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Would you harm a fly?
An introduction to *Drosophila suzukii* and alternative methods for controlling this invasive pest

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Abstract
The Green Revolution has greatly changed agricultural production methods. Agriculture has become more specialized and intensive, and the use of phytopharmaceutical products, including insecticides, has intensified. However, these are harmful to the environment and human health. At the same time, globalization has led to the introduction of alien species (called invasive), whose establishment in Europe has been facilitated by the abundance of nutritive resources and the absence of natural enemies. These observations are particularly true with *Drosophila suzukii*. This fly is now considered as the main fruit pest in the world. Thus, it is becoming urgent to find alternative control methods to insecticides to counter the economic damage caused by this new pest. However, the development of an integrated pest management approach requires an excellent understanding of the biology and ecology of the species.
In this paper, we first present the state of knowledge on the life cycle, host plants and phenology of *D. suzukii*. The current geographical distribution and the history of invasion of this pest are detailed, before estimating the extent of the economic losses caused. In a second part, the known alternative control methods against *D. suzukii* are listed: cultural practices, post-harvest treatments, sterile insect releases, uses of natural enemies and behavioral manipulations (visual and olfactory). Finally, in a third part, we will see how these methods can be combined to improve the control of this pest.
Keywords: Spotted-Wing Drosophila (SWD), semiochemicals, bait, predators, parasitoids, microbial control

Résumé
Feriez-vous du mal à une mouche ? Une introduction à *D. suzukii* et aux méthodes alternatives pour contrôler cette espèce invasive. La Révolution Verte a fortement modifié les méthodes de production agricoles. L'agriculture est devenue plus spécialisée et intensive, et l'usage des produits phytopharmaceutiques, parmi lesquels les insecticides, s'est intensifié. Ceux-ci sont cependant néfastes pour l'environnement et la santé humaine. En parallèle, la mondialisation a conduit à l'introduction d'espèces exotiques envahissantes (dites invasives), dont l'établissement en Europe a été facilité par l'abondance en ressources nutritives et l'absence d'ennemis naturels. Ces constats sont particulièrement vrais avec *Drosophila suzukii*.

Cette mouche est aujourd'hui considérée comme le principal ravageur des fruits dans le monde. Ainsi, il devient urgent de trouver des méthodes de lutte alternatives aux insecticides pour contrer les dégâts économiques causés par ce nouveau ravageur. Cependant, le développement d'une approche par lutte intégrée requiert une excellente compréhension de la biologie et de l'écologie de l'espèce.
Dans ce document, nous présentons dans un premier temps l'état des connaissances sur le cycle de vie, les plantes hôtes et la phénologie de *D. suzukii*. La répartition géographique actuelle et l'historique d'invasion de ce ravageur sont détaillés, avant d'estimer l'ampleur des pertes économiques causées. Dans une seconde partie, les méthodes alternatives de lutte connues contre *D. suzukii* sont répertoriées : pratiques culturales, traitements post-récoltes, lâchés d'insectes stériles, utilisation d'ennemis naturels et manipulation comportementale (visuelle et olfactive). Finalement, dans une troisième partie, nous verrons comment ces moyens de lutte peuvent être combinés afin d'améliorer le contrôle de ce ravageur.
Mots clés : drosophile à ailes tâchées, sémiochimiques, piège, prédateurs, parasitoïdes, contrôle microbien

1. Introduction

After the Second World War, the world population growth has created the need for a marked increase in food production and food security (self-sufficiency). The Green Revolution of the 1960s met this need by doubling the production of food worldwide (Mann, 1999). This was achieved partially through the use of insecticides to protect crops from pests (Baulcombe et al., 2009; Mahmood et al., 2016). The intensification of the use of these chemical products has rapidly brought to light many problems related to human health. Pesticide residues are found in food, leading to cancers and diseases (about 3 million cases of pesticide poisoning per year) (Kim et al., 2017; Nasreddine & Parent-Massin, 2002). Pesticides also have a negative impact on the environment due to their low specificity and high dispersal ability. They decrease biodiversity by killing non-target organisms and degrading their habitats (Pisa et al., 2014; Robinson & Sutherland, 2002; Schwarzenbach et al., 2010). Moreover, the law pushes to reduce the use of insecticides (Epstein et al., 2021, 2022). Finally, beyond the adverse effects on human health and the environment, pesticide use is very costly for farmers (up to around €6.06 billion per year worldwide in total) (Alavanja et al., 2004; Mostafalou & Abdollahi, 2017).

The Green Revolution has also transformed the structure of agriculture by creating monocultures. Agriculture has become more specialized and intensive, driven by new crop breeding for higher yield, increase in mechanization and in the area of land under cultivation (Baulcombe et al., 2009). At the same time, the processes of free exchange (commercial and human) have intensified. Globalization facilitates the introduction and establishment of invasive species (Daane et al., 2018; Meyerson & Mooney, 2007; Pyšek & Richardson, 2010). These pests establish themselves in new areas, where no natural enemies are present to limit their propagation and where resources are unlimited for them due to monocultures (Altieri, 2020). Thus, the intensification of monocultures and globalization allows the emergence of pests that decrease yields (Martinet & Meiss, 2020). With a further increase in human population expected to reach about 9 billion people by 2050, current projections indicate that food production will have to double over the two coming decades (Baulcombe et al., 2009). We therefore face a three-fold challenge: how to increase production while changing our means of production, mostly by reducing chemical inputs, and controlling native and invasive pests?

This challenge is particularly true with the vinegar fly *D. suzukii*. Also called the Spotted-Wing Drosophila (SWD), this pest is now present on almost the entire globe and its expansion does not stop. It develops inside soft-skinned fruits, causing damages and therefore important economic losses (Little et al., 2017). Although many ecofriendly alternatives are being developed, insecticide (mainly spinosad) is the most common method to control this pest (Bruck et al., 2011; Van Timmeren & Isaacs, 2013). In addition to adverse effects of chemical products, SWD is physiologically and behaviorally resistant to many chemical products. Indeed, when an insecticide is used, *D. suzukii* takes refuge in wild plants and then recolonizes crops (Kenis et al., 2016; Tonina, Mori, et al., 2018). Moreover, the required dose of insecticide to manage the fly population is increasing, as demonstrated recently in California (Gress & Zalom, 2019; Van Timmeren et al., 2018). Wholesalers and retailers apply a zero-tolerance policy and reject the fruits when they detect infestation. This pushes the growers to use chemical control, taking the risk of increasing the resistance and reducing the efficacy of the few chemical products available (Asplen et al., 2015; Tait et al., 2021).

Integrated Pest Management (IPM) could optimize control of *D. suzukii* in an environmentally friendly and economical manner (Ehler, 2006). IPM includes efficient monitoring of populations, modeling their demography and distribution, preventing new introductions and the use of alternative methods to pesticides (Cini et al., 2012). Nevertheless, a good knowledge of the pest is a silver bullet for a successful IPM (Vreysen et al., 2007). Thus, we describe the biology and ecology of *D. suzukii*, its invasion and economic impacts. Then, we report the different alternative methods. Finally, we discuss how to combine these methods to work towards a global IPM.

2. Drosophila suzukii

2.1. Biology and ecology

2.1.1. Morphology and life cycle

Drosophila suzukii (Matsumara 1931) is a fly species of the Diptera order and the Drosophilidae family. It has a size of 2 to 3 mm, red eggs, yellow-brown abdomen and thorax with black streaks on the abdomen (Asplen et al., 2015; Walsh et al., 2011). Females are slightly larger than the males (Calabria et al., 2012). The first are recognized by serrated saw-like ovipositor (Hauser, 2011), while the males are differentiated from those of other species by their black spot at the end of each wing (Walsh et al., 2011). However, immature stages of SWD (egg, larvae and pupal) are indistinguishable from other *Drosophila* species (Okada, 1968).

Mating can occur on the first day of adult life and female lay its eggs in the fruit the next day (Cini et al., 2012) but mating activity strongly increases the first 3 days (Revadi et al., 2015). Females lay during all its life, which represents an average of 380 eggs per female, which is considered as a rather high fecundity (Asplen et al., 2015; Mitsui et al., 2010). Generally, SWD life cycle lasts between 13 to 18 days but is impacted by temperature, and adults live between 3 to 9 weeks (Cini et al., 2012; Weydert & Mandrin, 2013) (Figure 1). Thus, up to 15 generations per year are possible (Cini et al., 2012). Therefore, the short generation time and the high fecundity of this pest lead to exponential population growth, explaining the very high infestation pressure during fruit ripening period (Asplen et al., 2015).

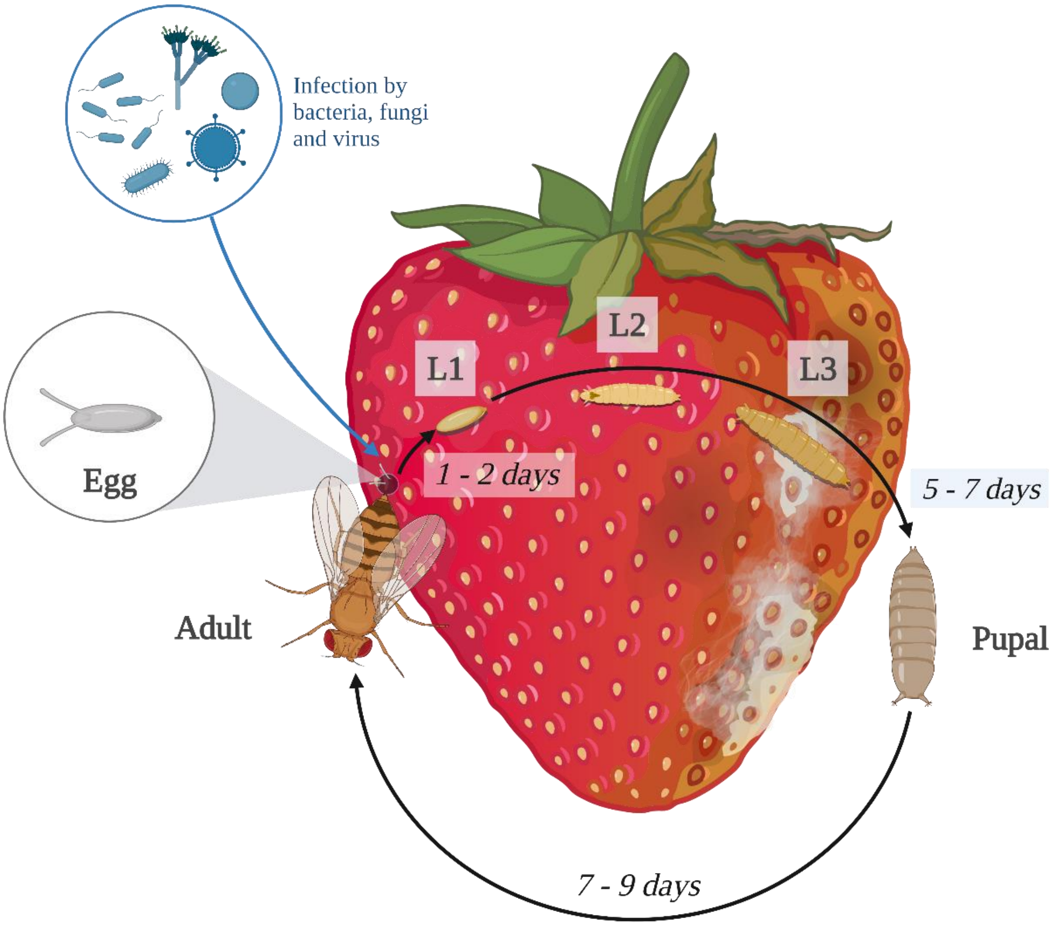

Figure 1. Life cycle of *Drosophila suzukii* with direct and indirect damages. L1, L2 and L3 correspond respectively to the larval stage 1, 2 and 3. Made with Biorender ®

2.1.2. Damages and hosts

Thanks to its ovipositor, SWD lays its eggs in ripe or ripening soft-skinned fruits (Mitsui et al., 2006; Walsh et al., 2011). This oviposition causes direct damage, via the consumption of the fruit by the larva. Oviposition also causes indirect damages: the scar left during the oviposition favors bacterial and fungal infections (Cini et al., 2012; Walsh et al., 2011) (Figure 1). In both cases, fruits rot and are unmarketable. *D. suzukii* has a wide host range of over 150 species (cultivated and wild plants) (Lee et al., 2015; Stockton et al., 2019; Thistlewood et al., 2019). Principal hosts are cultivated plants such as strawberries, raspberries and blueberries (Bellamy et al., 2013). Wild hosts are used as refuges during winter and promote dispersion (Elsensohn & Loeb, 2018). Indeed, wild berries at the margins of fields are oviposition sites for *D. suzukii*, promoting its dispersal during the ripening period. In addition, forests also contain non-cultivated hosts that provide overwintering habitat for adult *D. suzukii* (Buck et al., 2022; Rossi-Stacconi et al., 2016; Shearer et al., 2016; Stockton et al., 2019).

2.1.3. Phenology

Drosophila suzukii is considered as a species with a high thermal tolerance (hot and cold) (Asplen et al., 2015; Cini et al., 2012). Its ability to resist cold temperatures allows it to survive winter in temperate climates (Rossi-Stacconi et al., 2016; Shearer et al., 2016; Stockton et al., 2019). Indeed, adult females change their phenotype following abiotic changes of the environment which gives them a greater cold tolerance (Shearer et al., 2016; Stockton et al., 2018). However, the mechanisms related to this seasonal polyphenism are still poorly understood (Lee et al., 2011; Panel et al., 2018). Immature stages (egg and larvae) also have similar resistance abilities which allow them to survive transportation between continents via containers (Rossi-Stacconi et al., 2016; Shearer et al., 2016; Stockton et al., 2019).

Although SWD adults are mainly active from spring to fall, they represent only 10% of the fly population, which is made for 90% of immature stages (eggs, larvae, pupae) (Grassi et al., 2018; Wiman et al., 2014). SWD populations vary according to biotic and abiotic factors but are at their maximum in autumn, decline during winter and then increase again with the arrival of spring (Dos Santos et al., 2017; Little et al., 2020). Also, this pest is more active at dawn and at dusk (Hamby et al., 2013; Tait et al., 2020). *D. suzukii* has a dispersal ability linked to its physiological needs and to abiotic factors (temperature, food availability, humidity...etc.) (Tait et al., 2021). In early spring, SWD uses wild host plants to lay eggs. As the population increases, it moves from crop to crop finding refuge in wild plants (Klick et al., 2016; Leach et al., 2016; Tait et al., 2020). In summer, *D. suzukii*, thanks to its ability to disperse over long distances, colonizes crops at higher altitudes (Briem et al., 2017; Kenis et al., 2016). At the end of the summer, this pest pullulates at lower altitudes, continuing to move from crop to crop and finally finding refuge in uncultivated plants where it creates its overwintering phenotype to spend the winter (Tait et al., 2021).

2.2. Distribution and invasion

The first records of SWD are in 1916 in Japan. From the 1930s, the infestations in cherry production were found to be common (Lee et al., 2011). In 1949, its presence was confirmed in Korea and China (Tan, 1949). Although its exact country of origin is not certain, it is however clear that it is native from East and Southeast Asia (Briem et al., 2017) (Figure 2).

The presence of *D. suzukii* outside its native region was then first confirmed in the 1980s in Hawaii. In 2008, SWD was reported in California (USA), Spain (Europe) and Italy (Europe) and spread across Europe and North America in the following years (Cini et al., 2012; Hauser, 2011). In 2013, this pest was detected in South America (Andreazza et al., 2017; Deprá et al., 2014) and in 2017 in Africa (Boughdad et al., 2021; Hassani et al., 2020). Based on genetic analyses, three native populations would be at the origin of the global invasion (Fraimout et al., 2017). Recent modelling research suggests that the invasion of this pest will continue, particularly in Africa and Australia (Boughdad et al., 2021; Dos Santos et al., 2017) (Figure 2). Thus, *D. suzukii* has been able to adapt to very diverse regions and landscapes (Asplen et al., 2015).

This global and rapid spread is partly due to the biology of this pest: short development time, high fertility and wide host-range, important thermal resistance, long-distance dispersal.

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But the transport of infected fruits likely is the main driver (Lewald et al., 2021; Westphal et al., 2008).

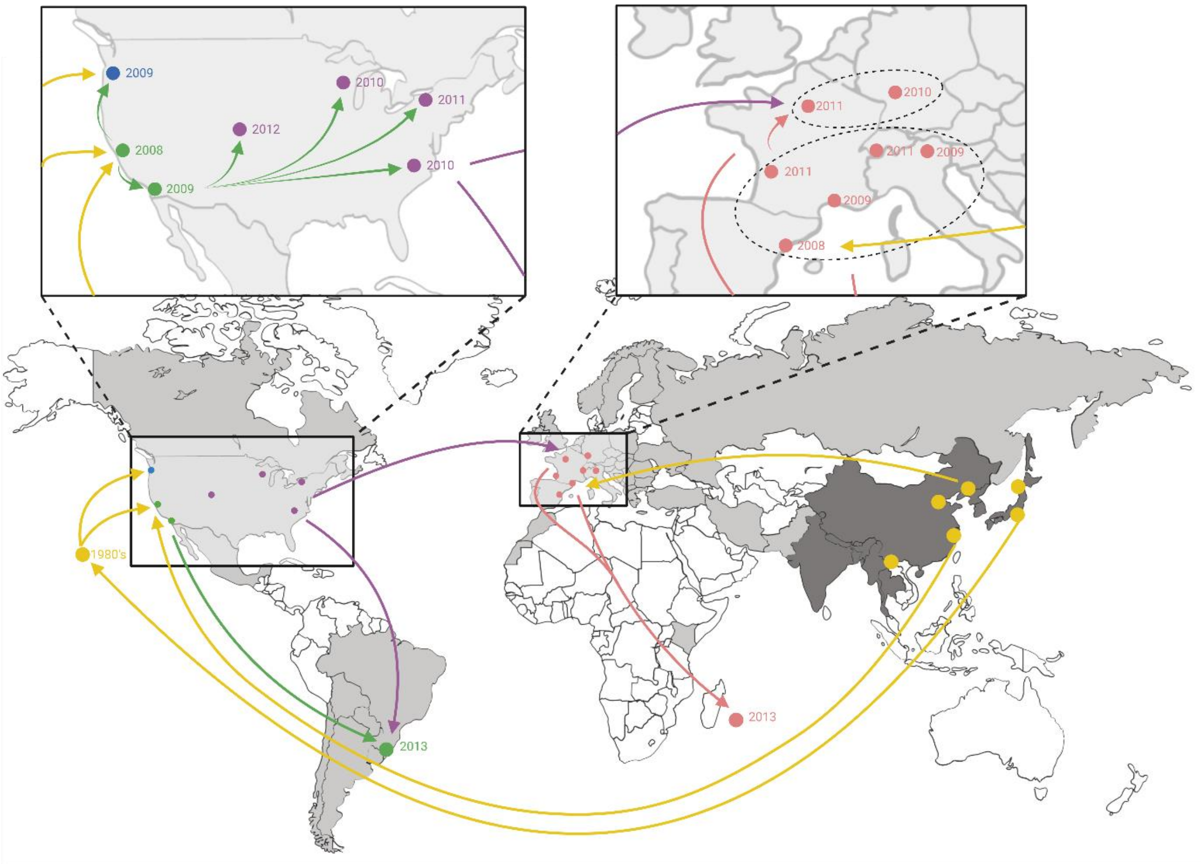

Figure 2. Worldwide invasion scenario of *D. suzukii*. The native range is in dark grey, and the invasive range is in light-grey (Lewald et al., 2021; Westphal et al., 2008). The circles represent the sampling sites followed by the date of the first year when *D. suzukii* was observed. The colors for the sample sites and arrows correspond to the different genetic groups. The arrows indicate the most probable invasion pathways (Fraimout et al., 2017). Adapted from Fraimout et al 2017 with Biorender ®

2.3. Economic impact

The economic impact of *D. suzukii* is hardly estimable. Indeed, the yield losses depend on the type of crops and regions (Tait et al., 2021). However, the main hosts are crops with high added value (strawberries and raspberries), leading to very important economic losses (De Ros et al., 2013). Only one year after its arrival in the USA, SWD's damages were estimated at 20% to 80% of yield loss in three states (California, Oregon and Washington) on five main crops (strawberries, raspberries, blueberries, blackberries and cherries), for an estimated loss of 500 million USD (Bolda et al., 2010; Goodhue et al., 2011). In 2017, raspberry yield losses were estimated at 2 to 100% in Minnesota (USA) (DiGiacomo et al., 2019). The findings are the same in Europe with damage up to 100% on strawberries, cranberries and cherries, representing 3 million € of economic losses in 2011 (Asplen et al., 2015; De Ros et al., 2013; Weydert & Mandrin, 2013). More recently, the total losses linked to *D. suzukii* have been estimated at more than 800.000 € in one year in the province of Trento (Italy) while growers used control methods (De Ros et al., 2021). These examples do not include the increase in management costs for growers. However, this parameter is essential for a good estimation, since all control methods do not have the same effectiveness and cost (De Ros et al., 2015; Farnsworth et al., 2017; Yeh et al., 2020).

3. Alternative methods against *D. suzukii*

3.1. Cultural management

The literature highlights several cultural practices that have a positive impact on *D. suzukii* control.

Humidity influences survival, fecundity and development of *D. suzukii* (Fanning et al., 2018; Kirk Green et al., 2019). Drip irrigation, in particular, reduces the relative humidity and therefore the emergence of the pest (Rendon & Walton, 2019).

Regular pruning of cultivated plants helps to modify the habitat and egg-laying sites of the pest. Indeed, the density of the leaves increases the activity of the adults and their reproduction. Thus, crops with little foliage experience reduced infestation by *D. suzukii* (Diepenbrock & Burrack, 2017; Schöneberg et al., 2021).

Managing wild hosts, especially those in the proximity of crops, is essential to control this pest (Leach et al., 2019). Several wild plants species serve as refuges for SWD and are potential sources of infestation, including seedling cherries and Himalayan blackberries (Leach et al., 2019; Tait et al., 2020).

Frequent harvesting of fruit reduces SWD infestation (Walsh et al., 2011). Moreover, destruction of overripe fruit prevents the spread of rot, bacteria or pests (Leach et al., 2016, 2018).

Crops can be protected by nets (mesh size 0.98 mm), which act as a physical barrier to limit infestation (Cini et al., 2012; Cormier et al., 2015; Leach et al., 2016). This technique has been effective on raspberry and grape crops (Ebbenga et al., 2019; Rogers et al., 2016). However, the cost of netting is high and it also hinders beneficial insects from entering the crop (Schöneberg et al., 2021).

Finally, some varieties are less attractive to the pest and can result in lower infestation. The Müller-Thurgau and Pinot Blanc grape varieties are less susceptible to *D. suzukii* attack than the Pinot Noir variety (Weißinger et al., 2019).

3.2. Postharvest control

Exposing fruits to cold (0.5, 1.1, 3.9 and 5.0 °C) for 24 to 72 hours after harvest reduces adult emergence (Kraft et al., 2020; Saeed et al., 2019).

The irradiation (with X-ray) of fruits also allows to decrease the emergence of adults. Although the X-ray doses are different according to the developmental stages (40 Gy for the first and second larval stage and 80 Gy for the pupal stage), a minimum dose of 80 Gy is recommended (Follett et al., 2014; Kim & Park, 2016). A higher dose (150 Gy), on the immature stages of SWD present in the fruits, causes sterility of the adults and thus reduces their infestation pressure (Kim & Park, 2016).

3.3. Sterile insect release

This technique consists of breeding the pest in large numbers, sterilizing it with ionizing radiation (gamma or X-rays), and releasing these sterile insects above the infested crops (Lanouette et al., 2017). The sterile insects will then mate with the non-sterile ones and produce non-viable eggs, leading to a significant decrease in the number of pests. Usually, sterilization is done on males (Knipling, 1979). This means of control is specific to the target pest, therefore respectful of the environment, and has no effect on humans. Moreover, it can be used in difficult to access areas (Dyck et al., 2005).

SWD females are completely sterile with a dose of 50 Gy (Lanouette et al., 2017) or 75 Gy while 200 Gy is required to sterilize males (Krüger et al., 2018). This dose can be decreased if the adults are infected with *Wolbachia* bacteria (Nikolouli et al., 2020). Recently, releases of sterile males suppressed the wild female SWD population by up to 91% (Homem et al., 2022). However, that did not stop the females from damaging the fruits via oviposition allowing the infection of the fruit by bacteria or fungi (Cini et al., 2012; Lanouette et al., 2017). Moreover, the physiological characteristics of the pest (high fecundity, short generation time, ability to migrate) could very quickly eliminate sterile individuals from the population (Nikolouli et al., 2018).

3.4. Natural ennemies

The use of natural enemies (macro- or micro-organisms), called biological control, allows to reduce the density of the pest population (Gurr & Wratten, 1999). Biological control can have three approaches. The first is the introduction and the establishment of natural enemies from the pest's native range (classical biological control) (Harris, 1991). Another approach, called augmentative biological control, consists of a release of native natural enemies to help them build larger populations (Van Lenteren & Bueno, 2003). Finally, conservation biological control tends to modify or preserve natural environments in order to increase the number of local natural enemies (Gurr et al., 2016).

3.4.1. Macro-organisms

3.4.1.1. Predators

The predators of SWD are very diverse: earwigs, spiders, ants, carabids, true bugs but also birds and mammals (Lee et al., 2019). Although predators can attack adults, the main cases of predation are on the immature stages (eggs, larvae, pupae) (Lee et al., 2019; Wang et al., 2020).

Pupae on the soil surface undergo a higher predation rate (80% to 100 %) than those remaining in the fruit (61% to 91%) (Ballman et al., 2017; Woltz & Lee, 2017). However, the results are highly variable ranging from 1% (Kamiyama et al., 2019) to 100 % (Ballman et al., 2017; Woltz & Lee, 2017). Larvae predation is less effective with a maximum rate of 49% in blueberry crops.

Immature stages are hidden in the fruit (except when the pupal fall to the ground), making it difficult for SWD predators to find prey (Lee et al., 2019). Moreover, the use of SWD predators, in biological control by augmentation, represents a very significant cost. However, predators (crickets, spiders, carabids, earwigs and ants) of SWD are very abundant in organic crops (Ballman et al., 2017; Lee et al., 2019; Woltz et al., 2017).

3.4.1.2. Parasitoids

A parasitoid is an insect that lays its eggs in another organism, using them as a host. The parasitoid uses the nutrients of its host to develop and emerge later. The parasitoid will systematically kill the host in which it has developed (Lee et al., 2019). SWD parasitoids can attack larvae or pupae.

The two main parasitoids of pupae are *Trichopria drosophilae* (Hymenoptera: Diapriidae) and *Pachycrepoideus vindemia* (Hymenoptera: Pteromalidae) (Rossi-Stacconi et al., 2015). However, they do not seem to be very effective (Mazzetto, Marchetti, et al., 2016; Miller et al., 2015). Indeed, although *T. drosophilae* has a preference for SWD pupae (Woltering et al., 2019), releases showed only a 34% reduction in infested fruit (Rossi-Stacconi et al., 2019). Release of *P. vindemmiae* have also shown mixed results (Hogg et al., 2022). However, both parasitoids show a potential for rapid adaptive evolution by increasing, after only 3 generations, their developmental success from 88 to 259% (Jarrett et al., 2022). Although they are the most widely used and effective, pupal parasitoids intervene after damage is already caused by *D. suzukii*.

Larval parasitoids, originating from the same region as SWD, seem to be very effective against *D. suzukii* (Giorgini et al., 2019; Girod et al., 2018; Mitsui et al., 2007). The main species are *Leptopilina japonica* (Hymenoptera: Figitidae), *Asobara japonica* (Hymenoptera: Braconidae) and *Ganapsis brasiliensis* (Hymenoptera: Figitidae) which had a parasite rate on SWD from 47.8% (Giorgini et al., 2019) to 75.1% (Girod et al., 2018). Concerning European larval parasitoids, three species were tested: *Asobara tabida* (Hymenoptera: Braconidae), *Leptopilina heterotoma* and *Leptopilina boulardi* (Hymenoptera Eucoilidae). *A. tabida* is not able to parasitize *D. suzukii* and both species of Leptopilina parasitize but without causing the death of the larva. Indeed, the immune system of the larvae allows them to fight against these parasitoids. These results suggest that host change is difficult for European specialist parasitoids (Chabert et al., 2012).

The control of SWD with parasitoids could be achieved by introducing Asian larval parasitoids (*L. japonica* and *A. japonica*) (classical biological control) but also by releasing European pupal parasitoids (*T. drosophilae* and *P. vindemmiae*) (augmentative biological control).

3.4.1.3. Competitors

A competitor will not kill the pest but will use the resources (egg-laying site or food) and thus limit the impact of the pest. *Drosophila melanogaster* and *D. suzukii* use the same egg-laying sites. Indeed, in laboratory, both species lay eggs in fruits that have already been parasitized by the other (Dancau et al., 2017; Shaw et al., 2018). Competition mechanisms are effective because *D. melanogaster* reduce the number of SWDs (Dancau et al., 2017). *Drosophila melanogaster* cannot have an impact on the marketed fruits because it lays its eggs in rotten fruits (Gao et al., 2018). However, at the end of the season, when SWD uses rotten fruits (Stemberger, 2016), *D. melanogaster* can interfere and reduce SWD populations before winter (Lee et al., 2019).

3.4.2. Micro-organisms

3.4.2.1. Virus

Five viruses are lethal for SWD with an injection in the thorax: Drosophila A virus, La Jolla virus, Drosophila C virus, Cricket paralysis virus and Flock house virus. 100% of adults die after 17 to 19 days (Carrau et al., 2018; Lee & Vilcinskas, 2017). However, lethality can be greatly reduced if the adults are in symbiosis with the *Wolbachia* bacteria. Indeed, the lethality reaches 100% without its presence and 0% when it is present with the Drosophila C virus and Flock house virus (Cattel et al., 2016). This finding compromises the search for viruses against *D. suzukii* because 17% of the adults in North America and 46% in Europe are in symbiosis with *Wolbachia* bacteria (Cattel et al., 2016; Hamm et al., 2014).

3.4.2.2. Nematodes

Many entomopathogenic nematodes (EPN), at the juvenile infectious stage, kills up to 69% of larvae (Cuthbertson & Audsley, 2016; Garriga et al., 2018; Renkema & Cuthbertson, 2018; Woltz et al., 2015). EPN are less effective on the pupae (Ibouh et al., 2019; Lee et al., 2019) because they have difficulties to penetrate pupae (Garriga et al., 2018; Hübner et al., 2017). The most effective nematode species currently is *Oscheius onirici* which kills up to 78.2% of SWD larvae (Foye et al., 2020). The dose of nematode applied may partly explain the differences of efficacy in results (Hübner et al., 2017; Woltz et al., 2015). Furthermore, nematodes need a humid environment and are therefore mainly used against soil pests. Field trials are needed to evaluate their efficacy against SWD (Labaude & Griffin, 2018).

3.4.2.3. Bacteria

The most commonly used bacteria for pest control is *Bacillus thuringiensis* (Biganski et al., 2018; Lacey et al., 2015). Five serovars are very lethal against SWD larvae, killing between 75 to 100% of the individuals. However, this bacterium cannot naturally come into contact with the larvae because it does not reach the internal part of the fruit (Biganski et al., 2020; Cahenzli et al., 2018; Cossentine et al., 2016). So far bacteria are not an option for *D. suzukii* management.

3.4.2.4. Fungi

Entomopathogenic fungi (EPF) are very effective natural pathogens against flies (Lacey et al., 2015). Six products containing EPF have a mortality rate ranging from 0% to 100% against SWD (Alnajjar et al., 2017; Cahenzli et al., 2018; Cossentine et al., 2016; Cuthbertson et al., 2014; Gargani et al., 2013; Rhodes et al., 2018; Woltz et al., 2015). These results are difficult to compare because the methods of infection vary considerably. The findings are the same with EPFs strains from universities (Alnajjar et al., 2017; Naranjo-Lázaro et al., 2014; Yousef et al., 2018). Laboratory tests must consider the reality of the field for the selection of effective EPF strains.

3.5. Behavioral manipulation

Behavioral manipulation consists in disrupting the communication (olfactory, visual and vibratory) of the pest in order to limit its damage on the crops (Foster & Harris, 1997). Currently, behavioral manipulation on *D. suzukii* focuses primarily on mass trapping. It consists of using attractive signals to attract the pest into a trap from which they cannot escape and where they die (Rodriguez-Saona et al., 2009). *D. suzukii* uses visual signals to orient itself at long distance and olfactory stimuli at short distance (Cha et al., 2012; Little et al., 2019). Although several commercial products exist for the capture of *D. suzukii*, their efficacy and selectivity are highly variable depending on the crop and the time of the season (Brilinger et al., 2021; Larson et al., 2021; Whitener et al., 2022).

3.5.1. Visual

Color and shape are strong stimuli for *D. suzukii* (Renkema et al., 2014; Rice et al., 2016). SWD has a high sensitivity for short wave colors (380 nm to 570 nm) (Little et al., 2019). Although the red and black objects are very attractive for SWD (Bolton et al., 2021; Kirkpatrick et al., 2016; Little et al., 2019), the contrast between the foreground and background colors would be more important (Kirkpatrick et al., 2016; Little et al., 2019). This is because its hosts are red fruits on dark foliage (green) (Kirkpatrick et al., 2016; Little et al., 2019).

3.5.2. Olfactive

Semiochemicals are odorant molecules that allow living beings to adapt their behavior. They are divided into several categories (Table 1).

Table 1. The different categories of semiochemicals with their effects on the emitter and receiver; + when the effect is beneficial and - when the effect is negative

Semiochemicals		Type of communication	Effect on emitter	Effect on receiver	Example
Pheromone		Intraspecific	+	+	Mate finding, alarm, aggregation
Allelochemical	*Allomone*	Interspecific	+	−	Defense
	Kairomone		−	+	Predation
	Synomone		+	+	Pollination

3.5.2.1. Attractants

Pheromones are very effective in behavioral manipulation. When they are sexual or aggregation, they allow to attract the pest. However, *D. suzukii* has lost the ability to produce the pheromone (cis-11-octadecenyl acetate) which is present in the melanogaster group (Dekker et al., 2015). However, SWD's neural system has retained the ability to perceive and react to this pheromone (Dekker et al., 2015). Thus, the search for attractive kairomone has been strongly developed (Cloonan et al., 2018).

The main attractants for *D. suzukii* are apple cider vinegar (Burrack et al., 2015; Hampton et al., 2014; Huang et al., 2017; Iglesias et al., 2014; Jaffe et al., 2018; Landolt, Adams, Davis, et al., 2012; Lasa et al., 2020; Toledo-Hernández et al., 2021; Tonina, Grassi, et al., 2018), wine and vinegar blend (Cha et al., 2014; Landolt, Adams, Davis, et al., 2012) and fermented apple juices (Feng et al., 2018). Studies have sought to simplify the latter two lures so that they are more stable over time (Table 2).

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Table 2. Main simplification of the attractive bait against *D. suzukii* and the main outcomes

Original attractant	Simplication of attractant	Outcomes	References
Wine and vinegar	Acetic acid and ethanol	Main constituent and responsible of the attractiveness	(Landolt, Adams, & Rogg, 2012; Landolt, Adams, Davis, et al., 2012)
	Acetic acid, acetoin, ethanol, and methionol	Attractiveness like wine and vinegar blend	(Cha et al., 2012, 2014)
		More attractive than apple cider vinegar	(Cha et al., 2018)
		More selective for non-target insects	(Cha et al., 2015)
	Ethanol and acetoin	As attractive as wine and vinegar	(Galland et al., 2020)
Fermented apple juice	Acetic acid, acetoin, ethyl octanoate, ethyl acetate and phenetyl alcohol	More attractant than apple cider vinegar	(Larson et al., 2020)
		More attractive than acetic acid, acetoin, ethanol, and methionol	(Larson et al., 2021)

These lure simplifications increase the attractiveness of *D. suzukii* by using volatiles produced by host plants and fruits (Abraham et al., 2015; Baena et al., 2022; Bolton et al., 2019, 2022; Dewitte et al., 2021; Keesey et al., 2015; Liu et al., 2018; Revadi, Vitagliano, et al., 2015; Urbaneja-Bernat et al., 2021), yeasts (Bueno et al., 2019; Jones et al., 2021; Lasa et al., 2019; Mori et al., 2017; Rehermann et al., 2022; Scheidler et al., 2015), acetic (Alawamleh et al., 2021; Đurović et al., 2021) and lactic bacteria (Mazzetto, Gonella, et al., 2016).

3.5.2.2. Repellent

The main repellent odors for *D. suzukii* are geosmin, 1-octen-3-ol (Wallingford et al., 2016) and essential oil of peppermint (Renkema et al., 2016). Citral, known to be a repellent against many insects, is less repellent than peppermint essential oil (Galland et al., 2020). More recently, 2-penthylfuran has been shown to be more repellent than 1-octen-3-ol (Cha et al., 2021).

4. Future directions in the control of *D. suzukii*

Research on alternative methods against *D. suzuki*i is extensive. However, very few of them combine these different methods (Figure 3).

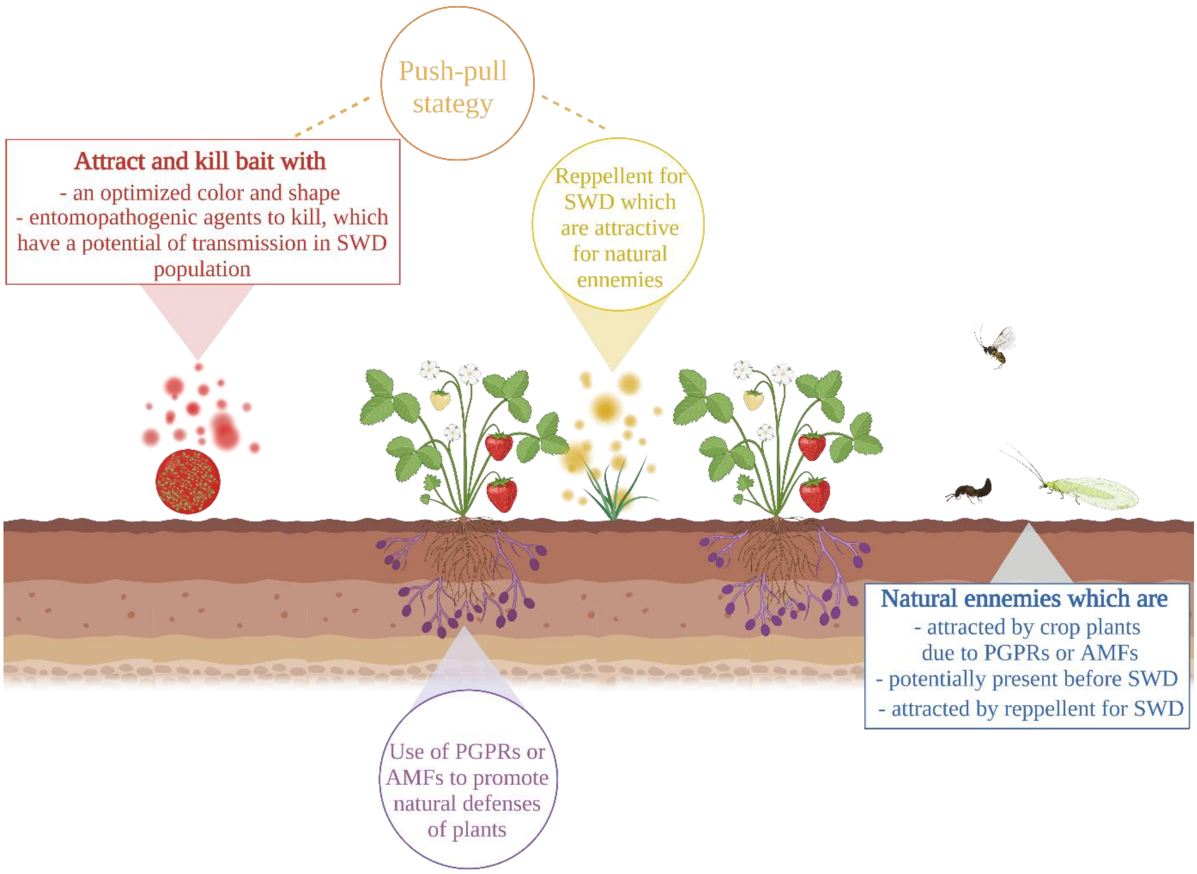

Figure 3. Diagram of future directions in the control of Spotted Wing Drosophila (SWD). Attract and kill bait (red) associated with repellent (yellow) could induced push-pull strategy (orange). Natural defenses of plant could be increased with Plant Growth-Promoting Rhizobacteria (PGPRs) or with Arbuscular Mycorrhiza Fungi (AMFs) (purple). Attraction of natural enemies could be promoted (blue). Made with Biorender®

4.1. Designing effective traps: associated olfactive and visual stimuli

Visual stimuli enhance the attractiveness of SWD for semiochemicals (Basoalto et al., 2013; Iglesias et al., 2014). Blue combined with blueberry fruit odor showed synergy in one study (Keesey et al., 2019) but decreased attraction in another (Bolton et al., 2021) (Table 3).

Table 3. Main outcomes of the study by Bolton et al, 2021. For blueberry odor, the synergies are ranked in descending order

Odors	Visual	Outcomes
β-cyclocitral	Yellow	Synergy
Yeast odor (*Saccharomyces cerevisiae*)	Red	Synergy
Blueberry odor	Black, Green, Red, Yellow, Purple	Synergy

4.2. Push and pull: associated attractants and repellents

Push-pull strategies combine repellents to push the pest out of the crop and outdoor attractants to attract it (Pyke et al., 1987). Repellents could also attract natural enemies of the pest to the crop, thereby increasing pest control (Fountain et al., 2021; Wallingford et al., 2018).

Field trials of a push-pull strategy have shown low efficacy on *D. suzukii* (Wallingford et al., 2018). However, placing the repellents at the entrance of the crops would reduce the infestation of *D. suzukii* (Galland et al., 2020). In addition, the discovery of new repellents could allow a more efficient push-pull (Cha et al., 2021; Dam et al., 2019). Future research should focus on a SWD repellent that is an attractant for natural enemies.

4.3. Attract and kill: associated attractants and pathogens

Attract and kill strategies use signals (usually semiochemicals) to attract the pest where it will encounter a toxic substance causing its death. Currently, attract and kill strategies against SWD mainly use insecticides (Babu et al., 2022; Klick et al., 2019; Rice et al., 2017). Currently, two autoinoculation devices with entomopathogenic fungi have been tested in the laboratory on SWD (Cossentine et al., 2016; Yousef et al., 2018). This research should be more important. Indeed, many pathogens, especially fungi, against SWD were discovered. Using attractants with entomopathogenic micro-organisms would reduce the use of insecticides but also be more selective than mass trapping. Indeed, generally the pathogens are specific to the pest (Cloonan et al., 2018; El-Sayed et al., 2009). Furthermore, the use of entomopathogens allows infected individuals to transmit the pathogen within the population. This would allow an even better control of the pest.

Future research against *D. suzukii* should focus on the association between attractants and entomopathogens. The latter will need to be tested on beneficial insects prior to their use in the field. In addition, the transmission capacity of the pathogen within the SWD population can be evaluated.

4.4. Recruit beneficials insects: associated SWD natural enemies and natural defense of plants

Plants naturally use Volatile Organic Compounds (VOCs) to defend themselves against pests. Natural enemies use these chemical signals to find their prey. In addition, these VOCs emitted by the plant give information on the identity, abundance and developmental stage of the pest (Heil & Karban, 2010; Peñaflor, 2019). Moreover, when a plant is infested, it emits specific VOCs: Herbivore Induced Plant Volatils (HIPVs). In addition to their ability to attract natural enemies, these HIPVs inform the undamaged organs of the plant, as well as other plants, of the presence of the aggressor. They also serve as a deterrent and cause behavioral changes in pests (Dicke & Baldwin, 2010; Gebreyesus Gebreziher, 2020; War et al., 2011). Recently, a study showed that the VOCs emitted by a blueberry infected with SWD were more attractive for a parasitoid than when the blueberry was not attacked (de la Vega et al., 2021).

The study of VOCs would allow the recruitment of natural enemies (Liu et al., 2021; Rodriguez-Saona et al., 2020) potentially before the arrival of *D. suzukii*, thus limiting its damage. In addition, natural plant defenses (including VOC emissions) could be increased via

Plant Growth-Promoting Rhizobacteria (PGPRs) and Arbuscular Mycorrhizal Fungi (AMFs). Thus, plants could better defend themselves against SWD.

5. Conclusion

Due to the important economic impacts and the rapid spread of *D. suzukii*, research concerning this pest is essential. The use of insecticides must be limited or even eliminated. Indeed, in addition to their harmful effects on the environment and human health, insecticides are less effective against SWD because this species shows resistance. Alternative methods must therefore be the priority to manage *D. suzukii*. Currently, cultural methods are already used. Considering the phenology of the insect, the management of wild hosts must be a priority. The application of these methods must be generalized.

Innovative pest management biotechnologies (sterile male release, use of *Wolbachia*) show promising results in the control of SWD. In view of the short life cycle of the pest, these methods must prove their efficiency over several generations.

Natural enemies (predators and parasitoids) contribute to the control of SWD. However, the lack of field trials means that their real impact on the pest population cannot be quantified. The integration of natural enemies into IPM could include the introduction of Asian larval parasitoids (classical biological control), the release of European pupal parasitoids (augmentative biological control) and the management of cultural practices to favor predators (conservation biological control). In other way, microorganisms could be associated with behavioral manipulation to increase their effectiveness.

The next step should be the studies of the association of these methods which unfortunately is lacking for now. These must be studied to interact in synergy to have a global and effective IMP against *D. suzukii*.

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Further information

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Conflicts of interest

The author declares no conflict of interest.

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