

Review

Drosophila suzukii (Diptera: Drosophilidae): A Decade of Research Towards a Sustainable Integrated Pest Management Program

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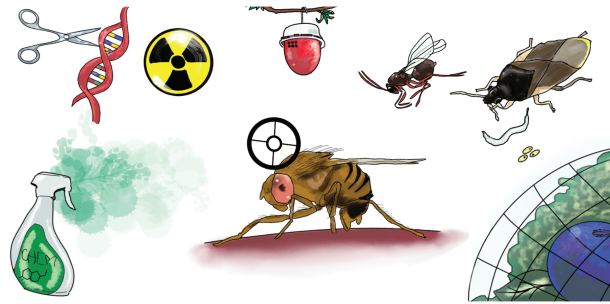
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Abstract

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) also known as spotted-wing drosophila (SWD), is a pest native to Southeast Asia. In the last few decades, the pest has expanded its range to affect all major European and American fruit production regions. SWD is a highly adaptive insect that is able to disperse, survive, and flourish under a range of environmental conditions. Infestation by SWD generates both direct and indirect economic impacts through yield losses, shorter shelf life of infested fruit, and increased production costs. Fresh markets, frozen berries, and fruit export programs have been impacted by the pest due to zero tolerance for fruit infestation. As SWD control programs rely heavily on insecticides, exceedance of maximum residue levels (MRLs) has also resulted in crop rejections. The economic impact of SWD has been particularly severe for organic operations, mainly due to the limited availability of effective insecticides. Integrated pest management (IPM) of SWD could significantly reduce chemical inputs but would require substantial changes to horticultural management practices. This review evaluates the most promising methods studied as part of an IPM strategy against SWD across the world. For each of the considered techniques, the effectiveness, impact, sustainability, and stage of development are discussed.

Graphical Abstract



Key words: spotted-wing drosophila, integrated pest management, fruit crop, control method

Globalization as characterized by increased trade and human movement, along with environmental change facilitates the introduction and establishment of invasive species outside their native geographical area (Pyšek and Richardson 2010, Cini et al. 2014, Daane et al. 2018). The vinegar fly *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), also known as spotted-wing drosophila (SWD), is one such pest species that develops within and damages soft-skinned fruit (Fig. 1). Native to southeast Asia, it was first detected in Europe and North America in 2008 (Hauser 2011, Walsh et al. 2011, Cini et al. 2012, Rota-Stabelli et al. 2020), in South America in 2013 (Deprá et al. 2014, Andreatza et al. 2017), and in northern Africa in 2017 (Hassani et al. 2020). Modeling the ecological niche of the pest suggests additional large-scale expansions, including Africa and Australia (Santos et al. 2017, Boughdad et al. 2020, Kwadha et al. 2021). The success of SWD's invasion may be partly explained by tolerance to a wide range of climatic conditions. It has the capacity to overwinter for many months and has the ability to survive transportation between continents in egg, larval, and adult life stages within fruit or shipping containers (Hoffmann et al. 2003, Ometto et al. 2013, Rossi-Stacconi et al. 2016, Shearer et al. 2016, Toxopeus et al. 2016, Stockton et al. 2019). This insect has a high fecundity (Emiljanowicz et al. 2014), a wide host range (Lee et al. 2015, Kenis et al. 2016, Stockton et al. 2019, Thistlewood et al. 2019), and high passive and active dispersal potential.

Environmentally friendly and cost-effective strategies are urgently needed to manage infestations of SWD with both local and area-wide approaches. Local area pest management is defined as the management of a particular pest within a size-restricted area such as specific fields or production units, which can be subject to constant reinvasion (Dhillon et al. 2005, Tait et al. 2020a). Even though many local control methods are under investigation and development, the most common

management techniques primarily rely on insecticides (Bruck et al. 2011a, Van Timmeren and Isaacs 2013). The use of broad-spectrum insecticides negatively affects beneficial arthropods, and their application is limited to managed crops; thus, pest re-infestations often occur shortly after treatment from surrounding vegetation (Van Timmeren and Isaacs 2013, Haye et al. 2016). Moreover, insecticide resistance to spinosad has been observed in SWD in California (Van Timmeren et al. 2018, Gress and Zalom 2019). By using chemical control as a standalone tactic there is the risk that growers may lose the few available effective chemistries. An integrated pest management (IPM) strategy promotes sustainable SWD suppression through a combination of tactics including biological and behavioral controls, habitat manipulation, cultural practices, and the use of resistant plant varieties (Asplen et al. 2015, Haye et al. 2016).

Successful IPM is only possible with a clear understanding of the biology and ecology of the insect (Vreysen et al. 2007). A large body of

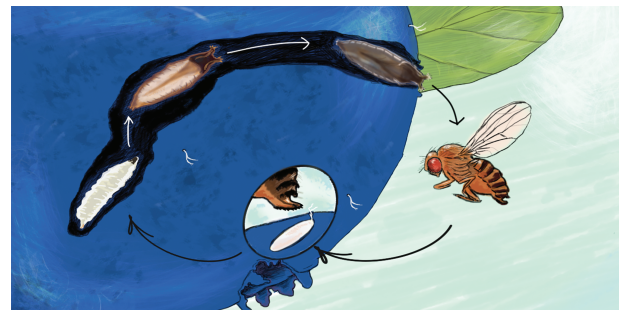


Fig. 1. *Drosophila suzukii* is a direct pest laying its eggs in ripe fruit, rendering them unmarketable (Avosani).

work was created during the period since SWD emerged as an economically damaging insect. Production systems differ between regions, and the economics of specific techniques need to be assessed together with key ecological and economic factors. Growers also need to be able to determine risk by using various techniques, including monitoring, population models, and determination of fruit susceptibility. This knowledge forms the foundation of any IPM program, ultimately impacting management decisions. The goal of this paper is to describe past studies within this context to help highlight possible strategies to manage SWD. Some of the strategies have been implemented, while others are still under development. Moreover, attempts to provide insights for continued development of an IPM system against SWD are presented.

Economics and IPM for SWD

Studies of the economic impacts can be broadly grouped into two categories: evaluation and documentation of economic impacts due to SWD damage; and comparison of growers' profit with the adoption of IPM control strategies relative to calendar-based insecticide sprays. Researchers have estimated significant economic losses due to SWD damage in different regions within and among countries (Bolda et al. 2010, Walsh et al. 2011, De Ros et al. 2015, Farnsworth et al. 2017, DiGiacomo et al. 2019, Yeh et al. 2020). For instance, during the earlier years when SWD first became established in the U.S., the total annual revenue losses for the West Coast berry and cherry industries were estimated at over \$500 million (Bolda et al. 2010). Early impact assessments focused on yield losses due to SWD to measure economic losses. However, more recently, attention has turned to the economic impact of prevention or control of SWD (Farnsworth et al. 2017, Knapp et al. 2021). This literature underscores the economic challenges caused by SWD. Understanding how growers manage SWD in practice is critical to design the most suitable IPM program. Studies based on surveys from various regions showed that most growers tend to follow calendar-based spray schedules (Mazzi et al. 2017, DiGiacomo et al. 2019, Knapp et al. 2021). To understand the pros and cons of various control strategies, researchers compared several management strategies in a variety of crops and regions using tools such as cost-benefit analysis, economic modeling, and simulations (Fava et al. 2017, Fan et al. 2020, Yeh et al. 2020). Although optimal SWD control may depend on the crop and region, most studies indicated that adopting IPM strategies are more effective than sole

reliance on calendar-based sprays, especially when environmental costs of insecticide use are considered (Fan et al. 2020). Moreover, Del Fava et al. (2017) and Yeh et al. (2020) found that optimal SWD control depends on perceived pest risk and that insecticidal sprays at low pest pressure may result in decreased profit. Although economic studies have been valuable to identify economically viable SWD control strategies, future work should examine economic incentives for growers to transition from calendar-based sprays to newly developed IPM strategies. This is especially important when new control strategies involve large initial capital investments such as spray equipment and postharvest cooling machinery (Kraft et al. 2020). Growers advised by public extension services are more likely to adopt sustainable preventive measures for SWD, illustrating the importance of strong extension and education programs in order to optimize economic sustainability (Wuepper et al. 2020). These data illustrate the value of stakeholder and academic collaboration.

Future efforts should evaluate control options with a more in-depth understanding of how grower characteristics, monitoring methods (fruit sampling or adult SWD trapping), as well as marketing channels (domestic, exporting, U-pick, etc.), may affect growers' decisions in choosing the most optimal management practices.

Seasonal Dynamics (Biology and Ecology)

An important component of any IPM system is the ability to evaluate the risk caused by the pest agent. Understanding seasonal SWD population dynamics, coupled with crop susceptibility is especially important to help guide grower management practices. During different times of the year, the life stage distribution of SWD varies considerably. During the summer months, when temperatures are warm and reproduction peaks, the population's life stage distribution is primarily skewed towards nonadult life stages (Wiman et al. 2014). This population ratio is about 90% immature life stages (eggs, larvae, and pupae) to 10% adult insects (Emiljanowicz et al. 2014, Grassi et al. 2018) (Fig. 2). These data indicate that targeting mobile adult flies may not be the most effective means of managing this pest. Indeed, many insecticides effectively target immatures within the fruit, including phosmet, malathion, methomyl, spinetoram, and zeta-cypermethrin (Wise et al. 2015, Mermer et al. 2021, Beers et al. unpublished data). Additional research has focused on the timing of insecticide applications during the summer period when population

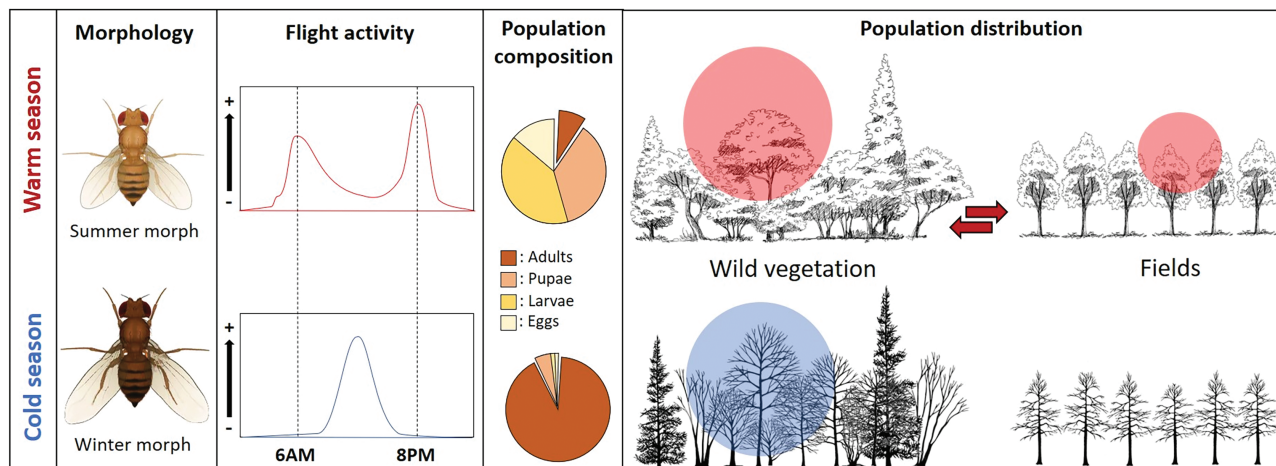


Fig. 2. *Drosophila suzukii* is highly adaptable, both in morphology and behavior on a daily and seasonal basis, population structure also changes dependent on seasonal conditions (Rossi-Stacconi).

growth occurs rapidly and coincides with peak fruit production (Shaw et al. 2019, Mermer et al. 2021).

Drosophila suzukii has the ability to tolerate a wide range of environmental conditions. Also has the capability to persist through cold winters *D. suzukii* and escape detection, particularly during the spring and early summer when small overwintering populations are likely building in noncrop areas (Fig. 2). *D. suzukii* is seasonally active from spring to autumn, but persist through cold winters by surviving mostly as adult females (Rossi-Stacconi et al. 2016, Shearer et al. 2016, Stockton et al. 2019). The following sections describe our current understanding of the seasonal biology of this pest, particularly as it relates to overwintering biology, movement, and population dynamics.

Overwintering Biology

Like many temperate drosophilids, SWD displays seasonal polyphenism following changes in the abiotic environment (Hoffmann et al. 2003, Shearer et al. 2016). Summer morphotype flies, which generally develop when ambient temperatures are greater than 20°C, are smaller and lighter in cuticular pigmentation than winter morphotype flies (Fig. 2), although the development and extent of these traits occur along a continuum as the temperature decreases to approximately 10°C (Shearer et al. 2016, Stockton et al. 2020). Larval development is not known to happen below this temperature. In contrast, the thermal threshold for female oviposition occurs at lower temperatures, even below 10°C (Rendon et al. 2019b). For the last decade, there has been debate about the success of adult overwintering based on the survival thresholds observed in more northern climates, including northern Italy and the Great Lakes regions of the United States (Jakobs et al. 2015, Stephens et al. 2015, Rossi-Stacconi et al. 2016, Bal et al. 2017, Guédot et al. 2018, Panel et al. 2018, Tait et al. 2018a, Leach et al. 2019). However, current data indicate that SWD can survive at temperatures as low as 0°C for as long as 3 d given adequate acclimation and gradual reduction in temperatures (Stockton et al. 2018) that presumably allow time for biochemical mechanisms conferring cold tolerance (Dalton et al. 2011, Wallingford and Loeb 2016, Cloutier et al. 2021). Unlike some species, which enter a biologically dormant state that does not recover until spring regardless of daily temperature fluctuations (Sinclair 1999), it is believed that SWD can recover full metabolic activity as soon as temperatures increase above freezing. Here, the reproductive function also recovers when the reproductive temperature range persists (Plantamp et al. 2016, Toxopeus et al. 2016). Further, it appears that unless SWD is in a state of chill coma, which occurs just below freezing (Stockton et al. 2018), individuals likely require a carbohydrate resource in order to survive, thereby requiring continual feeding (Rendon et al. 2018, 2019b).

Current knowledge of overwintering has several implications. First, SWD likely forages throughout the winter when conditions are mild enough to permit short-range movement. Second, this activity suggests that the site of overwintering must include a food source. Recent data suggest saprotrophic fungi including mushrooms and decomposing plant materials may be a sufficient nutrient source during this period (Stockton et al. 2019, Park 2020). Indeed, landscape-level movement research indicates that SWD most likely overwinters in wooded areas where refuge and nutrients are more abundant, although the exact location remains elusive (Thistlewood et al. 2018, Tonina et al. 2018, Leach et al. 2019). Additional management options may be developed if overwintering populations can be successfully located and targeted. Increasingly, there is interest in trapping overwintering flies using specialized baits that capitalize on

the nuanced nutritional needs of these populations. Ongoing genetic and behavioral research is currently focused on determining attractants specific to overwintering populations. If such tools were developed, it would greatly enhance our ability to detect overwintering population hotspots and would enable the development of off-season management strategies that targets vulnerable populations.

Seasonal Movement and Dispersal

Understanding seasonal trends of SWD populations is important for determining relative risk to susceptible fruit crops. Research over the past decade has shown that SWD is highly adaptable and has successfully invaded a diverse array of regions and landscapes (Asplen et al. 2015). Fluctuations in populations are driven by a combination of biotic and abiotic factors including temperature, humidity, and nutrient availability (Rendon et al. 2019b, Tochen et al. 2016, Evans et al. 2017, Eben et al. 2018, Little et al. 2020). *Drosophila suzukii* dispersal may be understood as a combination of short- and long-range movements, reflecting biological needs within the context of seasonal phenology, nutrient availability, and the abiotic environment. During the growing season, noncrop hosts surrounding cultivated areas drive the daily dispersion of SWD (Klick et al. 2016, Leach et al. 2019, Tait et al. 2020a). These forces can regulate small-scale population dynamics and, consequently, impact pest pressure in nearby crops (Delbac et al. 2020). Moreover, laboratory and field trials have shown diel SWD activity, with peak movement during dawn and dusk, when temperature and humidity conditions are more suitable, especially during the summer (Fig. 2) (Hamby et al. 2013, Evans et al. 2017, Tait et al. 2020a). Longer-range SWD dispersal patterns have been studied between high and low elevations. Such dispersal behavior may locate more suitable ambient conditions for development and improve access to essential nutritive or reproductive resources (including host plants) as they become available at higher elevation from spring into summer (Mitsui et al. 2010, Tonina et al. 2016, Tait et al. 2018a) (Fig. 3). Conversely, during late summer this trend reverses, allowing insects to exploit available food resources, suitable climatic conditions, and adequate overwintering sites at lower elevations.

Although longer-range and elevational migration patterns of cold-tolerant SWD populations need additional study, current approaches focus on population genetics, gene flow, and genetic drift among populations using single nucleotide polymorphism (SNP) detection. Some reports suggest that yearly movement likely does occur in the U.S. Studies have demonstrated such movement, particularly along the East Coast from southern regions such as Georgia and North Carolina to New York, Maine, and Michigan (Lewald et al. unpublished). More information is however needed to determine the frequency and extent of this movement and whether it occurs directly due to the biology and movement of the pest, or indirectly due to human-driven movement and trade (Cini et al. 2014). The outcome of these studies may affect future approaches to population monitoring and management.

Seasonal Population Dynamics

Currently, the primary means for estimating populations are through adult trap captures using baits and/or lures (Zengin and Karaca 2019, Rodriguez-Saona et al. 2020). While traps are an imperfect tool, monitoring over multiple years has provided a predictable pattern in relative abundance and activity levels of SWD (Thistlewood et al. 2018, Leach et al. 2019). In more northerly regions, the first adult flies are captured in late June/early July



Fig. 3. Seasonal and daily movement and dispersal is highly dependent on microclimate. *Drosophila suzukii* will move to more suitable climates as resources become available and when environmental conditions are relatively more suitable. Often surrounding vegetation is more suitable compared to exposed environmental conditions found within production units (Avosani).

(Champagne-Cauchon et al. 2020), while in warmer temperate regions flies are captured year-round (Rossi-Stacconi et al. 2016, Thistlewood et al. 2018). In many regions, fly populations increase steadily over the course of summer, culminating in a population peak in fall (Briem et al. 2018, Leach et al. 2019, Thistlewood et al. 2019). However, in regions where summers are hot and dry, populations peak in spring and fall are lower in summer and winter (Harris et al. 2014, Wiman et al. 2016, Wang et al. 2016, 2019). In colder regions, the capture of flies declines in late fall/early winter as temperatures decrease until flies can no longer be detected during the coldest periods of winter (Guédot and Perry 2016, Leach et al. 2019, Thistlewood et al. 2019, Stockton et al. 2019). This late fall/early winter decline is also present in warmer regions, although flies can still be detected throughout winter (Thistlewood et al. 2019). Understanding seasonal population trends of SWD and the factors that influence them is important for developing tools for IPM. To this end, research has focused on developing population models to predict SWD seasonal trends (see optimized management through modeling in this manuscript).

Determination of Risk

Monitoring

Accurate and sensitive monitoring tools are necessary to understand SWD population dynamics and allow effective risk mitigation. Direct monitoring for SWD larvae can be conducted using a fruit dunk flotation technique, similar to methods developed for other drosophilid pests (Yee 2014). Such methods involve placing crushed fruit in sugar- or salt-water and counting the larvae that float on the surface of the liquid (Shaw et al. 2019). Recent modifications involve using a reusable coffee filter to separate larvae from the flotation liquid allowing for quicker and more accurate detection of larvae in infested fruit, sometimes using a microscope (Van Timmeren et al. 2017). The method was further optimized, allowing for the assessment of samples within a shorter time frame (Van Timmeren 2021). Monitoring for larvae within fruit has the advantage of providing real-time information that growers can use to adjust insecticide applications and/or harvest schedules. Additional research is required to determine how to best integrate larval monitoring into different production systems.

In addition to monitoring for larval infestation, traps can be used to monitor SWD adult activity (Grassi et al. 2012, Cha et al. 2012, Huang et al. 2017). The most common baits used to attract SWD include apple cider vinegar (ACV), as well as yeast and sugar (Grassi et al. 2012, Walsh et al. 2011, Landolt et al. 2012, Burrack et al. 2015, Mazzetto et al. 2016a). Early studies used ACV-based liquid traps to monitor SWD. Key attractive volatiles from vinegar and red wine at ratios of 75% ACV, 25% red wine, and 4g l⁻¹ raw brown sugar (Grassi et al. 2012 demonstrated effective attraction under field conditions (Cha et al. 2012, Landolt et al. 2012). Further improvements to red wine-vinegar attractants included adding specific strains of lactic acid bacteria, *Oenococcus oeni* (Đurović et al. 2021). Yeast-based solutions were highly attractive (Hamby et al. 2014, Iglesias et al. 2014). Results from this study contrasted with previous findings on wine and vinegar mixtures, and it was determined that the attractiveness of more acidic solutions is sub-optimal (Huang et al. 2017). Commercially available food baits with a custom mixture of 60% wine to 40% apple cider vinegar and 20g l⁻¹ brown molasses, were more attractive than other baits, yet less attractive than ripe blackberry fruit (Wollmann et al. 2019). Agricultural grade apple cider vinegar, especially with the addition of apple nectar, had superior attractivity compared to standard, commercially available apple cider vinegar (Lasa et al. 2020). Sugar and a small drop of liquid soap added to the liquid bait lure helped to reduce water surface tension in order to minimize escape (Grassi et al. 2014).

The most effective early plastic bottle traps contained ~200 ml of liquid bait and had a 5–10 mm diameter entry hole. Larger entry areas corresponded to greater trap counts, red- or black-colored traps were more attractive compared to other colors (Basoalto et al. 2013, Lee et al. 2013). Even though trap cups containing attractive liquid baits are more commonly used, dry sticky traps offer various practical advantages including ease of use to growers (Kirkpatrick et al. 2018).

Despite the important function of traps, adult catches do not always represent population numbers accurately, nor do they reliably predict infestation in fruit. As a matter of fact, the odor preference of flies changes over the season in relation to their nutrient, reproductive or physiological state (Kirkpatrick et al. 2018, Wong et al. 2018, Clymans et al. 2019, Piñero et al. 2019, Cloonan et al. 2019, Crava et al. 2020). Fruit availability at the peak of commercial production has been shown to reduce the sensitivity of

traps (Singh et al. 2021). Trap catches are likely also affected by temperature and humidity (Tochen et al. 2014, 2016, Wiman et al. 2014, Hamby et al. 2016, Wang et al. 2016, Rendon and Walton 2019a). For example, when temperatures drop below 10°C, most SWD summer morph females do not lay eggs, ultimately resulting in gradual population decline. Fields surrounded by fruiting wild host plants, as compared to fields surrounded by nonhost plants, display increased SWD risk (Klick et al. 2016, Rodriguez-Saona et al. 2020). However, a comparison of model simulations and actual fly captures reveals the difficulties in accurately assessing the actual size of SWD populations (Kirkpatrick et al. 2018). Currently, the impact of temperature on trapping efficiency is not known and needs to be addressed. Altogether, more sensitive and efficient traps can play an important part in threshold development, although trap active distance needs additional studies to enable use on a larger scale (Kirkpatrick et al. 2018, Spies and Liburd 2019).

SWD monitoring techniques need additional development in order to provide growers with actionable information. There are some regions where adult trap monitoring has been largely abandoned, while other regions still use trapping as an important part of management. The initial lack of correlation between trapping data and fruit infestation ultimately may have resulted in the abandonment of this practice. In addition, the labor and training required to sort through nontarget captures and identify SWD reduces the feasibility of grower-led monitoring, especially for smaller operations. The majority of adult trap monitoring is currently conducted during the early portion of the season in order to determine possible risks later during fruit ripening. Ultimately, successful SWD monitoring programs may end up incorporating several different monitoring techniques including adult trapping, and egg and larval fruit infestation determination. This method shows potential as a risk tool for the industry.

Determination of Fruit Susceptibility

Green unripe fruits are generally not susceptible to SWD oviposition, and fruit susceptibility increases as the fruit ripens (Lee et al. 2011a). Several physiological changes occur as fruit ripen, such as color changes, increased total soluble solids (sugar and other compounds, Brix), decreased force required to break through the fruit skin (firmness or penetration force), softening of fruit pulp (flesh firmness) and reduced acidity. Typically, increasing sugar and decreasing skin firmness is associated with significantly increased crop risk. Pulp composition (Tochen et al. 2014, Lee et al. 2016), host plant volatiles (Cai et al. 2019, Urbaneja-Bernat et al. 2020), and color as indicated by short-wavelength reflectance (Little et al. 2020) can directly impact fruit susceptibility and suitability.

Fruit susceptibility has been studied in-depth among grapes and blueberries. Firmness is the driving factor of susceptibility to oviposition (Ioriatti et al. 2015, Baser et al. 2018, Rezazadeh et al. 2018, Entling et al. 2019, Shrader et al. 2019). In blueberry, domestication and agronomic practices are also associated with several physical and chemical characters that result in increased SWD susceptibility compared to uncultivated fruit (Rodriguez-Saona et al. 2019a). Within cultivated blueberry, varieties with higher pH displayed higher adult emergence and a shorter developmental time from egg to adult (Molina et al. 2020).

Relative SWD risk between fruit types provided an index of suitability, based on no-choice and choice oviposition tests. Cherry was classified as most preferred, followed by strawberry, blueberry, grape, banana, and apple as least preferred (Cai et al. 2019).

Additional studies on SWD susceptibility were largely similar with the highest to lowest ranking being raspberry, strawberry, blackberry, cherry, blueberry, and grape (Lee et al. 2011a, Bellamy et al. 2013, Burrack et al. 2013). Injured fruit of less-susceptible crops displayed increased SWD oviposition levels (Grant and Sial 2016, Holle et al. 2017, Pelton et al. 2017, Cai et al. 2019, Shrader et al. 2019, Acheampong et al. 2020).

Coatings that alter skin characteristics also affect SWD oviposition. An edible carnauba wax-based coating was found to increase skin penetration force in blueberries (Swoboda-Bhattarai and Burrack 2014). Here, edible coatings applied to blueberry and raspberry fruit reduced oviposition by SWD in the laboratory, and both carnauba and carnauba plus kaolin coating reduced survivorship of immature SWD in raspberry fruit. Applications of foliar calcium fertilizers targeting blueberry fruit increased skin penetration force, resulting in a reduction of oviposition by up to 70% (Ochmian 2012, Lee et al. 2016). Additional investigation to reduce SWD oviposition through edible coatings is thus warranted. Some coatings have further benefits: preharvest applications of calcium sulfate delayed postharvest softening of blueberry kept in storage (Angeletti et al. 2010, Strik 2016), and hence may improve the marketability of fruit as postharvest freshness is related to firmness. The knowledge of fruit susceptibility has become a useful tool for growers to reduce chemical treatments and management costs against SWD.

Cultural Practices

Successful cultural management practices include sanitation measures, the timing of harvest, pruning, irrigation, mulching, and exclusion netting (Schöneberg et al. 2021). Ripe, ripening, overripe, or fermented fruit can host SWD reproduction. Fruit compost and dropped fruit are also susceptible to SWD infestation (Bal et al. 2017). Research demonstrated that raspberries harvested every 1–2 d have fewer SWD larvae compared to a 3-day harvest schedule (Leach et al. 2018). Thus, sanitation measures that remove host resources can be effective for SWD management.

Sanitation practices include the management of surrounding vegetation such as Himalayan blackberry (*Rubus armeniacus*) and seedling cherry, two highly suitable host species that can directly affect SWD temporal dynamics (Klick et al. 2014, Leach et al. 2019, Tait et al. 2020a). Noncrop habitat, and wild hosts plants are utilized by SWD during fruit ripening and may serve as potential sources of infestation to nearby highbush blueberry fields (Urbaneja-Bernat et al. 2020).

Temperature and humidity affect the development, survivorship, and reproductive output of SWD (Kinjo et al. 2014, Ryan et al. 2016, Fanning et al. 2019, Kirk Green et al. 2019). Canopy manipulation by pruning may impact SWD oviposition activity by changing habitat conditions and altering oviposition sites within the canopy of a crop host (Schöneberg et al. 2021). Plant canopy density affects both humidity and light penetration, and SWD adult activity and larval infestation are higher in the interior of the canopy in caneberries (Diepenbrock and Burrack 2017, Rice et al. 2017). A lower canopy densities created by heavy pruning can, in some regions, experience slightly lower levels of SWD infestation (Schöneberg et al. 2021). Drip compared to overhead sprinkler irrigation in blueberry reduced relative humidity, which in turn decreased survival and emergence of SWD adults from sentinel pupal (Rendon and Walton 2019a). Woven weed fabric mats combined with sawdust may provide additional microclimate modification (Strik and Davis 2021). Weed fabric can increase temperatures and reduce field suitability for SWD, but can

also create a barrier that prevents larvae from reaching favorable pupation microhabitats underground (Rendon et al. 2019a). Fruit can be protected from SWD damage by creating a physical barrier by covering canopies using 0.98 mm mesh screens (Kawase et al. 2008, Cini et al. 2012, Leach et al. 2016, Rogers et al. 2016). Fall raspberry plots covered with exclusion netting placed on high tunnel structures had significantly lower SWD infestation compared to uncovered open plot treatments (Rogers et al. 2016). Exclusion netting also prevented SWD damage to grapes in Minnesota (Ebbenga et al. 2019).

Cultural control often requires investment in materials (e.g., drip line, netting) and can be labor-intensive, which often makes them more expensive than other management tactics (Schöneberg et al. 2021). The production and deployment of cultural control materials may also have negative environmental impacts (e.g., plastic mulches). Additionally, these approaches cannot be used as stand-alone tactics and minimally reduce SWD populations. However, cultural practices sometimes provide multiple horticultural benefits. Appropriate pruning improves crop quality and yield (Prange and DeEll 1997, Strik and Cahn 1999, Strik et al. 2003, Bushway and Pritts 2008), while potentially mitigating SWD populations (Schöneberg et al. 2021). Drip irrigation delivers water to the plant more efficiently, while suppressing weeds (Rendon and Walton 2019a) and conserving water. Weed fabrics reduced water use, increased yield levels, and provided weed suppression (Kasirajan and Ngouajio 2012, Kader et al. 2017, Strik and Davis 2021). The use of protective coverings provided increased bird control, decreased sunburn, and protection against hail and freeze events (Santoiemma et al. 2020). These practices have the additional benefit to reduce SWD risk, increasing the likelihood of adoption, and resulting in an overall economic benefit.

Future Directions in Cultural Management

Cultural control strategies are key to SWD management. Many practices are possible but can bring both advantages and disadvantages. Exclusion netting, drip irrigation, and mulch may require high initial capital investment but are commonly used by many growers, resulting in additional horticultural benefits. Shortened harvest intervals and the removal of unmarketable or leftover fruit are usually not practical for u-pick farms that rely on consumers to harvest the majority of fruit and may not have the budget to train harvest crews or perform additional harvests. Overall, despite the economic input required, we believe that many of these cultural strategies should be adopted within a holistic fruit production system (Table 1). These techniques can have synergistic effects to improve production efficiency and improved fruit quality.

Biological Control

Biological control is an IPM strategy using predators, parasitoids, and/or entomopathogens. There are three main approaches, which rely on: 1) protecting locally occurring natural enemies in the ecosystem (conservation biocontrol); 2) augmenting extant natural enemies in the ecosystem to strengthen their impact on pest population (augmentative biocontrol); and 3) introducing and establishing self-perpetuating populations of natural enemies from the pest's native range (classical biocontrol) (Wang et al. 2020). Significant progress has been made on evaluations of various natural enemies, especially parasitoids for potential applications in biological control of SWD over the last decade (Lee et al. 2019, Wang et al. 2020). Considering these significant recent contributions this review will attempt to summarize key advances.

Predators

Several commercially available predators including *Orius insidiosus* (Say), *Orius majusculus* (Reuter), *Orius laevigatus* (Fiber) and *Anthocoris nemoralis* (Fabricius, 1794) (all Hemiptera: Anthocoridae), *Dalotia coriaria* (Kraatz, 1856) (Coleoptera: Staphylinidae), and *Chrysoperla carnea* (Stephens, 1836) (Neuroptera: Chrysopidae) showed promise under laboratory conditions (Gabarra et al. 2015, Woltz et al. 2015, Renkema and Cuthbertson 2018, Wolf et al. 2018, Bonneau et al. 2019, Englert and Herz 2019). The European earwig, *Forficula auricularia* L. (Linnaeus, 1758) (Dermaptera: Forficulidae) preys on larvae and pupae rather than adults reducing SWD populations in orchards, but overall effects were limited (Bourne et al. 2019). Few predators were tested in open field trials. Predation efficacy is believed to be limited due to the cryptic occurrence of SWD eggs and larvae (Fig. 1). In pitfall traps, SWD pupae were attacked by ants, spiders, harvestmen, crickets, carabid beetles, and earwigs (Gabarra et al. 2015, Ballman et al. 2017, Ballman and Drummond 2017, Woltz and Lee 2017). Overall, predators are more abundant in unmanaged or organic farms than conventional farms and generalist predators may have some SWD control capability especially through conservation biocontrol (Lee et al. 2019).

Parasitoids

Parasitoids of the genera *Asobara* (Hymenoptera: Braconidae) as well as *Leptopilina* and *Ganaspis* (Hymenoptera: Figitidae) (Carton et al. 1986) are capable of developing from SWD larvae despite a high level of resistance by SWD against these larval parasitoids in the fly's invaded regions (Fleury et al. 2009, Kacsoh and Schlenke 2012, Poyet et al. 2013, Abram et al. 2020, Puppato et al. 2020, Seehausen et al. 2020). Generalist pupal parasitoids include *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae), *Trichopria*

Table 1. Potential current and future use of selected integrated management practices for *Drosophila suzukii*

Practice	Currently active	Prime time	Early stage	Some promise	Literature of reference
Cultural	Sanitation, timing of harvest, pruning, irrigation, mulching, exclusion netting				Schöneberg et al. 2021
Biological control	Generalist parasitoids	Specialist parasitoids	Nematode, Fungi	Predator, microsporidia, bacteria, virus	Wang et al. 2021
Chemical control	Conventional and organic				Shawer 2020
Behavioral manipulation	Mass trapping, postharvest control	Attract-and-kill, arrestant	Deterrent, push-pull techniques	Sterile Insect technique, CRISPR/Cas9, gene drive system, RNA interference	Wallingford et al. 2017

drosophilae (Perkins, 1910) (Hymenoptera: Diapriidae) (Gabarra et al. 2015, Rossi Stacconi et al. 2015, Mazzetto et al. 2016b, Knoll et al. 2017, Rossi Stacconi et al. 2018, Gonzalez-Cabrera et al. 2019, Hougardy et al. 2019, Wolf et al. 2019, Puppato et al. 2020) and *Trichopria anastrephae* (Lima) (Vieira et al. 2020). However, these pupal parasitoids appear unable to provide adequate SWD suppression of SWD (Gabarra et al. 2015, Miller et al. 2015, Mazzetto et al. 2016b). In contrast, multiple species of larval parasitoids were found in Japan (Mitsui et al. 2007, Girod et al. 2018), South Korea (Daane et al. 2016), and China (Girod et al. 2018, Giorgini et al. 2019). Among them, *Asobara japonica* (Belokobylskij) (Hymenoptera: Braconidae), *Ganaspis brasiliensis* (Ihering) (Hymenoptera: Figitidae), and *Leptopilina japonica* (Novković & Kimura) (Hymenoptera: Braconidae) are dominant (Daane et al. 2016, Giorgini et al. 2019, Girod et al. 2018). Both *G. brasiliensis* and *L. japonica* are the two major larval parasitoids attacking SWD infesting fruits, with parasitism of larval hosts by *G. brasiliensis* reaching 47.8% in China (Giorgini et al. 2019) and as high as 75.1% in Japan (Girod et al. 2018) (Fig. 4). These two species in particular are good candidates for classical biological control releases. *Asobara japonica* was the major parasitoid collected from fruit-baited traps infested predominantly by other drosophilids (Mitsui et al. 2007, Daane et al. 2016).

Techniques to increase the effectiveness of parasitoid release involves the use of infested fruit placed inside fine mesh cages (*augmentoria*) through which only (the much smaller) parasitoids can enter, parasitize SWD and reproduce; thereby increasing the abundance of the parasitoid populations (Rossi Stacconi et al. 2015, 2019). Augmentative releases should be timed carefully in order to optimize both temperature and host availability, allowing both survival and reproduction of the parasitoid (Pfab et al. 2018, Rossi Stacconi et al. 2019). In conjunction with other control methods, properly planned augmentative biological control can therefore provide an effective control mechanism for growers. Additional research is necessary to determine situations where it is a cost-effective IPM program component.

Entomopathogens

Fungi. Entomopathogenic fungi (EPFs) are dominant natural pathogens found to be effective against a number of fruit and vinegar flies (Lacey et al. 2015). Commercial EPFs (primarily the genera *Metarhizium* Sorokīn, *Beauveria* Vuillmin, *Lecanicillium* W. Games & Zare and *Paecilomyces* Samson) can penetrate cryptic habitats, including fruits or soil (Lacey et al. 2015). Commercial EPFs fungi tested against SWD have provided mixed success, possibly because

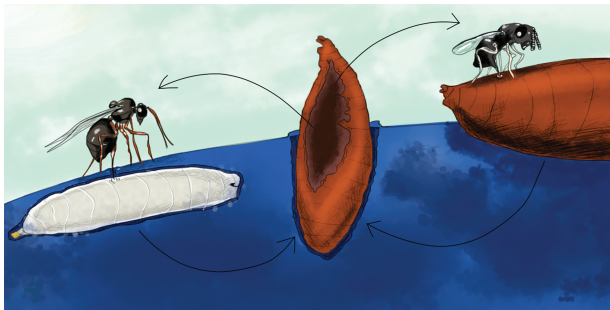


Fig. 4. The most dominant classes of parasitoids that attack SWD are larval (left) and pupal (right) parasitoids. Larval parasitoids show tremendous promise for control through classical and augmentative biological control (Avosani).

of suboptimal field conditions (Lee et al. 2019). This method of control could be improved by using autochthonous strains that are better adapted to local conditions (Haye et al. 2016, Cossentine and Ayyanath 2017). Alternative use strategies of EPF-based control include a lure-and-infect or lure-and-kill device (Cossentine et al. 2016, Yousef et al. 2018), where fungal spores are contained within a baited auto-inoculator that protects them from environmental degradation. Trials using a noncommercial fungal strain killed 96% of adults after a 24h exposure, showing excellent potential to provide selective and cost-efficient control of SWD (Yousef et al. 2018).

Microsporidia. Microsporidia are unicellular obligate eukaryotic parasites of many animal species. Several entomopathogenic microsporidia have been well-described because they cause diseases of beneficial arthropods, and their potential to be used as biocontrol agents of agricultural pests is being investigated (Bjørnson and Oi 2014). Microsporidia have been isolated from infested SWD individuals recently (Biganski et al. 2020); however, further studies are needed to determine their capacity for biological control.

Nematodes. Heterorhabditid and steinernematid entomopathogenic nematodes (EPNs) are used as infective juveniles (IJs), the only free-living stage, or by application of infected hosts from which emerge (Lacey et al. 2015). Laboratory trials using *Heterorhabditis bacteriophora* (Poinar) (Rhabditida: Heterorhabditidae), *Steinernema carpocapsae*, (Weiser) (Rhabditida: Steinernematidae), *Steinernema feltiae* (Rhabditida: Steinernematidae) Filipjev, and *Steinernema kraussei* Steiner (Rhabditida: Steinernematidae) (Woltz et al. 2015, Cuthbertson and Audsley 2016, Hübner et al. 2017, Garriga et al. 2018, Renkema and Cuthbertson 2018) show promise to kill SWD larvae when directly applied to the insect surface, whereas pupae appear to be less susceptible (Brida et al. 2019, Ibouh et al. 2019, Lee et al. 2019). Fruit-surface-applied EPNs were less effective because of the tendency of larvae to penetrate into the fruit pulp. Recently, a rare EPN species isolated from Wisconsin, *Oscheius onirici* (Andrassy) (Rhabditida: Rhabditidae), was highly pathogenic against SWD larvae. This nematode maintained efficacy when applied on the fruit surface, effectively reducing SWD survivorship by 77% (Foye and Steffan 2020). Field-testing is needed to confirm the efficacy of this promising biocontrol agent for SWD.

Bacteria. A relatively small number of entomopathogenic bacteria have been commercially developed for the control of insect pests. Among these, the most widely used bacterium is *Bacillus thuringiensis* (Bt) (Flexner et al. 1986, Lacey et al. 2015, Biganski et al. 2018). Several Bt serovars have been tested against SWD populations with Bt var. *thuringiensis*, *kurstaki*, *thompsoni*, *boliviana*, and *pakistanii* resulting in high mortality rates in first instar larvae. However, these bacteria cannot not reach the internal part of the fruit, where the larvae are located (Cossentine et al. 2016, Cahenzli et al. 2018, Biganski et al. 2020). A variant of Bt serovar, var. *thuringiensis*, is effective against adults but cannot be commercialized because it also produces exotoxins toxic to invertebrates (Cossentine et al. 2019). *Chromobacterium subtsugae* (Bergonzini) can reduce SWD infestations in the field, and is used as a rotational organic product with spinosad (Fanning et al. 2018). Entomopathogenic bacteria associated with SWD under natural conditions have been isolated from field screening of moribund SWD in Germany (Hiebert et al. 2020). The lactic acid bacterium, *Leuconostoc pseudomesenteroides* (Farrow et al. 1989), caused adult SWD mortality through oral ingestion (Hiebert et al. 2020).

Endosymbiont bacteria can strongly interfere with the biology of their host biology. SWD can host a specific *Wolbachia* variant, denoted *wSuz* (Kaur et al. 2017, Ross et al. 2019), which is found in populations from North American and Europe, and its mean occurrence is 17% and 46%, respectively (Zabalou et al. 2004, Hamm

et al. 2014, Cattel et al. 2016). However, *wSuz* does not produce cytoplasmic incompatibility, thus it is not suitable for population suppression programs. Two other *Wolbachia* variants identified in other *Drosophila* species (*wTei* and *wHa*) have been experimentally introduced in SWD and induced strong cytoplasmic incompatibility when infected males were crossed with uninfected females (Cattel et al. 2018), providing a potentially promising avenue for SWD management (Nikolouli et al. 2020).

Viruses. Two RNA viruses, Drosophila A virus (DAV) and La Jolla virus (LJV) from moribund SWD larvae in Germany can reduce SWD survival by intrathoracic injection (Carrau et al. 2018). Meta-transcriptomics analysis revealed eighteen new RNA viruses associated with SWD in the wild (Medd et al. 2018). Additional model viruses (Drosophila C virus, Cricket paralysis virus, and Flock house virus) trigger adult mortality when infected with intrathoracic injections. Additional work is needed to determine how viruses can be delivered and spread amongst SWD in the field as IPM strategies.

Future Directions in Biological Control

Altogether, data from the past decade provide multiple approaches that may be applied alone or synergistically with other compatible IPM practices (Lee et al. 2019, Wang et al. 2020). In particular, parasitoids, predators, and endosymbiont *Wolbachia* may help reduce the impact of SWD (Biondi et al. 2021). Promising results may be achieved after consistent and methodic releases and field studies of these agents over multiple years to demonstrate efficacy. Some biological control agents will require commercialization and the affordability of these products will additionally determine their usefulness. Future studies are needed to improve understanding of the field ecology of these key natural enemies, developing optimal release strategies for parasitoids and conservation strategies to reduce nontarget impacts of other control measures on natural enemies as well as developing recommendations for field use of entomopathogens.

Chemical Control

Currently, many fruit producers are reliant on insecticides to protect their fruit from SWD infestation, due to the high market value of fruit and zero tolerance for infested fruits (Haye et al. 2016). This is partly because other techniques for organic and conventional production (cultural, mechanical, and biological) are insufficient as standalone practices (Diepenbrock et al. 2016). The rapid invasion and explosive population increase of SWD, coupled with its seasonal population structure (Hamby et al. 2014) result in growers needing highly effective fruit protection tactics. Sprays are typically conducted using calendar scheduling, with application based on the duration of protection provided by different sprays (Van Timmeren and Isaacs 2013, Fanning et al. 2018, Shaw et al. 2019). Most broad-spectrum insecticides target the adult stage of SWD but can affect the survival of the immature stages, e.g., eggs and larvae (Wise et al. 2015, Shaver et al. 2018). Common effective conventional chemical classes include organophosphates, pyrethroids, carbamates, and diamides. Reduced-risk chemicals include spinosyns, and the certified organic insecticide spinosad is a mainstay for organic production (Zehnder et al. 2007, Van Timmeren and Isaacs 2013, Gress and Zalom 2019). These classes provide a variety of modes of action e.g., acetylcholinesterase (AChE) inhibitors, sodium channel modulators, nicotinic acetylcholine receptor (nAChRs) allosteric modulators, and ryanodine receptor modulators (Fig. 5). This allows for resistance management through the rotation of chemical classes in successive spray applications.

Conventional Production

Many insecticides are effective and provide sufficient mortality both under laboratory and field conditions (Bruck et al. 2011b, Pavlova et al. 2017, Rosensteel and Sial 2017, Schlesener et al. 2019). The residual effect of malathion, spinetoram, and spinosad were tested on cherry. Here, mortality generally ranged around 90% (Beers et al. 2011). Malathion, spinetoram, lambda-cyhalothrin, and spinosad treatments resulted in relatively equivalent toxicity in males but

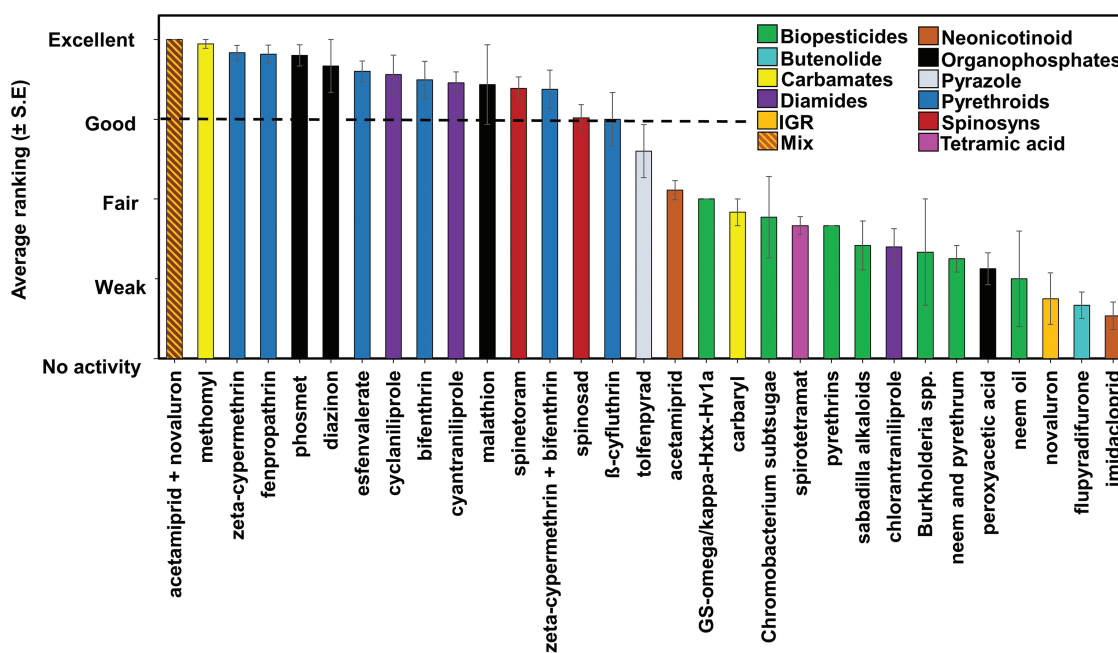


Fig. 5. Ranking of insecticide efficacy by United States-based insect management experts in a 2020 survey of applied entomologists with experience studying SWD. Rankings for each listed active ingredient were provided using a range from 0 (ineffective) to 4 (excellent), and values presented are average \pm S.E. of the rankings provided (Isaacs).

malathion was found to be the most toxic against females followed by spinetoram and spinosad (Smirle et al. 2017) (Fig. 5).

Label restrictions limit the number of insecticide applications that can be made in a season and/or, or the number of successful applications of the same chemical class. The ultimate goal is to rotate chemical classes throughout the season, thereby delaying the development of insecticide resistance (Mishra et al. 2018). The most common insecticides for SWD control used by conventional growers in the United States are Delegate 25 WG (spinetoram, Dow AgroSciences LLC, Indianapolis, IN), Mustang Maxx (zeta-cypermethrin, FMC Corp, Philadelphia, PA), and Malathion 8 EC (malathion, Arysta LifeScience North America, LLC, Cary, NC) (Mermer et al. 2020). Seasonal programs of these and other broad-spectrum insecticides can provide effective control of this pest across a range of crop systems and environmental conditions (Beers et al. 2011, Bruck et al. 2011b, Diepenbrock et al. 2016, 2017).

Organic Production

Several National Organic Program (NOP) approved insecticides have recently been evaluated in a series of laboratory and semi-field experiments (Van Timmeren and Isaacs 2013, Guédot and Perry 2016, Iglesias and Liburd 2017, Wise et al. 2017, Fanning et al. 2018, Sial et al. 2019). Organic growers have a limited number of effective insecticides including Entrust (spinosad, Dow AgroSciences LLC, Indianapolis, IN), Pyganic (pyrethrin, McLaughlin Gormley King Co., Minneapolis, MN), and Grandevo (fermented product of *Chromobacterium subsugae*, Marrone Bio Innovations, Davis, CA). Additionally, azadirachtin, hydrogen peroxide + peroxyacetic acid, *Burkholderia* spp., and pending promising biopesticides including sabadilla alkaloids may have the potential for organic production.

These products represent various unknown modes of action. Spinosad is currently known to be the most effective insecticide for organic producers (Bruck et al. 2011b), but the label requires rotation with a different mode of action for resistance management. Lower activity on SWD has been recorded for the insecticide Pyganic. In fact, only direct-sprays against SWD adults resulted in reduced activity without any form of residual effectiveness in field trials (Bruck et al. 2011a).

Some level of effectiveness has been found for azadirachtin, *C. subsugae*, and sabadilla alkaloids. Generally, these compounds have lower levels of effectiveness with limited residual efficacy beyond 3 d after application (Sial et al. 2019). An insecticidal spider venom peptide, GS-omega/kappa-Hv1a, and azadirachtin were not effective against SWD and are not recommended for rotation with spinosad (Fanning et al. 2018). Lime-sulfur showed promise in reducing fly activity. Adjuvants can increase pesticide efficacy by improving deposition, enhancing rainfastness, reducing drift, protecting active ingredients from environmental degradation, and/or increasing plant tissue penetration (Foy and Pritchard 1996). In some cases, adjuvants can also increase pesticide toxicity or are directly toxic to insects (Stark and Walthall 2003, Stark et al. 2004, Ciarlo et al. 2012, Mullin et al. 2015, Chen et al. 2018). Organic adjuvants (alcohol ethoxylate (AEO), poly-1-p-menthene (P1PM), polyether-polymethylsiloxane-copolymer polyether) were evaluated for SWD control and some adjuvant-insecticide combinations increased insecticide efficacy; however, expected benefits were not realized (Roubos et al. 2019).

Rainfastness

Both the intensity and the quantity of precipitation may impact insecticides. Insecticide efficacy was compared under simulated rainfall to determine SWD adult mortality and immature survival. Here,

the residual effects of zeta-cypermethrin, spinetoram, and phosmet were significantly reduced after a rain event. The residual effects of phosmet and spinetoram decreased after the simulated rainfall event showing that these compounds were more influenced by rainfall than zeta-cypermethrin (Andika et al. 2020). Additional studies on the active ingredients spinosad, spinetoram, cyantranilprole, malathion, and zeta-cypermethrin also demonstrated a significant reduction of efficacy after rainfall (Gautam et al. 2016). The adjuvant Nu Film 17 combined with zeta-cypermethrin, malathion, spinosad, and spinetoram increased efficacy after simulated rainfall (Gautam et al. 2016). The intensity and quantity of precipitation may impact the efficacy of insecticides. Van Timmeren and Isaacs (2013) found that 2 cm of precipitation can affect adult mortality for most active ingredients except for methomyl, phosmet, and zeta-cypermethrin.

Improving Efficacy and Nontoxic Control

To increase the effectiveness of insecticides against SWD, sucrose, and yeast have been tested as phagostimulants (Cowles et al. 2015, Knight et al. 2016, Gullickson et al. 2019). Multiple studies have demonstrated that various combinations of non-nutritive erythritol and sucrose have detrimental effects on SWD adults. Non-nutritive sugars fed to *D. melanogaster* (Meigen) reduced the fly's longevity, motor coordination, and reproduction (Baudier et al. 2014, O'Donnell et al. 2016, 2018). Non-nutritive sugars also have insecticidal properties against SWD at various concentrations and formulations and also reduce fecundity (Goffin et al. 2017, Sampson et al. 2017, 2019, Tang et al. 2017, Choi et al. 2017, 2019). Erythritol molecules are not utilized as carbohydrate energy, or converted into a storage form like glycogen, so they rapidly accumulate in the body, and cause the fly to have high osmotic pressure or physiological imbalance. Erythritol is directly transported from the midgut and is eventually excreted. (Tang et al. 2017). Despite encouraging results using this compound, several concerns need to be addressed, including whether flies will feed on other naturally-occurring sugar sources such as fruit juice or floral nectar instead of the treated berries in the field (Kaçar et al. 2017). In the laboratory trial, erythritol combined with sucrose reduced the longevity of fly adults regardless of the presence of wounded blueberries as natural naturally occurring sugar sources (Choi et al. 2019). For practical application in the field, non-nutritive sugars must be registered as a pesticide. As phagostimulants, non-nutritive sugars, can be combined with other insecticides or baits which may increase insecticide efficacy (Roubos et al. 2019). Studied baits included fermented strawberry juice, the SWD-associated yeast *Hanseniaspora uvarum* (Niheaus), and a combination of two plant extracts. Insecticides included spinosad, cyantranilprole, and lambda-cyhalothrin. Such combinations resulted in increased mortality, and reduced oviposition on both summer and winter morphs of SWD (Noble et al. 2019).

Application Techniques

A study on commonly-used sprayers (cannon, electrostatic, and airblast) indicated that electrostatic sprayers displayed the least variability on canopy deposition, while airblast sprayer deposition rates were highest in the middle of the canopy (Mermer et al. 2020), where SWD infestation is generally most concentrated (Diepenbrock et al. 2016). In the laboratory bioassays, improved spray coverage on raspberry fruit increases adult mortality (Lewis and Hamby 2020). Further research is needed to explore alternative application techniques that are more efficient, more effective, and can reduce the need for frequent repeated applications.

Insecticide Resistance

Concern for insecticide resistance in SWD was expressed shortly after its widespread establishment (Cini et al. 2012) due to its short generation time, high fecundity, and repeated exposure to insecticides applied for its control (Asplen et al. 2015). The limited number of insecticide classes registered for SWD host crops in both conventional and organic production systems further increases selection pressure. Although insecticide resistance has not been observed in most North American berry and cherry growing regions to this time, reduced sensitivity to spinosyns was found in Michigan and California (Van Timmeren et al. 2018, Gress and Zalom 2019). However, 30 generations of selection with malathion did not result in resistance development in a SWD laboratory colony (Smirle et al. 2017). Malathion toxicity is related to time of day and level of detoxification gene activity i.e., cytochrome P450 (Hamby et al. 2013). Significant differences in chronotoxicity were found when comparing malathion (highest susceptibility) at 6 am and peak activation of cytochrome P450 at the same time, and maybe related to bioactivation of malathion (Hamby et al. 2013). The potential for insecticide resistance in SWD field populations has led to development of a discriminating dose contact bioassay technique. This rapid and simple bioassay is available to identify the presence of insecticide resistance for most insecticides commonly used to control SWD (Van Timmeren et al. 2019).

Maximum Residue Levels and Nontarget Impacts

Maximum Residue Limits (MRLs) are limits on the level of pesticide residue allowed on imports, and violations of MRLs could result in the inability to sell to certain international markets with severe economic consequences (Goodhue et al. 2011, Farnsworth et al. 2017, Rodriguez-Saona et al. 2019b). A side effect of insecticide use is the disruption of natural enemy populations, including parasitoids and predators (Desneux et al. 2007). Several certified organic insecticides were tested for their impacts on natural enemies (e.g., *Chrysoperla rufilabris* (Burmeister) (Neuroptera: Chrysopidae), *O. insidiosus*, *Aphidius colemani* (Viereck)). Spinosad is highly toxic to many natural enemies. Several adjuvants, including polyether-polymethylsiloxane-copolymer polyether showed similar toxicity levels to these natural enemies. All tested insecticides were harmful to natural enemies resulting in reduced oviposition and egg hatch levels (Sarkar et al. 2020). Insecticides currently remain a critical component of SWD management but can result in significant economic and environmental cost.

Future Directions in Chemical Management

Future directions in chemical management should focus on continued development of alternative strategies, allowing for a return to more sustainable programs. Additional biopesticide research is needed for organic growers who currently have few options with moderate efficacy. For example, several alternative products including thyme, *Leptospermum ericoides*, *L. scoparium*, erythritol plus sucrose, the chitinase of *Euphorbia characias*, and perillaldehyde or perilla aldehyde all are potentially promising alternatives for SWD management. To enhance the activity of insecticides against SWD, additional research is needed optimized adjuvant use and improved application methods.

Behavioral Manipulation

D. suzukii employs multiple mechanisms to find reproductive hosts. For example, short- and long-distance attraction is based on both odor cues and visual stimuli (Cha et al. 2012, Little et al. 2019).

After contact, feeding and/or oviposition behavior is likely impacted by volatile compounds on the fruit surface, either directly from plants, or from conspecific flies (Tait et al. 2020b, Elsensohn et al. 2021). In this section, we review research of host attraction and host acceptance as they relate to pest management.

Mass Trapping

Mass trapping for the suppression of a pest population uses attractive stimuli to lure insects to a trap where they are confined and presumably die (Rodriguez-Saona and Stelinski 2009). For SWD, it is believed that a dense crop perimeter barrier of traps baited with lures reduces pest immigration (Hampton et al. 2014, Alnajjar et al. 2017). It is recommended to place 30 to 50 traps per hectare, placed up to 2 meters apart. These traps should be serviced weekly (Lee et al. 2011b, Spies and Liburd 2019). The costs associated with materials and labor using this strategy are likely a barrier to adoption, especially for large-scale production. It may be possible that the use of attractive odors as a lure can cause hotspots of elevated crop injury in the vicinity of traps, likely caused by uncaptured ovipositing flies (Hampton et al. 2014). While currently not a viable stand-alone approach to manage SWD, mass trapping could contribute to integrated management (Profaizer et al. 2015, Spies and Liburd 2019).

Attract and Kill (A&K)

This method uses attractive stimuli to lure insects to a toxicant, where contact or consumption of the toxicant leads to death. Attracticidal spheres with a wax cap containing sugar feeding stimulant and toxicant have been demonstrated to reduce SWD infestation when deployed in small-scale raspberry field trials (Rice et al. 2017, Stockton et al. 2021). HOOK-SWD (ISCA Technologies, Riverside, CA) is a sprayable attract-and-kill formula containing attractive olfactory and gustatory stimuli combined with spinosad, and has been demonstrated to reduce SWD infestations in blueberry and raspberry crops when applied to leaves (Klick et al. 2019). Registration and commercial availability of products containing insecticides remain a regulatory barrier to the adoption of attract-and-kill approaches. There is growing interest, therefore, in developing adjuvants that include attractive odors plus a feeding stimulant such as sugar, that can be mixed with insecticide and applied to the crop (Noble et al. 2019).

Arrestants

Arrestants act to disrupt foraging behaviors upon contact. Detection of sucrose arrests SWD foraging behavior and stimulates flies to feed. The addition of sucrose to insecticides targeting SWD has been shown to enhance lethality in some laboratory, semi-field, and field tests (Cowles et al. 2015, Knight et al. 2016, Cloutier et al. 2018) but not in others (Fanning et al. 2018, Roubos et al. 2019). A SWD arrestant in the form of an attractant gum matrix was proposed as an alternative management approach (Tait et al. 2018b). The gum matrix is highly competitive with ripening fruits in reducing SWD oviposition in commercial crops. Semiochemical volatiles from the gum significantly alters damaging SWD behavior, resulting in the protection of fruit (Rossi Stacconi et al. 2020). This technology is distinct from attract-and-kill systems that employ both semiochemicals and a toxicant to kill adult SWD populations (Klick et al. 2019).

Spatial Repellents and Oviposition Deterrents

Aversive odors could be used to avoid crop injury by repelling SWD away from crop space entirely or by deterring female SWD from ovipositing in fruit when they come in contact with susceptible crops. Several aversive compounds have been identified for SWD,

including plant-, insect-, and microbe-derived compounds, as well as DEET-inspired anthranilates (Ebrahim et al. 2015, Pham and Ray 2015, Renkema et al. 2016, Wallingford et al. 2016b, Bernardi et al. 2017, Cha et al. 2021), and the effects of natural products and compounds have been recently reviewed (Dam et al. 2019). Various plant-derived essential oils offered high levels of repellency and some caused contact or fumigant toxicity, but more testing is needed before essential oils and other promising compounds can be successfully used in the field (Dam et al. 2019).

Maintaining relatively high concentrations of aversive odors is critical to reduce crop injury and remains a barrier to implementation. Butyl anthranilate painted on blueberries provided several days of protection from oviposition in a laboratory setting (Pham and Ray 2015); however, direct application of a compound imparting its own flavor to fruit is likely not practical. Gullickson et al. (2019) found that EcotrolPLUS (rosemary and peppermint oils and geraniol) sprayed at weekly intervals reduced SWD infestation in raspberries but not blueberries, but they did not report on whether spray residual could affect fruit flavor. More, the strong smell compounds could have a negative effect on the organoleptic profile of treated fruits (Bedini et al. 2020).

Methods that place aversive odors near, rather than on, ripening fruit may be preferred over foliar application. Passive release methods include incorporating compounds into laminate polymer flakes, mineral oil, or other waxy substrates (e.g., SPLAT; ISCA Technologies, Riverside, CA) so that the compound will slowly volatilize from dispensers. In some cases, these approaches have resulted in reduced SWD infestation but whether SWD can eventually overcome these aversive odors still needs to be tested (Renkema et al. 2016, 2017, Wallingford et al. 2016a, Wallingford et al. 2017, Cha et al. 2021). Advances in the identification of bioactive aversive compounds and their effective field doses are essential for optimizing their application. For example, placing hops (*Humulus lupulus*) pellets in perforated plastic cups near ripening berries did not affect SWD oviposition in the field, even though pellets were repellent in the laboratory (Reher et al. 2019). Active release methods include automated aerosol puffers that release a standard amount of a compound on a regular schedule. Automated puffers can reduce SWD infestation over several days, using the oviposition deterrent, 1-octen-3-ol (Stockton et al. 2020).

Using plants from which the most SWD-repellent compounds in the laboratory were derived may provide a constant release of volatiles over extended periods. Peppermint (*Mentha × piperita*) was interplanted in strawberry and potted blueberry since peppermint oil was effective in the laboratory (Renkema et al. 2016). However, there were no reductions in berry infestation with a peppermint intercrop (Renkema et al. 2018, Gowton 2020). Initial observations showed that sweet alyssum (*Lobularia maritima*) planted on the edge of a strawberry field reduced drosophilid captures. Cut sweet alyssum flowers repelled SWD from raspberries in the laboratory (Renkema and Smith 2020), and potted sweet alyssum reduced SWD infestation in fruit in cage experiments (Renkema unpublished data, Lee unpublished data). Adding sweet alyssum to berry fields may not only help reduce SWD fruit infestation through repellency or deterrence, but it may also attract and maintain populations of beneficial insects (Berndt and Wratten 2005).

Push-Pull Techniques

Push-pull refers to an approach that combines the “push” of aversive stimuli combined with the “pull” of attractive stimuli. This terminology implies that insects are diverted from crop space using spatial repellents, into traps baited with long-distance attractants. However,

any of the described behavioral manipulations used in combination could be considered push–pull. For example, Wallingford et al. (2017, 2018) found that mass trapping combined with an ovipositional deterrent (1-octen-3-ol) resulted in lower SWD infestations than either approach alone, but this effect was most likely additive; authors found no evidence that the deterrent was “pushing” flies towards mass trapping devices.

It is worth mentioning that a survey of SWD hosts in France revealed some “trap plants”, attract females for egg-laying without allowing the emergence of adults (Ulmer et al. 2020). These noncrop dead-end hosts could be cultivated on the edge of a field as a form of functional biodiversity, although this idea needs to be tested.

Future Directions in Behavioral Management

Development of behavioral control of SWD should focus on large-scale production. There is both great potential and demand for more research. Pest behavioral manipulation is a standard practice in several other horticultural systems. For example, GF-120, an attract and kill technique that combines attractant volatiles and a feeding stimulant with insecticide, is commonly used for managing tephritid pests such as apple maggot (*Rhagoletis pomonella*) (Diptera: Tephritidae), blueberry maggot (*Rhagoletis mendax*) (Diptera: Tephritidae) and western cherry fruit fly (*Rhagoletis indifferens*) (Diptera: Tephritidae). This example provides hope that similar tools can be developed against SWD. Effective repellants are needed, given the advent of insecticide resistance development. Arrestant chemicals that can reduce fruit damage without the use of insecticides can also contribute to a behavior-based management system (Tait et al. 2018b, Cha et al. 2021).

Developmental Disruption

Sterile Insect Technique (SIT)

This technique is a species-specific and environmental-friendly method for pest management. This approach has been used successfully to suppress or eradicate pest populations (Nikolouli et al. 2018). First developed for the eradication of the New World screwworm fly *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) from North America, Mexico, and Central America (Wyss 2000, Scott et al. 2017), sterile insect technique has been effectively and increasingly used against many crop and livestock pests and disease vectors, such as tephritid fruit flies, tsetse flies and Lepidoptera (Hendrichs et al. 2002, Marec and Vreysen 2019). This approach consists of mass-rearing of the insect pest, sterilization by exposure to ionizing radiation and sustained area-wide releases of sterile insects at regular intervals (Lanouette et al. 2017). Thus, to develop a sterile insect technique for SWD mass-rearing technologies need to be developed and a radiation dose that produces sterile males that are competitive in the field must be identified. The radiation dose should also fully sterilize females. Fortunately, SWD females are fully sterilized by a dose of 50 (Lanouette et al. 2017) or 75 Gy (Krüger et al. 2018). A much higher radiation dose of 200 Gy was required to achieve over 99% male sterility but this dose did not appear to impact male flight ability or longevity (Krüger et al. 2018). Two groups have reported development of economical methods for mass rearing SWD using a yeast-based diet (Sassù et al. 2019, Aceituno-Medina et al. 2020). The use of a cage with a wax panel appears to be an effective method for collecting eggs that produce high-quality insects (Sassù et al. 2019). Additional studies are needed to determine whether mass-reared radiation-sterilized males are competitive and can suppress a population in cage trials.

The sterile insect technique is more efficient if only sterile males are released. This is because sterile females compete with fertile females for mating with the sterile males (Rendón et al. 2004). Further, sterile SWD females could still mechanically damage the soft fruits while laying their sterile eggs, permitting secondary infections and compromising fruits marketability (Cini et al. 2012, Lanouette et al. 2017). Drosophilid female are known to mate multiple times, and can store sperm for up to two weeks (Bangham et al. 2003). Such long-term sperm storage may negatively affect SIT efficiency (Scolari et al. 2014).

Biotechnology-Enhanced Sterile Insect Technique

A genetic sexing strain (GSS) provides a means for releasing only sterile males. Mediterranean fruit fly GSS is homozygous for a recessive temperature-sensitive lethal (*tsl*) mutation and carries a translocation of the functional *tsl⁺* gene to the Y chromosome (Franz, 2005). Consequently, only females survive at the nonpermissive temperature. A SWD genetic sexing strain could be made by random chemical mutagenesis and selecting for *tsl* mutations or more directly by using CRISPR/Cas9 gene editing. For CRISPR/Cas9, the guide RNA (gRNA) and Cas9 protein can be delivered into the organism in the form of DNA, RNA, or protein (Bassett and Liu 2014). Indeed, methods for CRISPR/Cas9 gene editing have been developed for SWD (Li and Scott 2016, Kalajdzic and Schetelig 2017). The CRISPR/Cas9 system allows site-specific mutations down to the change of a single nucleotide. Since there is no stable introduction of exogenous DNA, CRISPR/Cas9 changes are considered nontransgenic and, in several countries, may be regulated differently than transgenic organisms. To make a genetic sexing strain, mutations could be made in selected genes based on known *tsl* mutations in *D. melanogaster*. Li and Handler (2017) took a similar approach to make temperature-sensitive mutations in the SWD *transformer-2* gene, which is essential for female development (Li and Handler 2017). At the permissive temperature (16–20°C), XX chromosomal females developed normally but at 26°C they developed as intersexes with some male features (Li and Handler 2017). The inability to rear SWD at higher temperatures (29°C) likely prevented full sex reversal of XX flies and would appear to limit the development of genetic sexing strain based on the production of only males at the elevated nonpermissive temperature. Genetic sexing or male-only strains have been made using other designs for several species through transgenic technology and can inform future biotechnology-enhanced SIT in SWD (Heinrich and Scott 2000, Fu et al. 2007). In these strains, females die due to sex-specific activation of a lethal gene that is otherwise repressed through addition of tetracycline to the diet. A SWD GSS has been developed that produced only males on diet without tetracycline (Li et al., 2021). Repeated releases of an excess of GSS males suppressed SWD populations in laboratory cage trials. In the U.S., a transgenic male-only strain of the diamondback moth was approved and tested in an open field trial, indicating that it would be possible to obtain approval for field trials of SWD male-only strains.

Gene Drive Systems

D. sukukii carrying gene drive systems could be effective for suppression of wild SWD populations (Li and Scott 2016). A gene drive is defined as a “process that promotes or favors biased inheritance of certain genes from generation to generation” and is “composed of one or more genetic elements that can cause the biased inheritance in its favor” (Alphey et al. 2020). For population suppression, one approach that appears particularly promising are homing gene drives (Deredec et al. 2008, Kyrou et al. 2018). In these strains, Cas9

and guide RNAs (gRNAs) are expressed in the germline and are inserted within an exon of a gene essential for female development of fertility. The guide RNA would target the functional copy of the gene carrying the Cas9-gRNA insertion. In hemizygotes (i.e., one copy of Cas9 and guide RNA genes), the wild-type gene is cleaved by the Cas9/gRNA complex and repaired by either the homology-directed or nonhomologous end-joining pathways. The former leads to copying of Cas9 and guide RNA genes and homozygosity for the disrupted gene in the germline. Consequently, most of the offspring carry one copy of the disrupted gene with the Cas9-guide RNA insertion. As the disrupted gene is essential for female development or fertility, the release of males carrying the transgene can lead to population suppression (Kyrou et al. 2018, Li et al. 2021). This approach should be much cheaper than the sterile insect technique as far fewer insects would need to be released to achieve suppression. However, the production of resistance alleles due to nonhomologous end-joining repair or pre-existing natural variation in the population can cause the drive to fail after a few generations (Unckless et al. 2017).

Several other gene drive systems have been developed and tested in *D. melanogaster* (Buchman et al. 2018, Oberhofer et al. 2019, Webster et al. 2020). One of them, *Medea*, was also evaluated in SWD (Buchman et al. 2018). Most of these systems were originally developed for population modification or replacement of mosquito disease vectors and not for population suppression. These gene drive systems could be used for control of SWD if they favor a gene that has low fitness cost at the time of release but is detrimental to survival at a later time. For example, susceptibility to a chemical or a parasitoid (Buchman 2018, Webster 2020). The regulatory process for approval for field release of gene drive organisms is currently being actively discussed (James et al. 2020). It should be noted that the degree of spread and temporal dynamics is quite different for different gene drive systems. For example, strains with homing and *Medea* gene drive systems are expected to have low release thresholds and could spread well beyond the release site. In contrast, killer-rescue gene drive systems are self-limiting (temporally limited) whereas underdominance systems have high-release thresholds and are localized. Thus, the genetic system used in the gene drive organism will likely be a significant factor in any risk-benefit analysis of a proposed field release.

RNA interference (*RNAi*) is the process by which the presence of double-stranded RNA (dsRNA) triggers a post-transcriptional sequence-specific gene silencing of the complementary mRNA. The application of *RNAi* technology for insect pest management has significantly progressed. Two breakthrough reports demonstrated that insects feeding on transgenic plants engineered to produce specific double-stranded dsRNA resulted in the suppression of target gene expression in the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae) (Mao et al. 2007) and the western corn rootworm, *Diabrotica virgifera* (Coleoptera: Chrysomelidae) (Baum et al. 2007). In insects, it has been shown that ingestion of double-stranded RNA targeting essential genes can lead to larval stunting and mortality (Baum et al. 2007, Taning et al. 2016). *RNAi* can theoretically target any nonconserved gene that results in high mortality when knocked down.

Although *RNAi* technology is a promising tool for insect pest management, there are technical challenges: 1) selection of suitable target genes; 2) development of a practical *RNAi* delivery mechanism, and 3) providing cost-effective double-stranded RNA production. The identification of effective *RNAi* targets with a high level of gene silencing would result in insect developmental arrest and/or death (Zhang et al. 2013). Using the annotated SWD genome sequences (Chiu et al. 2013, Paris et al. 2020), various SWD

genes for potential RNAi targets such as housekeeping, neurohormones, and their receptors have been investigated (Murphy et al. 2016, Taning et al. 2016, Choi et al. 2017). This, coupled with the sequence-specific nature of the silencing, makes RNAi an excellent candidate as a species-specific insecticide.

The oral delivery of dsRNA is feasible for practical application in the field, but its efficacy is limited due to the dsRNA degradation in the SWD gut (Yoon et al. 2021). RNAi to control pest populations can be implemented either by spraying double-stranded RNA on infested plants or by genetically engineering crops to produce double-stranded RNA. Both mechanisms have advantages and disadvantages. Spray application of double-stranded RNA fits well with current pesticides delivery infrastructure but is not cost-effective because production of necessary quantities in vitro synthesized double-stranded RNA is expensive. Plant-incorporated dsRNA expression, on the other hand, can be cost-effective in the long term but would require growers to plant transgenic crops (Baum et al. 2007, Mao et al. 2007). Another approach takes advantage of low-cost microbial-based RNA production to generate large quantities of double-stranded RNA. Both bacteria- or yeast-expressed double-stranded RNA targeting housekeeping genes have been developed to control SWD and have been proven to reduce SWD larval survivorship (Abrieux and Chiu 2016, Murphy et al. 2016, Taning et al. 2016, Ahn et al. 2019). This method is cost-effective, but there are concerns for the containment of transgenic microbes, since when applied in the field, it can be carried from one location to another by flying adults. Besides the specific limitations of the approaches mentioned above, the use of RNAi, in general, is hindered by public hesitancy in accepting transgenic organisms (Taning et al. 2016). For practical application, the oral delivery of RNAi should be considered.

Future Directions in Developmental Disruption

Although the effort required for the advancement and future implementation of Sterile Insect Technique on SWD is still considerable, the novel prospective offered by CRISPR/Cas9 gene-editing technology and new SWD genomic resources opens a range of avenues that will foster this process. If successful, we believe Sterile Insect Technique can be easily integrated with other biological control strategies (parasitoids, predators, and pathogens). Regulation on the use of genetically modified organisms in the field remains a notable limitation, placing doubt on the utility of these tools in the immediate future. While there are already field tests of sterile insect technique in US and Europe, the risks associated with these techniques are of concern. What will be the direct and indirect effects on the biotic structure of fly populations, how practical and cost-effective would this technique be, what are the ethical and public concerns? It may be prudent for companies investing in this approach to conduct risk–cost–benefit analysis as a step towards the future use of these approaches. The Sterile Insect Technique (SIT) could be easily integrated with other biological control strategies discussed previously (parasitoids, predators, and pathogens). Indeed, there is potential in using synergistic suppressive actions by combining SIT with area-wide releases of parasitoids (Knipling, 1998). SWD strains infected with *Wolbachia* appear particularly promising for SIT as a much lower dose of radiation is required to achieve male sterility (Nikolouli et al 2020). For biotechnology enhanced SIT and RNAi-based methods for pest suppression, the next steps would be testing in large cages in contained greenhouse trials. Open-field testing would be a longer-term prospect and would require regulatory approval. Whether or not transgenic male-only/male-sterile or RNAi approaches would be used by growers for SWD control will depend upon several factors including public support for the technology. The

development of gene drive strains for SWD suppression is still at the beginning stages and would be a longer-term prospect. In contrast, considerable effort and progress has been made in developing and testing transgenic mosquito gene drive strains for population suppression. The recently released WHO *Guidance framework for testing genetically modified mosquitoes* will no doubt serve as a useful guide for those developing SWD strains.

Optimized Management Through Modeling

Mathematical models can be used to simulate the dynamics of SWD populations and their responses to pest control interventions. Such simulations can enhance our understanding of different control strategies and help to optimize single or combined interventions, both under experimental and real-world conditions. Current approaches for modeling SWD population dynamics include statistical methods such as degree-day (DD) estimates for the onset of the reproductive period (Drummond et al. 2019a, Kamiyama et al. 2020), as well as stage-structured models (Wiman et al. 2014, 2016) and on continuous time differential equations (Gutierrez et al. 2016, Langille et al. 2017, Pfab et al. 2018, Mermer et al. 2020, Mermer et al. 2021). Such models have been used in case studies to optimize the timing of augmentative parasitoid releases (Pfab et al. 2018), and pesticide treatments against SWD populations (Mermer et al. 2021). Modeling has helped reveal key seasonal bottleneck periods allowing for future timed control strategies and improving our understanding on how to combine control strategies. More, developmental stage-based models and degree-day models have been created to provide insight into population structure within a specific region (Wiman et al. 2014, 2016, Pfab et al. 2018, Kamiyama et al. 2020). These models are based on degree-days, physiological parameters, and population ecology, and can be used to estimate the timing of important risk events such as first adult fly detection and peak activity (Kamiyama et al. 2020). In addition, environmental factors such as extreme winter events are associated with decreased fly abundance the following year (Rossi-Stacconi et al. 2016, Thistlewood et al. 2018, Drummond et al. 2019b, Leach et al. 2019). Data from these models can provide valuable information regarding large-scale population trends within a specific region, thus allowing growers to anticipate management needs in their crops. For early- and mid-season ripening crops, this could mean reducing or increasing the number, sequence, and frequency of insecticide applications. Likewise, harvest schedules can potentially be adjusted based on the capture of adults and model predictions (Drummond et al. 2019a). It is important to be aware of the limitations of predictive phenology models, especially for a pest such as SWD that has multiple overlapping generations and rapid reproductive rates. Here, simple degree-day models tend to have less value, as opposed to more complex models that take into consideration population structure and size. Such models have not only been used to optimize pesticide application strategies, but also have also provided valuable insights that can be integrated into existing IPM programs (Mermer et al. 2021). These models should be further refined and validated against real-world scenarios to improve value.

In addition to case studies, growers and horticulturalists could benefit from a user-friendly interface that use various inputs such as weather data, current SWD infestation status, and type and status of the crop to make a more informed prognosis for ongoing or future SWD outbreaks aiding in planned interventions. Generic case studies and custom simulations can together broaden our understanding of SWD population dynamics and help further development of efficient and sustainable pest control strategies.

Postharvest Control

Postharvest practices have the potential to negatively affect immature SWD and to potentially salvage a crop with the low-level infestation as part of an IPM program. Generally, postharvest approaches for SWD management include: 1) irradiation; 2) chemical treatments; and 3) cold temperature treatments. While a radiation dose of 40 Gy applied to first- and second-instar larvae is enough for preventing adult emergence (Follett et al. 2014), a radiation dose of 80 Gy applied to late-stage pupae is necessary to eliminate F1 adults. Overall, a minimum absorbed dose of 80 Gy is recommended for quarantine control of SWD. A dose of 150 Gy of postharvest X-ray irradiation of fruit induces adult sterility and limits further dispersal of SWD (Kim et al. 2016). Postharvest chemical treatments include the use of methyl bromide (Walse et al. 2012). The use of methyl bromide is regulated internationally via the Montreal Protocol on ozone-depleting substances under the Quarantine Pre-shipment (QPS) Exemption (Ristaino and Thomas 1997). Exposing SWD to commercial methyl bromide fumigation (8.3 to 12.2 ($\pm 0.5^\circ\text{C}$) can provide comparable results when subjected to commodity fumigation ($T = 13.9 \pm 0.5^\circ\text{C}$) (Walse et al. 2016). The potential of stand-alone ethyl formate treatments and a combined treatment of ethyl formate and cold temperature as postharvest controls for SWD in blueberry proved effective against all life stages of SWD and had no apparent negative impact on the quality of blueberries (Kwon et al. 2021). Ethyl formate fumigation (70.0 gm^{-3}) at low-temperature conditions (e.g., 5°C) could be especially beneficial to meet the temperature requirements for the cold chain necessary to maintain quality of blueberries when shipping to destination countries (Kwon et al. 2021). Extended cold temperature treatments of 1.1, 3.9, and 5.0°C for periods up to 72 h can result in longer developmental times and decreased SWD survivorship (Aly et al. 2017, Kraft et al. 2020), providing an effective postharvest management strategy for local small-fruit growers. Investment in suitable cold storage facilities would

result in an economic breakeven point in about 4 yr. Postharvest control is an essential and key required management strategy against SWD. Even though results are extremely promising, more work has to be done in order to refine optimal postharvest treatments of fruit type and on different berry varieties. Additional evaluation is needed on the quality parameters including flavor, firmness, weight, color, and longer-term storage conditions.

Discussion

The majority of key fruit production regions around the world have experienced a continuous geographic expansion of SWD since 2008. This phenomenon is most likely due to the increased global trade of fruit crops (Haye et al. 2016). Multiple studies have been conducted with the goal of obtaining new strategies to manage this insect using an integrated approach. The relative efficacy of management options differs in terms of the level of adoption, cost, regulation, and ease of use.

Management of SWD is challenging (Fig. 6). Horticultural management tactics already in place in many production regions include drip irrigation, the incorporation of weed mat, appropriate plant canopy management, sanitation of the crop through regular harvesting, cleanup of dropped fruit, and protective netting. Many of these practices also provide horticultural benefits, resulting in widespread adoption.

D. suzukii management largely relies on repeated applications of insecticides such as carbamates, pyrethroids, organophosphates, diamides, and spinosyns (Pérez-Guerrero and Mateus 2019, Valtierra-de-Luis et al. 2019). Insecticides can effectively protect fruit, but recent studies indicate widespread resistance to spinosyns and pyrethroids in major California berry production regions (Ganjisaffar and Zalom, pers. comm.). Fortunately, insecticide resistance has not been confirmed elsewhere in North America

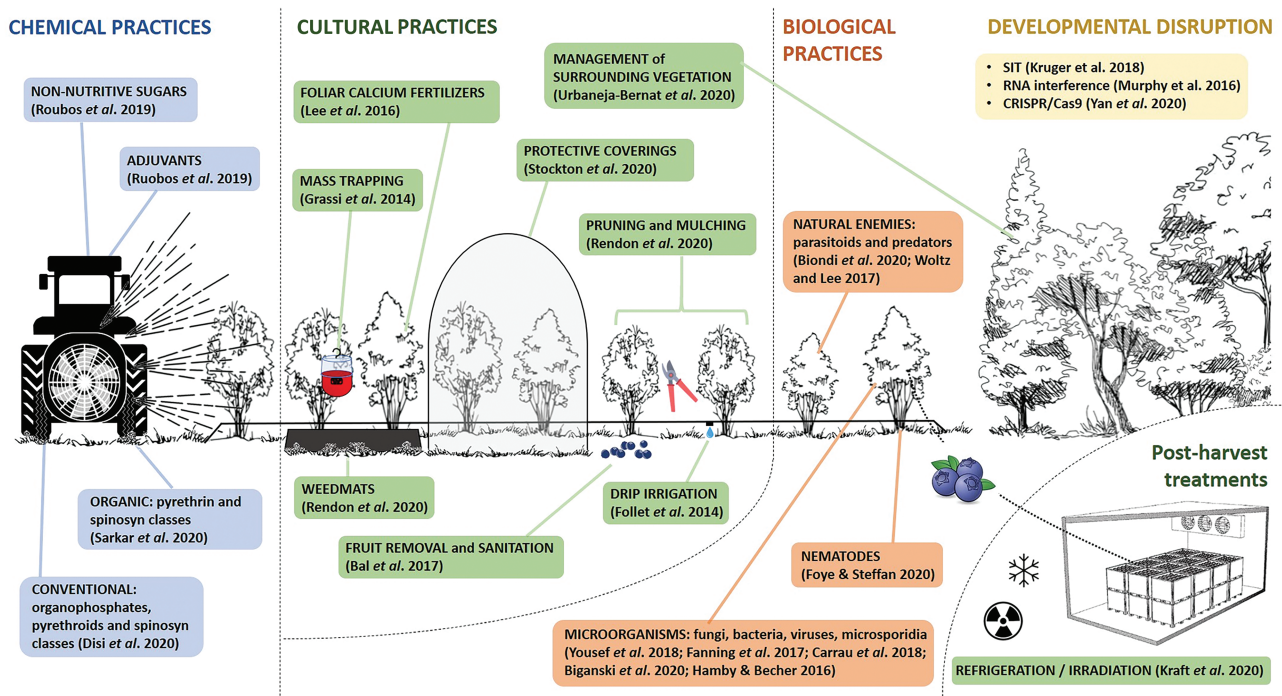


Fig. 6. *Drosophila suzukii* management is challenging with few current technologies that provide relief as a standalone option. Growers are urged to use an integrated approach from basic horticultural practices to postharvest treatments to manage this highly adaptive insect (Rossi-Stacconi).

to date. While coastal California's long berry harvest season, mild year-around weather, and extensive contiguous planted area of susceptible host crops are particularly favorable to SWD populations that generally require insecticide applications over a longer period of time than in other production regions. Growers in California and elsewhere should be cautioned to adopt management practices that maintain insecticide efficacy. Insecticide applications leave toxic residues on fruit, and can negatively impact natural enemies and pollinators (Sponsler et al. 2019). Research on alternative management technologies must therefore be focused on reduced-risk strategies, that increase impacts of natural controls including biological control agents (Biondi et al. 2012). Optimal timing and methods of insecticide applications are key to successfully manage this insect. This can be done by focusing on certain compounds that can provide control of all insect life stages, and making sure to use seasonal spray programs that rotate modes of action to minimize insecticide resistance development.

Biological control agents, including predators, parasitoids, fungi, nematodes, and bacteria are all likely to contribute to suppression of SWD populations, although their direct impacts (ability to effectively reduce the population size of SWD) have not yet been demonstrated. We believe that the inclusion of biological control in the IPM program will result in sustainable and effective SWD control. Here classical biological control, which includes active release of parasitoids may play a key future role. Advantages of biological control include self-sustaining populations and minimal financial inputs from growers. New behavioral strategies based on push-pull (Wallingford et al. 2017, 2018), attract and kill (Klick et al. 2019), and arrestants (Tait et al. 2018b) are options that warrant consideration and additional development. Innovative pest management biotechnologies or *Wolbachia*-based population suppression methods must be sufficiently developed to demonstrate their efficacy and sustainability before implementation. Tools such as risk mapping through modeling should be further developed to optimize control strategies. Cost-effectiveness analysis should be carried out to guide policy decisions. It is possible that emerging technologies will become more widely accessible to affected industries. Given the fact that SWD is firmly established as a key insect pest in all affected fruit industries, future funding towards the continued development of sustainable pest management technologies is essential. The development of such strategies however requires collaboration between both national and international specialists.

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