Chapter 4
The Biology and Ecology of *Drosophila suzukii* (Diptera: Drosophilidae)

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Abstract Preference of egg laying in ripe (or in ripening process), healthy, soft, small fruits (berries and stone fruits) still attached to the plant makes *Drosophila suzukii* (spotted wing *Drosophila*, SWD) a severe, harmful pest, capable of producing huge food and economic losses to Asia, Europe, and America. The high degree of polyphagy shown by SWD either in their native region, Eastern and Southeastern Asia, or in the invaded continents, besides its seasonal phenotypic plasticity that allows it adaptations to adverse thermal periods, greatly favors SWD establishment and dispersion into new environments. In view of its high-damaging profile and rapid adaptability to settle in different world regions, several authors have focused on the study of biological and ecological features of this invasive pestiferous insect. In this regard, the chapter provides summarized information on life cycle, oviposition preference, larva feeding effects on fruits, crop and non-crop host plants world-

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wide range, host preference, continental dispersal, seasonal biology, population dynamic, thermal susceptibility, reproductive behavior, interspecific and intergeneric interactions with other frugivorous dipterans, and relationships with natural enemies in native and introduced regions. A deep knowledge of the relationships between SWD and ecological components of newly invaded landscapes is critical for designing effective, environmental-friendly, SWD management strategies.

Keywords Spotted wing Drosophila · Biological invasions · Host range · Fruit pests · Seasonal biology · Natural enemies

4.1 Introduction

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), commonly known as the spotted wing *Drosophila* (SWD), is a major invasive global pest of small, soft, and stone fruits. Originally from Eastern and Southeastern Asia, SWD causes significant economic damage to fruit production in invaded regions of Europe and the American continent (Lee et al. 2019). From the earliest records on a specific invaded continent, SWD was characterized by its rapid range expansion within fruit-growing areas (Asplen et al. 2015). Based on this fact, and taking into account the very damaging profile of SWD, several authors have been giving special attention to biological and ecological features of SWD to understand its adaptation and dispersal strategies to invade and settle in different world regions. Thus, this chapter reviews over a large number of publications and provides summarized information on: (1) life cycle, oviposition preference, and feeding effects; (2) crop and non-crop host plants worldwide range, host preference and continental dispersal; (3) seasonal biology and population dynamics; (4) adult and immature stages thermal susceptibility; (5) mating behavior and sex ratio; (6) interspecific and intergeneric interactions with other frugivorous dipterans; and (7) relationships with natural enemies in native and introduced regions.

4.2 Life Cycle, Oviposition Preference, and Feeding Effects

Two exclusive features of SWD make it an economically dangerous pest: its preference for healthy, ripening fruit and the powerful, sclerosed, and serrated ovipositor of the female, which penetrates the fruit epidermis causing physical damage. Frequently, these oviposition wounds provide access to secondary fruit-feeding organisms, both insects (i.e., other frugivorous drosophilids) and pathogens (fungi and bacteria), which together cause additional losses (Walsh et al. 2011). Eggs develop into larvae within the fruit mesocarp, causing its rapid softening and rotting, bringing as consequence enormous yield losses, with significantly negative economic impact. Nevertheless, SWD may also lay eggs in wounded and/or fermenting fruit (Kienzle et al. 2020). The SWD may thrive well in fallen fruit, when the preferred fruit stages are unavailable or scarce (Bal et al. 2017; Kienzle et al.

2020). As a result, SWD individuals can emerge from eggs laid on berries either intact or injured (Mazzetto et al. 2020; Kienzle et al. 2020).

SWD females lay eggs with an erratic distribution pattern across fruits, which can be explained by random visits of females to fruits and the production of clutches of mostly single eggs (Mitsui et al. 2006; Schlesener et al. 2017). SWD females tend to oviposit at softer parts of the fruit, which imply that they examine fruits very carefully to locate the most suitable parts for egg laying (Kinjo et al. 2014). Tests carried out with different *Vaccinium* spp. cultivars showed more egg laying in softer fruit blueberry varieties than in firmer fruit varieties (Kinjo et al. 2013). A SWD female may lay 20–419 eggs in a lifetime, depending on the environmental conditions (Hamby et al. 2016). Once the larva hatched, it feeds inside fruit pulp. SWD larvae develop through three instars; the mature larva tends mainly to migrate out of the fruit to pupate in the soil (Woltz and Lee 2017; Lee et al. 2019). A total of 13–14 days is needed for the fly to develop from egg to adult at 22 °C (egg stage duration 1.4 day, larval stage 6 days, and pupal stage 6 days) (Tochen et al. 2014). Adults of both summer and winter morphotypes may live up to 30–179 days in the lab when provided food depending on temperature (Shearer et al. 2016; Rendon et al. 2019; Stockton et al. 2019). Females have a short pre-ovipositional period, during which they mostly feed. After first mate, 1- to 5-day-old females start laying eggs under standard lab conditions (Hamby et al. 2016).

4.3 Host Plants and Continental Dispersal

The SWD has a broad crop and non-crop host plants range, mainly throughout Asia, Europe, and America (Asplen et al. 2015), and with potential for adaptation and establishment in Oceania and Africa (Dos Santos et al. 2017). Soft-skinned and stone fruits such as berries and cherries are highly susceptible to infestation (Mitsui et al. 2010; Cini et al. 2012; Bellamy et al. 2013; Burrack et al. 2013; Lee et al. 2015). In addition to cultivated host species, the SWD can develop in both native and exotic fruit of wild and ornamental non-crop hosts. This occurs in various habitats, such as forests, forest edges, meadows, hedges of agricultural areas, urban gardens and parks, whereby this insect may switch among host plants and environments when ripe fruits are available (Lee et al. 2015; Asplen et al. 2015; Kenis et al. 2016). This feature, besides other biological factors, greatly facilitates its dispersion in invaded fruit-growing regions (Lee et al. 2011a, b, 2012; Cini et al. 2012, 2014; Kenis et al. 2016).

4.3.1 Asia

A total of 58 host plant species, belonging to 11 families, were recorded in Asia (Table 4.1). This complete list includes crop and non-crop fruit species from southeastern Asia, including China, Japan, South Korea (the region where SWD is native), and Turkey. Four species were cited only at the generic level, such as *Prunus* sp., *Rubus* sp., *Morus* sp., and *Vaccinium* sp. About 16% of the host plant species are cultivated, while the majority are non-crop fruits, upon which SWD multiplies. Most of the SWD host plant species belongs to the Rosaceae (53.4%), in which 55% and 26% belong to *Prunus* L. and *Rubus* L., respectively. All of the host plant species cited for Asia had naturally SWD-infested fruits (Table 4.1). Additionally, two of them, *Prunus donarium* Siebold (Mitsui et al. 2006) and *P. avium* L. (Kasuya et al. 2013), were infested under lab conditions as well. The SWD has mainly caused economic damage in cherry (*Prunus tomentosa* Thunb. and *P. avium*), blueberry (*Vaccinium* spp.), wax-myrtle (*Myrica rubra* Sieb. Et Zucc.), and autumn olive (*E. umbellate* Thunberg) crops (Asplen et al. 2015).

4.3.2 Europe

From the first report of *D. suzukii* in Europe during 2008 in both Spain (Calabria et al. 2012) and Italy (Cini et al. 2012), the SWD widely spread in 6 years across the continent (Asplen et al. 2015). Severe damage in several small fruit crops, such as sweet cherry (*Prunus avium*), sour cherry (*Prunus cerasus* L.), strawberry (*Fragaria x ananassa* Duch.), raspberry (*Rubus idaeus* L.), blackberry (*Rubus fruticosus* aggr.), and blueberry (*Vaccinium* spp.), was mainly recorded at numerous European locations (Cini et al. 2012; Weydert and Mandrin 2013; Asplen et al. 2015; Weydert et al. 2016; Mazzi et al. 2017). SWD infestations have also been reported in cultivated peach (*Prunus persica* (L.) Stokes), apricot (*Prunus armeniaca* L.), plum (*Prunus domestica* L.), apple (*Malus domestica* (L.) Borkh.), and fig (*Ficus carica* L.), although without economically significant damage (Grassi et al. 2011; Weydert and Mandrin 2013; Asplen et al. 2015; Kenis et al. 2016). Similarly, infestations in grape (*Vitis vinefera* L.) varieties were recorded in both Italy (Grassi et al. 2011; Cini et al. 2012; Kenis et al. 2016) and Germany (Asplen et al. 2015). Although grape cultivars with soft-skinned berries are more susceptible for egg laying (Mazzetto et al. 2020), successful SWD adult development is limited (Asplen et al. 2015). Late-ripening grape varieties were mainly infested by SWD in Italy, probably because of an increase in the number of flies and/or the reduction of alternative hosts (Mazzetto et al. 2020). In fact, surrounding wild vegetation suitable for SWD oviposition increased the capture of flies inside vineyards as well as in other crops (Poyet et al. 2015; Kenis et al. 2016; Mazzetto et al. 2020).

In Europe, 126 species of crop and non-crops fruits belonging to 27 families were recorded as SWD hosts (Table 4.2). From a total of SWD host species cited in Table 4.2, 91 were found producing natural infestations, while the remaining 35 were infested only under lab conditions. However, in 13 of these lab-infested fruit species, *D. suzukii* laid eggs, but there was no adult emergence (Table 4.2). The highest percentage of host species (41%) belongs to the Rosaceae family, with *Prunus* as the genus with more host species (24%), followed by *Cotoneaster* Medik. (14%) and *Rubus* (12%). Caprifoliaceae, Ericaceae, Solanaceae, Adoxaceae, and Cornaceae also have numerous SWD host species (Table 4.2). Several non-crop host plants such as *Rubus* spp., *Sambucus* spp., *Prunus* spp., *Lonicera* spp., *Arbutus*

Table 4.1 Crop and non-crop host species of *Drosophila suzukii* recorded in Asia

Plant family	Plant species	Host plant status		Fruit-collection country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Adoxaceae	*Sambucus adnata* Wallich ex Candolle	–	Yes	CN	Yes	–	Giorgini et al. (2019)
	Sambucus williamsii Hance	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
	Viburnum dilatatum Thunberg	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
Caprifoliaceae	*Lonicera maacki* (Rupr.) Herder	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
Coriariaceae	*Coriaria nepalensis* Wall.	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
Cornaceae	*Alangium platanifolium* (Sieb. et Zucc.)	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Aucuba japónica Thunberg	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Cornus controversa Hemsl. ex Prain	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Cornus kousa F. Buerger ex Miq.	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
Ebenaceae	*Diospyros kaki* Thunberg	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
Elaeagnaceae	*Elaeagnus multiflora* Thunberg	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
	Elaeagnus umbellate Thunberg	Yes	–	KR	Yes	–	Asplen et al. (2015)
Ericaceae	*Gaultheria adenothrix* (Miq.) Maximovich	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Vaccinium smallii A. Gray	–	Yes	JP	Yes	–	Kasuya et al. (2013)
	Vaccinium ovalifolium Sm.	–	Yes	JP	Yes	–	Kasuya et al. (2013)
	Vaccinium sp.	Yes	–	CN	Yes	–	Asplen et al. (2015)
		–	Yes	JP	Yes	–	Sasaki and Sato (1995), Mitsui et al. (2010), Girod et al. (2018a, b, c)
Moraceae	*Morus alba* L.	–	Yes	JP	Yes	–	Lee et al. (2015)
	Morus australis Poiret (= *bombycis*)	–	Yes	JP	Yes	–	Lee et al. (2015)
	Morus bombycis Koidz	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Mitsui et al. (2010)
	Morus sp.	–	Yes	JP	Yes	–	Lee et al. (2015), Girod et al. (2018a, b, c)

(continued)

Table 4.1 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country^a	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Myricaceae	*Myrica rubra* Sieb. Et Zucc.	Yes	–	JP	Yes	–	Asplen et al. (2015)
		–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
Phytolaccaceae	*Phytolacca americana* L.	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
Rosaceae	*Cerasus jamasakura* (Siebold ex Koidz.)	–	Yes	JP	Yes	–	Kasuya et al. (2013)
	Eriobotrya japónica (Thunbergerg) Lindley	–	Yes	JP	Yes	–	Lee et al. (2015)
	Fragaria x *ananassa* Duch.	Yes	–	TR	Yes	–	Orhan et al. (2016); Efil (2018)
	Fragaria moupinensis Cardot	–	Yes	CN	Yes	–	Giorgini et al. (2019)
	Malus domestica (Borkh.)	Yes	–	KR	Yes	–	Daane et al. (2016)
	Malus pumila Miller	–	Yes	JP	Yes	–	Lee et al. (2015)
	Princepia utilis Royle	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
	Prunus armeniaca L.	–	Yes	JP	Yes	–	Lee et al. (2015)
	Prunus avium L.	Yes	–	JP	Yes	–	Mitsui and Kimura (2010)
		–	Yes	JP	–	Yes	Kasuya et al. (2013)
		–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
		Yes	–	CN	Yes	–	Asplen et al. (2015)
	Prunus buergeriana Miquel	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
	Prunus cerasoides BuCN-Ham. Ex d. Don	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
	Prunus cerasus L.	–	Yes	JP	Yes	–	Lee et al. (2015)
	Prunus donarium Siebold	–	Yes	JP	Yes	–	Kasuya et al. (2013), Lee et al. (2015)
		–	Yes	JP	–	Yes	Mitsui et al. (2006)
	Prunus japónica Thunberg	–	Yes	JP	Yes	–	Lee et al. (2015)
	Prunus mahaleb L.	–	Yes	JP	Yes	–	Lee et al. (2015)

	Prunus nipponica Matsumura	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Prunus padus L.	–	Yes	JP	Yes	–	Girod et al. (2018a, b, c)
	Prunus persica (L.) Batsch	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
	Prunus salicina Lindley *(= P. triflora)*	–	Yes	JP	Yes	–	Lee et al. (2015)
	Prunus sargentii Rehder	–	Yes	JP	Yes	–	Lee et al. (2015)
	Prunus serrulata Lindl.	–	Yes	JP	Yes	–	Girod et al. (2018a, b, c)
	Prunus sp.	–	Yes	JP	Yes	–	Mitsui et al. (2010)
	Prunus tomentosa Thunb.	Yes	–	KR	Yes	–	Asplen et al. (2015)
	Prunus yedoensis Matsumura	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
	Rubus crataegifolius Bunge	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Rubus ellipticus Sm.	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
	Rubus foliosus Weihe	–	Yes	CN	Yes	–	Giorgini et al. (2019)
	Rubus microphyllus L.f.	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
	Rubus niveus Thunb.	–	Yes	CN	Yes	–	Giorgini et al. (2019)
	Rubus parvifolius L. (= *triphyllus)*	–	Yes	JP	Yes	–	Sasaki and Sato (1995), Lee et al. (2015)
	Rubus sp.	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
		Yes	–	KR	Yes	–	Daane et al. (2016)
	Rubus ulmifolius Schott	Yes	–	KR	Yes	–	Daane et al. (2016)
Solanaceae	*Solanum lycopersicum* L.	–	Yes	JP	Yes	–	Lee et al. (2015)
	Solanum nigrum L.	–	Yes	CN	Yes	–	Girod et al. (2018a, b, c)
Styracaceae	*Styrax japonicas* Siebold & Zuccarini	–	Yes	JP	Yes	–	Mitsui and Kimura (2010)
Taxaceae	*Torreya nucifera* (L.) Siebold & Zuccarini	–	Yes	JP	Yes	–	Mitsui et al. (2010), Lee et al. (2015)
Vitaceae	*Vitis vinifera* L.	Yes	–	KR	Yes	–	Asplen et al. (2015)

[a] ISO Country Codes: CN = China, JP = Japan, KR = Republic of Korea (South Korea), TR = Turkey

Table 4.2 Crop and non-crop host species of *Drosophila suzukii* recorded in Europe

Plant family	Plant species	Host plant status		Fruit-collection country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Actinidiaceae	*Actinidia arguta* (Siebold & Zucc.) Planch. ex Miq.	Yes	–	AT	Yes	–	Asplen et al. (2015)
	Actinidia chinensis Planch.	Yes	–	IT	Yes	–	Kenis et al. (2016)
Adoxaceae	*Sambucus ebulus* L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Sambucus nigra L.	–	Yes	IT	Yes	–	Grassi et al. (2011), Kenis et al. (2016)
		–	Yes	ES	Yes	Yes	Arnó et al. (2016)
		–	Yes	NL, CH	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Sambucus racemosa L.	–	Yes	IT, NL, CH	Yes	–	Kenis et al. (2016)
		?	?	CH	–	Yes	Baroffio et al. (2014)
	Sambucus spp.	Yes	Yes	AT, DE, NL	Yes	–	Asplen et al. (2015)
	Viburnum lantana L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
		?	?	CH	–	Yes	Baroffio et al. (2014)
	Viburnum opulus L.	?	?	CH	–	Yes	Baroffio et al. (2014)
		–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
	Viburnum rhytidophyllum Hemsl.	–	Yes	NL	Yes	–	Kenis et al. (2016)
Aquifoliaceae	*Ilex aquifolium* L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
Araceae	*Arum italicum* Mill.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Arum maculatum L.	–	Yes	FR	–	Yes	Poyet et al. (2015)
		?	?	CH	–	Yes	Baroffio et al. (2014)
Araliaceae	*Hedera hélix* L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)

Asparagaceae	*Asparagus officinalis* L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
	Ruscus aculeatus L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
Berberidaceae	*Mahonia aquifolium* (Pursh) Nutt.	–	Yes	NL	–	Yes	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Mahonia x media Brickell	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Mahonia ES	–	Yes	IT	Yes	–	Kenis et al. (2016)
Caprifoliaceae	*Bryonia cretica* (Jacq.)	–	Yes	ES	–	Yes	Arnó et al. (2016)
	Lonicera alpigena L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
		?	?	CH	–	Yes	Baroffio et al. (2014)
	Lonicera caerulea L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Lonicera caprifolium L.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Lonicera ferdinandii Franch.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Lonicera nigra L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Lonicera nitida E. H. Wilson	–	Yes	NL	–	Yes	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Lonicera periclymenum L.	?	?	CH	–	Yes	Baroffio et al. (2014)
	Lonicera ES	–	Yes	IT	Yes	–	Grassi et al. (2011)
		?	?	NL	Yes	–	Kenis et al. (2016)
	Lonicera xylosteum L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
		?	?	CH	–	Yes	Baroffio et al. (2014)
	Symphoricarpos albus (L.)	–	Yes	NL	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Symphoricarpos x chenaultii Rehder	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)

(continued)

Table 4.2 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Cornaceae	*Cornus alba* L.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Cornus kousa Hance	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Cornus mas L	– ?	Yes ?	IT, NL, CH CH	Yes –	– Yes	Kenis et al. (2016) Baroffio et al. (2014)
	Cornus sanguinea L.	– ? –	Yes ? Yes	IT, NL, CH FR	Yes – –	– Yes Yes[b]	Kenis et al. (2016) Baroffio et al. (2014) Poyet et al. (2015)
	Cornus sericea L.	–	Yes	FR	–	Yes	Poyet et al. (2015)
Dioscoreaceae	*Tamus communis* L.	–	Yes	IT, CH	Yes	–	Kenis et al. (2016)
Elaeagnaceae	*Elaeagnus* x *ebbingei* (hybrid)	–	Yes	NL	Yes	–	Panel et al. (2018)
	Hippophae rhamnoides L.	Yes –	Yes Yes	CH FR	Yes –	Yes Yes	Kenis et al. (2016), Baroffio et al. (2014) Poyet et al. (2015)
Ericaceae	*Arbutus unedo* L.	– –	Yes Yes	ES IT	Yes Yes	– –	Gabarra et al. (2012), Arnó et al. (2012) Kenis et al. (2016)
	Gaultheria procumbes L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
	Gaultheria x wisleyensis M. & M.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Vaccinium corymbosum L.	Yes	–	IT	Yes	–	Grassi et al. (2011)
	Vaccinium myrtilloides Michx.	Yes	Yes	NL	Yes	–	Kenis et al. (2016)
	Vaccinium myrtillus L.	Yes Yes	Yes Yes	IT CH	Yes Yes	Yes –	Grassi et al. (2009, 2011), Kenis et al. (2016) Kenis et al. (2016)
	Vaccinium oldhamii Miquel.	Yes	Yes	NL	Yes	–	Kenis et al. (2016)
	Vaccinium praestans Lamb.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Vaccinium uliginosum L.	?	?	FR	–	Yes	Poyet et al. (2015)
	Vaccinium vitis-idea L.	–	Yes	NL	Yes	–	Kenis et al. (2016)

Garriaceae	*Aucuba japonica* Thunb.	–	Yes	FR	–	Yes	Poyet et al. (2015)
Liliaceae	*Polygonatum multiflorum* (L.) All	–	Yes	NL, CH	Yes	–	Kenis et al. (2016)
Melanthiaceae	*Paris quadrifolia* L.	—	Yes	IT, CH	Yes	–	Kenis et al. (2016)
Moraceae	*Ficus carica* L.	Yes	–	IT	Yes	–	Grassi et al. (2011), Kenis et al. (2016)
		Yes	–	CH	Yes	–	Kenis et al. (2016)
	Morus nigra L.	–	Yes	IT	–	Yes	Grassi et al. (2011)
	Morus ES	–	Yes	FR	–	Yes	Poyet et al. (2015)
Onagraceae	*Fuchsia* ES	?	?	FR	–	Yes	Poyet et al. (2015)
Phytolaccaceae	*Phytolacca americana* L.	–	Yes	IT, NL, CH	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
		?	?	CH	–	Yes	Baroffio et al. (2014)
	Phytolacca esculenta Van Houtte	–	Yes	NL	Yes	–	Kenis et al. (2016)
Rhamnaceae.	*Frangula alnus* Mill.	–	Yes	IT	Yes	–	Grassi et al. (2009), Kenis et al. (2016)
		–	Yes	NL	Yes	–	Kenis et al. (2016)
		–	Yes	CH	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Rhamnus cathartica L	–	Yes	NL	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
Rosaceae	*Amelanchier lamarckii* F.G. Schr.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Amelanchier ovalis Medik.	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Cotoneaster bullatus Boiss.	?	?	FR	–	Yes	Poyet et al. (2015)
	Cotoneaster franchetii Boiss.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Cotoneaster horizontalis DecNL	?	?	CH	–	Yes	Baroffio et al. (2014)
		–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
	Cotoneaster lacteus W.W. Smith	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Cotoneaster rehderi Pojark.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Cotoneaster salicifolius Franch.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)

(continued)

Table 4.2 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
	Cotoneaster x *watereri* Exell.	?	?	FR	–	Yes	Poyet et al. (2015)
	Crataegus chrysocarpa Ashe	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Crataegus monogyna Jacq.	– –	Yes Yes	NL FR	Yes –	– Yes[b]	Kenis et al. (2016) Poyet et al. (2015)
	Duchesnea indica (Andr.) Focke	– ?	Yes ?	IT, NL, CH FR	– –	Yes Yes	Kenis et al. (2016) Poyet et al. (2015)
	Eriobotrya japonica (Thunb.) Lindl.	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Fragaria x ananassa Duch.	Yes Yes Yes	– – –	IT ES FR	Yes Yes Yes	– Yes –	Grassi et al. (2011) Sarto and Sorribas (2011), Gabarra et al. (2012), Arnó et al. (2016) Weydert and Mandrin (2013)
	Fragaria vesca L.	– – ? –	Yes Yes ? Yes	IT, NL, CH FR CH DE	Yes – – –	– Yes Yes Yes	Kenis et al. (2016) Poyet et al. (2015) Baroffio et al. (2014) Gong et al. (2016)
	Malus baccata (L.) Borkh.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Malus domestica Borkh.	Yes	–	FR	Yes	–	Weydert and Mandrin (2013)
	Photinia beauverdiana C. K. Schn.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Photinia villosa (Thunb.) DC.	–	Yes	NL	Yes	–	Kenis et al. (2016)

	Photinia prunifolia Lindl.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Prunus armeniaca L.	Yes	–	IT	Yes	–	Grassi et al. (2011), Kenis et al. (2016)
		Yes	–	FR	Yes		Weydert and Mandrin (2013)
	Prunus avium L.	Yes	Yes	IT	Yes	–	Grassi et al. (2011), Cini et al. (2012)
		Yes	Yes	NL, CH	Yes	–	Kenis et al. (2016)
		Yes	Yes	FR	Yes	Yes	Weydert and Mandrin (2013), Poyet et al. (2015), Weydert et al. (2016)
		Yes	–	CH	Yes	–	Mazzi et al. (2017)
	Prunus cerasifera Ehrh	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Prunus cerasus L.	Yes	Yes	IT	Yes	–	Kenis et al. (2016)
		Yes	–	DE	Yes	–	Asplen et al. (2015)
	Prunus domestica L.	Yes	–	CH	Yes	–	Kenis et al. (2016)
		Yes	–	HU	Yes	–	Asplen et al. (2015)
	Prunus laurocerasus L.	–	Yes	IT	–	Yes	Grassi et al. (2011)
		–	Yes	IT, NL, CH	Yes	–	Kenis et al. (2016)
	Prunus lusitanica L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
			Yes	FR	–	Yes	Poyet et al. (2015)

(continued)

Table 4.2 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country^{a}	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
	Prunus mahaleb L.	–	Yes	ES	Yes	–	Arnó et al. (2016)
		–	Yes	IT	Yes	–	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Prunus padus L.	–	Yes	NL, CH	–	Yes	Kenis et al. (2016)
		–	Yes	FR	–	Yes^{b}	Poyet et al. (2015)
	Prunus persica (L.) Stokes	Yes	–	FR	Yes	–	Weydert and Mandrin (2013)
		Yes	–	HU	Yes	–	Asplen et al. (2015)
	Prunus serotina Ehrh.	–	Yes	FR	Yes	Yes	Poyet et al. (2013, 2015)
		–	Yes	NL	Yes	–	Kenis et al. (2016)
	Prunus spinosa L.	–	Yes	IT, NL, CH	–	Yes	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
		–	Yes	DE	Yes	–	Asplen et al. (2015)
	Pyracantha coccinea M. Roem.	–	Yes	FR	–	Yes^{b}	Poyet et al. (2015)
	Pyracantha ES	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Pyrus calleryana Decne	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Ribes nigrum L.	–	Yes	FR	–	Yes^{b}	Poyet et al. (2015)
	Ribes rubrum L.	Yes	–	NL, CH	–	Yes	Kenis et al. (2016)
		–	Yes	FR	–	Yes	Poyet et al. (2015)
	Ribes sanginium Pursh.	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Rosa acicularis Lindl.	–	Yes	NL	Yes	–	Kenis et al. (2016)

	Rosa canina L.	–	Yes	ES	–	Yes	Arnó et al. (2016)
		–	Yes	NL	Yes	–	Kenis et al. (2016)
	Rosa glauca Pourr.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Rosa pimpinellifolia L.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Rosa rugosa Thunb.	–	Yes	NL	Yes	–	Kenis et al. (2016)
	Rubus caesius L.	–	Yes	IT, NL	Yes	–	Kenis et al. (2016)
	Rubus fruticosus aggr.	Yes	Yes	IT, NL, CH	Yes	–	Cini et al. (2012), Kenis et al. (2016)
		Yes	Yes	FR	Yes	Yes	Weydert and Mandrin (2013), Poyet et al. (2015), Weydert et al. (2016)
		Yes	–	AT, DE	Yes	–	Asplen et al. (2015)
	Rubus idaeus L.	Yes	Yes	IT	Yes	–	Grassi et al. (2011), Kenis et al. (2016)
		Yes	–	ES	Yes	–	Arnó et al. (2012, 2016)
		Yes	Yes	NL, CH	Yes	–	Kenis et al. (2016)
		Yes	Yes	FR	Yes	Yes	Weydert and Mandrin (2013), Poyet et al. (2015), Weydert et al. (2016)
		?	?	H	–	Yes	Baroffio et al. (2014)
		Yes	–	AT, DE, HU	Yes	–	Asplen et al. (2015)
	Rubus phoenicolasius Maxim.	Yes	–	CH	Yes	–	Kenis et al. (2016)
	Rubus saxatilis L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Rubus ulmifolius Schott	–	Yes	ES	Yes	–	Arnó et al. (2016)
	Sorbus aria (L.)	–	Yes	IT	Yes	–	Kenis et al. (2016)
	Sorbus aucuparia L.	–	Yes	NL	Yes	–	Kenis et al. (2016)
Rubiaceae	*Rubia tinctorum* L.	–	Yes	FR	–	Yes[b]	Poyet et al. (2015)
Santalaceae	*Viscum album* L.	–	Yes	FR	–	Yes	Poyet et al. (2015)

(continued)

Table 4.2 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Solanaceae	*Atropa belladona* L.	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Lycium barbarum L.	Yes	Yes	IT	Yes	–	Kenis et al. (2016)
	Physalis alkekengi L.	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Solanum chenopodioides Lam.	–	Yes	ES	–	Yes	Arnó et al. (2016)
	Solanum dulcamara L.	– – –	Yes Yes –	ES NL, CH FR	– Yes –	Yes – Yes	Arnó et al. (2016) Kenis et al. (2016) Poyet et al. (2015)
	Solanum dulcamara L. *f. littorale*	–	Yes	FR	–	Yes	Poyet et al. (2015)
	Solanum nigrum L	– – – ?	Yes Yes Yes ?	ES NL, CH FR CH	– Yes – –	Yes – Yes Yes	Arnó et al. (2016) Kenis et al. (2016) Poyet et al. (2015) Baroffio et al. (2014)
	Solanum villosum Mill. (= *S. luteum*)	–	Yes	ES	Yes	–	Gabarra et al. (2012), Arnó et al. (2012)
Taxaceae	*Taxus baccata* L	– – ?	Yes Yes ?	IT, NL, CH FR CH	Yes – –	– Yes Yes	Kenis et al. (2016) Poyet et al. (2015) Baroffio et al. (2014)
Thymelaeaceae	*Daphne mezereum* L.	–	Yes	IT	Yes	–	Kenis et al. (2016)
Vitaceae	*Parthenocissus inserta* (A. Kern.) FrIT	–	Yes	FR	–	Yes[a]	Poyet et al. (2015)
	Parthenocissus quinquefolia (L.)	–	Yes	IT, CH	Yes	Yes	Grassi et al. (2011), Cini et al. (2012), Baroffio et al. (2014)
	Vitis vinifera L.	Yes Yes	– –	IT DE	Yes Yes	Yes –	Grassi et al. (2011), Cini et al. (2012), Kenis et al. (2016) Asplen et al. (2015)

[a] AT =Austria, CH = Switzerland, DE = Germany, ES = Spain, FR = France, HU = Hungary, IT = Italy, NL = Netherlands

[b] Fruit with *D. suzukii* eggs but there was no adult emergence

unedo L., and *Frangula alnus* Mill. (Table 4.2) have been constantly found throughout Europe with high natural infestation rates, and SWD switch between these hosts depending on the fruit seasonality (Arnó et al. 2012, 2016; Asplen et al. 2015; Poyet et al. 2015). Those host plants could be potential resources for SWD population increase in Europe (Asplen et al. 2015; Arnó et al. 2016; Kenis et al. 2016). Green fruits of the wild host *Rubus ulmifolius* Schott collected at an altitude of 1273 m in Spain were highly infested (Arnó et al. 2016), which shows that SWD can be found within a broad range of altitude.

4.3.3 North America

SWD was first recorded on berry crops in California (USA) in 2008 and from that year it was dispersed through the soft and stone fruits-producing regions of mainland United States and Canada (Table 4.3) (Asplen et al. 2015). The most important economically affected crops in these countries include blueberries, raspberries, blackberries, strawberries, and cherries (Lee et al. 2011a, b; Bellamy et al. 2013). In 2011, SWD was detected in traps in Mexico (García-Cancino et al. 2015), but then it was found infesting *Psidium guajava* L. (Myrtaceae) crops (Lasa et al. 2017). A total of 85 crop and non-crop fruit species belonging to 21 families were recorded as SWD hosts in North America (Canada, United States, and Mexico) (Table 4.3). Four host plant species were only recorded at the generic level, e.g., *Sambucus* sp., *Lonicera* sp., *Morus* sp., and *Rubus* sp. The 93% of recorded SWD host plant species was naturally infested, while six fruit species were infested only under lab conditions. Most SWD host species are non-crop fruits, while 23% are cultivated species. The main SWD host plant family is Rosaceae, which includes 27% of the total fruit species recorded as hosts. Both *Prunus* and *Rubus* species represented 39% and 31%, respectively, of all Rosaceae species. Other important plant families with numerous SWD host species are Caprifoliaceae, Cornaceae, Adoxaceae, and Ericaceae (Table 4.3).

4.3.4 South America

SWD was first recorded in Brazil in 2013 (Deprá et al. 2014), and then in other South American countries, such as Uruguay (Gonzales et al. 2015), Argentina (Santadino et al. 2015), and Chile (Morales 2020). In 7 years, 31 crop and non-crop fruit species belonging to 10 families were recorded as SWD hosts in South America (Table 4.4). Two host plant species were only recorded at the generic level, such as *Butia* sp. and *Rubus* sp. All host fruit species recorded in Table 4.4 were naturally infested by SWD. Most SWD host species (58%) are crop fruits of economic importance. Damage caused by SWD in *Rubus idaeus* L., *R. fruticosus, R. ulmifolius* Schott, *Vaccinium corymbosum* L., *V. myrtillus* L., and *Fragaria* x *ananassa* has

Table 4.3 Crop and non-crop host species of *Drosophila suzukii* recorded in North America

		Host plant status		Fruit-collection US state or country[a]	Infestation type		
Plant family	Plant species	Crop	Non-crop		Nat.	Lab.	Source
Adoxaceae	*Sambucus* sp.	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
	Sambucus canadensis L.	Yes	–	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Sambucus nigra L.	–	Yes	US-Or	Yes	–	Lee et al. (2015)
	Viburnum lantana L.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
Berberidaceae	*Berberis aquifolium* Pursh	–	Yes	US-Or	Yes	–	Lee et al. (2015)
Buxaceae	*Sarcococca confusa* Sealy	–	Yes	US-Or	Yes	–	Lee et al. (2015)
Cactaceae	*Opuntia streptacantha* Lem.	–	Yes	US-Ca	Yes	--	Wang et al. (2019a, b)
Cannabaceae	*Celtis occidentalis* L.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
Caprifoliaceae	*Lonicera* sp.	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
	Lonicera caerulea L.	–	Yes	US-Or	Yes	–	Lee et al. (2015)
	Lonicera japonica Thunberg	–	Yes	US-Va	Yes	–	Shrader (2017)
	Lonicera morrowii A. Gray	–	Yes	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Lonicera tatarica L.	–	Yes	US-Va	Yes	–	Shrader (2017)
		–	Yes	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Symphoricarpos albus (L.) S.F. Blake	–	Yes	US-Or	Yes	–	Lee et al. (2015)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
Basellaceae	*Basella alba* L.	–	Yes	US-Sd	Yes	–	Diepenbrock and McPhie (2018)
Cornaceae	*Cornus alternifolia* L.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Cornus amomum Miller	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Cornus foemina Miller	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
	Cornus kousa Hance	–	Yes	US-Or	Yes	–	Lee et al. (2015),

	Cornus racemosa Lam.	–	Yes	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Cornus sericea L.	–	Yes	US-Or	Yes	–	Lee et al. (2015)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
Ebenaceae	*Diospyros kaki* L.	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
Elaeagnaceae	*Hippophae rhamnoides* L.	–	Yes	CA	–	Yes	Little et al. (2017)
Ericaceae	*Elaeagnus umbellata* Thunberg	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
	Vaccinium corymbosum L.	Yes	–	US-Or	Yes	Yes	Dreves (2008), Lee et al. (2011a, b)
		Yes	–	US-Mn	Yes	–	Sward (2017)
		Yes	–	CA	–	Yes	Little et al. (2017)
	Vaccinium macrocarpon Aiton	Yes	Yes	US-Wi	Yes	Yes	Steffan et al. (2013)
	Vaccinium vitis-idaea L.	–	Yes	CA	–	Yes	Little et al. (2017)
Lauraceae	*Lindera benzoin* (L.) Blume	–	Yes	US-Mi	Yes	–	Lee et al. (2015)
Lythraceae	*Punica granatum* L.	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
Moraceae	*Ficus carica* L.	Yes	Yes	US-Ca	Yes	–	Lee et al. (2015), Wang et al. (2019a, b)
		Yes	–	US-Ca	Yes	–	Yu et al. (2013)
	Morus spp.	–	Yes	US-Ca	Yes	–	Yu et al. (2013)
	Morus alba L.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Morus alba x rubra	–	Yes	US-Ca	Yes	–	Yu et al. (2013)
	Morus nigra L.	–	Yes	US-Or	–	Yes	Lee et al. (2015)
	Morus rubra L.	–	Yes	US-Fl	–	Yes	Lee et al. (2015)
Myrtaceae	*Eugenia uniflora* L.	–	Yes	US-Fl	Yes	–	Lee et al. (2015)
	Psidium guajava L.	Yes	–	MX	Yes	–	Lasa et al. (2017)

(continued)

Table 4.3 (continued)

Plant family	Plant species	Host plant status		Fruit-collection US state or country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Phytolaccaceae	*Phytolacca americana* L.	–	Yes	US-Mi	–	Yes	Lee et al. (2015)
		–	Yes	US-Va	Yes	–	Shrader (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
Rhamnaceae	*Frangula purshiana* (de Candolle) A. Gray	–	Yes	US-Or	Yes	–	Lee et al. (2015)
	Rhamnus cathartica L.	–	Yes	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Sd	Yes	–	Agbaba (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
Rosaceae	*Aronia melanocarpa* (Mitchx.) Elliot	–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Cotoneaster lacteus W.W. Smith	–	Yes	US-Or	Yes	–	Lee et al. (2015)
	Duchesnea indica (Andr.) Focke	–	Yes	US-Va	–	Yes	Shrader (2017)
	Eriobotrya japonica (Thunb.) Lindl.	–	Yes	US-Fl	Yes	–	Wang et al. (2019a, b)
	Fragaria x ananassa Duch.	Yes	–	US-Ca	Yes	–	Bolda (2008)
		Yes	–	US-Or	Yes	–	Lee et al. (2011a, b)

	Malus domestica Borkh.	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Prunus armeniaca L.	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Prunus avium L.	Yes	Yes	US-Or	Yes	–	Lee et al. (2011a, b, 2015)
		–	Yes	US-Va	Yes	–	Shrader (2017)
		Yes	–	US-Ca	Yes	Yes	Hauser (2011), Stewart (2015), Wang et al. (2019a, b)
		Yes	–	US-Ca,US-Wa	Yes	–	Beers et al. (2011)
	Prunus domestica L.	Yes	–	US-Ca	–	Yes	Wilson et al. (2013)
		Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Prunus laurocerasus L.	–	Yes	US-Or	–	Yes	Lee et al. (2015)
	Prunus lusitanica L.	–	Yes	US-Or	Yes	–	Lee et al. (2015)
	Prunus persica (L.) Stokes	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Prunus serotina Ehrh.	–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Prunus tomentosa Thunb.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
	Prunus virginiana L.	–	Yes	US-Sd	Yes	–	Agbaba (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
		–	Yes	CA	–	Yes	Little et al. (2017)
	Pyrus communis L.	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Rubus spp.	–	Yes	US-Va	Yes	–	Shrader (2017)
	Rubus allegheniensis Porter	–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Rubus armeniacus Focke	–	Yes	US-Or	Yes	–	Lee et al. (2015)

(continued)

Table 4.3 (continued)

Plant family	Plant species	Host plant status		Fruit-collection US state or country[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
	Rubus fruticosus L.	Yes	–	US-Or	Yes	Yes	Lee et al. (2011a, b)
		Yes	–	US-Nc	Yes	–	Burrack et al. (2013), Swoboda-Bhattarai and Burrack (2016)
		Yes	–	MX	–	Yes	Lasa et al. (2017)
	Rubus idaeus L.	Yes	–	US-Or	Yes	Yes	Lee et al. (2011a, b)
		Yes	–	US-Mn	Yes	–	Sward (2017)
		Yes	–	US-Sd	Yes	–	Agbaba (2017)
		Yes	–	CA	Yes	–	Little et al. (2017)
		Yes	–	US-Ca	Yes	–	Bolda (2008), Hamby et al. (2014)
		Yes	–	US-Nc	Yes	–	Burrack et al. (2013), Swoboda-Bhattarai and Burrack (2016)
	Rubus occidentalis L.	–	Yes	US-Mn	Yes	–	Sward (2017)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Rubus spectabilis Pursh	–	Yes	US-Fl	Yes	–	Lee et al. (2015)
Rutaceae	*Citrus* × *sinensis* (L.) Osbeck	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Citrus reticulata Blanco	Yes	–	US-Ca	Yes	–	Wang et al. (2019a, b)
	Murraya paniculata (L.) Jack	–	Yes	US-Fl	Yes	–	Lee et al. (2015)
Solanaceae	*Solanum dulcamara* L.	–	Yes	US-Fl, US-Or	–	Yes	Lee et al. (2015)
		–	Yes	US-Ny	Yes	–	Elsensohn and Loeb (2018)
	Solanum lycopersicum L.	Yes	–	US-Fl	–	Yes	Lee et al. (2015)
Vitaceae	*Vitis vinifera* L.	Yes	–	US-Or	Yes	–	Dreves (2008), Lee et al. (2011a, b)
		–	Yes	US-Sd	Yes	Yes	Agbaba (2017)
		Yes	–	US-Va	–	Yes	Shrader (2017)

[a] **ISO Country code:** CA = Canada, MX = Mexico; US = United States. **US state code:** Ca = California, Fl = Florida, Mi = Michigan, Mn = Minnesota, Nc = North Carolina, Ny = New York, Or = Oregon, Sd = South Dakota, Va = Virginia, Wa = Washington; Wi = Wisconsin

Table 4.4 Crop and non-crop host species of *Drosophila suzukii* recorded in South America

Plant family	Plant species	Host plant status		Fruit-collection country^{a}	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Arecaceae	*Butia* sp.	–	Yes	BR	Yes	–	Alexandre (2016)
Caricaceae	*Carica papaya* L.	–	Yes	BR^{c}	Yes	–	Junior et al. (2018)
Ebenaceae	*Dispyros kaki* L.	?	?	UR	Yes	–	Lauyé (2017)
Elaeocarpaceae	*Aristotelia chilensis* (Molina) Stuntz	–	Ye	CL	Ye	–	Morales (2020)
Ericaceae	*Vaccinium ashei* Reade	Yes	–	UY^{b}	Ye	–	Gonzales et al. (2015)
	Vaccinium corymbosum L.	Yes	–	BR	Yes	–	Vilela and Mori (2014), Bezerra Da Silva et al. (2019)
		Yes	–	AR	Yes	–	Santadino et al. (2015), Funes et al. (2018a, b)
		Yes	–	UY	Yes	–	Lauyé (2017)
		Yes	–	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019), Morales (2020)
Moraceae	*Ficus carica* L.	Yes	–	UY	Yes	–	Lauyé (2017)
Myrtaceae	*Acca sellowiana* Burret		?	UY	Yes	–	Lauyé (2017)
	Eugenia involucrata DC.	–	Yes	BR	Yes	–	Geisler et al. (2015)
	Eugenia uniflora L.	–	Yes	BR	Yes	–	Müller and Nava (2014), Nunes et al. (2014), Andreazza et al. (2015), Geisler et al. (2015)
	Luma apiculate (DC.) Burret	–	Yes	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019)
	Psidium cattleianum Sabine	–	Yes	UY	Yes	–	Lauyé (2017)
		–	Yes	BR	Yes	–	Müller and Nava (2014), Andreazza et al. (2015), Junior et al. (2018)
	Psidium guajava L.	– –	Yes Yes	BR^{d} AR^{e}	Yes Yes	– –	Nunes et al. (2014), Andreazza et al. (2015), Andreazza et al. (2016c) Escobar et al. (2018)
	Ugni molinae Turcz	–	Yes	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019)

(continued)

Table 4.4 (continued)

Plant family	Plant species	Host plant status		Fruit-collection country^{a}	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
Rosaceae	*Eriobotrya japonica* (Thunb.)	–	Yes	BR	Yes	–	Andreazza et al. (2016b), Geisler et al. (2015)
	Fragaria x *ananassa* Duch.	Yes	–	BR	Yes	–	Deprá et al. (2014), Santos (2014), Nava et al. (2015), Andreazza et al. (2016b, c), Wollmann et al. (2016), Junior et al. (2018)
		Yes	–	BR	–	Yes	Schlesener et al. (2017)
		Yes	–	AR	Yes	–	Lochbaum (2017)
		Yes	–	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019)
	Malus domestica L.	Yes	–	BR	Yes	–	Oliveira et al. (2015)
	Prunus avium L.	Yes	–	AR	Yes	–	Lochbaum (2017)
		Yes	–	CL	Yes	–	Morales (2020)
	Prunus cerasifera Ehrh.	–	Yes	CL	Yes	–	Morales (2020)
	Prunus cerasus L.	Yes	–	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019), Morales (2020)
	Prunus persica L.	Yes	–	BR	Yes	–	Geisler et al. (2015), Borba et al. (2016)
	Pyrus communis L.	¿?	–	UY	Yes	–	Lauyé (2017)
	Rosa rubiginosa L.	–	Yes	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019)
	Rubus spp.	Yes	–	BR	Yes	–	Wollmann et al. (2016), Junior et al. (2018), Schlesener et al. (2018), Krüger et al. (2018a, b, 2019)
	Rubus L. subgen. *Rubus* Watson	Yes	–	AR	Yes	–	Dagatti et al. (2018)
	Rubus fruticosus L. agg.	Yes	–	AR	Yes	–	Lochbaum (2017), Funes et al. (2018a, b)
	Rubus idaeus L.	Yes	–	AR	Yes	–	Cichón et al. (2015), Escobar et al. (2018), Lochbaum (2017), Funes et al. (2018a, b), Lavagnino et al. (2018)
		Yes	–	BR	Yes	–	Alexandre (2016)
		¿?	–	UY	Yes	–	Lauyé (2017)
		Yes	–	CL	Yes		SAG Servicio Agrícola y Ganadero (2019)
	Rubus ulmifolius Schott	Yes	–	UY	Yes	–	Lauyé (2017)
		–	Yes	CL	Yes	–	SAG Servicio Agrícola y Ganadero (2019), Morales (2020)

Rutaceae	*Citrus* x *sinensis* (L.) Osbeck	Yes	–	UY	Yes	–	Lauyé (2017)
Vitaceae	*Vitis vinifera* L.	Yes	–	UY	Yes	–	Lauyé (2017)
		Yes	–	BR	–	Yes	Andreazza et al. (2016a)

[a] ISO Country Codes: AR = Argentina, BR = Brazil; CL = Chile; UY = Uruguay

[b] Fruit rotting on the ground

[c] In damaged fruit, over-ripen or decayed

[d] Fruit with symptoms of infestation by several pests

[e] SWD was found in healthy, ripe fruit attached to the trees and in damaged fruit collected from the ground

been reported for Argentina, Brazil, Chile, and Uruguay (Table 4.4). All of these fruit species are primary SWD hosts (Deprá et al. 2014; Andreazza et al. 2016a; Lauyé 2017; Funes et al. 2018a, b; Bezerra Da Silva et al. 2019; SAG Servicio Agrícola y Ganadero 2019; Wollmann et al. 2016, 2019; Morales 2020).

Other cultivated plant species, such as *Malus domestica* L., *Prunus persica* L., *Prunus cerasus* L., *Pyrus communis* L., *Citrus sinensis* (L.) Osbeck, *Carica papaya* L., *Psidium guajava* L., *Ficus carica* L., and *Vitis vinifera* L. can be used by SWD as secondary hosts or reservoirs (Nunes et al. 2014; Oliveira et al. 2015; Geisler et al. 2015; Andreazza et al. 2015, 2016c, 2017; Borba et al. 2016; Lauyé 2017; Junior et al. 2018; Morales 2020). However, at least for some apple (Oliveira et al. 2015) and peach (Andreazza et al. 2017) cultivars, SWD females showed low oviposition frequencies, without economic damage in the fruit. Interestingly, *V. vinifera* varietal susceptibility studies carried out under lab conditions in Brazil showed that only some cultivars were vulnerable to SWD attack (Andreazza et al. 2016a). In field studies, the SWD has showed preference for different species within the genus *Rubus*, being *R. idaeus* much more attractive to SWD than *R. fruticosus* (Funes et al. 2018a). Furthermore, preference for determined *R. fruticosus* varieties has been detected for other frugivorous dipeterans (Funes et al. 2017), which could also be the case for the SWD.

Rosaceae is the plant family with the most SWD host species (45.2%) followed by Myrtaceae (23%) and Ericaceae (10%) (Table 4.4). Wild myrtaceous species (Table 4.4) are particularly alternative SWD hosts in South America (Müller and Nava 2014; Geisler et al. 2015; Alexandre 2016; Andreazza et al. 2015, 2016c; Lauyé 2017; SAG Servicio Agrícola y Ganadero 2019; Morales 2020). SWD pupae were usually recovered from healthy fruit, but there were some exceptions, e.g. SWD pupae were also found from damaged, over-ripen, or decayed *Vaccinium ashei* Reade fruit (Gonzales et al. 2015) or *P. guajava* fruit (Escobar et al. 2018), and from *Carica papaya* rotting fruit on the ground (Junior et al. 2018).

4.3.5 Africa and Oceania

SWD's potential for further invasions to Africa and Oceania is predicted, due to the environmental suitability of these areas for this species (Dos Santos et al. 2017). In Africa, SWD has been found on berry crops since 2013 in Morocco (North Africa) and on Reunion Island (EPPO European and Mediterranean Plant Protection Organization 2019). Only three crop fruit species were recorded as hosts of the SWD in this continent (Table 4.5). In Oceania, SWD was introduced into Hawaii in the 1980s (Kaneshiro 1983), and recorded in traps in the French Polynesia since 2017 (EPPO European and Mediterranean Plant Protection Organization 2019). Only two crop and two non-crop fruit species were cited as SWD hosts in Hawaii (Table 4.5).

Table 4.5 Crop and non-crop host species of *Drosophila suzukii* recorded in Africa and Oceania

Plant family	Plant species	Host plant status		Fruit-collection country, state or territory[a]	Infestation type		Source
		Crop	Non-crop		Nat.	Lab.	
AFRICA							
Ericaceae	*Vaccinium myrtillus* L.	Yes	–	FR-Ri	Yes	–	EPPO European and Mediterranean Plant Protection Organization (2019)
Rosaceae	*Fragaria* x *ananassa* Duch.	Yes	–	FR-Ri	Yes	–	EPPO European and Mediterranean Plant Protection Organization (2018, 2019); CABI EPPO Centre for Agricultural Bioscience International, European and Mediterranean Plant Protection Organization (2016)
	Rubus idaeus L.	Yes	–	MA, FR-Ri	Yes	–	EPPO European and Mediterranean Plant Protection Organization (2019)
OCEANIA							
Ericaceae	*Vaccinium reticulatum* (Smith)	–	Yes	US-Hi	Yes	–	Kaneshiro (1983); O'Grady et al. (2002); Magnacca et al. (2008); Hauser 2011; EPPO European and Mediterranean Plant Protection Organization (2014); Fraimout et al. (2015); CABI EPPO Centre for Agricultural Bioscience International, European and Mediterranean Plant Protection Organization (2016); Dos Santos et al. (2017); Koch et al. (2020)
Myrtaceae	*Psidium cattleianum* Sabine	Yes	–	US-Hi	Yes	–	Koch et al. (2020)
Rosaceae	*Rubus hawaiiensis* Gray	--	Yes	US-Hi	Yes	–	Koch et al. (2020)
	Rubus idaeus L.	Yes	–	US-Hi	Yes	–	Koch et al. (2020)

[a] MA = Morocco, FR-Ri = Reunion Island, US-Hi = Hawaii

4.4 Seasonal Biology and Population Dynamics

In temperate climate regions, such as Asia, Europe, and North America, adult SWD populations markedly decrease from winter onward (Kinjo et al. 2014; Wang et al. 2016a, b, c; Grassi et al. 2018). In Europe, SWD adult populations frequently reach peaks in spring and autumn, to decline again in the early winter (Weydert and Mandrin 2013; Asplen et al. 2015; Mazzetto et al. 2015; Zerulla et al. 2015; Arnó et al. 2016; Rossi-Stacconi et al. 2016; Zengin and Karaca 2019). This population dynamic is too similar to that reported in California, USA (Harris et al. 2014; Wiman et al. 2014; Wang et al. 2016a, b, c) where SWD populations increase in early spring, decrease during the hottest months of the year but increase again in autumn. Thus, cherries are usually the first commercial fruits available to SWD in Europe (Grassi et al. 2011; Cini et al. 2012; Poyet et al. 2015; Kenis et al. 2016; Mazzi et al. 2017). Damages to cherry crops during spring can be mainly explained by two SWD's biological abilities. Firstly, SWD adults can adapt to seasonal climate changes and survive harsh conditions through physiological and morphological adaptations (Shearer et al. 2016). These winter adaptations involve: (1) a reproductive diapause in which females have undeveloped ovaries and males produce very few sperm (Zerulla et al. 2015; Rossi-Stacconi et al. 2016; Shearer et al. 2016; Grassi et al. 2018), and (2) a phenotypic plasticity that allows a specific seasonal morphological change, which produces differences between a winter morphotype fly and a summer morphotype fly. The former has higher cold tolerance (10–15°C), darker pigmentation, and a larger body and longer wings than the latter (Asplen et al. 2015; Shearer et al. 2016; Fraimout et al. 2018; Stockton et al. 2018). Seasonal morphologies of SWD adults are unalterable, whereas reproductive dormancy is not; females can develop mature eggs when weather conditions are favorable (Rossi-Stacconi et al. 2016; Wallingford et al. 2016). Therefore, winter morphotype females that mated in autumn and overwintered may have mature eggs in early spring to infest the earliest ripening cherries and any other suitable non-crop fruits occurring at the same time (Panel et al. 2018), which facilitate the development of the summer morphotype SWD first generation, increasing pest population in late spring (Panel et al. 2018). Secondly, winter SWD survivors can use several early spring fruiting non-crop host plants for food and reproduction (Kenis et al. 2016; Grassi et al. 2018). Cases in point as *Viscum album* L. in Germany (Briem et al. 2016), *Hedera helix* L. in Italy (Grassi et al. 2018), and *Aucuba japonica* Thnb. in The Netherlands (Panel et al. 2018) are believed to be the earliest SWD reproductive hosts in early spring. Even though fitness of SWD adults emerging from these non-crop host species is poor, they could potentially attack the first available commercial crops (Grassi et al. 2018; Panel et al. 2018).

In subtropical climate regions like southern Brazil, a fruit-growing area invaded by SWD quite recently, SWD pattern of occurrence and population peaks were similar to those observed in berry-producing areas of the USA in late spring and mid-autumn (Wollmann et al. 2019). Probably, the growth of SWD population in autumn was determined by the occurrence of cooler conditions than in summer, with temperatures within a similar range than that of the fly's native region (Deprá et al. 2014). The gradual temperature increase in spring favored not only SWD activity but also triggered the onset of the fruiting season for both, commercial berry crops and non-crop fruits, such as strawberry guava (*Psidium cattleianum* Sabine) and Surinam cherry (*Eugenia uniflora* L) in southern Brazil (Wollmann et al. 2019). Although some SWD population peaks occurred during the spring-summer period, a significant decrease in the pest activity was detected at temperatures near 30°C, which are considered limitant for SWD oviposition (Wiman et al. 2014). In southern Brazil, SWD can survive at low population levels in alternative hosts such as loquat (*Eriobotrya japonica* Thunb.) even in winter, with thermal variations between 9 and 10.7°C (Wollmann et al. 2019). Alike in North America and Europe, SWD winter morphotypes were found in subtropical regions of South America, such as southern Brazil, demonstrating that seasonal phenotypic plasticity allows SWD to remain in the same habitat year after year. Similar SWD seasonal activity was found in blueberry crops in northwestern Argentina, another subtropical, South American fruit-growing region**.** High population peaks were detected in late spring, but the permanence of SWD in blueberry orchards was verified throughout the year, regardless of the presence of blueberry fruit in the area (Funes et al. 2018a). During the fruitless period, from early summer to mid-winter, there were low levels of SWD adult catches in traps (Funes et al. 2018b), which would indicate that SWD females use alternative host fruits, such as *P. guajava*, in wild vegetation areas between mid-summer and late-autumn (Escobar et al. 2018). SWD winter morphotypes were caught in peach crops in fruit-producing areas of the central-eastern region of Argentina as well (Gonsebatt et al. 2017).

4.5 Thermal Susceptibility

Seasonal temperature variations affect SWD population abundance (Wiman et al. 2014; Zengin and Karaca 2019), as well as daily temperature variations influence SWD adult dispersal between different habitats (Tait et al. 2020). In addition, temperature substantially influences SWD developmental, survival, and reproduction periods (Tochen et al. 2014). High temperatures would be responsible for SWD population summer decline in several temperate and subtropical regions (Arnó et al. 2016; Wollmann et al. 2019). SWD's activities are null or reduced when temperatures are out of the 10°–31°C range (Kimura 2004; Kinjo et al. 2014; Tochen et al. 2014; Zerulla et al. 2015; Rossi-Stacconi et al. 2016; Grassi et al. 2018). Although SWD adult detection is often difficult in Europe's and North America's winter, winter trapping has caught wild SWD individuals despite temperatures below 0°C (Hamby et al. 2016; Rossi-Stacconi et al. 2016; Thistlewood et al. 2018). This is a clear evidence of SWD's ability to overwinter locally (Rossi-Stacconi et al. 2016; Grassi et al. 2018; Stockton et al. 2018). Thus, these SWD winter morphotype adaptive features allow adult insects to absorb and retain heat throughout the winter (Kimura 1988; Tonina et al. 2016). Furthermore, in contrast with summer morphotypes, winter morphotypes may reduce water loss, improve immune function, and extend their longevity at cold temperatures (Stephens et al. 2015; Shearer et al. 2016; Toxopeus et al. 2016; Wallingford et al. 2016) through physiological changes that prevent ice crystals formation within the hemocoel, and fly death (Lee 1991; Shearer et al. 2016; Toxopeus et al. 2016).

Several studies on SWD thermal tolerance have used static and/or dynamic acclimation protocols in order to learn more about this biological capacity, taking into account closer approximations to natural temperature changes (Kimura 2004; Dalton et al. 2011; Kellermann et al. 2012; Jakobs et al. 2015; Stephens et al. 2015; Shearer et al. 2016; Wallingford et al. 2016; Stockton et al. 2018). In the static acclimation procedure, SWD individuals are kept at a single constant cool temperature for the duration of the acclimation period prior to testing, while a dynamic acclimation process involves gradually subjecting the insect to cold hardening temperatures (Stockton et al. 2018). Static acclimation procedure induces cold tolerance in SWD adults, which survived to temperatures below 0°C for up to 1 h and reached a lower lethal limit at −7.5°C (Jakobs et al. 2015). However, dynamic acclimation significantly improved SWD winter morphotype adults' survival since the survival rate was 50% after 72 h at −7.5°C (Stockton et al. 2018). Therefore, both acclimation and a suitable overwintering site may allow the survival of small founder populations of SWD winter morphotypes in the spring (Wallingford et al. 2016). Some models of *D. suzukii* potential distribution relate temperature with pest spread (Dos Santos et al. 2017). According to these models, annual mean temperature, maximum temperature of the warmest month (values >33°C), mean temperature of the coldest quarter (values <−10°C), and annual precipitation are the environmental variables with more influence on SWD distribution. Consequently, SWD potential geographical distribution range includes world subtropical regions with high rainfall throughout the year or during part of it.

There are no records on SWD overwintering as larva or pupa. Both immature stages have lesser cold tolerance compared to adults, and show little survival at temperatures below 5°C (Dalton et al. 2011; Stephens et al. 2015; Aly et al. 2017; Enriquez and Colinet 2017). Pupal survival drops noticeably below 0°C regardless of the dynamic acclimation procedure (Stockton et al. 2018).

Temperature is crucial for SWD development and establishment. According to studies carried out by Schlesener et al. (2020) in Brazil, for egg-to-adult survival, the lowest thermal threshold was 7.8 °C and optimum temperature was 23–25 °C. No SWD emergence occurred at 30–33 °C. The shortest egg-to-adult development time (10 days) was observed at 25–28 °C. The intrinsic rate of population increase was the highest at 23–25 °C. SWD body size is strongly affected by temperature, with 13°C and 28 °C causing the largest and the smallest body sizes, respectively. The annual number of generations ranged from 17.1 to 27.2 in cold and warm regions, respectively.

4.6 Reproduction

A high reproductive potential is one of the strongest reasons for the rapid worldwide spread of the polyphagous SWD. Courtship in drosophilids might involve aerial vibrations, visual displays, substrate-borne vibrations, and sex pheromones (Hamby et al. 2016). SWD sexual behavior is characterized by distinct facts of male courtship leading to female acceptance for mating. Furthermore, it has been reported that time of day and male age modulate *D. suzukii* mating activity (Revadi et al. 2015). The SWD displays characteristic courtship behavior, but to what extent the different sensory modalities are involved remains unclear. The importance of substrate-borne vibrations produced during male courtship has been demonstrated (Mazzoni et al. 2013), but the role of pheromonal and visual components in courtship remains unknown. Unlike most other drosophilids (e.g., *Drosophila melanogaster* Meigen), *D. suzukii* does not produce the male pheromone cis-vaccenyl acetate (Dekker et al. 2015). In this direction, female pheromones such as cuticular hydrocarbons (CHCs) were also studied in SWD since female sexual maturity is accompanied by a quantitative increase in these olfactory signals (Revadi et al. 2015). Despite of having been shown that CHCs were not needed to induce male courtship in *D. suzukii*, it turned out that these pheromones significantly increased male sexual behavior and that interfering in their naturally occurring ratios disrupts mate recognition (Revadi et al. 2015; Snellings et al. 2018).

Sex ratios are among the most basic of demographic parameters and provide an indication of both the relative survival of females and males and the future breeding potential of a population (Skalski et al. 2005). The production of males and females in a 1:1 ratio is usually the most prevalent evolutionary steady strategy, governed by frequency-dependent natural selection owing to competition for mates among individuals of the same sex (Sapir et al. 2008). SWD sex ratio is subjected to variations, depending on several factors. In SWD, sex ratio fluctuations throughout the year seem to be very conservative regardless the plant environment within the same region, but not between regions. In Italy (Gargani et al. 2015), in a trapping net implemented from January to December, sex ratio fluctuation patterns over time were almost the same in a vineyard than in a botanical garden, in Siena. However, in another location (Gosseto), the sex ratio fluctuation curve was different to that of Sienna, in three orchards surveyed (vineyard, apricot, and blueberry). Nevertheless, sex ratio fluctuation patterns were very similar among the three fruit crops. Besides, the sex ratios (expressed as percentage of females) varied between 0 and 50 in Siena, and from 0 to 100 in Grosseto. The highest sex ratios (biased to females) occurred at different seasons, depending on the location (winter in Siena, autumn in Grosseto). The lowest sex ratios (biased to males) were registered in spring. There was not SWD catches in none of the two locations in summer.

SWD sex ratio (% of females) decreased in parallel with host's fruit production (berries, and stone and pome fruits) from January to March, in semiarid high-elevation valleys with temperate summers and cold winters, in northwestern Argentina (CF Funes pers. comm.). As food supply slowed down, SWD sex ratios went from female-biased (January, plenty of fruit) to male-biased (March, scarce fruits). SWD sex ratio may vary between undamaged fruit collected from the plant and undamaged fruit lifted from the ground below the tree, as reported by Lasa et al. (2017), who worked in guava (*P. guajava*) in Mexico. In both cases, sex ratios were female-biased, varying within a range of 58–68%. Drummond et al. (2019) reported that across a 7-year survey, the relative abundances of sexes were slightly male-biased. Sex ratio (% of males) declined linearly between 2012 and 2018. The sex ratio of newly emerging adults remained more or less constant, with a mean of 0.98 males per female (Emiljanowicz et al. 2014).

No effect of egg density was observed on the sex ratio of SWD adults that emerged from attached pupae. Conversely, in detached pupae, sex ratio decreased linearly as egg density increased (Bezerra da Silva et al. 2019). A female-biased sex ratio for *D. suzukii* cultures probably results from the greater sensitivity of males to dietary ethanol. Without dietary alcohol, the sex ratio for *D. suzukii* stabilized near that of *D. melanogaster*, ~1:1 (Sampson et al. 2016).

4.7 Interspecific and Intergeneric Interactions with Other Frugivorous Dipterans

Selective pressure might have facilitated the evolution of *Drosophila* morphological traits such as a serrated ovipositor in *D. suzukii*. For instance, interspecific and intraspecific competitors could induce changes in SWD behavior of either female adult oviposition or larvae. The presence of competitors around fallen fruits on the ground probably suppressed *D. suzukii* oviposition on the fallen fruits and facilitated oviposition on non-fermenting substrates in nature, driving *D. suzukii* to use ripening fruits on the tree instead (Kidera and Takahashi 2020). Two species co-habiting similar niches would compete to either coexist or exclude the other. Interestingly, *D. suzukii* and *D. melanogaster* may have separate ecological niches, but *D. melanogaster* was observed ovipositing in fruit injuries caused by *D. suzukii* oviposition (Vilaire et al. 2011).

The presence of *D. melanogaster* in a substrate significantly reduced SWD emergence and egg laying; conversely, more SWD eggs were laid in blank media, not pre-inoculated with *D. melanogaster* (Shaw et al. 2018). Chemical cues or signs of previous oviposition by heterospecifics, such as *D. melanogaster*, can deter *D. suzukii* female from ovipositing in the same fruit (Shaw et al. 2018; Kidera and Takahashi 2020). This may be due to repellent olfactory cues such as trace amounts of the male *D. melanogaster* sex pheromone, cis-vaccenyl acetate, transferred to fruit during oviposition. In direct interspecific competition situations, *D. melanogaster* larvae have greater survival than *D. suzukii* larvae (Gao et al. 2018). This is due in part to higher tolerance to ethanol produced through decay and fermentation of fruit damaged by larval feeding and that higher levels of ethanol are produced in fruit containing *D. melanogaster* larvae than fruit containing *D. suzukii* larvae

(Sampson et al. 2016; Gao et al. 2018). Although SWD females prefer to oviposit in ripe fruit, they are able to shift ecological niches and use ripening fruit to avoid competitive pressures and reduce potential ethanol exposure to their larvae (Little et al. 2020).

Zaprionus indianus flies would not be capable of laying eggs in healthy fruit because they lack a serrated ovipositor, but they might take advantage of other dipeterans oviposition punctures for placing their own eggs (Lasa et al. 2017; Shrader et al. 2020). Guavas attached to the tree infested with *Z. indianus* were also infested with *D. suzukii*, *Anastrepha* spp., or both. Therefore, the infestation was possible because of previous injuries caused by the other two frugivorous dipterans (Lasa et al. 2017). Competition from *Z. indianus* limited *D. suzukii* numbers in interspecific laboratory studies (Shrader et al. 2020). When reared with grapes, *Z. indianus* also affected *D. suzukii* mortality, and increased developmental times to pupation and adult emergence, compared with the intraspecific SWD controls. Pupal volume was scarcely reduced, and it occurred only with the highest interspecific larval densities (Shrader et al. 2020). In laboratory trials with strawberry ripe fruits, there was a significant and positive interaction between damage caused by *D. suzukii* and infestation by *Z. indianus* (Bernardi et al. 2017).

4.8 Natural Enemies–*Drosophila suzukii* Relationships

Reviews on SWD natural enemies were published by Asplen et al. (2015), Haye et al. (2016), Garcia et al. (2017), and Lee et al. (2019), involving several parasitoid, predator, and entomopathogenic species. Parasitoids represent the most numerous and most studied group of SWD's natural enemies. In total, 30 parasitoid species associated with SWD were recorded throughout the world, either through field collections or through laboratory host specificity tests (Table 4.6). Nine of them are pupa parasitoids and 21 are larva parasitoids. The 40% of the parasitoid species recorded are Asian-native species, the SWD's origin region. The 75% of Asian parasitoid species belong to the genus *Asobara* Foerster (Braconidae, Alysiinae), such as *Asobara brevicauda* van Achterberg & Guerrieri, *A. elongata* van Achterberg & Guerrieri, *A. mesocauda* van Achterberg & Guerrieri, *A. triangulata* van Achterberg & Guerrieri, *A. unicolorata* van Achterberg & Guerrieri, *A. leveri* (Nixon), *A. japonica* Belokobylskij (Guerrieri et al. 2016), *A. pleuralis* (Ashmead) (Girod et al. 2018a), and *A. tabida* (Nees) (Mitsui et al. 2007), while 35% are eucoilines (Figitidae: Eucoilinae), such as *Ganaspis xanthopoda* (Ashmead) (Kasuya et al. 2013), *Ganaspis brasiliensis* (Ihering), and *Leptopilina japonica* Novkovic & Kimura (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). However, the association between *G. xanthopoda* and *D. suzukii* is doubtful because *G. xanthopoda* individuals from Japan, reported by Mitsui et al. (2007) and Kasuya et al. (2013), have been assigned to *G. brasiliensis* by Bufington and Forshage (2016) and Nomano et al. (2017). In turn, *G. xanthopoda* individuals tested under lab conditions by Kacsoh and Schlenke (2012) would appear to be *G. brasiliensis* (Nomano et al. 2017).

Table 4.6 Country list of hymenopteran parasitoid species associated with *Drosophila suzukii*

Parasitoid Family	Parasitoid species	Host stage attacked	Parasitism conditions		Successful development on the host	Country[a]	Source
			Lab	Field			
Braconidae	*Asobara brevicauda* van Achterberg & Guerrieri	Larva	– –	Yes Yes	Yes Yes	CN KR	Guerrieri et al. (2016) Daane et al. (2016)
	Asobara citri Fisher	Larva	Yes	–	Yes	US	Kacsoh and Schlenke (2012), Poyet et al. (2013)
	Asobara elongata van Achterberg and Guerrieri	Larva	–	Yes	Yes	CN	Guerrieri et al. (2016)
	Asobara japonica Belokobylskij	Larva	– – – Yes Yes	Yes Yes Yes – –	Yes Yes Yes Yes Yes	JP CN KR US CH	Mitsui et al. (2007), Ideo et al. (2008), Guerrieri et al. (2016) Daane et al. (2016) Kacsoh and Schlenke (2012), Poyet et al. (2013), Wang et al. (2018a, a, b, 2020) Girod et al. (2018b, c)
	Asobara leveri (Nixon)	Larva	– –	Yes Yes	Yes Yes	CN KR	Guerrieri et al. (2016) Daane et al. (2016)
	Asobara mesocauda van Achterberg and Guerrieri	Larva	–	Yes	Yes	CN	Girod et al. (2018a)

	Asobara pleuralis (Ashmead)	Larva	–	Yes	Yes	CN	Girod et al. (2018a)
			Yes	–	No	JP	Nomano et al. (2015)
			Yes	–	No	US	Kacsoh and Schlenke (2012)
	Asobara tabida (Nees)	Larva	–	Yes	Yes	JP	Mitsui et al. (2007)
			Yes	–	No	JP	Nomano et al. (2015)
			Yes	–	No	CH	Knoll et al. (2017)
			Yes	–	No	US	Kacsoh and Schlenke (2012)
	Asobara triangulata van Achterberg & Guerrieri (likely *Asobara* sp. TK1)	Larva	–-	Yes	Yes	JP	Nomano et al. (2015), Guerrieri et al. (2016),
			–	Yes	Yes	CN	Girod et al. (2018a)
	Asobara unicolorata van Achterberg & Guerrieri	Larva	–-	Yes	Yes	CN	Guerrieri et al. (2016)
Diapriidae	*Trichopria drosophilae* Perkins	Pupa	Yes	–	Yes	CH	Knoll et al. (2017), Woltering et al. (2019)
			Yes	–	Yes	IT	Rossi-Stacconi et al. (2013), Mazzetto et al. (2016)
			–	Yes	Yes	US	Miller et al. (2015), Wang et al. (2016a, b, 2018b)
			Yes	–	Yes	US	Kaçar et al. (2017)
			Yes	–	Yes	FR	Chabert et al. (2012)
			–	Yes	Yes	ES	Gabarra et al. (2015)
			–	Yes	Yes	KR	Daane et al. (2016)
			–	Yes	Yes	CN	Giorgini et al. (2019)
			Yes	–	Yes	CN	Yi et al. (2020)
			–	Yes	Yes	MX	García-Cancino et al. (2015)
			Yes	–	Yes	MX	Gonzalez-Cabrera et al. (2019)
	Trichopria anastrephae Lima	Pupa	–	Yes	Yes	BR	Wollmann et al. (2016)
			Yes	–	Yes	BR	Schlesener et al. (2019), Krüger et al. (2019)
	Trichopria sp.1	Pupa	Yes	–	Yes	US	Kacsoh and Schlenke (2012)
	Trichopria sp.	Pupa	–	Yes	Yes	AR	Funes et al. (2019)

(continued)

Table 4.6 (continued)

Parasitoid Family	Parasitoid species	Host stage attacked	Parasitism conditions		Successful development on the host	Country[a]	Source
			Lab	Field			
Figitidae	*Dieucoila* sp.	larva	–	Yes	Yes	AR	Funes et al. (2019)
	Ganaspis brasiliensis (Ihering)	Larva	–	Yes	Yes	CN	Girod et al. (2018a), Giorgini et al. (2019)
			–	Yes	Yes	JP	Nomano et al. (2017), Matsuura et al. (2018),
			Yes	–	Yes	CH	Girod et al. (2018a)
			–	Yes	Yes	KR	Girod et al. (2018b)
			Yes	–	Yes	US	Daane et al. (2016) Wang et al. (2018a)
	Ganaspis hookeri Crawford	Larva	–	Yes	Yes	AR	Lue et al. (2017)
	Ganaspis xanthopoda (Ashmead)[b]	Larva	–	Yes	Yes	JP	Mitsui et al. (2007), Kasuya et al. (2013)
			Yes	–	No	US	Kacsoh and Schlenke (2012), Poyet et al. (2013)
	Ganaspis sp.1	Larva	Yes	–	Yes	US	Kacsoh and Schlenke (2012)
	Ganaspis sp.	Larva	–	Yes	Yes	AR	Funes et al. (2019)
	Hexacola sp.	Larva	–	Yes	Yes	AR	Funes et al. (2019)
	Leptopilina boulardi Barbotin, Carton & Kelner-Pillault	Larva	–	Yes	Yes	AR	Garrido et al. (2018)
			–	Yes	Yes	MX	García-Cancino et al. (2015)
			Yes	–	Yes	MX	Gonzalez-Cabrera et al. (2019)
			–	Yes	Yes	BR	Wollmann et al. (2016)
			Yes	–	No	US	Kacsoh and Schlenke (2012)
			Yes	–	No	CH	Knoll et al. (2017)
			Yes	–	No	FR	Chabert et al. (2012)
			Yes	–	No	IT	Mazzetto et al. (2016)
	Leptopilina clavipes (Hartig)	Larva	Yes	–	No	US	Kacsoh and Schlenke (2012)
			–	Yes	Yes	AR	Lue et al. (2017)

	Leptopilina heterotoma (Thomson)	Larva	Yes	–	No	CH	Knoll et al. (2017), Girod et al. (2018a, b)
			Yes	–	Yes	IT	Rossi-Stacconi et al. (2015, 2017)
			Yes	–	No	IT	Mazzetto et al. (2016)
			Yes	–	No	IT, US	Miller et al. (2015)
			Yes	–	No	US	Poyet et al. (2013)
	Leptopilina japonica Novkovic & Kimura	Larva	–	Yes	Yes	JP	Novkovic et al. (2011), Kasuya et al. (2013)
			Yes	–	Yes	US	Wang et al. (2018a)
			–	Yes	Yes	CN	Giorgini et al. (2019)
			–	Yes	Yes	KR	Daane et al. (2016)
			Yes	–	Yes	CH	Girod et al. (2018b, c)
Pteromalidae	*Muscidifurax raptorellus* Kogan & Legner	Pupa	Yes	–	Yes	CA	Bonneau et al. (2019)
	Pachycrepoideus vindemmiae Rondani	Pupa	Yes	–	Yes	CH	Knoll et al. (2017)
			–	Yes	Yes	IT	Rossi-Stacconi et al. (2013)
			–	Yes	Yes	US	Miller et al. (2015), Wang et al. (2016b, 2018b)
			Yes	–	Yes	US	Kaçar et al. (2017)
			Yes	–	Yes	CA	Bonneau et al. (2019)
			Yes	–	Yes	FR	Chabert et al. (2012)
			–	Yes	Yes	ES	Gabarra et al. (2015)
			–	Yes	Yes	CN	Giorgini et al. (2019)
			–	Yes	Yes	KR	Daane et al. (2016)
			–	Yes	Yes	MX	García-Cancino et al. (2015)
			Yes	Yes	Yes	BR	Schlesener et al. (2019)
			–	Yes	Yes	AR	Funes et al. (2019)
	Spalangia erythromera Förster	Pupa	Yes	–	Yes	CH	Knoll et al. (2017)
	Spalangia simplex Perkins	Pupa	–	Yes	Yes	MX	García-Cancino et al. (2015)
	Vrestovia fidenas (Walker)	Pupa	Yes	–	Yes	CH	Knoll et al. (2017), Wolf et al. (2019)

[a] ISO Country Codes: AR = Argentina, BR = Brazil, CA = Canada, CH = Switzerland, CN = China, ES = Spain, FR = France, IT = Italy, JP = Japan, MX = Mexico, KR = Republic of Korea (South Korea), US = United States

[b] Dubious association (Nomano et al. 2017)

Interestingly, *G. brasiliensis* would involve four lineages with different geographic distribution and host ranges (Nomano et al. 2017). These morphologically identical lineages could be a complex of cryptic species (Giorgini et al. 2019).

Among the other parasitoid species, 33.4% are native to America, 10% to Europe, and one of them (3.3%), *Asobara citri* Fisher, to Africa (Kacsoh and Schlenke 2012). The remaining 13.3% are present worldwide, such as *Pachycrepoideus vindemmiae* Rondani (Pteromalidae), *Trichopria drosophilae* Perkins (Diapriidae) (Rossi-Stacconi et al. 2013; Wang et al. 2016a, b, c; Daane et al. 2016), *Leptopilina boulardi* Barbotin, Carton & Kelner-Pillault, and *L. clavipes* (Hartig) (Figitidae: Eucoilinae) (Wollmann et al. 2016; Lue et al. 2017). Of the 10 American parasitoid species associated with SWD, six (60%) are undescribed species of eucoilines and diaprines (Table 4.6). The remaining four species are represented by one drosophilid larval parasitoid, *Ganaspis hookeri* Crawford (Lue et al. 2017), and by three generalist parasitoids that attack cycloraphic dipterous pupae, such as the pteromalines *Muscidifurax raptorellus* Kogan & Legner (Bonneau et al. 2019) and *Spalangia simplex* Perkins (García-Cancino et al. 2015) and the diaprine *Trichopria anastrephae* Lima (Krüger et al. 2019). Of the three European parasitoid species, one is drosophilid larval parasitoid, *Leptopilina heterotoma* (Thomson) (Figitidae) (Rossi-Stacconi et al. 2015), and two are generalist pupal parasitoids, *Spalangia erythromera* Förster and *Vrestovia fidenas* (Walker) (Pteromalidae) (Knoll et al. 2017).

Although more larval parasitoids than pupal parasitoids have been associated with the SWD, few species can successfully overcome the defense response of the SWD larva. Parasitoid eggs or larvae are usually encapsulated (Kacsoh and Schlenke 2012; Poyet et al. 2013). Therefore, Asian-native larval parasitoid species have mainly shown high capacity of developing successfully in SWD. Among them, *L. japonica*, *G. brasiliensis*, and *A. japonica* are the most significant parasitoid species, due to their high natural parasitism rate and greater specificity to SWD (Daane et al. 2016; Girod et al. 2018a; Matsuura et al. 2018; Giorgini et al. 2019). Thus, these three Asian parasitoid species were imported for evaluation as classical biological control agents in North America and/or Europe (Daane et al. 2016; Girod et al. 2018b, c; Wang et al. 2018a, 2019a, b; Giorgini et al. 2019).

Among the generalist parasitoid species, pupal parasitoids *P. vindemmiae*, *M. raptorellus, V. fidenas, T. drosophilae*, and *T. anastrephae* have been mainly evaluated under laboratory conditions, for both their ability to successfully parasitize SWD and their efficiency in reducing the target population (Wang et al. 2016a, b, 2018b; Bonneau et al. 2019; Krüger et al. 2019; Schlesener et al. 2019; Wolf et al. 2019; Yi et al. 2020). Since all of them can attack other dipterous species, their field effectiveness is doubtful. Nevertheless, *T. drosophilae* has a potential as SWD's biological control agent (Mazzetto et al. 2016; Kaçar et al. 2017; Rossi-Stacconi et al. 2017; Pfab et al. 2018; Wang et al. 2018b; Yi et al. 2020). This potentiality was verified through *T. drosophilae* releases in berry fields at Colima and Jalisco, Mexico, where this strategy reduced 50–55% SWD wild populations (Gonzalez-Cabrera et al. 2019). Mass releases of *T. drosophilae* have been recently accomplished in northern Italy (Bioplanet 2020).

Arthropod predators such as ants, spiders, earwigs, and rove beetles have been found attacking SWD larvae and/or pupae inside field-infested fruit (Woltz and Lee 2017). Similarly, several generalist hemipteran species such as *Dicyphus tamaninii* Wagner (Hemiptera: Miridae), *Orius laevigatus* (Fieber), *Cardiastethus nazarenus* Reuter, and *C. fasciventris* Garbiglietti (Hemiptera: Anthocoridae) have also been observed predating on SWD eggs, larvae, and/or pupae, inside fallen fruit in berry growing areas of Northern Spain (Arnó et al. 2012; Gabarra et al. 2015). In addition, *Labidura riparia* Pallas (Dermaptera: Labiduridae) has been recorded as a common and effective SWD larvae and pupae predator, in Spain (Gabarra et al. 2015). Furthermore, several commercially available predator species have been tested under lab conditions for potential use as SWD's biological control agents. The evaluated predator species were *Orius insidiosus* Say (Hemiptera: Anthocoridae), *Dalotia coriaria* Kraatz (Coleoptera: Staphylinidae), *Podisus maculiventris* Say (Hemiptera: Pentatomidae), *Dicyphus hesperus* Knight (Hemiptera: Miridae), and *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) (Cuthbertson et al. 2014a; Renkema et al. 2015; Woltz et al. 2015; Renkema and Cuthbertson 2018; Bonneau et al. 2019).

Similarly, several commercial entomopathogenic agents, such as nematodes [*Heterorhabditis bacteriophora* Poinar (Rhabditida: Heterorhabditidae), *Steinernema carpocapsae* (Weiser), *S. feltiae* (Filipjev) and *S. kraussei* (Steiner) Travassos (Rhabditida: Steinernematidae)], and fungi [*Metarhizium brunneum* (= *M. anisopliae*) (Metchnikoff) Sorokin, *Isaria fumosorosea* (= *Paecilomyces fumosoroseus*) (Wize) Brown & Smith, *Lecanicillium (= Verticillium) lecanii* (Zimm.), and *Beauveria bassiana* (Balsamo-Crivelli) Vuillemin (Ascomycota; Hypocreales)], have been tested against SWD under lab conditions (Cuthbertson et al. 2014b; Woltz et al. 2015; Cossentine et al. 2016; Cuthbertson and Audsley 2016; Renkema and Cuthbertson 2018; Yousef et al. 2018; Lee et al. 2019). Bacteria and viruses have been also reported from laboratory trials or natural infestation (Lee et al. 2019). Commercial *Bacillus thuringiensis* var. *kurstakii* or *B. thuringiensis* var. *israeliensis* were tested against SWD in lab trials (Biganski et al. 2018; Cahenzli et al. 2018). More details on the use of SWD's natural enemies as a biological control strategy can be seen in Chap. 8 of this book.

4.9 Concluding Remarks

In brief, egg-laying preference for ripening and ripe healthy small, soft and stone fruits attached to the plant makes SWD a severe and harmful pest for fruit-producing regions of Asia, Europe, and America. Most of the worldwide host fruit species preferred by SWD belong to Rosaceae, a plant family involving several economically important cultivated fruits, such as caneberries, cherries, strawberries, and stone and pome fruits, and a large list of non-crop species. Besides, both non-crop and crop *Vaccinium* L. plants (Ericaceae) have been recorded as recurrent SWD hosts in all continents. In addition to wild species of Rosaceae and Ericaceae families, several Adoxaceae (*Sambucus* spp.), Caprifoliaceae (*Loricera* spp.), and Rhamnaceae (*Rhamnus cathartica* L. and *Frangula* spp.) are crucial host plants for SWD population growth and seasonal dynamics in Europe and the USA. In Mexico and South America, Myrtaceae are fruit species highly susceptible to SWD, playing the important role of facilitating SWD multiplication in wild habitats adjacent to host crop fields.

The high degree of polyphagy shown by SWD either in their native region or in the invaded continents, added to the seasonal phenotypic plasticity that allows adaptations to adverse thermal periods, greatly favors SWD establishment and dispersion in the invaded regions. In turn, complex landscape structures such as forests with alternative non-cultivated host plants, shrub vegetation and flowering field margins, and the distance of these structures to host crops in the different invaded areas, facilitate SWD daily spread between different habitats, which can also determine infestation levels.

In both temperate and subtropical climate regions, the SWD seasonal dynamic is essentially related to temperatures more suitable for its movement between habitats, development, survival, and reproduction. The warmest, as well as the coldest, months of the year reduce, with more or less intensity, SWD populations in summer and winter, respectively. Therefore, SWD populations mostly generate two population peaks, in late spring and mid-autumn. However, as SWD can overwinter locally, adults can be captured throughout the year in the invaded areas.

A better understanding of the relationships between SWD and the components of newly invaded landscapes, in terms of reproductive behavior and interspecific and intergeneric interactions, especially with other frugivorous dipterans, and biological controllers would be very important to achieve. This will allow designing efficacious, efficient, and environmental friendly pest management strategies, maximizing the benefits provided by ecosystem services.

A diverse suite of local predators and parasitoids associated with SWD are found in wild vegetation areas surrounding fruit crop fields in the different invaded regions. These natural enemies should be conserved in their natural habitats. Furthermore, it should be noted that the recently found specialist Asian parasitoids could be significant SWD's biocontrol agents. In addition, several entomopathogens have been laboratory tested, but their suppressive effects on SWD wild populations remains unknown and should be assessed.

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