (*L. j. formosana*) (Novkovic et al. 2011). The larval parasitoid *L. boulardi* and the pupal parasitoid *P. vindemiae* were collected from other drosophilids. *Asobara brevicauda*, *A. triangulata*, and *A. mesocauda* are newly described species (Guerrieri et al. 2016). Parasitism of SWD by these larval parasitoids varied according to geography, season, and collection methods, ranging from 0 to 28.6% (Daane et al. 2016). *Ganaspis brasiliensis* and *L. japonica* were the major parasitoids found in fresh fruits infested by SWD, whereas *A. japonica* was the major parasitoid collected from fruit bait traps infested predominantly by other drosophilids (Daane et al. 2016). A total of 3266 and 20,358 *Drosophila* puparia were collected in 2013 and 2014, respectively, from a variety of locations, and *A. japonica*, *G. brasiliensis*, and *L. japonica* accounted for 85.7% of all larval parasitoids emerged (Daane et al. 2016). In 2016, a total of 11,575 SWD puparia were collected from several wild *Rubus* fruits, and *G. brasiliensis* and *L. japonica* accounted for 87.1% of total parasitoids emerged (Daane et al. 2016).

In China, Girod et al. (2018a) conducted surveys in the provinces of Yunnan, Jilin, Beijing, Hubei, and Sichuan by collecting wild and commercial fruits, and Giorgini et al. (2019) conducted surveys in Yunnan Province using banana-baited traps and wild fruit collections. Collected fruits were often co-infested by *Drosophila. pulchrella* Tan, Hsu & Sheng in Yunnan or by *D. subpulchrella* Takamori in other regions of China. These two species are also characterized by a

serrated ovipositor, like SWD, that allows them to attack fresh fruits. Because the pupae of these three *Drosophila* spp. are indistinguishable, it was impossible to determine from which host the parasitoids emerged from (Giorgini et al. 2019; Girod et al. 2018a). At least nine larval parasitoids, *A. leverii*, *A. mesocauda*, *A. unicolorata*, *A. pleuralis* (Ashmead), *Areotetes striatiferus* Li, *G. brasiliensis* (or *G. cf. brasiliensis*), *L. japonica*, *Tanycarpa chors* Belokobylskij, and *Leptopilina* sp., and the pupal parasitoid *T. drosophilae* were collected in China. The most abundant and frequently collected larval parasitoids were *G. brasiliensis* and *L. japonica*. For example, Giorgini et al. (2019) collected a total of 11,683 SWD and *D. pulchrella* puparia from four wild host fruits (*Rubus foliosus* Weihe, *R. niveus* Thunberg, *Fragaria moupinensis* Cardot, and *Sambucus adnate* Wallich ex de Candolle) at four different locations during 2016 in Yunnan, China. The majority of emerged parasitoids were *G. brasiliensis* (63.7%) and *L. japonica* (33.2%), accounting for 97.1% of total parasitoids. These two parasitoids also accounted for 97.8% of all larval parasitoids emerged from 1792 *D. suzukii* and *D. pulchrella* puparia (Hoelmer et al. unpubl. data). The highest parasitism by *G. brasiliensis* was 47.8% and 42.0% by *L. japonica* in the 2016 collections in Yunnan, China (Giorgini et al. 2019). The banana traps yielded mainly other Drosophilidae (>99%) and seven *Asobara* species (primarily *A. mesocauda*) and six figitids (primarily *L. japonica*) as well as *T. drosophilae* and *P. vindemiae*. Only one *A. japonica* and one *G. xanthopoda* were collected, and *G. brasiliensis* was never collected from banana traps (Giorgini et al. 2019). The surveys showed that most flies emerging from fresh fruits were SWD or the closely related *D. pulchrella* and *D. subpulchrella*. This suggests that field collection of fresh fruits is a more reliable method to collect SWD parasitoids (Daane et al. 2016; Giorgini et al. 2019) (Fig. 8.1).

In Japan, at least six larval parasitoids (*A. japonica*, *A. tabida*, *L. japonica*, *G. xanthopoda*, *T. chors*, and *Asobara* sp.) have been reported to parasitize SWD and other frugivorous *Drosophila* species (Girod et al. 2018a; Ideo et al. 2008; Kasuya et al. 2013; Mitsui and Kimura 2010; Mitsui et al. 2007; Novkovic et al. 2011). *Ganaspis cf. brasiliensis* was the most abundant parasitoid collected from SWD in wild fruits with parasitism of 75.6% reported in Nara, Japan (Girod et al. 2018a). Matsuura et al. (2018) showed that *G. cf. brasiliensis* attacked SWD larvae in fresh fruits in the tree canopy, but rarely in fruits fallen on the ground, suggesting a specific adaptation of a Japanese strain to SWD infesting fresh fruits. An *Asobara* sp. that was recorded only from SWD in wild fruits (Girod et al. 2018a; Ideo et al. 2008; Nomano et al. 2015) may be more specific; it was speculated to be *A. triangulata* based on molecular analysis of specimens (Guerrieri et al. 2016). *Asobara japonica* was the major parasitoid collected in banana traps throughout Japan (Mitsui et al. 2007). Populations of *A. japonica* in the main islands of Japan and South Korea seem to be parthenogenetic, whereas those in the south-western islands of Japan apparently reproduce sexually (Daane et al. 2016; Murata et al. 2009).

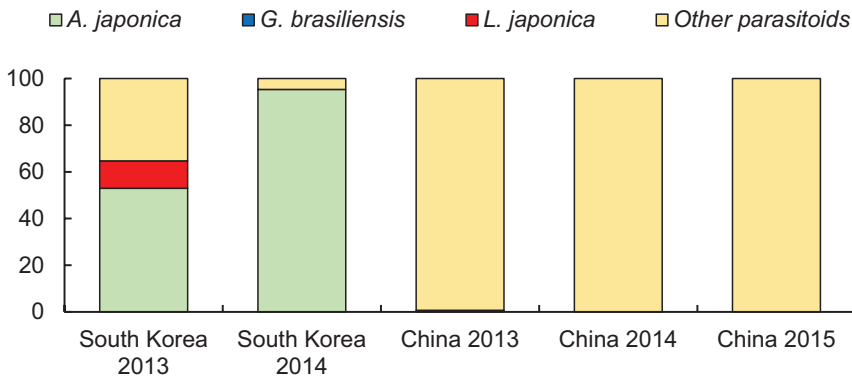
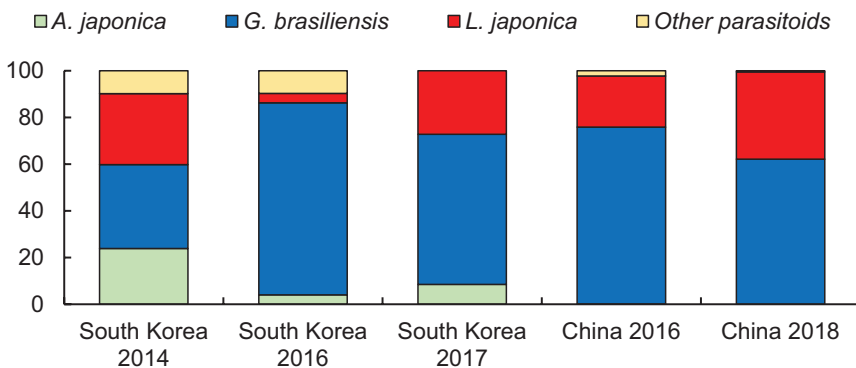
(A) Sentinel fruit traps**(B) Fruit samplings**

Fig. 8.1 Composition of major Asian parasitoids (*Asobara japonica*, *Ganaspis brasiliensis*, and *Leptopilina japonica*) of frugivorous Drosophilidae collected from (a) fruit-baited traps or (b) via sampling of fresh fruits in South Korea and China during 2013–2018 (for other parasitoid species, see the list on Table 8.1—parasitoid complexes). Data were compiled based on Daane et al. (2016), Giorgini et al. (2019), and unpublished data from recent collections

8.4 Prospects for Classical Biological Control

The Asian surveys suggest that *G. brasiliensis*, *L. japonica*, and *A. japonica* are the most dominant and widely distributed larval parasitoids attacking SWD (Fig. 8.1), whereas most other larval parasitoids showed a more restricted distribution and lower parasitism rates (8.1 and 8.2). These three larval parasitoids have been systematically evaluated for their efficiency, host specificity, climatic adaptability as well as potential interaction as classical biological control agents in North America and Europe (Biondi et al. 2017; Daane et al. 2016; Giorgini et al. 2019; Girod et al.

2018b, c; Wang et al. 2018a, 2019, 2020). All three parasitoids readily attack and develop from SWD (Table 8.2) and prefer to attack young host larvae (Wang et al. 2018a). At 23 °C, with SWD larvae in artificial diet, *G. brasiliensis* adult females survived 17.7 days and produced 98.3 offspring per female, and *L. japonica* survived 18.7 days and produced 107.2 offspring per female (Wang et al. 2018a), while *A. japonica* females lived 17.8 days and produced 117.3 offspring per female (Wang et al. unpubl. data). *Leptopilina japonica* eggs hatched the fastest, followed by *A. japonica* and then *G. brasiliensis* and consequently *L. japonica* outcompeted the other two parasitoids in multi-parasitized hosts (Wang et al. 2019). However, *G. brasiliensis* discriminated strongly against hosts parasitized by *L. japonica*, and *A. japonica* discriminated against hosts parasitized by *L. japonica*. The combined impacts on host suppression by *L. japonica* and *G. brasiliensis* were additive, likely due to the interspecific discrimination by *G. brasiliensis*. Indeed, both parasitoids coexist in all locations and plants sampled in China or South Korea (Daane et al. 2016; Giorgini et al. 2019), indicating they might synergistically improve the suppression of SWD.

Quarantine tests with a wide range of 24 different drosophila species showed that the South Korean and Yunnan *G. brasiliensis* populations developed from SWD and several other closely related hosts (*D. melanogaster* and *D. simulans*) but did not develop from more distant non-target drosophilid species (Giorgini et al. 2019). *Asobara japonica* developed from 19 of 24 tested host species, whereas *L. japonica* developed mainly from species in the *melanogaster* group (Daane et al. unpubl. data). By comparison, both *P. vindemiae* and *T. drosophilae* developed from all 24 tested drosophila species (Wang et al. unpubl. data). Other studies also showed that these two pupal parasitoids develop from nearly all tested hosts, preferentially attacking large hosts with correspondingly large progeny emerging (Chen et al. 2018; Wang et al. 2016a; Wolf et al. 2020; Yi et al. 2020). In Japan, field surveys and laboratory tests also found that *A. japonica* parasitized various indigenous and exotic drosophilid species (Ideo et al. 2008; Mitsui and Kimura 2010; Mitsui et al. 2007). In Switzerland, Girod et al. (2018b, c) tested six different European non-target fly species with these three larval parasitoids. Similarly, they found that *A. japonica* developed from all tested drosophilids, and *L. japonica* successfully parasitized *D. melanogaster* and *D. subobscura*. A Japanese population of *G. cf. brasiliensis* collected from SWD was strictly specific to SWD as reported by Kasuya et al. (2013), whereas another population from China parasitized SWD and *D. melanogaster* and sporadically parasitized *D. subobscura*. Thus, *A. japonica* is more of a generalist, whereas *L. japonica* appears to be a specialist on *melanogaster* species group. Currently, *G. brasiliensis* is considered as the first candidate for classical biological control of SWD due to its demonstrated specificity.

8.5 Diversity of the *Ganaspis brasiliensis* “Complex”

Buffington and Forshage (2016) first described *G. brasiliensis* as a new combination based on the specimens collected from SWD in South Korea (Daane et al. 2016) and historical specimens from the Neotropical region. Previously in Japan, Mitsui and Kimura (2010) reported that *Ganaspis* collected from *Drosophila lutescens* Okada readily parasitized *D. lutescens* and other drosophilids tested (>90% parasitism) but rarely accepted SWD (only 3.3% parasitism). These *Ganaspis* were initially assigned the name *G. xanthopoda* (Table 8.1). However, Kasuya et al. (2013) showed that SWD was the only drosophilid species infesting fresh wild cherries in Tokyo area, and *Ganaspis* individuals were the major parasitoids attacking SWD in wild cherry fruits. They reported that this *Ganaspis* population did not parasitize SWD in *Drosophila* medium and other *Drosophila* spp. in fresh cherries; and they identified the population as the *D. suzukii*-associated *G. xanthopoda* type. *Ganaspis* specimens previously assigned as *G. xanthopoda* are morphologically similar to specimens that were collected from South Korea and identified as *G. brasiliensis* by Buffington and Forshage (2016) and were thus reassigned to *G. brasiliensis* (Nomano et al. 2017).

Subsequent molecular analyses of different individuals based on nucleotide sequences of the mitochondrial cytochrome oxidase subunit 1 (CO1) gene, and the inter-transcribed spacers 1 and 2 (ITS1 and ITS2) suggest that individuals thus far morphologically identified as *G. brasiliensis* could be subdivided into five lineages (Nomano et al. 2017): G1, including individuals collected from SWD from Sendi and Tokyo in Japan; G2, including individuals from a subtropical Japanese island parasitizing *Drosophila ficusphila* Kikkawa & Peng; G3, including individuals from temperate regions of Japan and high mountains of Southeast Asia (Indonesia, Malaysia) parasitizing different species of *Drosophila*; G4, including individuals from Indonesia parasitizing *Drosophila eugracilis* Bock & Wheeler; G5, including individuals previously reported as *G. xanthopoda* or *Ganaspis* sp. from Thailand and the Philippines (Schilthuizen et al. 1998), Hawaii and Uganda (Kacsoh and Schlenke 2012), Indonesia (Kimura and Suwito 2012, 2015), Malaysia (Nomano et al. 2017), Benin, Puerto Rico and the Caribbean Sea (Carton et al. 1986), Brazil (Buffington and Forshage 2016), and Mexico (Gonzalez-Cabrera et al. 2020).

Phylogenetic analysis of COI sequences revealed that the *G. brasiliensis* specimens collected in Yunnan, China (Giorgini et al. 2019), consisted of 77% G1 and 23% G3. Similarly, the *G. brasiliensis* specimens collected in South Korea in 2017 (and similar sites reported in Daane et al. 2016) consisted of 65% G1 and 35% G3. These results suggest that these two lineages (G1 and G3) appear to be widely distributed in East Asia. They coexist in many locations and attack SWD and the closely related *D. pulchrella* and *D. subpulchrella* inhabiting fresh fruits, and have thus been considered sufficiently specific to SWD based on field collections and quarantine evaluations (Daane et al. 2016; Giorgini et al. 2019; Girod et al. 2018b, c; Kasuya et al. 2013). The host range of other lineages is unclear, and they have not been collected from SWD in fresh fruits nor tested in the laboratory with SWD,

except that some G5 individuals from Hawaii and Uganda have a capacity to parasitize SWD in laboratory tests but with no or low development (Kacsoh and Schlenke 2012). Thus, *G. brasiliensis* appears to be a complex of several cryptic strains with varying host specificity and distributions. Given the Asian origin of SWD and the common ancestor of different lineages likely occurs in Asia, the species have likely been introduced to the Neotropics and Africa (Buffington and Forshage 2016; Nomano et al. 2017).

Recent studies further suggest that G1 (called *G. cf. brasiliensis* in Girod et al. 2018a) and G3 may be two different species. Reeve and Seehausen (2019) compared the acid-soluble insect protein spectra among three different G1 populations collected from Tokyo, Japan, and Dali and Ximing, China and a G1 population collected from Hasuike, Japan, and found that the G3 is significantly different from all G1 specimens. Other ongoing studies indicate the absence of positive crossing between G1 and G3, and different host-searching behaviors. G1 prefers hosts infesting fruits, whereas G3 prefers hosts in rotting substrates (M. Kenis, personal comm.). Further research combining multiple gene analyses and crossing-mating experiments across geographical populations or lineages is clearly needed to fully understand the ecological and genetic diversity of the *G. brasiliensis* complex.

8.6 Predicted Geographical Ranges of *Ganaspis brasiliensis*

The CLIMEX model (Kriticos et al. 2015) has been used to predict the potential geographical range of *G. brasiliensis* based on the current known distribution of G1 and G3 lineages in Asia (Daane et al. unpubl. data). Geographical coordinates of 37 collection sites where parasitoids were found in China, South Korea, and Japan were obtained (Kasuya et al. 2013; Daane et al. 2016; Nomano et al. 2017; Matsuura et al. 2018; Giorgini et al. 2019). The model parameters were repetitively adjusted and the function “Compare location,” which describes the potential geographical distribution of species, as controlled by weather variables was subsequently run until the estimated potential *G. brasiliensis* range coincided best with the known distributions of the species in East Asia. The model predicted that *G. brasiliensis* would likely establish in the western, southeastern, and east coastal states in North America and most southern European countries where SWD is a major concern of small fruit crops (Fig. 8.2). Indeed, a recent survey in British Columbia, Canada, found that G1 has established in the Vancouver area, possibly through accidental introduction (P. Abram, personal comm.). It remains to be discovered whether *G. brasiliensis* will be able to colonize all invaded regions by SWD or whether it will be limited by climatic constraints. A comparative study on thermal performance between two populations originally from Yunnan Province of China and Gyeongsangnam-do Province of South Korea revealed the occurrence of a facultative diapause in *G. brasiliensis* below 17.2 °C (Hougardy et al. 2019). This cold temperature response varied between the populations: South Korean populations entered diapause at 17.2 °C, whereas only a proportion of its Chinese counterpart

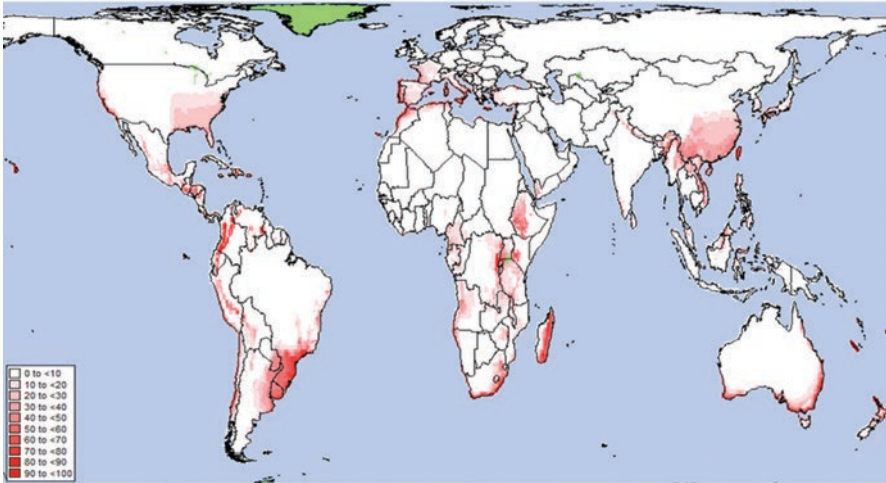


Fig. 8.2 Predicted distribution of *Ganaspis brasiliensis* worldwide based on CLIMEX climatic suitability indices. EI: <10 is not suitable; 10–50 moderate level of suitability; and >50 highly suitable for long-term survival

entered diapause at the same temperature. This suggests that some populations could be a better match for colder climates, or that mixing of populations from different origins could increase plasticity in response to cold seasons.

8.7 Future Directions with Parasitoids

Biological control using parasitoids could be a key component of areawide management programs for SWD by reducing fly populations at the landscape level. To date, three resident pupal parasitoids (*P. vindemiae*, *T. drosophilae*, and *T. anastrephae*) and one Asian larval parasitoid species or species complex (*G. brasiliensis* or *G. cf. brasiliensis*) have been identified as potentially promising biological control agents for SWD. A petition for release of the Asian *G. brasiliensis* in North America and Europe has been submitted, and a regulatory decision is currently pending. The resident pupal parasitoids already adapted to local ecological conditions and which can readily attack SWD could be manipulated either through conservation or augmentation to contribute to SWD suppression. However, the most effective and permanent biological control will likely be achieved by the introduction and augmentation of *G. brasiliensis*.

Future studies may include (1) the genetic improvement of natural enemies by selecting biological traits among different populations for selection or breeding that are important for effective biological control (Kruitwagen et al. 2018); (2) developing optimal rearing and release strategies for promising parasitoids to maximize establishment potential in different regions; (3) developing strategies to reduce the

impacts of non-target control measures such as selective pesticides or cultural management (Cossentine and Ayyanath 2017; Schlesener et al. 2019), (4) introducing different geographic *G. brasiliensis* strains that are adapted to different climate zones within invaded regions (Hougardy et al. 2019); and if necessary (5) exploration, importation, and evaluation of additional Asian larval parasitoids (such as the unidentified *Asobara* sp. TK1) that appear to be specific to SWD (Guerrieri et al. 2016; Nomano et al. 2015).

8.8 Predators

Since the 2019 review, earwigs, green lacewings, mirids, and stink bugs have been identified as potential predators. The European earwig, *Forficula auricularia* L. (Dermaptera, Forficulidae), readily consumed larval and pupal stages of SWD, but could not effectively catch adults in laboratory studies (Englert and Herz 2019). Similarly, *F. auricularia* reduced the emergence of SWD adults by 45% when confined to infested cherries in a growth chamber, and the reduction was likely due to predation on developing SWD and not removal of parental SWD (Bourne et al. 2019). Green lacewing larvae, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), have reduced emergence of SWD from infested raspberries by 32% (Bonneau et al. 2019), and from infested cherries by 33% (Englert and Herz 2019). The mirid *Dicyphus hesperus* (Knight) (Heteroptera: Miridae) preyed on exposed SWD eggs, and the stink bug *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) preyed on exposed larvae that were placed on leaves (Bonneau et al. 2019). Recent studies with minute pirate bugs further support previous work, as *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) reduced emergence from infested fruit by 49% (Bonneau et al. 2019), and *O. majusculus* (Reuter) (Hemiptera: Anthocoridae) reduced emergence by 31% (Englert and Herz 2019).

Previous assessments of field predation have revealed 61–100% removal of sentinel pupae on or below the soil surface, and a 19–49% reduction in emerging SWD from infested fruit in fields in Oregon and Maine, USA (Ballman et al. 2017; Woltz and Lee 2017). A recent survey in organic raspberry fields in Wisconsin documented 1–4% predation on sentinel pupae (Kamiyama et al. 2019). Therefore, actual predation levels can vary from field to field depending on the conditions. Predation has also been assessed by molecular analysis as first demonstrated by Wolf et al. (2018) which surveyed predators in organic farms in Germany. In Georgia blueberries, 0.4% of the 1600 collected predators tested positive for predation by molecular analysis (Schmidt et al. 2019). These included hunting spiders, a web-building spider, and one mantid. Both studies using molecular surveys reveal that generalist spiders prey on SWD.

To date, most work on parasitoids and predators has focused on field surveys, measuring natural predation and parasitism rates, or studied the efficacy of agents in enclosed arenas or field releases. More work remains to be done on conserving these natural enemies, and whether specific habitat manipulations will benefit natural

enemies and increase SWD control. A landscape-level analysis of blueberry fields revealed that organic systems and fields with vegetation between rows harbored more natural enemies (Schmidt et al. 2019). In their analysis, landscapes with greater composition of non-crop habitats also had higher SWD populations. This may be expected since SWD reproduces on many different wild hosts (Kenis et al. 2016; Lee et al. 2015), and SWD can move from wild fruit to nearby crops (Leach et al. 2018).

8.9 Entomopathogens

In 2019–2020, more studies were published on entomopathogenic nematodes than other pathogens. The recently discovered *Oscheius onirici* Torriani et al. (Nematoda: Rhabditidae) was sprayed on infested blueberries, reducing pupation by 78% in laboratory trials (Foye and Steffan 2020). Contrary to previous reports (Garriga et al. 2017; Hübner et al. 2017), SWD pupae have appeared to be more susceptible to nematode infections than larvae. For example, *Heterorhabditis bacteriophora* (Poinar) (Nematoda: Heterorhabditidae) and *Steinernema feltiae* (Filipjev) (Nematoda: Steinernematidae) caused 72% mortality among SWD pupae, and 20% mortality among larvae in Petri dish assays (Ibouh et al. 2019). Newly tested *Heterorhabditis amazonensis* (Andalo) and *H. indica* (Poinar) (Nematoda: Heterorhabditidae), as well as *S. carpocapsae* (Weiser) and *S. feltiae*, caused 35, 26, 13, and 43% mortality among SWD pupae, respectively (Brida et al. 2019).

Additional work has supported the effectiveness of *S. carpocapsae*, including recent assays with adult SWD. Adults exposed to *S. carpocapsae* had an infection rate of 65% compared to 4% by *S. feltiae* and *H. bacteriophora* (Garriga et al. 2020b). Moreover, when soil with buried SWD pupae was treated with *S. carpocapsae*, 89% of emerging adults were infected. Teneral adults may be especially vulnerable to infection, and 59% could not move up their plastic cylinder arena. In lab arenas, 21% of infected adults were able to fly, and the authors suggested that this may help with nematode dispersion. As with any pathogen, infected hosts can have defensive responses, and studies of SWD larvae infected with *S. carpocapsae* and its symbiont bacteria *Xenorhabdus nematophila* Thomas & Poinar revealed that the pathogen avoided cellular defenses and depressed humoral responses (Garriga et al. 2020a).

The fungal pathogens *Beauveria bassiana* (Bals.) Vuill and *Metarhizium anisopliae* (Metch.) Sorok. have been the most widely studied (reviewed in Lee et al. 2019). Recent work has shown them to cause 38% mortality of larvae, and 32–64% of adults when sprayed on SWD in Petri dishes (Ibouh et al. 2019). Interestingly, when grape berries were dipped in fungal suspensions, oviposition by SWD was reduced by 80% compared to the controls. Thus, while fungal treatments may not always directly contact adults when sprayed in the field, and require several days to induce adult mortality, the sprays provide additional protection to the fruit. Assays

conducted by Ibouh et al. (2019) exposed flies to grapes for 5 days under standard laboratory conditions, and the duration of fruit protection has still to be determined.

To find bacterial pathogens, Hiebert et al. (2020) collected SWD from infested fruits in the field, isolated, and screened the associated bacteria. Seven isolates were detrimental including the Gram-positive bacteria *Brevibacterium frigoritolerans* Delaporte & Sasson, *Bacillus simplex* (exMeyer and Gottheil), *Bacillus altitudinis* Schivaji et al., *Leuconostoc pseudomesenteroides* Farrow et al., *Paenibacillus dongdonensis* Son et al. and *Paenibacillus odorifer*, and the Gam-negative bacterium *Tatumella terreus* (Kageyama et al.). The mode of action was explored; *Paenibacillus dongdonensis* and *L. pseudomesenteroides* appeared to reduce food uptake in SWD larvae.

8.10 Competitors

Previous laboratory and greenhouse work has shown *Drosophila melanogaster* to be a promising competitor of SWD. The presence of *D. melanogaster* is not expected to pose a threat to harvested fruit since it attacks overripe or damaged fruit and could foreseeably compete with SWD during the late season when dropped fruit remains on the ground. The African fig fly, *Zaprionus indianus* (Gupta), was recently shown to compete with SWD in grapes in laboratory studies, and induce higher SWD mortality (Shrader et al. 2020). *Zaprionus indianus* generally does not lay eggs in intact fruit but can use the oviposition sites of SWD to lay eggs (Bernardi et al. 2017). Whether co-infestations occur often in the field or could be advantageous for IPM remains to be studied.

8.11 Compatibility of Biological Control

Recent work has investigated the compatibility of biological controls with other control approaches, especially with pesticides commonly used in SWD management. Organophosphates, pyrethroids, and neonicotinoids cause high mortality in the parasitoids *T. anastrephae* and *P. vindemiae* in lab bioassays (Schlesener et al. 2019). Spinosad is a commonly used organic insecticide which is unfortunately detrimental to *P. vindemiae* adults, and female wasps are unable to avoid treated SWD pupae (Cossentine and Ayyanath 2017). The same study also determined that the larval stage of *P. vindemiae* was susceptible to spinosad when SWD pupae were treated 1 week post-parasitization, but they survived better at the pupal stage when treated 2 weeks post-parasitization. A variety of organic insecticides were tested on two generalist predators of SWD; the green lacewing *Chrysoperla rufilabris* (Burmeister) was susceptible to spinosad, and the minute pirate bug *Orius insidiosus* was susceptible to fresh and aged residues of spinosad and sabadilla alkaloids

(Sarkar et al. 2019). Moreover, sublethal effects of insecticide exposure resulted in reduced egg hatch of *O. insidiosus*.

With the variety of pathogens being tested for SWD control, more work is needed to assess compatibility of pathogens with predators and parasitoids, especially if releases are anticipated. Recently, *T. drosophilae* was unaffected when parasitized SWD pupae were exposed to treatments of *B. bassiana*, *M. anisopliae*, *H. bacteriophora*, or *S. feltiae* and parasitoid emergence was subsequently monitored in the laboratory (Ibouh et al. 2019). Likewise, adults of *T. drosophilae* and rove beetle, *D. coriaria* (Kraatz), were unaffected by *H. bacteriophora*, *S. feltiae*, and *S. carpocapsae* in Petri dish assays (Garriga et al. 2019). However, the predator *O. laevigatus* (Fieber) experienced reduced survival from exposure to *S. carpocapsae* in Petri dish assays but not when nematodes were applied to a plant. This suggests that this predator would escape harmful effects in a field situation. Mulching and floor management have been examined as cultural practices to control SWD (Rendon et al. 2020; Rendon and Walton 2019), and specifically target SWD as they often wander to pupate in the soil (Woltz and Lee 2017). Such ground practices to make the soil less hospitable to SWD may however be incompatible with soil drench treatments with nematodes where a moist soil environment is necessary for infective juveniles to survive and find hosts.

8.12 Summary

Many researchers have been dedicated to advancing biological control of SWD as demonstrated by the nearly 100 publications at the time of writing this review. A longer-term approach relies on importing the parasitoid, *Ganapsis brasiliensis*, to invaded regions. With this parasitoid, there is a need to: breed more effective traits, develop efficient rearing and release strategies, and use geographic strains adapted to various climates. A variety of endemic predators in the field prey on SWD. Augmentative releases of predators have not yet been recommended since their cost-effectiveness and efficacy need determination. As for pathogens, new nematode species have been tested in the laboratory, and nematodes can affect ten-eral SWD adults as they emerge from treated soil. Moreover, several nematode and fungal pathogens appear to be compatible with common SWD parasitoids and predators. This is promising since many commonly used insecticides for SWD are harmful to these parasitoids and predators. Since most pathogen research has been conducted in the laboratory, field trials are required to develop recommendations. As more information becomes available with biological control agents, additional work is needed to integrate them into SWD management programs.

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