

A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management

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Abstract

The vinegar fly *Drosophila suzukii* (Matsumura) (Diptera Drosophilidae), spotted wing drosophila, is a highly polyphagous invasive pest endemic to South East Asia, which has recently invaded western countries. Its serrated ovipositor allows this fly to lay eggs on and damage unwounded ripening fruits, thus heavily threatening fruit production. *D. suzukii* is spreading rapidly and economic losses are severe, thus it is rapidly becoming a pest of great concern. This paper reviews the existing knowledge on the pest life history and updates its current distribution across Europe. *D. suzukii* presence has now been reported in nine European countries. Nonetheless, several knowledge gaps about this pest still exist and no efficient monitoring tools have been developed yet. This review is aimed at highlighting the possible research approach which may hopefully provide management solutions to the expanding challenge that *D. suzukii* poses to European fruit production.

Key words: spotted wing drosophila, cherry fruit fly, invasive species, berry fruit, insect control.

A new pest is threatening European fruit production

On the 2nd of December 2011 about 180 people attended the international meeting “*Drosophila suzukii*: new threat for European fruit production” in Trento. The meeting represented a unique occasion to exchange information about the spread and impact of *Drosophila suzukii* (Matsumura) (Diptera Drosophilidae), a new fruit pest which is invading Europe. Researchers, producers, representatives of local institutions and phytosanitary services from ten European countries attended the meeting, shared ideas, identified needs and tried to elaborate strategies for the near future. The fly *D. suzukii* (also known as spotted wing drosophila, SWD, in the USA) is an invasive pest endemic to South East Asia which recently invaded western countries where it is now threatening both the European and the American fruit industry, due to its egg laying and feeding on unwounded ripening fruits of many plant species.

D. suzukii has been reported so far in most of the Mediterranean countries in Europe and is rapidly spreading toward north and east. In most attacked countries *D. suzukii* caused extensive economic damage to small fruits (Goodhue *et al.*, 2011); for this reason, and because efficient monitoring and control tools are not yet available for this species, growers and producers at the Trento meeting pushed for immediate and efficient solutions. The European and Mediterranean Plant Protection Organization (EPPO) recently presented a pest risk assessment (PRA), in which it was concluded that *D. suzukii* is a threat for most parts of the EPPO region, where the pest will likely spread further, and that complete eradication is unfeasible and management difficult (information available at www.eppo.org).

Inspired by the meeting, we review the knowledge gained so far about *D. suzukii* life history traits in a European context. Extensive information can be found

in Kanzawa (1935; 1936; 1939), while more recent biological data in English are available in Walsh *et al.* (2011) and Lee *et al.* (2011b). We then provide an updated overview of its distribution across Europe. The understanding of basic biology, ecology and distribution is crucial for development of efficient management strategies. The presence of multiple gaps in the present knowledge was indeed clear in the aforementioned meeting, and only an integrated and multidisciplinary approach can face the challenge of understanding and ultimately controlling this pest. Efficient and rapid solutions will only arise from a coordinated network of diverse expertises, from molecular biology and neurophysiology to pest management techniques. The main focus of this review will thus be the possible research lines able to provide management solutions to the challenge *D. suzukii* poses to European fruit production. We draw up a draft research agenda in the hope that it will guide future research.

Where does the pest come from and where will it go?

What does *D. suzukii* look like?

D. suzukii adults are drosophilid flies (2-3 mm long) with red eyes, a pale brown or yellowish brown thorax and black stripes on the abdomen. Sexual dimorphism is evident: males display a dark spot on the leading top edge of each wing and females possess a large serrated ovipositor (Kanzawa, 1939; Walsh *et al.*, 2011). Despite these evident features, the identification of *D. suzukii* presents several challenges: adults can be easily misidentified, as it occurred for example in California, where it was initially erroneously identified as *Drosophila biarmipes* Malloch (Hauser, 2011).

The distinguishing features of the two sexes (serrated ovipositor and black wing spots) are present in other

Drosophila species, thus making species identification difficult in areas where they are sympatric. For example, *Drosophila subpulchrella* Takamori et Watabe males' black spots are very similar in shape and position to those of *D. suzukii* (Takamori *et al.*, 2006). Moreover, small or young *D. suzukii* males sometimes lack the wing spot, which becomes clearly visible circa two days after emergence (Hauser, 2011), which could lead to misidentification with other *Drosophila* males. Other characteristics may thus guide identification, such as the sex combs on the foretarsi (*D. suzukii* has one row of combs on the first and one row on the second tarsal segment) (Kikkawa and Peng, 1938; Parshad and Paika, 1965; Bock and Wheeler, 1972). Therefore, in many cases, only analyses of a full set of features, also including male genitalia (Hsu, 1949; Okada, 1954; Parshad and Paika, 1965; Bock and Wheeler, 1972), enable a reliable identification. Similar problems arise with females. On the basis of the shape and length of the ovipositor, *D. suzukii* can be easily discriminated from related species, as for example *D. biarmipes*, but not easily from other species such as *Drosophila immigrans* Sturtevant and *D. subpulchrella* (Takamori *et al.*, 2006) which possess very similar ovipositors (Hauser, 2011). In such cases, a final determination should rely on the relative size of spermatheca compared to ovipositor's size: it is thus feasible only for the trained eyes of taxonomists (Hauser, 2011). The situation is complex also for immature stages (eggs, larvae and pupae), where no reliable morphological diagnostic features have been identified (Okada, 1968). The *D. suzukii* egg has two respiratory appendages but this character is not species-specific. Therefore, DNA barcoding is the only fully reliable identification tool (Doczkal D., <http://barcodenews.net/2012/02/22/>).

A difficult tree for a fruit pest

D. suzukii belongs to the subgenus *Sophophora*, which is divided into several species groups. One of them, the *melanogaster* species group, also contains the famous "workhorse" of experimental biology and genetics, *Drosophila melanogaster* Meigen (Powell, 1997). The *melanogaster* group is further divided into species subgroups, one of which (the *suzukii* subgroup) composes, together with 6 other subgroups, the "oriental lineage" (Kopp and True, 2002; Schawaroch, 2002; van der Linde *et al.*, 2010).

However, relationships between and within these subgroups are still far from being resolved, and the *suzukii* subgroup itself is commonly regarded as polyphyletic (Kopp and True, 2002). A recent paper suggested *D. biarmipes* as the sister species of *D. suzukii* (Yang *et al.*, 2011), in accordance with previous findings (Kopp and True, 2002; Barmina and Kopp, 2007), but in contrast with Prud'homme *et al.* (2006) and van der Linde and Houle (2008), which instead supported *D. subpulchrella* as the sister species of *D. suzukii* (with *D. biarmipes* being the sister species of *D. subpulchrella* + *D. suzukii*). Conflicting results could be due to inadequate sampling of taxa and characters, as well as being due to the complex phylogenetic signal residing in different genes (Rota Stabelli, unpublished data).

D. suzukii is rapidly spreading across Europe

If phylogenetic relationships of *D. suzukii* have not been resolved yet, little is known about its geographical origin either. It was firstly described in Japan in 1916, where it was found to attack cherries, but it is still uncertain whether it is native to this area or possibly introduced around the turn of the last century (Kanzawa, 1936). The fly is also present in the eastern part of China (Peng, 1937), Taiwan (Lin *et al.*, 1977), North and South Korea (Chung, 1955; Kang and Moon, 1968), Pakistan (Amin ud Din *et al.*, 2005), Myanmar (Toda, 1991), Thailand (Okada, 1976), the Russian Far East (Sidorenko, 1992) and India (Kashmir region, Parshad and Duggal, 1965), where it was described as the *D. suzukii* subspecies *indicus* (Parshad and Paika, 1965).

D. suzukii is currently spreading in many areas, such as the USA (West and East coast), Canada, Mexico and Europe (a history of the introduction in North America is reviewed by Hauser, 2011). A key feature of its rapid spread was the initial lack of regulation over the spread of any *Drosophila*. In Europe it was first reported in autumn 2008 in Spain (Rasquera Province) (Calabria *et al.*, 2012), although a recent publication offers an update of its first findings in Europe. Malaise traps deployed in Tuscany (San Giuliano Terme, Pisa, Italy) in 2008, whose catches were examined only recently, caught *D. suzukii* adults contemporaneously with those deployed in Spain (Raspi *et al.*, 2011).

In 2009 *D. suzukii* adults were recorded in traps in other regions of Spain (Bellaterra, near Barcelona) France (Montpellier and Maritimes Alpes) and Italy (Trentino) (Grassi *et al.*, 2009; Calabria *et al.*, 2012). In Trentino, both first oviposition on wild hosts (*Vaccinium*, *Fragaria* and *Rubus* spp.) and economically important damage on several species of cultivated berries were reported (Grassi *et al.*, 2009).

By 2010-2011, the range of *D. suzukii* was further enlarged. In Italy it was reported in several other regions: Piedmont, Aosta Valley, Lombardy, Veneto, Emilia Romagna, Liguria, Marche and Campania (Franchi and Barani, 2011; Pansa *et al.*, 2011; Süss and Costanzi, 2011; Griffò *et al.*, 2012) and in France it was found from Corsica up to Île de France (Mandrin *et al.*, 2010; Weydert and Bourgoïn, 2011). Then, many other European countries made their first record: Switzerland (Baroffio and Fisher, 2011), Slovenia (Seljak, 2011), Croatia (Masten Milek *et al.*, 2011), Austria (Lethmayer, 2011), Germany (Vogt *et al.*, 2012) and Belgium (EPP0 Website).

The data presented and summarized in figure 1 reflect the current known distribution of *D. suzukii* in Europe. It appears to be spreading rapidly and all of continental Europe is at risk for invasion. We advocate an integrated, precise and area-wide monitoring network. It is worthwhile to note that the lack of reports from several areas is probably due to a lack of monitoring rather than to an actual absence of *D. suzukii*. Thus, the history of reports might reflect differences in the sampling effort and/or problems of awareness rather than the true *D. suzukii* distribution.

Considering the recent reports together with the outputs of the available degree-day phenological models

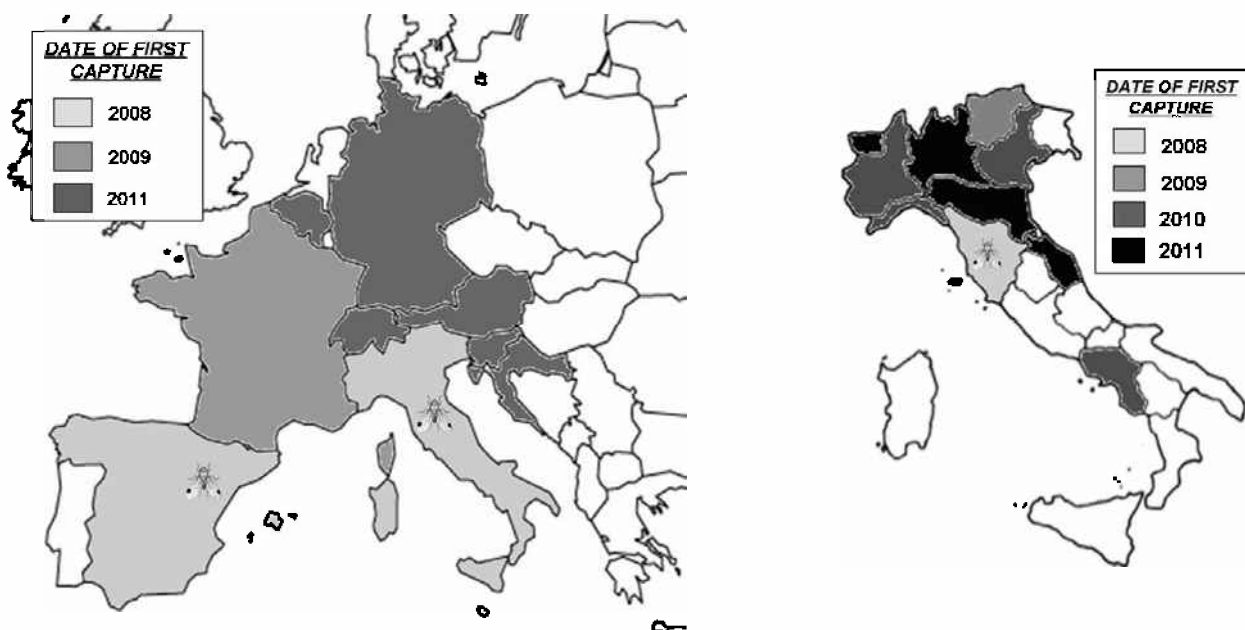


Figure 1. The escalating outbreak of *D. suzukii* in Europe. European countries and Italian regions are represented by different colours on the maps according to the year of the first finding. The fly drawings are placed in the areas of the first record.

(Damus, 2009; Coop, 2010) and analysis of *D. suzukii* host plants distribution (EPPO website), it is very likely that *D. suzukii* will spread all over Europe. Indeed, ecological simulations indicate the northern humid areas as more suitable ecosystems compared to the Mediterranean drier environments, especially because desiccation seems to be a limiting factor for drosophilids (Walsh *et al.*, 2011). If the current climate changes are taken into account, even Scandinavian countries can not be considered exempt from these risks of invasion. On a wider geographic perspective, according to *D. suzukii* biology, the global expansion in regions with climatic conditions spanning from subtropical to continental is highly likely to happen (Walsh *et al.*, 2011). Furthermore, niche shifts, as occurred for other pests (e.g. *Zaprionus indianus* Gupta, Da Mata *et al.*, 2010), should not be excluded (Calabria *et al.*, 2012), which suggests that *D. suzukii* could become a global problem for fruit production. It has yet to arrive in South America or Africa, but seems likely to reach there in the future.

Why is *D. suzukii* a threat for fruit production?

Unlike most other Drosophilidae, possibly exempting *D. subpulchrella*, *D. suzukii* is able to lay eggs in healthy, unwounded fruit thanks to the serrated female ovipositor and not only on damaged or overripe fruits (Sasaki and Sato, 1995). Hence, ripening fruits are preferred over overripe ones (Mitsui *et al.*, 2006).

Most damage caused by *D. suzukii* is due to larvae feeding on fruit flesh, however the insertion of the prominent ovipositor into the skin of the fruit can cause physical damage to the fruit, as it provides access to sec-

ondary infections of pathogens - such as filamentous fungi, yeasts and bacteria - that may cause faster deterioration and further losses. Additional costs are related to increased production costs related to pest control (monitoring and chemical input costs, increased labour and fruit selection, reduction of the fruit shelf life, storage costs) and to the decrease of foreign market appeal for production from contaminated areas (Goodhue *et al.*, 2011).

However, the oviposition habit itself is not enough to explain the dramatic impact of *D. suzukii* on production. In the next sections we show the main features making *D. suzukii* a threat of high concern for the European fruit production.

Extreme fecundity

Adults of *D. suzukii* reach maturity one or two days after emergence (during the warm season). Mating occurs from the first days of life and females start to lay eggs already from the second day from emergence. Females typically lay 1-3 eggs per fruit in up to 7-16 fruits per day; since they are able to oviposit for 10-59 days, they can lay up to a total of 600 eggs during their lifetime (around 400 eggs on average). Eggs hatch within 2 to 72 hours after being laid inside fruits, and larvae mature (inside the fruit) in 3 to 13 days. Pupae reside inside or, less frequently, outside the fruit, for 3 to 15 days. Depending on the temperature, a minimum of 8 days is required from oviposition to adult emergence. This very short generation time implies that *D. suzukii* can complete several generations in a single cropping cycle and up to 7 to 15 generations in a year, according to the specific climatic conditions, thus allowing an explosive population growth (life-cycle details can be found in Kanzawa, 1939; Mitsui *et al.*, 2006; Walsh *et al.*, 2011).

Tolerance of a wide range of climatic conditions

The ability to survive and reproduce in a wide range of climatic conditions is obviously a relevant factor for insects. Limiting temperatures for *D. suzukii* reproduction are between 10 and 32 °C for oviposition and up to 30 °C for male fertility (Sakai *et al.*, 2005). The peak of activity and development is around 20 to 25 °C (Kanzawa, 1939). *D. suzukii* can thus be considered a species with high thermal tolerance, being both heat tolerant (viable *D. suzukii* populations resist to the hot summers in Spain) and cold tolerant (*D. suzukii* is present in cold areas, such as mountain regions in Japan and Alpine areas).

Adults are particularly tolerant to cold compared to other drosophilids (Kimura, 1988) and mated females in reproductive diapause are considered to be the overwintering stage of *D. suzukii* (Kanzawa, 1939; Mitsui *et al.*, 2010; Walsh *et al.*, 2011). Whether this tolerance is physiological or mediated by behavioural adaptation is still unclear and several authors suggest that *D. suzukii* survival under harsh conditions might be increased by altitudinal migration (Mitsui *et al.*, 2010), acclimatization (Walsh *et al.*, 2011) and/or overwintering in man-made habitats or other sheltered sites (Kimura, 2004).

Wide host range

D. suzukii is able to develop on a very wide range of both cultivated and wild soft-skinned fruits with many host plants in the native and in the invaded areas, with berries being the preferred hosts. The following list of *D. suzukii* host plants grouped based on botanical family should be still considered tentative, since some information is not well documented: Rosaceae - *Fragaria ananassa* (strawberry), *Rubus idaeus* (raspberry), *Rubus fruticosus*, *Rubus laciniatus*, *Rubus armeniacus* and other *Rubus* species and hybrids of the blackberry group, *Rubus ursinus* (marionberry), *Prunus avium* (sweet cherry), *Prunus armeniaca* (apricot), *Prunus persica* (peach), *Prunus domestica* (plum), *Eriobotrya japonica* (loquat); Ericaceae - *Vaccinium* species and hybrids of the blueberry group; Grossulariaceae - *Ribes* species including the cultivated currants; Moraceae - *Ficus carica* (fig), *Morus* spp. (mulberry); Rhamnaceae - *Rhamnus alpina* ssp. *fallax*, *Rhamnus frangula* (buckthorn); Cornaceae - *Cornus* spp. (dogwood); Actinidiaceae - *Actinidia arguta* (hardy kiwi); Ebenaceae - *Diospyros kaki* (persimmon); Myrtaceae - *Eugenia uniflora* (Surinam cherry); Rutaceae - *Murraya paniculata* (orange jasmine); Myricaceae - *Myrica rubra* (Chinese bayberry); Caprifoliaceae - *Lonicera* spp. (honeysuckle); Elaeagnaceae - *Elaeagnus* spp.; Adoxaceae - *Sambucus nigra* (black elder); Vitaceae - *Vitis vinifera*, *Vitis labrusca* (Kanzawa, 1939; Grassi *et al.*, 2011; Lee *et al.*, 2011b; Seljak, 2011; Walsh *et al.*, 2011). However, current data suggest that host preference is heavily dependent upon the local abundance of hosts.

The *V. vinifera* case is still matter of verification. Despite laboratory experiments that showed a significantly lower oviposition susceptibility and developmental rate of *D. suzukii* on grapes than on berries and cherry (Lee *et al.*, 2011a), recent observations in vineyards in Northern Italy would indicate that *V. vinifera* can be-

come a field host (with soft skinned varieties being more impacted) (Griffo *et al.*, 2012).

The host-choice flexibility of *D. suzukii* is also demonstrated by the ability to develop also on tomato under laboratory conditions (not recorded so far as a host in the field, even if *D. suzukii* adults have been trapped in tomato crops in France (EPPO website).

The wide host range represents a pest management constraint not only because *D. suzukii* can cause damage to many species, but also because populations can survive almost everywhere, alternating hosts with different ripening times through the year, both cultivated and wild. Indeed, crop plants, usually cultivated in high density monoculture, allow rapid and impressive population growth, while wild hosts and ornamental plants may serve as refuges from management treatments, and provide later re-infestation sources and overwintering habitats (Klick *et al.*, 2012).

The wide host range and the ability to damage thick ripening fruits, gives to *D. suzukii* a wide but at the same time specialized ecological niche. However, overlapping niches and possible competition with other drosophilids needs to be investigated.

High dispersal potential

D. suzukii has a high dispersal potential (Hauser, 2011; Calabria *et al.*, 2012), which would seem to be confirmed by its rapid spread in invaded countries and its presence on several continents, as well as remote islands (i.e. Hawaii; Kaneshiro, 1983;). Passive diffusion due to global trade is likely the main cause of the spread of *D. suzukii*, as for many other invasive species (Westphal *et al.*, 2008). The apparently intact and healthy status (before larval activity) of the fruits infested with *D. suzukii* is likely to compound the problem, as it increases the risk that infestation will remain undetected and thus the risk of passive dissemination of *D. suzukii* (Calabria *et al.*, 2012).

A research agenda for integrated pest management

Estimating the costs associated with *D. suzukii* impact is a complex task, with several factors (direct and indirect costs) that must be taken into account, their interdependency and the dynamic nature of the system (Goodhue *et al.*, 2011; Walsh *et al.*, 2011). Preliminary studies in the USA indicate an annual loss of more than 500 million dollars in five affected crops (strawberries, blueberries, raspberries, blackberries and cherries) in three states (California, Oregon and Washington) (Bolda *et al.*, 2010). Because of regional monoculture, economical losses might be even larger in proportion at a local scale. A preliminary study estimated that Trento province (Northern Italy), the area devoted to small fruit cultivation (about 400 hectares) faced a loss around 500,000 € in 2010 and 3 million € in 2011 (Ioriatti *et al.*, 2011).

While fast answers to *D. suzukii* could be provided by changes in the pesticide regulations and by sanitation procedures, these management techniques will only

have short-term application and effects. Solutions that are effective and sustainable over the long term are hard to find in the absence of detailed knowledge of the pest species life history, as well as of its biological attributes and population dynamics. Research on fundamental aspects is thus a key step enabling future management solutions.

Below we propose a research agenda, which identifies the main relevant topics we consider to be fundamental. The research agenda is based on a paradigm we called the “3M framework”, which stands for Monitoring, Modelling and Managing. These steps should be tightly interconnected to each other in order to properly face a pest invasion challenge; however, for clarity, we will treat them separately in this review.

Monitoring

A reliable monitoring of the pest presence is the first step for a successful integrated pest management (IPM). So far, the monitoring of *D. suzukii* has been based on trapping methods available for other pests and for Drosophilidae in general, i.e. fermentation baits and vinegar, with the main baits being represented by one or a mix of the following substances: ripe bananas, strawberry puree, cherry juice, citronella oil, geranium oil, apple cider, vinegar, cherry wine, sugar and yeast mixtures (Wu *et al.*, 2007; Walsh *et al.*, 2011). A recent study showed a high level of attraction to a combination of vinegar and wine, possibly due to a synergistic effect of acetic acid, ethanol and other vinegar/wine volatiles (Landolt *et al.*, 2012).

While *D. melanogaster* and other drosophilids can complete all life stages on the same fermenting materials, gravid *D. suzukii* females need to find undamaged ripening fruits for oviposition. It is therefore likely that the odour produced by fermenting fruits represents a generic food cue to *D. suzukii*, whereas egg-laying females target volatiles from fresh fruits specifically. Unfortunately, the knowledge of the sensory and chemical ecology of *D. suzukii* in relation to feeding, mating and oviposition is still extremely poor. In particular, the identification of the most behaviourally-active volatiles emitted by fruits host of *D. suzukii* might allow the development of more selective and powerful attractant lures that could be released at controlled rates from dispensers. Knowledge of kairomones for *D. suzukii* will also form the basis of environmentally friendly strategies, such as mass trapping and attract and kill, which showed promising results in initial studies (Kanzawa, 1934; Wu *et al.*, 2007).

The trapping performance is also highly influenced by the trap's colour, shape and structure. Red and black have been shown to be the most attractive colours, hence coloured traps would be recommended (Mitsui *et al.*, 2006; Edwards *et al.*, 2012). The most currently used traps are plastic bottles or cups with multiple small lateral holes (diameter between 5-10 mm) containing the liquid bait. The addition of a small drop of surfactant or the placement of sticky cards inside the trap increases trapping efficiency by preventing the escape of flies (Walsh *et al.*, 2011). Even though some trapping protocols already exist (e.g. Dreves *et al.*, 2009), a

really highly performing and species-specific trap has not been developed yet (Walsh *et al.*, 2011). Further research on baits, trap design and trapping protocols is thus needed.

In addition to optimizing bait (with single or multiple components), trap shape, and colour, it is also important to study the effects of trap placement both in terms of space and time. Traps are currently either placed on the ground or hung on plants near fruits, and preliminary evidence indicates that traps perform best when placed in cool and shaded areas (Walsh *et al.*, 2011). Future research should investigate the importance of spatial variables, both on the microscale (e.g. height, on plants or on the ground) and on the mesoscale (e.g. inside crop areas or along the borders), as well as the importance of the timing of trapping. Here, e.g., mass trapping could be more effective at the onset of the season than later on, when the population has already reached high densities.

Modelling

Understanding ecological factors influencing feeding, survival, and reproduction is crucial in order to understand and forecast the current and future distribution and population dynamics of *D. suzukii*. Attention should be paid to both the spatial (distribution at large and small scales) and temporal scale (seasonal variation in abundance). Coupling high resolution techniques (such as georeferencing) with basic biological knowledge (e.g. life cycle, life history traits) will allow the prediction of the fine scale distribution, pest pressure maps and degree day models, allowing reliable estimates of *D. suzukii* impact and economic losses. This will improve the choices in sanitation, management and socio-economical procedures, and, as a consequence, improve the effectiveness of pest management decisions.

A landscape ecology approach would also be crucial to understand the movement of *D. suzukii* across the landscape, highlighting possible refuge areas as well as potential sources of re-infestation (Ohrn and Dreves, 2012). Modelling should also tackle the timing of *D. suzukii* population growth, starting from the first seasonal re-infestations to forecast the seasonal dynamics. This could help in understanding when to set the trap and deliver the chemical treatments. Degree-day models are currently being developed (Damus, 2009; Coop, 2010), but future research will result in more precise and specific models.

The interactions between *D. suzukii* and the several host plants should be taken carefully into account. This step could be facilitated by the availability of phenological models for many host species. However it may also be hindered by the great number of *D. suzukii* hosts. It is thus imperative to deepen our understanding of *D. suzukii*-host plant interactions and dynamics. Therefore, research should investigate host preference and the factors affecting *D. suzukii* choice of oviposition and feeding sites, such as local abundance, population history or prior experience. Interesting insights in this regard could be gathered through the study of *D. suzukii* biology in its native range, where such phytophagous-plant interactions evolved. Initial laboratory experi-

ments indicate that, while *D. suzukii* could show preferences toward certain host plants in nature, it could also show differences in the breeding success and thus in the level of impact on different hosts (Lee *et al.*, 2011a). The mechanisms of host reactions and differences in their susceptibility (among species, among varieties and across landscape and times) will thus be worth of investigating. The integration of crop phenology, pest life cycle and host-pest interactions will allow the prediction of spread and impact.

Managing

Preventing new introduction and re-infestation

D. suzukii is spreading across Europe and eradication and containment do not seem feasible (EPPO website). However, in order to keep *D. suzukii* populations at a manageable level, it is critical to avoid recurrent introductions and re-infestations.

From this perspective, it is crucial to understand where the pest comes from, by which vectors it has been and is still being introduced, and determine the most likely sources of re-introduction in a certain region and re-infestation of a specific crop area. International trade is considered a key factor increasing the likelihood of biological invasion (Westphal *et al.*, 2008) and undetected infested fruits are believed to be the most likely pathway of colonization for *D. suzukii* (EPPO website). Through population genetics it would be possible to disclose *D. suzukii* colonization patterns and dynamics (e.g. Fernandez Iriarte *et al.*, 2009 for a related species) and to trace the routes of invasion, which could allow prevention of recurrent introductions. Based on preliminary genetic results and on the similarities between the dates of introduction, Calabria *et al.* (2012) suggested that the *D. suzukii* invasions in North America and in Europe could be related.

Removing any possible source of *D. suzukii* either outside (wild hosts, sites in neighbouring grower fields and ornamental plants in backyard gardens) or inside the orchard (fruit production waste) is crucial in order to prevent re-infestations on local scale, and thus represents a key step in IPM (Walsh *et al.*, 2011). Any fruit that remains in the crop can be a food source or a breeding site for *D. suzukii*, thus acting as a potential re-infestation source. However, once removed, fruits must be destroyed. Several widely used techniques, e.g. composting could in fact worsen the problem, since the fruits and the larvae are not rapidly destroyed, but rather are able to develop rapidly in the warm environment produced by decomposition processes. Several options for effective disposal of potentially contaminated fruit material have been proposed, e.g. solarization, insecticide treatment, disposal in closed containers, crushing, cold treatment, bagging and burial (Walsh *et al.*, 2011; EPPO website). These sanitation procedures should be widely applied in the affected areas, in order to avoid the persistence of neglected re-infestation sources. Therefore, many local entities officially imposed sanitation measures to growers. Research is underway for the evaluation of other management methods based on physical barriers. As an example, in Japan it was dem-

onstrated that covering plants with netting (0.98 mm mesh size) fully prevented the *D. suzukii* infestations (Kawase *et al.*, 2007).

Chemical control

Current control efforts for *D. suzukii* rely heavily on the use of insecticides. Unfortunately, the insecticides which are currently available to growers for control of *D. suzukii* are not very effective, since the use of highly efficient broad spectrum chemicals is being progressively restricted. In particular, organic production is seriously threatened because only few natural insecticides are admitted and their efficacy against *D. suzukii* is either not known or lower than the conventional insecticides (Walsh *et al.*, 2011). Furthermore, the fast generation turnover requires many chemical interventions at the ripening stage, which can increase the risk of residues in fruits, promote insect resistance and negatively affect pollinators and other beneficial species.

However, due to the lack of specific insecticides against *D. suzukii* larvae within fruits, research has been focused on treatments based on chemicals targeting adults. Kanzawa (1939) found that camphor oil was the most effective of the treatments he employed, followed by nicotine sulphate, kerosene emulsion, and neoton but no treatment totally prevented oviposition and most of these materials are no longer used or acceptable. Recent laboratory and field studies both in the USA and in EU revealed that among the registered insecticides organophosphates, timely applications of pyrethrins and spinosyns can provide good contact activity and residual impact for up to 12-14 days (Beers *et al.*, 2011; Bruck *et al.*, 2011; Profaizer *et al.*, 2012). In contrast, the efficacy of the neonicotinoids as adulticides was not satisfactory (Bruck *et al.*, 2011).

Initial trials in the Trentino Province indicated that only lambda-cyhalothrin provided an adequate level of control. However, at high population densities repeated applications by alternating pyrethrins and spinosad in strawberry plantations only reduced the damage immediately after the treatment and had negligible impact at the end of the harvest time (Grassi *et al.*, 2012). Therefore, future research needs to address not only identification of effective chemicals, but must also consider how protocols for delivery of chemicals can be optimized. In addition, growers should undertake a pesticide rotation, in order to avoid or at least delay the evolution of insecticide resistance, which can be easy in *Drosophila* species (even associated with a single resistance allele, see Ffrench-Constant and Roush, 1991) also thanks to the numerous generations per year.

Control strategies based on interferences with communication

Among the environmentally safe strategies those based on the interferences with the insect communication, both intra- and inter-specific, are often the most effective and enduring ones (i.e. mating disruption, attract and kill, mass trapping). These approaches act either by reducing the population survival (attract and kill, mass trapping) and/or by interfering with its reproduction (mating disruption).

Although more research is needed to decipher the sexual communication of *D. suzukii*, advantage could be taken from the vast knowledge on the model organism *D. melanogaster*. *Drosophila* species use aggregation pheromones which often act in synergism with food odours (Bartelt *et al.*, 1985). It might be speculated that *D. suzukii* releases also cuticular hydrocarbons which act as sex pheromones for a short range attraction (Antony and Jallon, 1982).

In addition, both visual cues and air-borne sounds emitted by wing vibrations have been demonstrated to play a role in the short-range courtship of *D. suzukii* (Ewing, 1978; Fuyama, 1979). Similarly to *D. melanogaster*, sex peptides produced in the *D. suzukii* male accessory glands and transferred into the female during copulation were shown to suppress the female receptivity and to stimulate oviposition (Ohashi *et al.*, 1991; Schmidt *et al.*, 1993).

Whether the *D. suzukii* mating and oviposition behaviour is susceptible to be disrupted with affordable and effective methods based on synthetic pheromones, on mechanical signals (i.e. vibrational mating disruption; Eriksson *et al.*, 2012), or by combinations of them is still matter of conjecture, but is a promising area for future research.

Biological control

There are multiple biocontrol agents (fungi, bacteria, viruses and other natural enemies of the pest, such as predators and parasitoids) that could be employed in IPM for *D. suzukii*.

Biocontrol activity of microorganisms:

Recently, DNA viruses have been isolated also in *Drosophila* species (Unkless, 2011) and were found to be related to other viruses used for pest control. These findings open the way for the evaluation of control of *D. suzukii* based on viral pathogens and research is urgently needed on this subject.

Parasitoids:

Research on arthropods as biocontrol agents is also urgently needed, although a control approach based on arthropod natural enemies would probably be very difficult for a high-reproduction species like *D. suzukii*. Nevertheless, several valuable studies on this topic have been performed in Japan, in the native range of the species. Potentially, results from these studies could help identify novel management strategies based on introduction and permanent establishment of natural enemies of *D. suzukii* from its native range for a long-term control.

Early experiments tested the efficacy of *Phaenopria* spp. (Hymenoptera Diapriidae) under laboratory conditions, however, results were unsatisfactory (Kanzawa, 1939). More recent studies have explored the occurrence and biology of several *D. suzukii* parasitoids in Japan (Ideo *et al.*, 2008; Mitsui *et al.*, 2007; Kimura unpublished data). Species of the genus *Ganaspis* (Hymenoptera Figitidae) showed the highest rates of *D. suzukii* parasitism (ranging from about 2 to 7%). These species lay eggs in larvae that are feeding in fruits and exhibits a high level of specificity for *D. suzukii*. On the

other hand, *Leptopilina japonica* Novkovic et Kimura (Hymenoptera Figitidae) and *Asobara japonica* Belokobylskij (Hymenoptera Braconidae) were able to attack larvae and pupae only in fallen decaying fruits and attacked a wide range of drosophilid hosts (Mitsui and Kimura, 2010; Kimura unpublished data).

However, it has been recently demonstrated that increased constitutive hemocyte levels involved in encapsulation of parasitoid eggs enable *D. suzukii* larvae to produce a more vigorous immune response and resistance than *D. melanogaster* to their generalist parasitic wasps (Kacsoh and Schlenke, 2012).

Nevertheless, another approach for the biological control of *D. suzukii* would be to enhance the effect of beneficial organisms already present in the newly invaded areas, generalist and widespread species having *D. suzukii* in their host range or, otherwise, species able to adapt their selection strategies to the invader. Indeed, *Pachycrepoides vindemmiae* (Rondani) (Hymenoptera Pteromalidae), a generalist pupal parasitoid considered for a long time as a major natural enemy of *D. melanogaster* (Martelli, 1910), was recently found to be also associated with *D. suzukii* in USA (Brown *et al.*, 2011).

Two promising candidates are also *Asobara tabida* Nees and its sibling species *Asobara rufescens* Foerster (Hymenoptera Braconidae), which are the most common parasitoids of frugivorous drosophilids in Europe (Vet *et al.*, 1984) and shown able to develop on *D. suzukii* in the field in Japan (Mitsui *et al.*, 2007). Likewise and in accordance with observations in Japan, generalist species of the genus *Trichopria* (Hymenoptera Diapriidae) distributed in US and EU are likely to accept *D. suzukii* as an additional host (Kimura, personal communication). Furthermore, the impact on *D. suzukii* population of generalist predators, such as several *Orius* (Rhynchota Anthocoridae) species, is under evaluation in different laboratories.

Exploiting pest-endosymbionts associations:

A promising, but sometimes neglected method of reducing pest populations is the exploitation of the intimate association of the pest species with endosymbionts (Zindel *et al.*, 2011). Arthropods are frequently infected with one or more micro-organisms which can have beneficial, neutral or detrimental effects on their hosts. These interactions may directly or indirectly influence the population dynamics of many pest species and could thus potentially be of great interest for agricultural pest management (Zindel *et al.*, 2011).

For example, the obligate intracellular bacteria of the genus *Wolbachia* are estimated to infect more than half of the living insect species, whose reproduction they are able to manipulate by provoking several phenotypic effects (cytoplasmic incompatibility, induction of parthenogenesis, male killing and feminization) (Werren *et al.*, 2008; Zindel *et al.*, 2011).

Cytoplasmic incompatibility (CI) is the most common reproductive effect induced by *Wolbachia* in their hosts. CI prevents infected males from successfully mating with females with different *Wolbachia* infection status (non-infected or infected with different and incompatible strains) (Werren *et al.*, 2008). Thus, CI could be used to

suppress insect pest populations in a manner analogous to the sterile insect technique (SIT) by releasing males carrying CI-inducing endosymbionts (see Zabalou *et al.*, 2004). *Wolbachia* inducing CI have been widely discovered in several Drosophilidae (reviewed in Werren *et al.*, 2008) and preliminary results suggest that also *D. suzukii* is infected with *Wolbachia* (Siozios unpublished data). However, *Wolbachia* has complex phenotypic effects on its hosts, depending on strain, host genotype and interactions between them. In addition to CI, *Wolbachia* infection could have significant survival and fecundity effects in drosophilids (Fry *et al.*, 2004). It has recently been discovered that *Wolbachia* infection enhances fertility in *Drosophila mauritiana* Tsacas et David, with an average four-fold increase in the egg laying rate of infected flies, compared to uninfected individuals (Fast *et al.*, 2011). Future research should address the extremely high fecundity found in *D. suzukii*, in order to assess whether it is linked in a similar way to *Wolbachia* infections. Finally, due to the rapid spread of *Wolbachia* in insect population, these bacteria have also been suggested as vectors for desirable genetic modification that could be used in control efforts (Sinkins and Gould, 2006).

The control potential of *Wolbachia* is also related to the natural enemies of the pest species. Indeed, *Wolbachia* was shown to induce parthenogenesis in several hymenoptera parasitoids (Werren *et al.*, 2008), thus suggesting potential advantages in their rearing, releasing and efficacy. In addition, a fertility-enhancing effect similar to that found in *D. mauritiana*, has been revealed in the *D. suzukii* parasitoid *A. tabida* (Dedeine *et al.*, 2001).

On the other hand, *Spiroplasma* bacteria can rescue the sterilization effect induced by a nematode on *Drosophila neotestacea* Grimaldi, James et Jaenike (Jaenicke *et al.*, 2010), while *Wolbachia* infections in *D. melanogaster* flies reduce the impact of the fungal pathogen *Beauveria bassiana* (Panteleev *et al.*, 2007) and of viruses (Werren *et al.*, 2008). These three examples are of particular interests, since nematodes, fungal pathogens and viruses are three widely used options for biocontrol of pest insects and candidate biocontrol agents for *D. suzukii*.

Other IPM strategies

Reducing pest population is also possible by inundative releases of sterile insects. The development of the SIT represents a major breakthrough in pest management science (Vreysen *et al.*, 2006). Indeed, SIT has several advantages compared to other control strategies, e.g. being safe to non-target organisms and acting with an inverse density-dependent mechanism; in addition, SIT could be integrated with other control strategies (Vreysen *et al.*, 2006). Therefore, the feasibility, procedures and possible drawbacks of SIT applied to *D. suzukii* management, with male sterility either induced by irradiation or based on transgenic insect strains, should be investigated, to promote successful use of SIT in the management of several pest species (Dyck *et al.*, 2005). This would include a requirement for mass rearing of high quality and competitive insects. The short generation time and large field populations would present a challenge for control by SIT.

D. suzukii as a vector of plant pathogens

An important topic to address is whether *D. suzukii* could act as a vector of plant pathogens, thus provoking additional damages to the attacked species. Indeed, *Drosophila* flies have long been recognised as microorganism disseminators and the role of fungal disease vectoring has been demonstrated for *D. melanogaster*, which carries (both on its cuticle and inside its digestive tract) the fungus *Botrytis cinerea* (Louis *et al.*, 1996). While *D. melanogaster* only attacks overripe/rotten fruits, thus limiting the damage caused by *B. cinerea*, *D. suzukii* targets intact fruits, making it possible for the fungus to penetrate inside. Research should thus investigate the potential of *D. suzukii* as a carrier of other microbial diseases.

Indeed, a possible link between the *D. suzukii* spread and the expansion of two host plants diseases (*Monilinia* brown rots and *Botrytis* rots) in Slovenia has been suggested (Seljak, personal communication). Interestingly, also the occurrence of interactions between specific yeast species associated with *D. suzukii* and the yeast profile of the host fruits has recently been proposed, which paves the way for another intriguing field of research on this pest (Hamby *et al.*, 2011).

Taking advantage from a close relative: the model system *D. melanogaster*

This review highlighted that knowledge about *D. suzukii* is still limited but great advantage could be taken from the vast experience on the related excellent model organism, *D. melanogaster*. Their close relationship offers also fascinating opportunities for addressing some longstanding questions in the field of insect biology with a practical outcome.

For instance, comparative research in *D. melanogaster* will accelerate progress in improving the effectiveness of insecticides. In addition, comparisons with *D. melanogaster* could shed light on the evolution of ecological innovations (as shown in other *drosophila* flies, Dekker *et al.*, 2006) and help researchers in understanding what makes a species invasive.

By harnessing the biology workhorse *D. melanogaster*, as well as the high priority pest *D. suzukii*, the *Drosophila* genus will probably become a model also for agricultural and crop protection studies.

Conclusions

The rapid spread of the invasive fruit pest *D. suzukii* poses a challenge to fruit production in Western countries. The biology of *D. suzukii* suggests that an effective control effort requires an area wide IPM program. In order to accomplish this, research needs to address *D. suzukii* basic biology, the development of management tools, the transfer of knowledge and technology to users and, finally, the implementation of the IPM program also at a cultural and societal level (Lee *et al.*, 2011b; Dreves, 2011). While short term solutions to limit the current dramatic damage are strongly needed, only long-term and environmentally friendly manage-

ment approaches will allow a sustainable control of this pest. To this aim, research should be carried out to shed light on many knowledge gaps that are still present. The future will surely see a great increase in the knowledge of *D. suzukii* biology, impact and management.

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