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WORLDWIDE INVASION BY *DROSOPHILA SUZUKII*: DOES BEING THE "COUSIN" OF A MODEL ORGANISM REALLY HELP SETTING UP BIOLOGICAL CONTROL? HOPES, DISENCHANTMENTS AND NEW PERSPECTIVES

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RÉSUMÉ.— *L'invasion mondiale de* Drosophila suzukii *: être une espèce « cousine » d'un organisme-modèle aide-t-il réellement à établir un contrôle biologique ? Espoirs, désillusions et nouvelles perspectives*.— L'invasion récente et rapide de *Drosophila suzukii* en Europe et en Amérique du Nord a suscité de nombreuses études sur le terrain comme en laboratoire. Cette drosophile est en effet à la fois un ravageur important, du fait de son développement dans des fruits à maturité, et une « cousine » de l'espèce modèle *Drosophila melanogaster* dont la biologie et la génétique sont bien connues. Cet article s'appuie sur les données publiées par différentes équipes et sur des résultats préliminaires pour discuter de l'avancée des recherches et notamment des questions suivantes: en quoi nos connaissances sur *D. melanogaster* peuvent-elles ou non aider à comprendre et gérer l'invasion de *D. suzukii* ? Les résultats obtenus en condition de laboratoire avec cette espèce sont-ils représentatifs de sa biologie ? Comment mesurer l'impact écologique d'une espèce invasive si la niche qu'elle vient occuper est peu décrite localement en termes d'espèces présentes et de réseaux trophiques ? Cet article discute aussi des pistes et contraintes en termes de lutte biologique et de biocontrôle.

SUMMARY.— The recent and rapid invasion of Europe and North-America by *Drosophila suzukii* has generated numerous laboratory and field studies since this fly species is an agricultural pest that causes economical losses by laying eggs and developing in ripening fruits, but also because of its relatedness with the model species *Drosophila melanogaster* whose biology and genetics are well described. This commentary is based on recent data published by different research groups as well as some of our own preliminary results. It discusses the state of research on *D. suzukii* and addresses the main following questions: can the wide knowledge on *D. melanogaster* help us to understand and manage the *D. suzukii* invasion and how? Are lab results on *D. suzukii* really informative on its biology? How can the ecological impact of an invasive species be evaluated if the ecological niche is poorly described in terms of biodiversity and trophic network? We also outline constraints for the biological control of this pest species and suggest new possible approaches for its long-term management.

THE *D. SUZUKII* PROBLEM

Drosophila suzukii Matsumura (Diptera: Drosophilidae), the spotted-wing *Drosophila* (Fig. 1), is a native species from Southeast Asia that quite simultaneously and independently established in North America (California) and Europe (Italy and Spain) (Hauser, 2011; Walsh *et al*., 2011; Calabria *et al*., 2012; Adrion *et al*., 2014), likely as a result of the global trade intensification. Its subsequent expansion was extremely fast (several hundred kilometres per year), certainly because of the local complex fruit trade exchange system, thus preventing its eradication. In contrast to most *Drosophila* species, which lay eggs on wounded rotting fruits only, *D. suzukii* is able to oviposit in the flesh of soft skinned fruits thanks to its serrated ovipositor (Fig. 1). Accordingly, substantial to severe damages are observed on cultivated fruits, such as berries and stone fruits, that result from the fly larva development and subsequent infections by fungi and bacteria at the puncture site. At the moment, the management of this agricultural pest mainly relies on prophylaxis, mass trapping and the large use of insecticides. The required chemical treatments increase the production costs, result in the presence of residues in harvested fruits, and impact the biodiversity (Lee *et al*., 2011; Cuthbertson *et al*., 2014; Werts & Thomas, 2014). Besides, *D. suzukii* may rapidly evolve resistance to insecticides.

Figure 1.— Pictures of *D. suzukii* male and female. Left, adult male with distinctive dark spots on the wings. Right, ventral picture of a female showing the extended serrated ovipositor at the tip of the abdomen.

A main goal was thus to manage *D. suzukii* using environmentally friendly methods at the interface between agronomy, integrative biology and evolutionary ecology. This seemed *a priori* feasible, notably because of *D. suzukii* relatedness with the model species *Drosophila melanogaster*. At least three kinds of benefits were expected from the former investigations on *D. melanogaster* and other drosophilids: (i) well-established rearing processes and experimental methods; (ii) easier prediction of species interaction networks and identification of natural enemies thanks to the available knowledge on *Drosophila* community ecology; (iii) sequencing, assembly and annotation of the genome within a short-time, with prospects of development of specific insecticides or genetic engineering for SIT-like strategies[1]. These expectations have motivated scientific and agronomic actors to act collectively against this progressive threat, in France as in other countries. Three to four years after several Research and/or Development programs were initiated, we portray here a much contrasted situation, less favourable than expected. However, work is in progress and the “landscape”, e.g. networks, knowledge and/or know-how, will certainly evolve in the next few years, hopefully leading to efficient and safe methods to control this pest!

COMMENTS AND PERSPECTIVES

Among the main “disappointments”, one is likely the observed acute competition between “actors” - public and private laboratories, agronomic representatives - after the initial phase of enthusiasm. For instance, attempts to build a consistent consortium in France based on the pre-

[1] SIT (Sterile Insect Techniques): Mass release of sterile or sterilizing individuals of a pest species in order to definitively suppress (eradication) or temporarily limit its populations.

existing scientific community on *Drosophila* species has failed until now, except for one successful agronomic project[2]. Ongoing collaborations have thus emerged from local/restricted initiatives, a situation similar to the one observed in other European countries and probably elsewhere as well. Unfortunately, this situation, although particularly pervasive in the case of *D. suzukii*, only highlights a common dysfunction (e.g. redundancy, lack of collective added-value) in the management of invasive species.

A second disillusion came from the strong expectation of "experimental comfort". Despite substantial efforts, transposition or adaptation of the *D. melanogaster* rearing conditions to *D. suzukii* proved difficult and experiments on *D. suzukii* are not yet straightforward. We observed that some field-collected *D. suzukii* populations managed to develop on *D. melanogaster* "classical food" once in the lab. However, this seemingly occurred only when the population was founded with an "optimal" number of flies. Indeed, no population increase was observed with a small number of founders, likely because of the low reproduction rate of this species, whereas rearing flies at high densities resulted in a strong decrease in the survival rate. Addition of fruits in the food did not drastically improve the results. The exact optimal number of flies to be used and whether it also depends on the sampled fruits, the time of the year, or the previous adaptation of the fly to specific conditions is yet unknown. For instance, although yeast is essential for *D. melanogaster* physiology, behavior, and fitness, and also improves the fitness of *D. suzukii*, whether *D. suzukii* is associated with the same yeast lineages as *D. melanogaster* or even requires yeast in the wild, remains unclear (Hamby *et al*, 2012). More generally, there is no available information on the metabolism of *D. suzukii*.

In agreement with results on sampled populations, we observed that *D. suzukii* adults are quite difficult to maintain in vials and that high density negatively affects their survival, in contrast to results on *D. melanogaster*. Adults survived only one or two weeks when the fly number reached fifty to a hundred individuals whereas they could be maintained as long as one month when isolated in a tube in the same food conditions and supplied with water (Emiljanowicz *et al*, 2014; personal observations). Besides, *D. suzukii* females do not lay eggs during the first two days post-emergence and they reach the peak of egg production, only about 5 to 8 eggs per day, between the fourth and seventh day (Kanzawa, 1939; Chabert *et al*., 2013; Emiljanowicz *et al*., 2014; unpublished results). A single *D. melanogaster* female lays almost continuously 50-70 eggs per day, for at least two weeks, in laboratory conditions. These two species thus largely differ in their life history traits.

The lack of knowledge on *D. suzukii* biology, notably its food requirements and reproductive activity, strongly impacts the feasibility of experiments. As an example, we recently performed time-consuming experiments in population cages to understand the dynamics of interactions between *D. melanogaster*, *D. suzukii*, and their natural enemies, that were totally unsuccessful since *D. suzukii* was rapidly outcompeted by *D. melanogaster* (unpublished data). Strikingly, a contrasted result was obtained when setting up preliminary experiments under semi-natural conditions, i.e. when flies were offered plants bearing intact ripening fruits (Fig. 2) on which both *D. melanogaster* and *D. suzukii* managed to reproduce. Indeed, no apparent competition was observed when the experiment was performed with a mix of equal numbers of individuals of the two fly species (Fig. 2). This clearly highlights the difficulty in extrapolating data on life history traits from the laboratory to field conditions. The population dynamics of *D. suzukii* in the field is also an intriguing question, with few information available from the fly area of origin, except from Japan where *D. suzukii* was first described about a hundred years ago, and is widely distributed (Kanzawa, 1939; Mitsiu *et al*., 2007, 2010; Lee *et al.*, 2011; and references therein). Nuclear and mitochondrial phylogenetic analyses suggest that *D. suzukii* is a sister taxon of *D. biarmipes* and

[2] CASDAR (compte d'affectation spéciale « développement agricole et rural ») "*Drosophila suzukii*: connaissance du ravageur, caractérisation du risque et évaluation de méthodes pour sa maîtrise rapide et durable".

that it appeared in Asia and may have adapted to temperate mountainous environments in continental South-Asia (Ometto *et al*., 2013). Fly attacks on cherries, grapes and different crops have been reported in Japan (Kanzawa, 1939; Kinjo *et al*., 2013), but little is known - or data are not available - on the ecological and economic impact of the fly in other Asian countries.

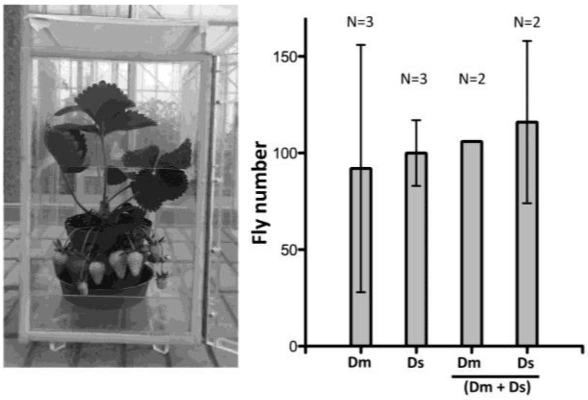

Figure 2.— Competition experiment between *D. suzukii* and *D. melanogaster* in « semi-natural » conditions. Left, picture of the experimental design: a strawberry plant with 10 fruits from green to mature was introduced in a plexiglas cage with one side aerated. The cage was maintained in a green house under natural light conditions (average daylight, 14h30) and temperature cycling (day/night 24.5/15.5°C). Six females and three males of a given species were introduced in each cage for the Ds (*D. suzukii*) or Dm (*D. melanogaster*) modality, or simultaneously for the Dm+Ds modality. The strawberries were harvested 10 days later and maintained in an aerated close box under the same conditions until fly emergence. Right, average number of emerged flies for each species and each modality. n, number of cage replicates. The same number of Dm flies was obtained in the two replicates of the Dm+Ds modality.

In newly invaded countries, one to three population peaks of *D. suzukii* per year are usually observed in crops (De Ros *et al.*, 2012; Weydert & Mandrin, 2013; Harris *et al*., 2014; see also for Swiss: http://www.agroscope.admin.ch). Yet, the timing of infestation and the population size, at one point or combined, vary largely in both space and time notably among the years. This heterogeneity is likely related to the sensitivity of *D. suzukii* to abiotic factors, combined with its high polyphagy. Lab-screening and field reports indeed reveal a tremendously high number of host plants, including some key-crops for invaded countries (Lee *et al*., 2011, 2015). This information must be taken into account when dealing with the prevision of agricultural risks. Altogether, the patterns of infestation in the field - local occurrence, infestation rates, and damages - are more complex than expected. In particular, the situation on grapes is ambiguous since various levels of damages (no damage to high damages) have been reported, in relation or not with particular environmental conditions or grape varieties (Rouzes *et al*., 2012; Linder *et al*., 2013; Van Timmeren & Isaacs, 2014), although this crop seems unfavourable for development of *D. suzukii* (Linder *et al*., 2013; Delbac *et al*., 2014). We also recently observed the presence of *D. suzukii* on unexpected crops, such as olives in South of France (unpublished data).

The final disenchantment came as a result of the evaluation of *D. suzukii* natural enemies. Although the communities of insect parasitoids associated to native *Drosophila* species are quite well known in Europe (at least in some agricultural landscapes; Fleury *et al*., 2004), none of these species seems currently able to regulate *D. suzukii*. This may result either from behavioural and/or physiological inadequacies, in relation with the specific ecological niche occupied by *D. suzukii*. For instance, all tested *Leptopilina* species, the main *Drosophila* larval endoparasitoids in Europe and USA, were unable to consistently develop in *D. suzukii* under laboratory conditions (Chabert *et al*., 2012; Kacsoh & Schlenke, 2012; Poyet *et al*., 2013; Rossi-Stacconi *et al*., 2013; Gabarra *et al.*, 2014), possibly because of the strong cellular immune response of *D. suzukii* to parasitism (Kacsoh & Schlenke 2012; Poyet *et al.*, 2013). In contrast, some pupal parasitoids (*Pachycrepoideus vindemmiae* and *Trichopria* cf. *drosophilae*), which are considered as generalists, successfully parasitize *D. suzukii* both in laboratory and in the field (Chabert *et al.*, 2012; Kacsoh & Schlenke, 2012; Rossi-Stacconi *et al*., 2013; Gabarra *et al.*, 2014). These species are also found in Japan where they have been reported amongst the few parasitoids emerged from field sampling of *D. suzukii* (Kanzawa, 1939; Mitsui *et al.*, 2007). Yet, their capacity to find and control natural *D. suzukii* populations remains to be determined. Similar information is required for larval parasitoids also emerged from Japanese *D. suzukii*, i.e. species of the genus *Asobara* (mainly *A. japonica* and *A. tabida*) and *Ganaspis* species not yet fully characterized (Mitsui *et al.*, 2007; Nomano *et al.*, 2015).

The use of some of these species (e.g. *Trichopria* cf *drosophilae* or *Pachycrepoideus* sp.) in augmentative biological control[3] is still under evaluation (Chabert *et al*., 2013). However, even if commercially and agronomically acceptable, this approach will likely be inefficient if fly populations are not also controlled in natural habitats. The use of biocontrol agents can thus only be considered in the frame of classical biological control[4]. This strategy is currently in progress but its development is hampered by several factors: i) as stated above, the community ecology around *D. suzukii* is still poorly documented, in both its native or formerly invaded areas (for Japan, see Mitsui *et al*, 2011; Nomano *et al*., 2015). The same statement also holds for close relative species (i.e. *D. subpulchrella*, a little studied fly also capable of puncturing the soft-fruit skin and having a similar feeding behaviour (Mitsui *et al*., 2010; Atallah *et al.*, 2014)) as well as more intensively studied drosophilids, which explains the restricted number of potential biological control auxiliaries yet identified; ii) although several invasive *Drosophila* species have already been described and investigated (da Silva *et al*., 2005; Pascual *et al*., 2007), their ecological impact on native communities - impact on resident *Drosophila* species, recruitment of natural enemies - are also poorly documented; iii) an important effort is required to describe the local biodiversity in the "wild and cultivated fruits" niche in Europe that could possibly be impacted by the arrival and establishment of *D. suzukii*. The lack of previous data may be detrimental since a "risks / benefits" assessment is required prior to introduction of any exotic biocontrol agent[5]. Several instances have indeed questioned the unexpected ecological issues that can be directly associated with exotic agents, e.g. when it turns out the agent impacts native communities, rather than target invasive species.

An attractive alternative to the "classical biological control" would be the development of sterile insect techniques (SIT) for *D. suzukii*. The use of SIT, and more specifically the radiation-induced sterilization of insects before release, has a long history with a vast body of experience, especially with fruit flies. However, it requires methods to sort out the males from the females, or even better, to obtain only males, as released sterile females could still be able to drill the fruit skin and induce damages. The use of female-lethal strains obtained by genetic engineering such as RIDL - Release of Insects carrying a Dominant Lethal (Alphey, 2002; Fraser, 2012) - may be a realistic goal, since such strains have already been produced in several pest species (Koukidou & Alphey, 2014; Leftwich *et al*., 2014). However, this method is still a matter of debate because the released insects are GMOs (Eckerstorfer *et al*., 2012). The recent development of new molecular

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[3] The intentional release of a living organism as a biological control agent with the expectation that it will control the pest for a more or less extended period, but not permanently (modified from Eilenberg *et al.*, 2011 to take into account both inundation and inoculative methods).

[4]The intentional introduction of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control (Eilenberg *et al.*, 2001).

[5] In France, the introduction of exotic macro-organisms as biological control agents is now regulated (NOR: AGRG1225395A - Journal Officiel de la République Française, 30 juin 2012) and it requires a positive expertise led by ANSES (Agence nationale de sécurité sanitaire de l'alimentation, de l'environnement et du travail).

tools may offer alternatives. For instance, genome editing techniques, such as CRISPR (Clustered, Regularly Interspaced, Short Palindromic Repeats) and TALEN (Transcription Activator-Like Effector Nucleases), which are used to induce specific mutations at targeted genomic sites, are known to be efficient in *D. melanogaster* (Housden *et al*., 2014). Given the availability of the *D. suzukii* genome sequence (Chiu *et al*., 2013; Ometto *et al.*, 2013), they can now be tested on this species, thus opening ways for new sterilizing methods.

The cytoplasmic incompatibility often induced by strains of the bacterial endosymbiont *Wolbachia*, largely present in insects, might also be used as a way to induce the sterilization of *D. suzukii* females in the wild. Preliminary studies did not allow identifying *D. suzukii Wolbachia* strains that induce CI but the possibilities of *Wolbachia* strain transfer from other *Drosophila* species could also be evaluated (Hamm *et al.*, 2014). However, all these tools will primarily require the successful and low-cost scale-up of rearing of *D. suzukii* in laboratory conditions.

CONCLUSIONS

In conclusion, the recent outbreaks of *D. suzukii* outside its native area and the phylogenetic relatedness of this pest with *D. melanogaster* have stimulated a strong scientific investment (75 % of the 117 papers in the Web of Science published since 2010). Despite this investment, unexpected locks have slowed the research progress with regard to (maybe too) optimistic expectations. The apparent proximity between the two fly species is likely a significant asset that may help dealing with *D. suzukii* rapidly, but support may come mainly from genetics and molecular biology. Yet, at least two strategies (classical biological control and SIT-like methods) are currently investigated in different laboratories, and long-term efforts are clearly required for a successful management of this invasive fly pest.

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