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Review Article

Scaphoideus titanus forecasting and management: *quo vadis?*

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With 2 figures and 1 table

Abstract: *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae) is a major pest for European viticulture due to its high efficiency in the transmission of one of the most destructive pathogens for grapevine, namely flavescence dorée phytoplasmas. Although it plays a major role in spreading this disease, *S. titanus* is part of a complex epidemiological cycle involving several alternative vectors with variable relevance for phytoplasma spread. Here we provide an updated review on *S. titanus* monitoring and modelling, as well as the available tools for management of this pest and for limiting phytoplasma transmission and, thus, also spread. Insecticide-based control is examined; additional emphasis is placed on innovative and low-impact control approaches, such as vibrational mating disruption, biocontrol, and methods to reduce vector competence. We also discuss the main emerging challenges to the implementation of effective and sustainable control programs against *S. titanus*.

Keywords: epidemiology; pest monitoring; modelling; Integrated Pest Management; vibrational mating disruption, biological control; plant resistance elicitors; RNA-interference; symbiotic control

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1 Introduction

In a recent review, Gonella et al. (2024a) examined the biology, ecology, and vector status of the Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae). The novel research advances outlined there are tightly connected with the implementation of monitoring and pest control strategies against this insect, which are the key to containing the spread of grapevine flavescence dorée (FD) phytoplasma across Europe (EFSA 2020). The control of *S. titanus* populations is definitely regarded as a major tool for managing FD infections, resulting in the establishment of compulsory insecticide treatments in several European Countries over the past 20 years (Boudon-Padieu 2003; Chuche & Thiéry 2014). However, several of the most effective insecticides are not available in Europe due to their environmental impact and public health issues. Hence in some situations the effectiveness of control measures is hampered by the reduced number of control options resulting from the ban of several active ingredients. The limited efficiency of *S. titanus* control depends on local variability of conditions such as population abundance, FD pressure, and preference for the cultivated grapevine varieties. The complexity of the vineyard agroecosystem further hampers the efficacy of pest control, as the presence of wild vegetation intermixed with cultivated grapevine has been shown to impact even a vine specialist like *S. titanus* (Oggier et al. 2023). Moreover, some additional vector species are involved in the multifaceted epidemiological cycle of FD, and variable abundance of these species may be observed according to the plant composition at the landscape level (Malembic-Maher et al. 2020). Such complexity highlights the need for an effective monitoring system to better determine the most critical entry point for new populations of *S. titanus* and possible alternative vectors. Due to the irregular success of insecticide applications (Tacoli et al. 2017; Prazaru et al. 2023), along with the need for insecticide-free solutions to satisfy Green Deal requirements, several studies have recently explored the use of innovative pest management tools, including plant resistance elicitors to reduce vector competence (i.e., the insect ability to transmit FDp), vibrational mating disruption, RNA-interference, and biocontrol (Miliordos et al. 2017; Ripamonti et al. 2022; Zaffaroni-Caorsi et al. 2022; Bocca et al. 2023).

Given this scenario, we reviewed current knowledge on monitoring, modelling, and management of *S. titanus*, shedding light on the complex epidemiological framework in which the vector is the focus. Its control will be discussed focusing both on current insecticide-based strategies as well as newly proposed sustainable approaches, which are intended to lay the foundations for future pest management.

2 The epidemiological role of *S. titanus* and alternative vectors on FD spread in different agroecosystems

For a long time, the transmission cycle of FD phytoplasmas (FDp) was considered to be restricted to grapevines and to involve only the ampelophagous *S. titanus*, resulting in single epidemiological cycle (Constable et al. 2010; Chuche & Thiéry 2014). However, the discovery of several natural plant reservoirs hosting FDp (*Alnus glutinosa* (L.) Gaertn., *Clematis vitalba* L., *Ailanthus altissima* (Mill.) Swingle, and *Corylus avellana* L.) (Angelini et al. 2004; Arnaud et al. 2007; Filippin et al. 2011; Casati et al. 2017) and a high genetic variability of FDp genotypes (Arnaud et al. 2007; Rossi et al. 2019; Malembic-Maher et al. 2020) have revealed the native European origin of FDp. Hence, a complex cycle of transmission has been recently depicted, with multiple epidemiological cycles also involving additional vectors (Filippin et al. 2009; Lessio et al. 2016; Malembic-Maher et al. 2020). Separate epidemiological cycles are recorded even in the same agroecosystem (Plavec et al. 2019; Krstić et al. 2022; Kogej Zwitter et al. 2023) involving different FDp genotypes that have been identified based on nucleotide sequence analyses of variable loci, such as the *map* and *Vmp* genes, either alone or following a multi locus sequence typing approach (Arnaud et al. 2007; Malembic-Maher et al. 2020). Three genetic clusters have been described based on the *map* gene, namely FD1, FD2, and FD3 (Arnaud et al. 2007), showing different geographical distributions and host variability (considering both plant and insect species). Additional variability has been recorded in *Vmp* genes, where three genetic clusters (named VmpA vectotypes I, II, III as they have been found to affect vector competence) were described as being transmitted by different vectors from distinct plant sources (Malembic-Maher et al. 2020) (Fig. 1). European alder trees (*A. glutinosa* and *A. incana*) have been repeatedly found to harbour diverse FDp genotypes in many European countries across a wide territory and were confirmed as mainly asymptomatic reservoir plants of genotypes belonging to VmpA vectotypes I and II. On the other hand, in northern Italy and Serbia, the climbing shrub *C. vitalba* has been proven to be a natural reservoir of genotypes belonging to FD3 VmpA vectotype III; a finding subsequently confirmed also in Slovenia, Hungary, Switzerland, Austria and in the wider territory of the Balkans (Filippin et al. 2009; Casati et al. 2017; Krstić et al. 2018, 2022; Plavec et al. 2019; Reisenzein & Strauss 2019; Rossi et al. 2019; Malembic-Maher et al. 2020; Radonjić et al. 2023). These plants are suitable hosts for native or introduced alternative insect vectors, and they are hence involved in movement of FDp from natural plants to grapevine in habitats with a mosaic of vineyards and natural vegetation. Genotypes associated with wild host plants are transmitted by specific alternative vectors. In particular,

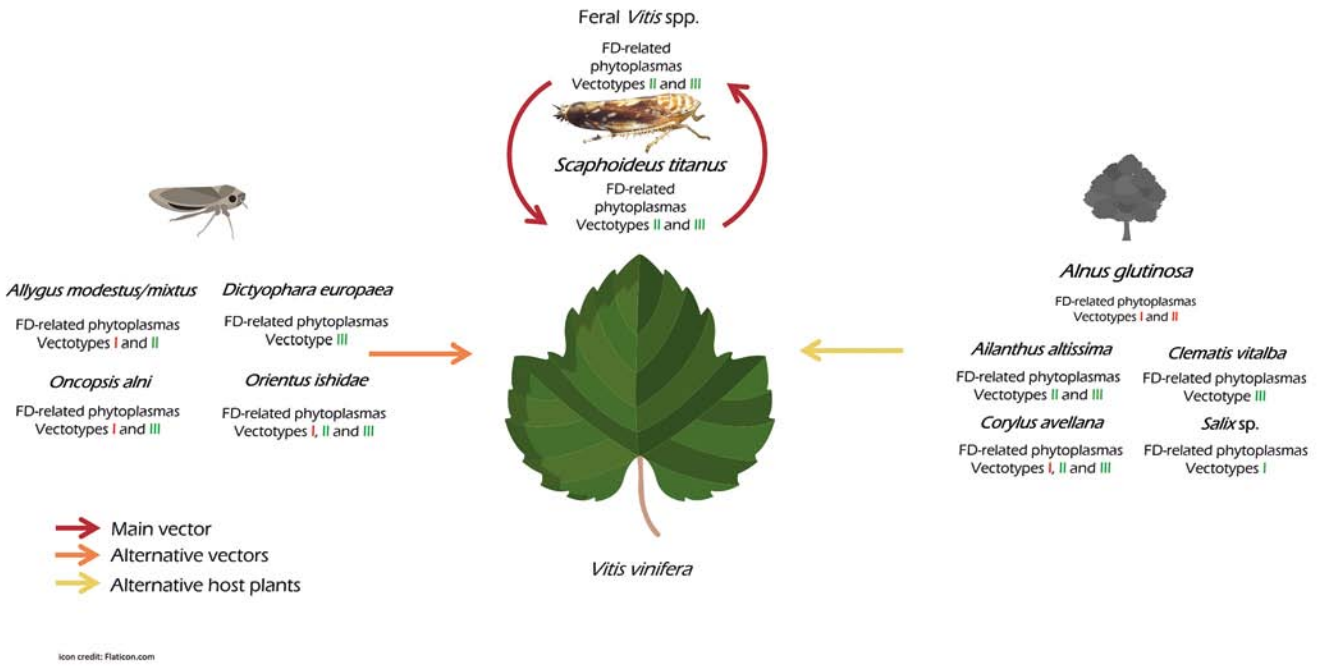

Fig. 1. Role of *Scaphoideus titanus* and alternative vectors in different agroecosystems. The phytoplasmas of vectotype I (in red) are transmitted from natural plant reservoirs (*Alnus glutinosa, Clematis vitalba, Ailanthus altissima, Corylus avellana*, and *Salix* sp.) (yellow arrow) to grapevine by alternative vectors (orange arrow) and are not transmissible by *S. titanus*. The phytoplasmas of vectotypes II and III (in green) are transmitted from natural plant reservoirs to grapevines by alternative vectors and are transmissible by *S. titanus* (red arrow).

the native leafhoppers *Oncopsis alni* (Schrank) (monophagous) and *Allygus modestus/mixtus* (polyphagous) transmit FD1 and FD2 genotypes (VmpA Vectotypes II and III) sourced from alders to alders and to an experimental host (broad bean) (Malembic-Maher et al. 2020). Additionally, the native planthopper *D. europaea* transmits FD3 (VmpA Vectotype III) from *C. vitalba* to grapevine (Filippin et al. 2009; Krstić et al. 2018). Recent research on the first occurrence of FDp (FD3, VmpA vectotype III) affecting grapevine in Montenegro vineyards underlined the role of *C. vitalba* as a reservoir of FD3 (VmpA vectotype III), together with alders, putative reservoirs of FD1 and FD2 (Radonjić et al. 2023). Additionally, an alien leafhopper species of Asian origin, *Orientus ishidae* (Matsumura), recently introduced into Europe has been identified as another potential vector (Lessio et al. 2016), possibly able to spread FD1 and FD2 genotypes in Slovenia, Italy, and France, while in Switzerland it was found to harbour all FDp genetic clusters (Casati et al. 2017; Malembic-Maher et al. 2020). Recently, *O. ishidae* was identified alongside *Allygus* spp. as an alternative vector of higher risk for FDp transmission from alder to grapevine in Germany (Jarausch et al. 2023).

Along with alders and *C. vitalba*, which are well known as FDp transmission sources, other host plants of native or introduced alternative insect vectors may act as additional FDp hosts, thus establishing further routes of transmission that could induce FDp outbreaks. It was recently found that *A. altissima*, a vigorous invasive plant species, harbours the FD3 genotype in Italy, Croatia, and Serbia (Filippin et al. 2011; Plavec et al. 2019; Krstić et al. 2022), and the FD2 genotype in Slovenia (Mehle et al. 2019), and could act as a reservoir for epidemics. Meanwhile, in a study in southern Switzerland (Casati et al. 2017), *O. ishidae* was found to be infected with FDp of all three *map* genetic clusters, all infecting *C. avellana* and FD1 infecting *Salix* spp., thus suggesting that both plants could be additional hosts and reservoirs for FDp epidemics. Finally, a native leafhopper, *Phlogotettix cyclops* (Mulsant & Rey), was recently identified to carry the FD2 genotype in Croatian vineyards (Plavec et al. 2019) whilst in Austria it was naturally infected with FD3 phytoplasma and frequently found on grapevine and neighbouring *C. vitalba* (Reisenzein & Strauss 2019). Preliminary results show that *P. cyclops* can acquire FDp from infected *C. vitalba*, but its ability to transmit the phytoplasma to grapevine still needs to be confirmed. Finally, in Southern Switzerland, a new alien leafhopper of North American origin, *Osbornellus auronitens* Provancher, was recently identified (Trivellone et al. 2017) in a mixed forest of *Castanea sativa* Mill., *C. avellana*, *A. glutinosa* and *Salix* spp. and it was found to be infected with FDp (Trivellone et al. 2022). This species was also recently recorded in Italy, where numerous specimens were collected on yellow sticky traps in vineyards and apple orchards (Ruzzier et al. 2023). This species is closely related to *S. titanus* having a similar external morphology and biology and thus it poses potential additional risks to European vineyards.

In the framework of such a complex epidemiological scenario, it is crucial to take into account not only the abundance of *S. titanus* but also other possible vectors in the vineyard agroecosystem to unveil the relative impact of each species according to local conditions. Monitoring of vectors is hence an essential step to support pest control measures, as only *S. titanus* can be contained through insecticide sprays due to its actual presence in vineyards.

3 *S. titanus* monitoring and pest forecasting, and impact of climate change on pest distribution

3.1 Trap-based monitoring techniques

Monitoring the potential presence of a pest is a fundamental step in Integrated Pest Management but it it is important to consider the sensitivity and cost-effectiveness of the available monitoring techniques. For *S. titanus*, classic monitoring methods, such as visual inspection of main leaves and suckers, beating net (frappage) and chromotropic sticky traps remain the best tools available (Chuche & Thiéry 2014). Their effective use requires that personnel be properly trained in order to correctly recognize *S. titanus* nymphs in the field as well as specimens caught on sticky traps using a stereo microscope. The greatest challenge is to design a monitoring strategy that allows for reliable early and cost-effective detection of the vector. Key factors such as monitoring technique(s), number of observations required (e.g., number of sticky traps or leaves to inspect per vineyard or ha) and, most importantly, location of suitable sites for monitoring the potential presence of *S. titanus* are often difficult to determine (Jeger et al. 2016). In addition, alternative habitats potentially hosting feral grapevines, abandoned vineyards or small private vineyard systems (e.g., pergolas), which may act as a suitable habitat for *S. titanus*, as well as inoculum reservoirs, should be included when designing a survey (Chuche & Thiéry 2014; Ripamonti et al. 2020; Oggier et al. 2023). As Lessio & Alma (2021) previously reported in their review, "*another issue needing investigation is not "when" but "where" an insect pest occurs. In this case, what matters is not time, but space*".

New smart trap types, coupled with cameras and assisted with automatic image analysis for the detection of adults, are already available from several manufacturers, e.g., xTrap Color by XFarm Technologies (https://xfarm.ag/en/crop-protection, accessed on 23 April 2024), BugSmartTrap by INESC TEC (https://www.inesctec.pt/en, accessed on 23 April 2024), iSCOUT® COLOR TRAP by Metos (https://metos.global/en/iscout/, accessed on 23 April 2024), etc. However, no literature on their efficacy and effectiveness, including species recognition accuracy, is currently available. Thus, the direct and indirect costs related to the installation and maintenance (including service subscriptions) of such new smart trap types for early detection are still not cost-effective compared to traditional monitoring techniques because of the large number of traps required to be placed over large geographic areas and the uncertainty of correct identification of *S. titanus* specimens at very low population densities.

3.2 Predictive models

In addition to active monitoring techniques, predictive models may contribute to risk assessment, help target surveillance, and facilitate adaptive control strategies. Available models usually describe and, in some cases, predict egg hatching, juvenile stage development and adult emergence in infested regions, usually based on temperature-dependent factors (Rigamonti et al. 2011, 2018; Maggi et al. 2013; Falzoi et al. 2014, 2016; Sciarretta & Trematerra 2014; Lessio & Alma 2021). Generally, the goal is to provide the optimal time window for well-targeted insecticide applications. However, predicting the potential presence and establishment of *S. titanus* in new areas necessitates other modelling approaches and should consider several additional factors, including vector adaptability to new temperature regimes, multiannual infestation patterns and the potential effects of climate change (Rigamonti et al. 2014; Jermini et al. 2019; Sneiders et al. 2019). The current and future potential distribution of FD and *S. titanus* in Europe were modelled in the "VitisCLIM" project by using CLIMEX® software (Steffek et al. 2011; ACRP 2013). The results were later used for the official EFSA report by Jeger et al. (2016). The predicted area of climate suitability for *S. titanus* covers almost all of continental Europe. Models were also generated for other regions where neither *S. titanus* nor FDp are currently present, such as for China (Ge & Wen 2006) and Chile (Quiroga et al. 2017). For the specific case of Europe, the published models do not properly consider specific biological requirements for successful spread of *S. titanus*. Indeed, considering its ampelophagy, without a vineyard continuum, it may be very difficult for *S. titanus* to actively invade new vineyards over long distances (Chuche & Thiéry 2014; Lessio et al. 2014; Riolo et al. 2014). Yet, involuntary introductions mediated by anthropogenic activities may, in fact, lead to the potential establishment of the vector in new areas. Such considerations accentuate the difficulties involved in designing a proper proactive monitoring strategy. In addition to wine growing regions neighbouring the currently known *S. titanus* distribution, important traffic routes and hubs are present nearby facilitating additional spread (e.g., Hulme et al. 2008). Moreover, FDp genotypes compatible with both grapevine and *S. titanus* may already be present in areas of natural vegetation containing known native host plants especially *Alnus* spp. (Filippin et al. 2009; Casati et al. 2017; Strauss & Reisenzein 2018; Malembic-Maher et al. 2020; Jarausch et al. 2021; Rizzoli et al. 2021). The potential arrival and establishment of *S. titanus* in such habitats may thus give rise to rapid epidemic spread (Rizzoli et al. 2021; Jarausch et al. 2023).

In general, in already infested areas, models should be used as an adaptive management tool in which new data (biotic and abiotic) are continuously integrated to improve prediction accuracy. The accompanying field surveys are essential for validating the models and for accommodating potential changes in the pest distribution due to climate change. In currently FD-free areas, the active surveillance of vineyard plots remains the only proper tool to detect the presence of *S. titanus*, as well as grapevines showing symptoms associated with Grapevine Yellows. The importance of detecting *S. titanus* at the earliest possible stage of invasion is crucial for the containment of FDp spread and, ideally, disease eradication (Jeger et al. 2016; Kopacka et al. 2017).

4 Management

4.1 Insecticide-based strategies

The control of FD is presently based on the application of insecticides against *S. titanus*, the removal of FDp-infected grapevines, and the use of certified propagation material (Tramontini et al. 2020). When the occurrence of *S. titanus* has been ascertained or is suspected, area-wide monitoring from egg-hatching to adult appearance is essential to estimate the vector population size and identify the proper timing for insecticide applications. Pavan et al. (2005) suggested two insecticide applications when large *S. titanus* populations and/or a high number of symptomatic grapevines occur in vineyards. Considering that insecticides target nymphs to avoid adult emergence, the first application is recommended when third instar nymphs are dominant in the population structure and the second about two weeks later to suppress newly hatched nymphs. A single application before adult occurrence (adults are more important for the spread of FDp than nymphs due to their migration ability) can be sufficient in cases of low leafhopper populations or low disease incidence. Due to the risk of immigrating infected adult leafhoppers, a third insecticide treatment to vineyard borders surrounded by natural vegetation or by abandoned vineyards has been suggested in late summer in the grape-growing areas with high FD incidence (Bocca et al. 2020). It is worth noting that the reduction in vector populations is greater following an area-wide insecticide application rather than multiple insecticide applications (Pavan et al. 2005). In this framework, phenological models and decision support systems can help to optimize the timing for insecticide applications (Rigamonti et al. 2011). In grapevine nurseries in areas where *S. titanus* is present/suspected, insecticide application is compulsory from the first hatching of *S. titanus* eggs to the last adult captures, according to schedules developed by national phytosanitary services to protect scion and rootstock mother plants. The number of applications conducted depends on the persistence of the insecticide employed (Chuche & Thiéry 2014) but information on persistence is limited.

The insecticides used in Europe until 2018 (organophosphates such as chlorpyrifos-ethyl and chlorpyrifos-methyl; chitin-inhibitors such as buprofezin and flufenoxuron; and neonicotinoids like thiamethoxam) were characterized by a remarkable contact activity and persistence reaching more than 90% efficacy (Pavan et al. 2005; Jermini et al. 2007; Zezlina et al. 2013). These active ingredients were withdrawn from the European market because of toxicological and eco-toxicological issues (Regulation (EC) No 1107/2009). They were replaced by other neonicotinoids (e.g., acetamiprid), butelonides (e.g., flupyradifurone) or pyrethroids (e.g., tau-fluvalinate). In organic vineyards, *S. titanus* control still relies on the use of pyrethrins. In 2022, the efficacy of the most used insecticides against *S. titanus* was evaluated in field and semi-field experiments carried out in Italy (Prazaru et al. 2023). In the first case, insecticides were applied against N2–N4 nymphs in large vineyard plots using a farm atomizer. Among conventional insecticides, acetamiprid and flupyradifurone were less effective than etofenprox and deltamethrin, whereas tau-fluvalinate and sulfoxaflor provided intermediate efficacy. Trials aimed at assessing insecticide persistence (semi-field experiments on N3–N4 nymphs and adults) stressed the prolonged effectiveness of pyrethroids on vectors compared to the remaining insecticides. However, the residual effect of pyrethroids in field conditions declined with temperatures above 30 °C. Field trials performed against N2–N4 nymphs with organic insecticides showed that pyrethrins were more effective than azadirachtin, *Beauveria bassiana*, and potassium salts of fatty acids; residual effects of organic insecticides were very low under semi-field conditions. The effect of six insecticides on egg hatching of *S. titanus* was evaluated using two-year-old cuttings as test material (Götsch et al. 2020). Etofenprox, spirotetramat, paraffin oil, azadirachtin, spirodiclofen and kaolin effectively reduced egg hatching. The latter study suggests the possibility of reducing *S. titanus* population size by decreasing egg hatching, but this strategy needs to be tested under a more realistic scenario.

It is important to note that the impact of insecticides on *S. titanus* populations can be affected by the kind of equipment used for applications (in particular the type of sprayer) and the volume of water used for treatments. In preliminary field trials, the same insecticide solution (same dose and volume) was applied against *S. titanus* using different sprayers; the best results in terms of efficacy were obtained using nebulisers and atomizers rather than tunnel sprayers (unpubl. data by F. Pavan and C. Duso). Specific factors accounting for differences in performances are under study. A multidisciplinary study is therefore needed to improve the impact of insecticide applications on vector populations. In this framework, cultural practices also play a crucial role. Branches from winter pruning should be destroyed (minced and/or buried under the soil), since they host leafhopper eggs (Bagnoli & Gargani 2011; Cara et al. 2013). Suckers should also be removed as they are preferred feeding sites for nymphs (Chuche & Thiéry 2014). Bunch leaf zone removal could improve insecticide coverage and reduce the favourable effects of dense canopies on leafhoppers. Another very important prophylactic measure is the cleaning of uncultivated areas hosting feral American vines surrounding vineyards, as well as the prompt removal of abandoned vineyards that host large potentially infected *S. titanus* populations (Pavan et al. 2012; Lessio et al. 2014; Ripamonti et al. 2020; Oggier et al. 2023).

The efficacy of kaolin, a white inert aluminosilicate mineral, was tested in Italy and in Switzerland as an alternative to natural pyrethrins (Tacoli et al. 2017; Linder et al. 2023). Kaolin was applied two to three times against nymphs (N2–N4), reducing leafhopper densities in most of trials. Results of trials carried out in Italy showed higher efficiency than those conducted in Switzerland but in both countries the efficacy of kaolin was lower than that obtained using pyrethrins. Additional field studies carried out in Italy confirmed this tendency: two applications with kaolin reduced *S. titanus* population densities by 45.5% compared to 70.8% by pyrethrins (Prazaru et al. 2023). In the same trials, formulations based on *Beauveria bassiana* achieved a reduction of 29.5%. These results suggest that the preventive use of kaolin and entomopathogens against the first nymphal instar can be useful for decreasing leafhopper populations prior to compulsory insecticide applications requested by phytosanitary services.

Insecticide use in areas affected by FD poses toxicological, ecotoxicological and technical (e.g., pesticide resistance and resurgence of minor pests) challenges. A five-year study carried out in Switzerland showed that it is possible to suspend the mandatory insecticide treatments in years when leafhopper population densities are low and poorly susceptible varieties are cultivated (Rizzoli et al. 2023). Such adaptive strategies should be promoted depending on regional or local conditions and on FD incidence, vector population size, cultivar susceptibility and demand for environmental sustainability. In such situations, the use of alternative or complementary control tools should be strongly encouraged.

4.2 Alternative pest control: vibrational mating disruption, natural enemies, and biocontrol

In view of the increasing need for additional pest control options, given the limitations of insecticide use, alternative control strategies targeting *S. titanus* are urgently needed. Vibrational mating disruption aims to reduce *S. titanus* populations by interfering with its intraspecific communication in order to prevent mating (Eriksson et al. 2012). Courtship of *S. titanus* relies on substrate borne vibrational signals falling within the frequency range of 150–200 Hz. Vibrational mating disruption operates through the transmission of synthesized disturbance signals to grapevines in the same frequency range, thus masking the natural mating signals produced by courting leafhoppers (Strauss et al. 2021; Thiéry et al. 2023). The first tests of this technique were conducted under laboratory conditions and showed that the playback of a rival male's disturbance signal, transmitted to a vine hosting *S. titanus* males and females, interrupted mating duet and prevented courtship (Mazzoni et al. 2009; Eriksson et al. 2012). Subsequently, field experiments were conducted in a vineyard trained by the Guyot system on couples of *S. titanus* released for 24 h in net sleeves that wrapped around grapevine shoots (Eriksson et al. 2012). The mating disruption effect was significant in all sleeves, with some reduction in effectiveness in the fifth sleeve, positioned 10 m away from the disturbance signal release source. Other field experiments showed that interruption of the disturbance signal from 12 AM to 3 PM did not reduce the disruptive effect. Good control was also obtained when disturbance devices were turned off from 9 AM to 4 PM (Polajnar et al. 2016). In contrast, any interruption during hours outside these time windows resulted in a drop of effectiveness. Laboratory trials revealed that an amplitude threshold value above 15 μm/s of substrate velocity (the "safety threshold") prevents 100% of mating, while values between 2.5 and 15 μm/s were still able to significantly reduce mating success but with lower efficacy (Polajnar et al. 2016; Mazzoni et al. 2019). From 2017 to 2022, a larger field experiment was conducted in a commercial organic vineyard of 1.5 ha ('Cabernet franc' cv., Guyot system) at Fondazione Edmund Mach, San Michele all'Adige (Italy) (Nieri & Mazzoni 2018; Mazzoni et al. 2019; Nieri et al. 2023). A significant reduction (up to −50%) was recorded in the population of *S. titanus* nymphs, especially in the first 3 years after application (2018–2020), followed by a loss of effectiveness in the last two years (2021–22). The declining effectiveness was related to a progressive loss in device performance over the years, with a reduction of the working distance that did not maintain the safety threshold over the entire row (Nieri et al. 2023). Despite reduction in nymphs, a substantial increase in male flight activity was observed in the disrupted area. Accordingly, Zaffaroni-Caorsi et al. (2022) showed a significant increase in "call-fly" behaviour for caged males and females of *S. titanus* on potted plants subjected to continuous disturbance signal. Interestingly, mated females increased their flight activity and showed some delay in oviposition, probably due to the exposure to a hostile environment and the related stress (Pekas et al. 2023).

Another control strategy that has been explored as a non-chemical control measure for *S. titanus* populations is the application of potential biocontrol agents, including arthropod natural enemies and entomopathogenic microbial strains. Several natural enemies associated with *S. titanus* were found, both in the native and introduced areas

(Table 1); however, they usually showed parasitism or predation rates below 1% (Arzone et al. 1994; Malausa et al. 2003; Malausa & Sentenac 2011; Bocca et al. 2020). Among them, both egg and nymphal parasitoids were recorded, as well as generalist predators. Some species were proposed for use in biological control programs, but with little success in a propagative and an augmentative approach (Malausa & Sentenac 2011).

Recently, the cuckoo wasp *Elampus bidens* (Förster) was reported to be associated with *S. titanus* in north-western Italy (Bocca et al. 2023). This parasitoid displays a combination of endoparasitic and cleptoparasitic behaviour, as it uses *S. titanus* to sustain development of the first larval stage, while subsequent instars can grow only if the leafhopper is consumed by zoophagous insects, which serve as the final host for *E. bidens*. At present, the final host species has not been identified; however, higher parasitism rates (reaching 25% in areas with low agricultural intensity) were observed for the cuckoo wasp compared to other Palearctic parasitoids of *S. titanus* (Bocca et al. 2023). These results suggest that a conservation biological control approach might be applied to reduce populations of *S. titanus* in uncultivated areas, where other control strategies cannot be pursued.

Among entomopathogenic organisms, only the fungus *Beauveria bassiana* has been indicated as a potential biocontrol agent against *S. titanus* eggs and nymphs, although field trials showed that the application of this fungal pathogen had low efficacy in controlling nymphal stages (Prazaru et al. 2023). The recent retrieval of nematode-related transcripts in *S. titanus* individuals (Abbà et al. 2022) belonging to putatively parasitic orders reveals a potential role of entomopathogenic nematodes in leafhopper biocontrol.

Additional investigations on the natural enemies in the native area of *S. titanus* may lead to identification of more efficient biocontrol agents. The proposal of novel biocontrol agents for managing *S. titanus* should consider their

Table 1. Natural enemies recorded on *Scaphoideus titanus*. References: 1, Arzone et al. 1994; 2, Malausa et al. 2003; 3, Malausa & Sentenac 2011; 4, Drieu & Rusch 2017; 5, Schvester et al. 1962; 6, Bernard & Du Fretay 1988; 7, Chuche &Thiéry 2014; 8, Chuche et al. 2011; 9, Bocca et al. 2023.

Attacked life stage	Kind of enemy	Class	Order	Family	Species	Area of recorded activity	Ref.
Egg	Parasitoid	Insecta	Hymenoptera	Aphelinidae	*Centrodora hexatricha*	Palearctic	1
				Mymaridae	*Polynema* spp.	Nearctic, Palearctic	1; 2
					Lymaenon spp.	Palearctic	1
					n.d.	Palearctic	3
				Trichogrammatidae	*Oligosita* spp.	Nearctic, Paleartcic	1; 2
Nymphs	Predator	Insecta	Dermaptera	Forficulidae.	*Forficula auricularia*	Palearctic	4
			Hemiptera	Reduviidae	n.d.	Palearctic	5
			Diptera	Syrphidae	n.d.	Palearctic	5
		Arachnida	Trombidiformes	Anystidae	*Anystis baccarum*	Palearctic	6
				Bdellidae	n.d.	Palearctic	7
			Araneida	Philodromidae	n.d.	Palearctic	8
				Salticidae	*Salticus scenicus*	Palearctic	4
			Opiliones	Phalangidae	*Phalangium opilio*	Palearctic	4
Nymphs / adults	Parasitoid	Insecta	Hymenoptera	Chrysididae	*Elampus bidens*	Palearctic	9
				Dryinidae	*Anteon masoni*	Nearctic	2
					Anteon pubicorne	Palearctic	3
					Esagonatopus niger	Nearctic	2
					Esagonatopus perdebilis	Nearctic	2
					Gonatopus spp.	Nearctic, Palearctic	1; 2; 3
					Lonchodryinus flavus	Nearctic	2
			Diptera	Pipunculidae	*Eudorylas* sp.	Palearctic	3

effectiveness as well as the potential impact on non-target organisms. Rules governing employment of biocontrol agents have been progressively modified with the issuing of legislative acts and technical documents by various international institutions. At the European Union level, biocontrol agents, specifically macro-organisms used to protect crops, are not currently the subject of specific legislation. However, substantial differences are found in the approaches of Member States that have national legislation related to biocontrol agents. In Italy, one of the countries where the problem of *S. titanus* control is particularly important, the possibility of presenting proposals for release of biocontrol agents has been recently allowed.

4.3 Innovative tools to reduce vector competence: plant resistance elicitors, RNA-interference, and symbiotic control

Recent advances in knowledge of the interactions between phytoplasmas and vectors have provided a foundation for several studies aimed at controlling FDp spread by reducing transmission competence rather than killing the vectors (Fig. 2). A promising strategy is RNA interference (RNAi), a sequence-specific mechanism in eukaryotes (Fire et al. 1998) that regulates gene expression at the post-trascriptional level, providing defence against nucleic acids from transposons or viruses (Bonning & Saleh 2021). RNAi is triggered by double-stranded RNAs (dsRNAs) which can silence specific target genes. RNAi recently became a powerful molecular tool for functional genomics and has been proposed as strategy in crop protection, with dsRNAs directly applied to plants to silence essential genes of target pests (insects, fungi or viruses) (Taning et al. 2020). The technology is based on the use of double-stranded RNAs (dsRNAs) to hinder expression of essential genes of a selected pest. The basic mechanism is known in arthropods, but knowledge gaps still exist. Several constraints still hamper open-field applications of RNAi in agriculture: (i) efficient delivery of dsRNAs to sap-sucking insects (Christiaens & Smagghe 2014), (ii) stability and integrity of dsRNA molecules when exposed to atmospheric agents (Yu et al. 2013), (iii) inconsistency in laws regulating the use of exogenous dsRNAs, so far approved in some non-EU countries (Mezzetti et al. 2020), iv) risk assessment protocols for undesirable off-target effects (Papadopoulou et al. 2020).

The occurrence of RNAi has been reported for phytoplasma leafhopper vectors (Abbà et al. 2019; Arricau-Bouvery et al. 2023; Canuto et al. 2023). In *S. titanus*, RNAi has been shown to occur after injection of dsRNAs in the insect (Ripamonti et al. 2022), as well as in insects that fed on plants treated by petiole absorption of dsRNAs (Rossi et al. 2024). These studies exploited RNAi as a functional genomic tool (i.e., to manipulate the phenotype by altering

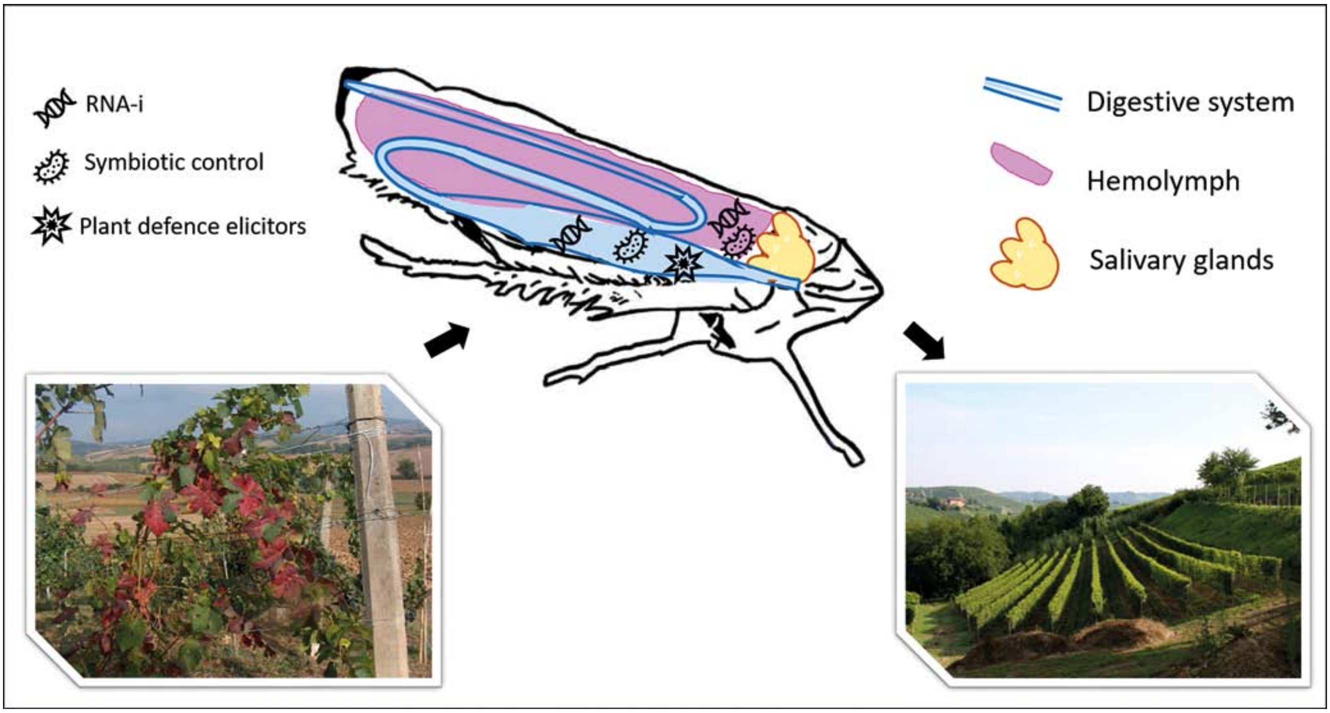

Fig. 2. Recent strategies to reduce FDp transmission efficiency of *Scaphoideus titanus*. The aim of these strategies is to reduce the vector-mediated disease spread even after *S. titanus* is feeding on phytoplasma-infected vines. Most factors that were shown to interfere with the phytoplasma in the vector's body are active in the gut after being ingested, or display their activity in the hemolymph after insect colonization or after being injected. In contrast, so far no direct antagonistic functions have been observed in salivary glands.

gene function), mainly to elucidate roles of insect genes in interactions with phytoplasma proteins, but the proof of concept that RNAi occurs in such species paves the way toward its application for the control of vector populations. However, dsRNA delivery to sap sucking insects, especially under field conditions, is an issue that still needs to be addressed. The occurrence of dsRNA translocation via the plant vascular system (phloem/xylem) is controversial (Biedenkopf et al. 2020; Sidorova et al. 2021); however, when exogenous dsRNAs are applied directly to the plant vascular system they are systemically distributed and could therefore trigger RNAi in piercing-sucking insects (Dalakouras et al. 2018).

Reducing transmission competence through the exploitation of microbial symbionts is another potential pest control strategy (Arora & Douglas 2017), and the management of phytoplasma-borne diseases is among the targets for such methods (Chuche et al. 2017; Gonella et al. 2019b). A promising candidate for symbiotic control is the reproductive parasitic bacterium *Cardinium* sp., which has been identified as a dominant member of the microbiome of European populations of *S. titanus*, but is apparently lacking in the native area (Marzorati et al. 2006; Abbà et al. 2022). The ability of *Cardinium* to manipulate insect host reproduction may support its potential role to drive anti-phytoplasma factors through a paratransgenesis approach (i.e. the genetic manipulation of microbial symbionts as pest control factors) (Abbà et al. 2022). Other potential symbiotic control agents are the acetic acid bacteria, *Asaia* sp. Bacteria in this genus have been proposed for paratransgenesis, to interact with pathogens in the insect vectors, altering their spread (Shane et al. 2018). Non-genetically modified strains of *Asaia* were proposed for use against FDp transmission. A selected isolate, producing an air-liquid interface biofilm, was shown to reduce phytoplasma acquisition in the model vector *E. variegatus* after oral delivery, suggesting that *Asaia* could affect the ability of the phytoplasma to cross the gut epithelia (Gonella et al. 2018). The entrapment of phytoplasma cells by flocculant bacterial masses produced by the *Asaia* strain was suggested to be responsible for reduced acquisition, together with the activation of a midgut-specific immune response, whereas the physical exclusion of phytoplasma attachment sites of the gut epithelia seemed to provide a minor contribution (Gonella et al. 2019a). Additionally, in the late phase of phytoplasma infection, insect immunity was activated in the haemolymph in specimens that were fed with the *Asaia* strain SF15.14 (Gonella et al. 2019a). The reduced acquisition did not completely prevent completion of the transmission process, when the phytoplasma escaped symbiont antagonistic activity in the gut and haemolymph; however, the final transmission rate was significantly reduced by an infection with these symbionts (Gonella et al. 2018).

Another way to reduce the transmission of FDp is by inducing plant defence factors. The use of specific chemical compounds or microbial agents to elicit a systemic resistance response has been proposed against FDp infections (Oliveira et al. 2019). Recovery of the plant from symptoms can be accomplished, as may occur after application of endophytic *Pseudomonas migulae* bacteria (Gamalero et al. 2017), although the phytoplasma load is not reduced in plant tissues, resulting in a poor effect on transmission efficiency by vectors. Conversely, delivery of Acibenzolar-S-methyl, a functional analogue of salicylic acid, resulted in the reduction of FDp transmission by vectors to grafted grapevine plants, even though the mechanisms inducing the effect are still unknown (Miliordos et al. 2017). In addition, spray treatments with a prototype biocomplex containing trace elements and soluble sugars on in vitro propagated grapevines affected the transmission efficiency of *S. titanus* (Gonella et al. 2024b). A combination of plant defence enhancement, direct antibacterial effect in the plant and the reduction of vector competence in insects that feed on the phloem of a treated plant have been suggested as factors contributing to the reduction of phytoplasma transmission (Gonella et al. 2024b).

5 Regulatory framework

Due to its role as a vector of FDp, *S. titanus* is a quarantine pest in many regions of the world where this leafhopper has not yet become established, such as South America and China. Conversely, this species is not regulated in Europe, although it is currently found in a relatively restricted area. In the EU, management of *S. titanus* is regulated only indirectly, since FDp is listed as a quarantine pest known to occur in the EU. The import into the EU of *Vitis* spp. plants from third countries, other than Switzerland, is prohibited, substantially limiting the possibility of new intentional introductions of *S. titanus* eggs contained in plant material from its native area; internal movement of *Vitis* plants is also regulated. Annual surveys are planned by local authorities throughout the European wine-growing areas to assess the presence of both the pathogen and the vector, with different intensity levels according to the reported presence or absence of *S. titanus* and/or FDp in a certain area. Within specifically demarcated areas, where FDp eradication is not possible, the application of appropriate treatments to control *S. titanus* are envisaged together with the removal and destruction of vines found infected by FDp. Specific measures are established for raising public awareness concerning the threat to grapevine production from FDp infections and the actions adopted to prevent its further spread outside of infected areas.

6 Conclusions and future challenges for Integrated Vector Management

At first glance, *S. titanus* may be considered as an easy-to-manage pest, due to its preference for *Vitis* plants and poor reproduction dynamics (Chuche & Thiéry 2014; Bocca et al. 2020). In contrast, the recent history of grapevine pest management clearly demonstrates that *S. titanus* cannot be easily eradicated from European vineyards, since more than 20 years of compulsory treatments in extensive areas showed little efficacy (Prazaru et al. 2023; Rizzoli et al. 2023). Increasing knowledge of this leafhopper's ecological, behavioural and genetic traits is beginning to reveal some of the reasons for the lack of success in managing *S. titanus*, including the complexity of its role in the framework of FD epidemiology, as well as the limitations of conventional insecticide treatments.

Although *S. titanus* is thought to play the primary role in FDp spread, the relative importance of alternative vectors in the epidemic expansion of FD remains poorly studied. Recent evidence suggests a continuous exchange of phytoplasma genotypes between vineyards and their surrounding environment (Filippin et al. 2009; Casati et al. 2017; Krstić et al. 2018, 2022; Plavec et al. 2019; Reisenzein & Strauss 2019; Rossi et al. 2019; Malembic-Maher et al. 2020; Radonjić et al. 2023), entailing a remarkable two-way movement that is only partly understood. The importance of polyphagous alternative vectors visiting grapevines has received increasing attention, but knowledge about the possible FDp movement from grapevine to other plants remains highly incomplete. The occasional phytoplasma acquisition from grapevine by polyphagous vectors, followed by their inoculation into wild plants, should be further explored in the future, as well as the sporadic inoculation by *S. titanus* adults visiting other plant species adjacent to grapevines. These events may explain the genotype renovation that is periodically observed in some vineyard agroecosystems (Plavec et al. 2019; Krstić et al. 2022; Kogej Zwitter et al. 2023), with significant implications for pest management, as nearby areas of natural or feral vegetation could further gain relevance as an important source for primary infections. If confirmed, such a dynamic epidemiology may severely affect the success of vector-targeted measures against FD, since it would involve a much broader and more diverse set of potential sources of phytoplasma infection compared with what is currently believed.

Under this scenario, the most important factors hindering effective pest control, currently believed to be mostly represented by the unavoidable presence of feral vines in grapevine growing areas, may be dramatically amplified by additional FDp reservoirs in the surrounding natural vegetation, which have been so far mostly neglected. Since these areas cannot be managed using insecticide treatments, they may represent serious hurdles to successful containment of FD. In addition to the increased relevance of natural vegetation as a phytoplasma source (Plavec et al. 2019; Malembic-Maher et al. 2020; Radonjić et al. 2023), suppression of *S. titanus* populations inside the vineyards is becoming more difficult, due to the reported reduction in efficacy of insecticide treatments (Prazaru et al. 2022). The ban of most organophosphates and chitin-inhibitors from the European market and the progressive withdrawal of authorization of neonicotinoids suggest that the development of resistance in *S. titanus* may become a serious threat. Investigations aimed to assess the susceptibility to the most common insecticides in *S. titanus* populations exposed to different insecticide pressures are needed to provide a scientific basis for insecticide resistance management strategies. Currently, IPM strategies are based on two IRAC groups, i.e. 3 and 4. Therefore, searching for new solutions and alternatives to insecticides has become urgent. We have reviewed several innovative approaches that have been recently proposed, although none of them may have the strong and immediate knockdown properties previously provided by the now banned chemicals. Only an integrated vision combining strategies aimed at controlling *S. titanus* populations with strategies to reduce phytoplasma transmission may successfully contain FD outbreaks.

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