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# Biology and ecology of the Flavescence dorée vector *Scaphoideus titanus*: a review

Julien Chuche · Denis Thiéry

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**Abstract** Flavescence dorée is a serious disease for European vine growers. Indeed, Flavescence dorée causes yield losses and lower grape quality. As a consequence, Flavescence dorée is costly and needs advanced control strategies. For instance, in 2005, 34 million Euro was given to Italian vine growers to compensate losses due to the disease. The infection by Flavescence dorée results from the association of a phytoplasma and the leafhopper vector, *Scaphoideus titanus*. Despite mandatory controls using insecticides, Flavescence dorée is still spreading in Europe. Here, we review the biology and ecology of *S. titanus* to suggest improved management techniques. The main findings are as follows. (1) The long-distance spread of *S. titanus* is mainly due to human activities, and all European vineyards are susceptible to be colonized. (2) *S. titanus* is an efficient vector because it can reach a high population level and it is specific to *Vitis* spp. (3) Current control and prophylaxis are insufficiently effective. (4) Variation in vector populations and vector capacities lead to differential risks of plant infection. Factors driving such population variations could be modeled to improve *S. titanus* control. (5) Feeding behavior is a key factor in the phytoplasma–vector relationship. (6) The infection risk is mainly limited by vector control. To decrease pesticide use, a cross survey of the vector population and of the infected stocks triggers mandatory treatments. (7) Alternative sustainable methods or strategies are required to reduce insecticide use and increase control efficiency. In the short term, new models could

support the establishment of more sustainable pest management operations. In the long term, innovative techniques involving symbionts, mating disruption and a push–pull strategy could improve *S. titanus* and Flavescence dorée control with less environmental impact.

**Keywords** *Scaphoideus titanus* · Grapevine · Insect · Vector · Phytoplasma · Leafhoppers

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## 1 Introduction

There are major concerns that pathogen transmission by animal vectors may cause major epidemics either in humans or in agronomic products (Lemon et al. 2008). Currently, most vector-borne epidemics are managed through vector control. In agricultural insect-borne epidemics, the alternative control to insecticides is the development of integrated pest management techniques or integrated vector management. Among these epidemics, phytoplasma-borne diseases are concerning. Phytoplasmas are wall-less bacterial pathogens, persistently transmitted in a propagative manner, that are responsible for hundreds of plant diseases worldwide (Lee et al. 2000; Bertaccini and Duduk 2009; Strauss 2009). In 2001, apple production alone suffered €25 million losses in Germany and €100 million in Italy (Strauss 2009) due to phytoplasma-borne diseases. The only currently available control approach for these diseases focuses on the vector since controlling the phytoplasma is not yet possible.



**Fig. 1** *Scaphoideus titanus* adult on a grapevine leaf

Currently, European viticulture is being confronted with two serious phytoplasma-borne diseases, Flavescence dorée and bois noir, with Flavescence dorée being caused by phytoplasma strains of the elm yellows group (16SrV) (Angelini et al. 2003) and Bois noir by “*Candidatus Phytoplasma solani*” (16SrXII) (Quaglino et al. 2013). Interestingly, the Flavescence dorée vector is highly species specific (Schvester et al. 1961), while the bois noir is not. The leafhopper vector of Flavescence dorée, *Scaphoideus titanus* (Hemiptera: Cicadellidae), is a specialist of *Vitis* in Europe and is the only known vector of Flavescence dorée from one grapevine to another in the field (Fig. 1). Thus, the vectorial capacity of *S. titanus* is the main limiting factor on disease progression.

In spite of the mandatory control of *S. titanus*, Flavescence dorée is still spreading in Europe.

For example, 40,000 vines with Flavescence dorée were detected in 2011 on 25,000 ha surveyed in the Bordeaux area of southwestern France, producing an average ratio of 1.6 infected vine stocks per hectare. From 2008 to 2010, vineyard area under mandatory control increased by 8 % in France (Trespaille-Barrau and Grosman 2011). Thus, it is necessary to improve current control techniques and to develop new control strategies. Vector age is one major trait influencing the vectorial capacity, and it could represent an interesting tool in epidemic management. Additionally, the effectiveness of other vector control strategies could be considered for *S. titanus*. As an example, controlling malaria and dengue fever has been attempted by managing the vector populations and especially the vector longevity (Cook et al. 2008).

In disease vectors, the vectorial capacity ( $V$ ) has been related to five main variables (Cook et al. 2008) and is adaptable to Flavescence dorée transmission by *S. titanus*.

$$V = \frac{ma^2p^n b}{-\ln p}$$

where  $m$  is the vector density;  $a$  the probability of the vector feeding on a host, which can be extended to all behaviors related to feeding (leaf choice, plant choice, and spatial dispersion);  $p$  the probability of vector survival;  $n$  the duration of the incubation period (IP);  $b$  the vector competence; and  $1/(-\ln p)$  is the longevity of a vector life after IP.

A higher vectorial capacity is attained when the insect vector has a wide range of host plants, is mobile to locate new host plants and new habitats, and has sufficient longevity to optimally acquire and transmit the pathogen. Feeding behaviors, like those of sucking insects with specialized mouthparts, allow for the efficient acquisition and transmission of pathogens. In vector-borne pathogens, the rate of transmission varies depending upon the vector or pathogens' life history traits, such as population sizes or strains, and environmental ecosystem parameters, such as resource availability and distribution (main

hosts), potential alternative hosts, natural enemies, and climatic conditions (Daugherty et al. 2010). Thus, the transmission rate of vector-borne pathogens is strongly correlated with the size and dynamics of the vector population (Jeger et al. 2004) as well as its biology and behavior.

By acting on these parameters, it is possible to affect the vectors' capacity and propose alternatives to chemical controls. With the Flavescence dorée epidemic expanding throughout European viticulture, an increasingly severe impact can be expected in the near future. It would, therefore, seem urgent to promote integrated strategies based on results from research projects involving in phytoplasma–plant interactions and those studying the vector. We review the vector research performed and examine the intimate relations between the vector, its host plant, and the phytoplasma. These intimate relations are keys to improving our understanding and control of the vector populations and, thus, the epidemic. Focusing on the insect biology, behavior and ecology, we attempt to identify gaps in the knowledge of *S. titanus* and suggest research perspectives that will improve Flavescence dorée management.

Among the different tools that may be implemented in an integrated pest management program for controlling the Flavescence dorée epidemic in vineyards, this review also identifies prospective integrated pest management components for future vector management: (1) managing the insect population's age structure; (2) developing methods targeting insect longevity; (3) affecting the host plant selection, feeding behaviour, and vector dispersion patterns based on push-pull strategies (Cook et al. 2007); and (4) that disrupt reproduction, as seen in some other agronomic pests.

## 2 Symptoms and impact of Flavescence dorée in viticulture

Flavescence dorée phytoplasma, which is a quarantined organism included in the A2 EPPO list (no. 2000/297CE directive),



**Fig. 2** Flavescence dorée symptoms in a Bordeaux vineyard. Diseased stocks have discolored and curled-down leaves. This is illustrated by the first stock in the *right* row



**Fig. 3** Symptoms of flavescence dorée. Yellowish leaves on the white cultivar Ugni blanc (on the *left*) and reddish leaves on the red cultivar Merlot (on the *right*)

is responsible for one of the most severely damaging diseases in European vineyards, with severe economic consequences in the major wine- and vine-producing countries (Fig. 2).

The first visible symptom of Flavescence dorée is either a delayed or lack of bud break on the most severely damaged vines (Caudwell 1964), with other characteristic symptoms appearing in the summer. The canes then droop because of a lack of lignification in the new shoots, with the leaves curling downwards and becoming yellowish in white cultivars or reddish in red ones (Fig. 3). Flavescence dorée also causes the death of inflorescences and berries (Caudwell 1964). By reducing photosynthesis activity and nutrient transport, which leads to decreased grape quality, the phytoplasma can also cause a 50 % reduction in yields (Credi 1989). At this point, plants can either die or recover, but they continue to be less productive (Credi 1989; Boudon-Padiou 2000).

In Switzerland, where Flavescence dorée was only found in Ticino (representing 7 % of all Swiss vineyards), the two mandatory buprofezin treatments cost €250,000 alone (Jermini, 2013, personal communication). In Serbia, primary economic losses due to vineyard destruction in the Aleksandrovac region were estimated at approximately €3.2 million in 2005 (Steffek et al. 2007). Flavescence dorée costs to growers include yield losses, vector control strategies, removing symptomatic grapevines, and low productivity of replacement plants. The control of Flavescence dorée also has an impact on the overall economy. For example, in Piedmont (northwest Italy), the regional administration spent approximately €1.5 million per year between 1999 and 2003 in disease control programs, while in 2005, the Italian government and the European Union compensated the growers with €34 million for yield losses and replanting (Belli et al. 2010). The cost of replacing symptomatic plants varies considerably

according to the cultivar, vineyard management, the yield, and age of the vineyard. In northeast Italy, the average annual cost of replacement was estimated at €0.28 per plant for a 25-year-old productive vineyard planted with “Merlot” at 3,000 plants ha<sup>-1</sup> with an 8 t ha<sup>-1</sup> grape yield, and at €6.50 for a 5-year-old productive vineyard planted with “Perera” at 1,500 plants ha<sup>-1</sup> with a 13 t ha<sup>-1</sup> yield (Pavan et al. 2012).

### 3 Introduction to Europe and spatial spread

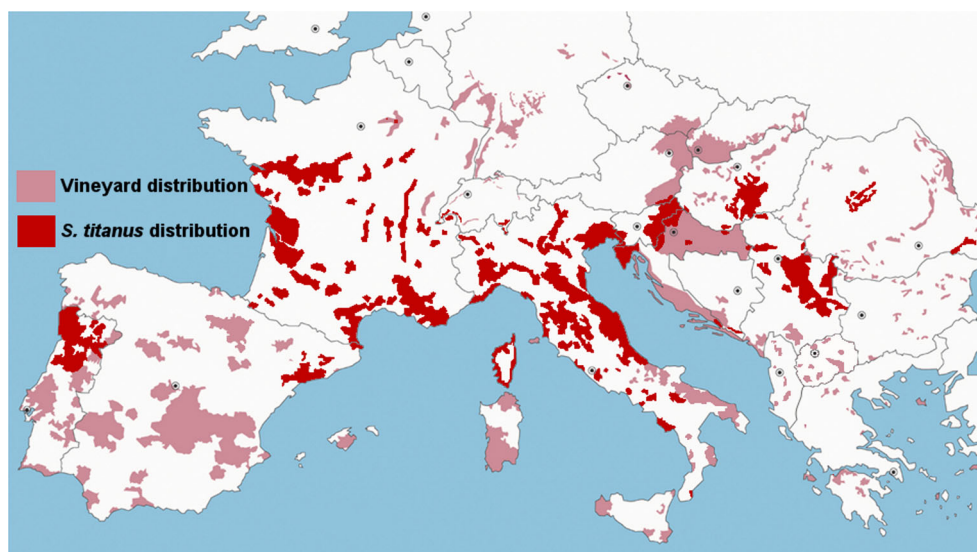
The introduction of *S. titanus* to Europe is now almost fully understood. It was first observed in France in 1958 (Bonfils and Schvester 1960), is attributed to human intervention, and originated in North America, probably in the northeastern region (Papura et al. 2012). A survey program conducted over the three following years recorded only low populations throughout southwest France (Bonfils and Schvester 1960). An inventory of the French Jassidae (now known as Cicadellidae) performed in 1927 did not mention *S. titanus* (Ribaut 1952). Thus, its introduction may have occurred between these two events. However, in the early 1960s, *S. titanus* individuals were discovered in other French and foreign vineyards, such as Charente Maritime, Haute Garonne, Hérault, Alpes Maritimes, Var, Vaucluse, and northwestern Italy (Schvester et al. 1962b; Vidano 1964), which calls into question the starting date of the vector’s biological invasion. However, *S. titanus* may have already been present in 1927, but at such a small spatial scale and population level that it was not recorded in the Ribaut’s inventories. The insect dissemination then extended to most French and European vineyards and is now found from west to east, from Portugal to Romania, and from north to south, from Champagne in France to Basilicata in Italy (Fig. 4; Table 1).

An important event in French viticulture, the Phylloxera crisis, occurred more than a century ago and was resolved by completely replanting the French vineyards (more than 800,000 ha) with new grapes grafted on American rootstocks (Granett et al. 2001). The importation of large amounts of American rootstocks occurred, and they were intensely multiplied in several nurseries, especially in southwestern France (Carton et al. 2007). Thus, the introduction of this insect at this time is a feasible hypothesis.

Population genetics studies reveal a much smaller genetic diversity in European *S. titanus* populations than in American populations, indicating that the former originated from a single introduction (Bertin et al. 2007; Papura et al. 2007, 2009, 2012), although an unusually high-frequency mitochondrial haplotype is present in Switzerland, suggesting at least one other introduction (Papura et al. 2012). The spread of the vector in Europe is based mainly on the dispersion of introduced populations rather than on multiple introductions (Pavan et al. 1997; Bertin et al. 2007; Papura et al. 2009). This dispersion also appears linked to human activities. The hypothesis that population dispersal is related to trading vine cuttings for planting (Bertin et al. 2007; Papura et al. 2009) is consistent with the low adult dispersal ability of *S. titanus*, which is estimated to be a distance of 25–30 m in the vineyards (Lessio and Alma 2004a; Beanland et al. 2006), and the role of roads in the spread of exotic species (Trombulak and Frissell 2000). Evidence for the long-distance dispersal of vector and phytoplasma by infested planting material is provided by the widespread distribution of the Flavescence dorée-2 strain, which has a high clonality level, in both France and Italy (Arnaud et al. 2007).

The small-scale dispersion ability of *S. titanus* does not exclude the larger scale passive dissemination of infectious *S. titanus* over longer distances by the wind, as is the case for aphids and fig wasps (Compton 2002). Initial observations on

**Fig. 4** Distribution of *Scaphoideus titanus* among European vineyards



**Table 1** European viticultural areas where *S. titanus* was recorded

Country	Region	First record	References
Austria	Southern Styria	2004	(Steffek et al. 2007)
Bosnia-Herzegovina	Trebinje (South)	2007	(Delic et al. 2007)
Bulgaria	North	2006	(Avramov et al. 2011)
Croatia	All regions	2003	(Budinišćak et al. 2005)
France	Alpes Maritimes	1961	(Schvester et al. 1962b)
	Ardèche	1986	(Caudwell and Larrue 1986)
	Aude		(Vidano 1964)
	Bouches du Rhône	1985	(Caudwell and Larrue 1986)
	Bourgogne		(Boudon-Padieu 2000)
	Champagne-Ardenne	2011	(DRAAF-SRAL and CIVC 2012)
	Charente		(Caudwell et al. 1974)
	Charentes	1961	(Schvester et al. 1962b)
	Corsica	1971	(Boubals and Caudwell 1971)
	Côtes du Rhône		(Caudwell et al. 1974)
	Dordogne		(Caudwell and Larrue 1986)
	Drôme		(Caudwell and Larrue 1986)
	Gard	1986	(Caudwell and Larrue 1986)
	Gers		(Bonfils and Schvester 1960)
	Gironde	1958	(Bonfils and Schvester 1960)
	Haute Garonne		(Vidano 1964)
	Hautes et Basses Pyrénées		(Bonfils and Schvester 1960)
	Hérault	1961	(Schvester et al. 1962b)
	Landes		(Bonfils and Schvester 1960)
	Languedoc		(Caudwell et al. 1974)
	Midi-Pyrénées		(Caudwell et al. 1974)
	Poitou		(Della Giustina 1989)
	Savoie	1986	(Della Giustina 1989)
Sud-Beaujolais	1987	(Della Giustina 1989)	
Var		(Vidano 1964)	
Vaucluse		(Vidano 1964)	
Yonne	1998	(Boudon-Padieu 2000)	
Hungary	South West		(Der et al. 2007)
	East		(Orosz and Zsolnai 2010)
Italy	Abruzzo	2001	(Belli et al. 2010)
	Basilicata	2002	(Viggiani 2002)
	Campania	2004	(Danise et al. 2005)
	Emilia-Romagna	1987	(Cravedi et al. 1993)
	Friuli-Venezia Giulia	1986	(Belli et al. 2010)
	Liguria	1964	(Vidano 1964)
	Latiun	2005	(Bagnoli et al. 2008)
	Lombardy	1975	(Osler et al. 1975)
	Marche	2001	(Belli et al. 2010)
	Umbria	2002	(Santinelli et al. 2003)
	Piedmont	1988	(Vidano et al. 1988)
	Tuscany	1998	(Santini and Lucchi 1998)
	Trentino-Alto Adige	1990	(Belli et al. 2010)
Valle d'Aosta	2006	(Belli et al. 2010)	
Veneto	1983	(Belli et al. 1985)	
Portugal	North	1998	(Quartau et al. 2001)
	Centre		(de Sousa et al. 2010)

**Table 1** (continued)

Country	Region	First record	References
	Madeira	2010	(de Sousa et al. 2010)
Romania	Transylvania (Blaj)	2009	(Chireceanu et al. 2011)
	Bucharest area	2009	(Chireceanu et al. 2011)
	Constanța County (Murfatlar)	2009	(Chireceanu et al. 2011)
Serbia	Centre and South		(Magud and Tosevski 2004)
	South		(Duduk et al. 2004)
Slovenia	All regions, except Pčinja		(Krnjajic et al. 2007)
	West		(Seljak 1987)
	South West	1983	(Seljak 1987)
	All regions		(Seljak 2008)
Spain	Catalonia		(Rahola et al. 1997)
Switzerland	Romandie, Geneva area	1996	(Clerc et al. 1997)
	Ticino	1968	(Baggiolini et al. 1968)
	Vaud and Geneva	2006	(Schaerer et al. 2007)

Flavescence dorée showed that secondary outbreaks were related to the wind (Caudwell 1957), suggesting the aerial dispersal of the vector. This hypothesis, which seems relevant, was used to explain the spread of *S. titanus* from Slovenia to Austria. Insects were found several kilometers from infested sites, and the captures were downwind in grapevine-free areas (Steffek et al. 2007). In Spain, the spatial distribution of Flavescence dorée in Catalonia suggests the influence of the tramontane (strong north to south wind) (Rahola et al. 1997).

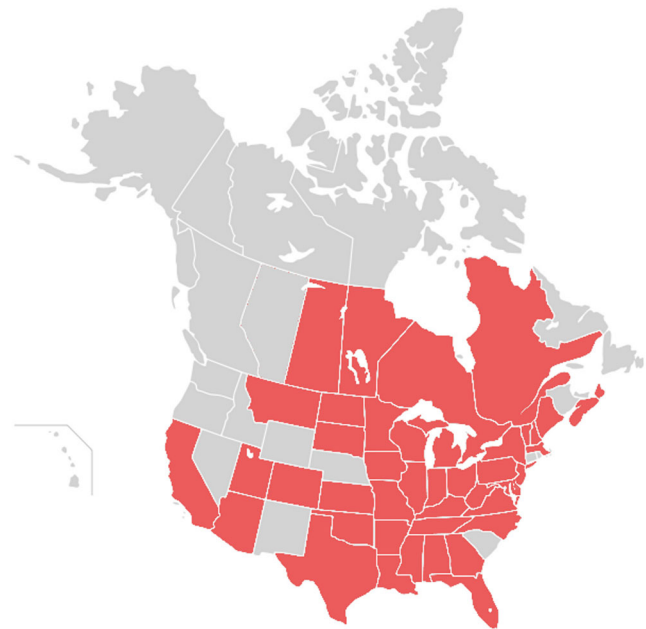
The spread of *S. titanus* in Europe has probably not yet ended. Several forecasting studies have found that populations of *S. titanus* could become established in certain wine regions of northern Europe, and even China because of favorable prevailing climatic conditions (Maixner 2005; Ge and Wen 2006; Steffek et al. 2007). Climate is certainly not the only factor effecting *S. titanus*' distribution since it has been recorded under different climatic conditions in many places in Canada and the USA (Fig. 5; Table 2). However, these observations should be accepted with caution because the number of morphologically similar *Scaphoideus* species present in North America makes them difficult to identify (Malausa et al. 2003). In addition, the morphological characteristics used for *S. titanus* identification, especially for males, show a high level of intraspecific variability and some may be similar to those of other *Scaphoideus* species (Barnett 1976). It should also be noted that these observations were made mostly before 1950 (Table 2), and the genus has been revised several times since then. Thus, in the revision of the genus *Scaphoideus* by Barnett, the species *S. cyprius*, *S. littoralis*, *S. amplus*, *S. brevidens*, *S. diutius*, *S. nigrellus*, *S. scelestus*, and *S. aduncus* are now known as *S. titanus* (1976). Lastly, this insect has rarely been studied in its native area, where it does not constitute an economic problem.

The long distance spread of *S. titanus* is mainly due to human activities and all European vineyards are susceptible to be colonized by this insect, which carries Flavescence dorée.

## 4 Biology

### 4.1 Life cycle

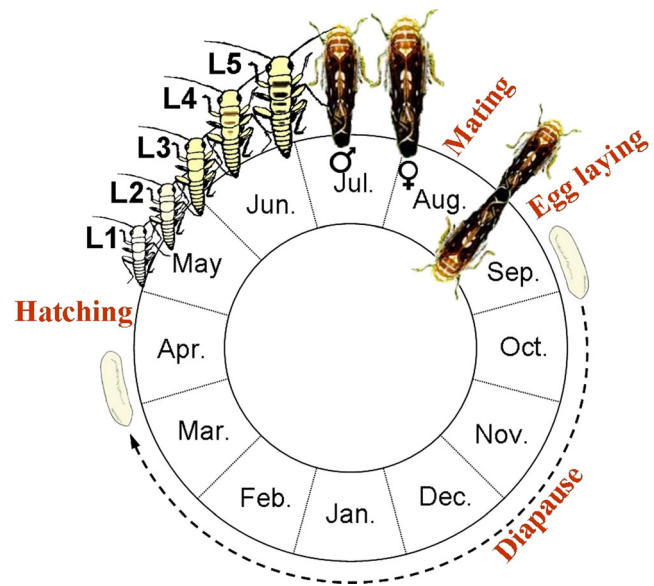
Eggs are laid in the late summer, from August through September, inside the excoriated bark of wood vines, either



**Fig. 5** States in the USA and Provinces in Canada where *Scaphoideus titanus* was observed

**Table 2** North American regions where *S. titanus* was recorded

Country	State/province	First description	References	
USA	Alabama		Barnett 1976	
	Arizona		Barnett 1976	
	Arkansas		Barnett 1976	
	California		Barnett 1976	
	North Carolina		Barnett 1976	
	Colorado		Barnett 1976	
	North Dakota		Barnett 1976	
	South Dakota	1946	Metcalf 1967	
	Delaware		Barnett 1976	
	Florida		Barnett 1976	
	Georgia	1955	Metcalf 1967	
	Illinois	1946	Delong 1948	
	Indiana		Barnett 1976	
	Iowa		Barnett 1976	
	Kansas		Barnett 1976	
	Kentucky		Barnett 1976	
	Louisiana	1936	Metcalf 1967	
	Maine		Barnett 1976	
	Maryland		Barnett 1976	
	Massachusetts	1932	Metcalf 1967	
	Michigan		Vidano 1966; Barnett 1976	
	Minnesota	1943	Metcalf 1967	
	Mississippi		Barnett 1976	
	Missouri		Barnett 1976	
	Montana		Barnett 1976	
	New Hampshire		Barnett 1976	
	New Jersey		Barnett 1976	
	New York		Maixner et al. 1993	
	Ohio	1936	Osborn and Knull 1946	
	Oklahoma		Barnett 1976	
	Pennsylvania	1936	Metcalf 1967	
	Tennessee	1936	Metcalf 1967	
	Texas		Barnett 1976	
	Utah		Barnett 1976	
	Vermont		Barnett 1976	
	Virginia		Beanland et al. 2006	
	West Virginia		Hamilton 1983	
	Wisconsin	1936	Metcalf 1967	
	Eastern States	1948	Delong 1948	
	South Eastern States	1949	Metcalf 1967	
	Central States	1949	Metcalf 1967	
	Canada	Manitoba		Maw et al. 2000
		Nova Scotia		Maw et al. 2000
		Ontario	1956	Beirne 1956
		Québec	1956	Beirne 1956
		Saskatchewan		Maw et al. 2000

**Fig. 6** Life cycle of *Scaphoideus titanus*. Dates are indicative and vary depending on year and location

individually or in groups (Schvester et al. 1962b; Vidano 1964; Bagnoli and Gargani 2011). Eggs have also been observed uncommonly on 1-year-old canes (Bagnoli and Gargani 2011). The fecundity of females is estimated at 10–15 eggs on average, but can reach up to 20 eggs (Vidano 1964; Cravedi et al. 1993; Bosio and Rossi 2001; Linder and Jermini 2007; Eriksson et al. 2012). One should note that this range was established using female dissections and bark examination. Therefore, such fecundity comparisons in the literature include a certain number of inaccuracies, such as the number of eggs lost during bark dissection, the number of females that oviposited, the female status when dissected, and possible egg resorption. In our opinion, the range indicated in the literature is probably underestimated. Since fecundity and fertility are key points for reproductive success and thus vector population size, an accurate evaluation is essential.

#### 4.1.1 Egg diapause outlet and cold requirements

Eggs pass the winter during a 6- to 8-month diapause stage (Fig. 6), and diapause does not require the exposure to cold temperatures to be broken (Chuche and Thiéry 2012). Hatching dynamics appear to vary a great deal according to vineyard latitude, altitude, and year. In France, hatching begins about 2 weeks earlier in Corsica than in Armagnac. It is also extended over time (Caudwell et al. 1974), more than 3 months in the former region compared with 1.5 months in the latter region (Caudwell and Larrue 1986). Such extensive hatching periods are characteristic of vineyards with mild winters, as in Corsica (Boubals and Caudwell 1971), where all stages of development (first instar to adult) can occur simultaneously. In Friuli-Venezia Giulia, hatchings begin in





**Fig. 7** Fifth nymphal instar of *Scaphoideus titanus* on a grapevine leaf

mid-May, but occur a few days earlier in the lower altitude than in the elevated vineyards, and the first nymphal instar can be found as late as the end of July or middle of August, depending on the year (Frausin 2000). These field data are perfectly matched by recent laboratory results showing that incubation temperatures regulate the beginning and length of the hatching dynamic. Cooling temperatures mainly affect the onset of hatching and are negatively correlated to cold exposure times. Most hatchings occur more quickly in cold rather than in mild winter conditions. In line with the Northern American origin of the vector, the diapause termination and, consequently, the timing regulation of egg hatching, requires cold winters (Chuche and Thiéry 2009; Chuche 2010). Females are more sensitive to incubation temperature variations. The different responses of males and females have consequences on the sex ratio dynamics of hatchings with less protandry after warm incubation temperatures (Chuche and Thiéry 2012).

#### 4.1.2 Nymphal instars

Five nymphal instars (Figs. 6 and 7) lead to adults in 7–8 weeks in France (Vidano 1964; Boudon-Padieu 2000), while this period is shorter, 5–7 weeks, in Spain (Rahola et al. 1997) and Italy (Vidano 1964). In addition to climatic conditions, additional factors probably govern larval growth speed, but they are poorly understood. Mortality is high between the first successive instars, 50 % between the first and second and between the second and third (Bernard and Du Fretay 1988). The first adults usually appear in summer, June, and July, and their lifetime is about 1 month, with females starting to lay eggs approximately 10 days after emergence (Schvester et al. 1962b). Even though *S. titanus* is univoltine, in 1987, the first nymphal instar was observed early in August in southern France. This was approximately 3 weeks after the last observation in mid-July of new-born nymphs, which was

confirmed by a similar observation for adult caged populations (Bernard and Du Fretay 1988). This interestingly suggests that *S. titanus* could produce a second generation under certain conditions, with females from the first generation producing non-diapausing eggs (Bernard et al. 1988). To our knowledge, this has not been observed another time in the field or in the laboratory. Even though the authors did not determine whether the eggs produced by a second generation underwent diapause, their results indicate the existence of a second generation in this very specific case. However, it seems very unlikely that individuals from this second generation have time to develop into adults.

Insect voltinism can undergo gradual shifts with the occurrence of partial generations in particular regions (Välimäki et al. 2008, 2013). The phenotypic plasticity in diapause induction, according to the environmental conditions, leads some species to stop their development in diapause or to produce an additional generation. As an example, the butterfly *Polygonia c-album* (Lepidoptera: Nymphalidae) is univoltine in Sweden, even though a partial second generation can occur in the southern region and a shift from one to two generations of Swedish populations is soon expected (Audusseau et al. 2013). In the same way, the planthopper *Hyalesthes obsoletus* (Hemiptera: Cixiidae), which is the vector of the phytoplasma disease bois noir in vineyards, is strictly monovoltin in Europe but is bivoltin in Israel (Sharon et al. 2005). The occurrence of a second generation should be investigated since multivoltinism is an evolutionary key in population increases, the adaptation and distribution of insects, and would have potential consequences on *S. titanus* spreading southwardly (Logan et al. 2003; Dalin 2011; Jonsson et al. 2011; Stoeckli et al. 2012).

Nymphs usually remain on the plant where they hatch (Maixner et al. 1993). However, their mobility allows them to easily travel from plant to plant. Young nymphs feed preferentially on suckers when they are not removed (Schvester et al. 1962b; Bernard and Du Fretay 1988; Posenato et al. 2001). All instars prefer the more sheltered lower and inner leaves, and even in favorable weather conditions, larvae can also be located at the apex (Bernard and Du Fretay 1988).

#### 4.1.3 Adult mating behavior

Mating among the Auchenorrhyncha, except for Cicadas, involves vibratory communication by signals transmitted via the plant (Čokl and Virant-Doberlet 2003). Males can emit calling signals within 24 h of emergence, while the earliest age of maturity in females is 6 days (Mazzoni et al. 2009b). At dusk, male *S. titanus* spontaneously emits a species-specific calling signal, thereby initiating a response from a receptive female (Mazzoni et al. 2009c). If the female responds, a mating duet will be established, with specific courtship vibratory signals being produced by the male (Mazzoni et al.

2009c). Mating lasts from 40 to 70 min and, while the males can mate several times, females only mate once (Lucchi et al. 2004; Mazzoni et al. 2009c). Mating disruption, competition, and opportunism can be observed. For example, a male close to a communicating male or female can disrupt the communication of the former and/or can silently approach the receptive female to mate with her (Mazzoni et al. 2009c). The substrate-borne vibrational signal can be transmitted from two neighboring plants, through the air beyond the boundary layer of the leaves (Eriksson et al. 2011). This facilitates long-distance communication in dense habitats such as vineyards, but the propagation, which depends on the distance between leaves, will vary with the vineyard architecture.

#### 4.2 Host range and population levels: the probability for the vector to feed on a host

*S. titanus* is mainly recorded on *Vitis vinifera* in Europe, while in North America, *Vitis labrusca* and *Vitis riparia* are reported as the preferred host plants (Vidano 1964; Maixner et al. 1993). In its native area, most individuals were found in the woods or hedges where these two wild grape species are present, while only a few individuals were observed in vineyards (Vidano 1966; Maixner et al. 1993; Beanland et al. 2006). Interestingly, this preference for American *Vitis* rather than *V. vinifera* is also observed in Europe where both species coexist (Lessio et al. 2007). However, the species of *Vitis* were not identified, and insecticide treatments targeting

the grapes may well have interfered with such observations. In Europe, *S. titanus* was also observed on *V. labrusca* and *Parthenocissus quinquefolia* (Table 3). It has also been observed occasionally on plants other than Vitaceae, such as *Salix viminalis* and *Prunus persica*, when growing in close vicinity to vines, and in large numbers on American elm (*Ulmus americana*) in the USA (Table 3). *S. titanus* was also recorded in North America on many additional plants whose host status has not yet been demonstrated (Table 3) and in various environments including forests, meadows, orchards, and bogs (Barnett 1976; Hill and Sinclair 2000). *S. titanus*, like other oligophagous species, accomplishes its whole life cycle on one genus (*Vitis*), but it can feed on other food plants. Studies on the survival of *S. titanus* on other plants outside the *Vitis* gender revealed that few species supported development to adulthood and those that did developed mainly from old nymphal instars, with a huge mortality rate (Schvester et al. 1962b; Caudwell et al. 1970; Trivellone et al. 2013). Feeding on others plants does not mean that these plants constitute host plants because no species outside of the *Vitis* genus has been shown to sustain the whole life cycle, from egg to egg, of *S. titanus*. However, that *S. titanus* can feed on other plants should be considered, particularly since they may act as pathogen reservoirs. The main scenario for the appearance of Flavescence dorée in vineyards implies a role for other vectors in introducing the phytoplasma to cultivated grapevines from wild plants. The leafhopper *Oncopsis alni* (Maixner et al. 2000; Arnaud et al. 2007) and the planthopper *Dictyophara*

**Table 3** Plants on which *S. titanus* was recorded

Family	Species	Comments	References
Amaranthaceae	<i>Amaranthus</i> sp.	Few individuals	Posenato et al. 2001
Apiaceae	<i>Daucus carota</i>	Wild grapevines and vineyards nearby	Drobnjakovic et al. 2011
Asteraceae	<i>Solidago</i> sp.		Barnett 1976
Chenopodiaceae	<i>Chenopodium</i> sp.	Few individuals	Posenato et al. 2001
Convolvulaceae	<i>Convolvulus</i> sp.	Few individuals	Posenato et al. 2001
Cupressaceae	<i>Juniperus virginiana</i>		Barnett 1976
Dryopteridaceae	<i>Onoclea sensibilis</i>		Barnett 1976
Fabaceae	<i>Vicia faba</i>	Laboratory host plant	Caudwell et al. 1970
Poaceae	–		Barnett 1976
Polygonaceae	<i>Polygonum</i> sp.		Barnett 1976
Rosaceae	<i>Crataegus</i> sp.		Barnett 1976
	<i>Prunus persica</i>		Barnett 1976; Schvester et al. 1962a
	<i>Malus</i> sp.		Barnett 1976
Salicaceae	<i>Salix</i> sp.		Barnett 1976
	<i>Salix viminalis</i>	In a vineyard, few individuals	Schvester et al. 1962a
Ulmaceae	<i>Ulmus americana</i>	Huge populations	Gibson 1973
Vitaceae	<i>Parthenocissus quinquefolia</i>	All instars, except eggs	Vidano 1964; Maixner et al. 1993
	<i>Vitis labrusca</i>		Vidano 1964; Viggiani 2002
	<i>Vitis riparia</i>	Preferred to <i>V. vinifera</i>	Maixner et al. 1993
	<i>Vitis vinifera</i>		Bonfils and Schvester 1960

*europaea* (Filippin et al. 2009) from *Alnus glutinosa* (Fagales, Betulaceae) and *Clematis vitalba* (Ranunculales, Ranunculaceae), respectively, could have acquired Flavescence dorée phytoplasma. This should be considered in Flavescence dorée epidemiology.

This specialization of *S. titanus* on *Vitis* could explain their reduced numbers of olfactory receptors and sensory neurons per *sensillum* as compared with other leafhoppers (Stacconi and Romani 2012). Despite such a reduction in olfactory sensory equipment, *S. titanus* can still detect *Vitis* leaves and shoot odours (Mazzoni et al. 2009a), but extended electrophysiological and behavioral studies have not been conducted.

In multicultivar vineyards, it is typical to observe different *S. titanus* population levels on each cultivar (Schvester et al. 1962b; Posenato et al. 2001). For example, Baco 22 A, which is sensitive to Flavescence dorée, could accommodate 5–57 times more insects than the white cultivar Villard 13 Couderc, which is more tolerant to Flavescence dorée (Schvester et al. 1962b). Differences in sensitivity were also observed in Corsica where, in a vineyard planted with Malvoisie de Corse and Grenache, the disease progressed in dense patches on the first cultivar, whereas only one vine of the second cultivar was seriously affected (Boubals and Caudwell 1971). This suggests that, although the two varieties are very susceptible, the higher frequency of contamination of Malvoisie vines was due to their higher attractiveness to the vector. In addition to investigations on cultivar sensitivity to Flavescence dorée phytoplasma (Jarausch et al. 2013), we urgently need large-scale investigations on cultivar sensitivity to the vector.

#### 4.3 Population biology: the vector density

In spring, following inoculation, phytoplasmas colonize the growing leaves via the phloem on which they multiply, thereby constituting a source of infection for *S. titanus*. However, as typical symptoms only appear in the plant in the summer following inoculation (Schvester et al. 1969), the newly infected stocks constitute an *inoculum* source for the spread of Flavescence dorée before the disease can be observed. As this pathogen has a high degree of specificity to its vector, and movements of the insect from one plant to another constitute the only natural transmission paths, the rate of infection in year  $n$  is strongly correlated with the vector population size that occurred in year  $n-1$  (Morone et al. 2007). Without any insecticide treatments, *S. titanus* populations can attain a magnitude range of 10,000 individuals per hectare (Schvester 1969). Without vector control, Flavescence dorée spreads epidemically, so that the number of infected vines can increase up to 10-fold every year and affect the entire field within a few years (EPPO/CABI 1997). In Pyrénées-Orientales (south-western France), the area affected by Flavescence dorée

abruptly increased in size by more than 300 times, from 60 ha in 1991 to 20,000 ha in 1993, in 2 years (Pueyo et al. 2008), probably because of a disease outbreak and intensifications in vineyard monitoring. In the French department of Aude, approximately 70 % of vineyards were infected only 6 years after Flavescence dorée was detected (Laurent and Agulhon 1989).

In the vineyards, the aggregated distribution of adults and larvae within plots seems to be a common pattern for this species (Bosco et al. 1997; Decante and van Helden 2006; Lessio and Alma 2006), but the spatial distribution of *S. titanus* needs further investigations to be fully understood.

*S. titanus* is crepuscular or nocturnal, and its flight activity is greatest between late afternoon and early morning (Lessio and Alma 2004b). This activity may be related to the crepuscular low dispersal ability, since night atmospheric lift is minimal (Taylor 1974) and sexual activity is highest between 18.00 and 20.00 (Mazzoni et al. 2009c). Flight activity increases with the daily minimum temperature, with maximum captures occurring above 22 °C. However, the flight activity of *S. titanus* mainly depends on the photoperiod, even though relative humidity is negatively correlated with flight (Lessio and Alma 2004b). The movement of *S. titanus* within the vineyard also depends on the vine density as well as on the canopy architecture (Lessio and Alma 2004a). This dual dependency of *S. titanus* is probably due to its movements being largely confined to the canopy (Lessio and Alma 2004a), where it moves along the vine row rather than transversely (Lessio et al. 2009a). Despite its low dispersal capabilities, in North America, there are seasonal population movements between vineyards and the surrounding forest vegetation (Weintraub and Beanland 2006).

Like in other vector-borne diseases, the estimated risk of plant infection differs greatly depending on the vector population size between years and also as a function of local environmental conditions (Gruber and Daugherty 2013). Models to improve the understanding of the spatiotemporal population and pattern of infective vector dynamics were developed. Most of them are phenology models that predict the dynamics of age structure, the beginning and the pattern of egg hatching, the occurrence of nymphal instars, and the emergence of adults (Rigamonti et al. 2011; Maggi et al. 2013; Rigamonti et al. 2013b). Others focused on biological parameters like the sex ratio (Lessio et al. 2009b), the seasonal progression of the proportion of infective vectors (Bressan et al. 2006; Lessio et al. 2009b), and the relationship between *S. titanus* population levels and diseased grapevines in the following year (Morone et al. 2007). Modeling is useful to better understand the biology of the insect and Flavescence dorée epidemiology and to better adjust *S. titanus* control. Recent modeling studies based on some of *S. titanus*' biological parameters may lead to further research that fills

knowledge gaps in the vector's population dynamics, both in time and space, and particularly on the ability of the vector to colonize *S. titanus*-free vineyards.

Variation in vector populations and vector capacities leads to differential risks of plant infection. Climatic and trophic factors driving such population variations in different geographical settings could be modeled to improve *S. titanus* control.

## 5 Relationships with phytoplasma: the vector competence

### 5.1 Feeding behavior and vectorial capacity

Food is taken in by probing the conducting vessels of the leaves, preferentially the phloem, and also on the xylem and parenchyma (Carle and Moutous 1965). Surprisingly, although the presence of typical structures, like the joint presence of a well differentiated filter chamber and aquaporins (LeCaherec et al. 1997), suggests xylemophagous habits, the phloemophagy of *S. titanus* is confirmed by the vection of phytoplasma. An early study by Carle and Moutous (1965) of the salivary sheath's path inside the vine leaves confirms that *S. titanus* may draw in the xylem sap. Perforation of the epidermis is made between two cells. The path of the stylets within plant tissues is linear, oriented toward vascular tissue, and is intra- or intercellular, according to the arrangement of the cells encountered. The formation of the setal sheath begins at the cortical parenchyma. Less than 20 % of the stylet bifurcations attain the wood parenchyma, the rest being divided equally between the xylem and phloem. No probing difference between males and females has ever been demonstrated. The nymphs prefer to feed on the small veins of the leaf blade, and the adults feed more readily on the larger veins or petioles. This preference is probably due to the difference between young instars and adult stylet lengths, but this could also be related to sap pressure. The study of these feeding behavior traits, only poorly known so far, should greatly benefit from the development of the electropenetrography technique that allows the fundamental processes of piercing–sucking insect feeding behavior to be studied (Chuche et al. 2011b).

From the first larval stage of *S. titanus*, phytoplasmas are passively acquired during feeding on infected plants (Schvester et al. 1969; Boudon-Padieu et al. 1989). A minimum feeding period is necessary to become infective, and the longer it lasts, the more likely the insect is to acquire the phytoplasma (Purcell 1982). Once infected, the insect remains a vector for the rest of its life (Christensen et al. 2005). The phytoplasma is drawn from the phloem by the stylets, then passes through the intestinal barrier, joins the hemolymph, and colonizes most of the vector organs. An incubation period of about 1 month, during which time the phytoplasma multiplies and colonizes the vector's body, is required before the vector

becomes infectious (Boudon-Padieu 2000). In the insect, phytoplasmas first multiply in the cytoplasm of gastrointestinal tract cells, particularly those of the filter chamber, foregut, and midgut (Lefol et al. 1994). Phytoplasmas then reach the hemolymph by passing between the intestinal cells and colonizing all organs, including the fat body and brain, but not the sex glands. The salivary glands are a site of intense proliferation (Lefol et al. 1993, 1994). The phytoplasma load increases in the hemolymph, and then in the salivary glands, suggesting either that the hemolymph is a late breeding site, or that it is colonized by the production of infected organs (Lefol et al. 1994). Once the concentration of phytoplasma in the salivary glands reaches a sufficient level, the infectious agent can be transmitted at an infectious dose to a healthy plant with every intake, until the death of the leafhopper. Unfortunately, several epidemiological traits, including the amount of phytoplasma ingested, the multiplication rate in *S. titanus*, and the amount of phytoplasma transmitted, are poorly known. However, the multiplication rate in the plant is known to be negatively related to temperature (Galetto et al. 2011). In the experimental Flavescence dorée leafhopper vector *Euscelidius variegatus*, D'Amelio et al. (2007) measured a Flavescence dorée phytoplasma titer increase from  $1.4 \times 10^3$  phytoplasma genome units per nanogram of insect vector DNA 14 days after a 7-day acquisition period to  $2.5 \times 10^6$  33 days after acquisition period.

The vertical transmission of Flavescence dorée is thought to be impossible because Flavescence dorée phytoplasma have never been observed in sexual organs (Schvester et al. 1969; Bressan et al. 2005a). However, since the 16SrI phytoplasma has been observed to transmit in this manner in *S. titanus*, sexual transmissibility seems to depend on the particular type of phytoplasma (Alma et al. 1997).

### 5.2 Interactions between *S. titanus* and the phytoplasma causing Flavescence dorée: the longevity of vector life after IP

Several vector-borne pathogens drive their vectors, with various effects on their biology and behavior (Maramorosch and Jensen 1963; Purcell 1982; Mayer et al. 2008; Sisterson 2009). Those effects can either be deleterious (García Salazar et al. 1991; D'Amelio et al. 2008; Malagnini et al. 2010) or, conversely, beneficial, particularly in terms of longevity and fertility (Purcell 1988; Beanland et al. 2000; Ebbert and Nault 2001; Sugio et al. 2011). Flavescence dorée phytoplasma reduces the lifespan of infected males and females and also reduces female fecundity and fertility, leading ultimately to smaller offspring (Bressan et al. 2005a). Pathogenicity decreases with the age of vector–pathogen relationships, which suggests a recent association of *S. titanus* with Flavescence dorée phytoplasma (Madden and Nault 1983; Ebbert and Nault 2001; Elliot et al. 2003; Weintraub and Beanland 2006). However, the rather homogenous distribution over large areas in Europe will

counterbalance a reduction in the virulence of the pathogen towards the vector (Elliot et al. 2003).

The transmission of phytoplasma strains responsible for Flavescence dorée is species specific in Europe, and *S. titanus* cannot transmit other phytoplasmas responsible for grapevine yellows in Europe (Carraro et al. 1994). However, *S. titanus* can transmit phytoplasma from the 16SrI group. Thus, several strains were found in natural populations, and these could be transmitted in the laboratory to broad bean (*Vicia faba*) (Alma et al. 1997). Laboratory transmission assays were successful with other phytoplasmas of the same group. Thus, a phytoplasma identified as belonging to the 16SrI-C called  $\varphi$  (Boudon-Padieu et al. 1990) was experimentally transmitted to the vine by *S. titanus* (Caudwell et al. 1971). In addition, a 16SrI-B group phytoplasma was experimentally transmitted to *Glebionis carinata* (syn. *Chrysanthemum carinatum*), but with a low efficiency (Alma et al. 2001). *S. titanus* is also able to transmit Flavescence dorée to *V. faba* and probably also to *C. carinatum* (Caudwell et al. 1970). In North America, phytoplasmas related to Flavescence dorée were detected in *S. titanus* via enzyme-linked immunosorbent assay (Maixner et al. 1993) and PCR (Olivier et al. 2008), but they could not be identified more accurately.

In addition, *S. titanus* was expected to transmit the virus causing grapevine corky-bark disease (Moutous and Hevin 1986), whose major vector is the mealybug (Namba et al. 1991), but the Grapevine Virus B causing the disease was not known at the time. Thus, Koch's postulates could not be demonstrated, and transmission rates were only checked by symptom expression on susceptible grape cultivars. The putative role of *S. titanus* in corky-bark disease transmission needs to be confirmed by new studies.

Several parameters influence the transmission efficiency of Flavescence dorée. The transmission rate of the phytoplasma in the laboratory is higher in males than in females (Schvester et al. 1969). The same phenomenon was observed for the transmission by *S. titanus* of yellows close to Flavescence dorée in New York State (Maixner et al. 1993) and also in *E. variegatus* (Kuszala 1986; Boudon-Padieu et al. 1989). In addition, the proportion of males carrying phytoplasma is always higher in vineyards than that of females, and both rates increase during the season (Lessio et al. 2009b). Phytoplasma can be acquired from hatching, and the proportion of vectors carrying phytoplasma increases with the instar (Bressan et al. 2006). The more effective phytoplasma acquisition by older instars may be partly explained by the increased concentration of phytoplasma in phloem over time (Bressan et al. 2005b), and by different forms of feeding behaviors. Plant quality also has an influence on feeding behavior and, therefore, on the effectiveness of the acquisition of phytoplasma by *S. titanus*, with several known susceptible grape cultivars being better sources of inoculum (Bressan et al. 2005b). Different concentrations of phytoplasmas among tolerant and

sensitive varieties (Bosco and Marzachi 2011; Eveillard et al. 2012), and a possible difference in feeding behavior on the two kinds of grapes, may explain the different rates of acquisition (Bressan et al. 2005b). The effectiveness of phytoplasma acquisition also depends on the infected plant species. Alma et al. (2001) have shown that the same phytoplasma could be acquired by three leafhopper species, *Macrosteles quadripunctulatus*, *Euscelidius variegates*, and *Euscelidius incisus*, depending on the host plant species. Thus, the acquisition of Flavescence dorée phytoplasma by *S. titanus* on broad bean is more efficient than on vine (Bressan et al. 2005b).

Feeding behavior is a key factor in the phytoplasma–vector relationship and, therefore, in the Flavescence dorée epidemic. The deleterious effects of Flavescence dorée phytoplasma on *S. titanus* suggest a recent association between the pathogen and the vector.

## 6 Vector management: current options

There is, as yet, no efficient way to control phytoplasma in the plant or vector. As in many insect-borne diseases, controlling the vector is the only current strategy. In addition to the use of insecticides, some prophylactic actions could be performed to decrease the risk of Flavescence dorée.

### 6.1 Vector control

Flavescence dorée phytoplasma is a quarantined pest in the EPPPO region and was declared a quarantined pest by the European Union in 1993 (Directive 77/1993 amended 92/103). The declaration of the disease and the various control measures were made mandatory by two ministerial decrees in France (April 17, 1987 and April 1, 1994) and one in Italy (May 31, 2000). Control of the Flavescence dorée epidemic requires mandatory use of insecticides against the vector. Vector control is primarily directed against mobile instars (nymphs and adults) and is based on the use of insecticides. Treatments against eggs can also be applied in the winter. Currently, the mandatory control of *S. titanus* is based on one or two treatments a year in Italy (Belli et al. 2010), two in Switzerland (Jermini et al. 2007), and three, or possibly two, depending of the size of the vector population, in France (Trespaille-Barrau and Grosman 2011). Thus, in 2011, more than 450,000 ha were under mandatory control, representing almost 50 % of French vineyards (Trespaille-Barrau, 2012, personal communication). Presently, pyrethrinoids are used, with basic products costing between 4 and 25 €ha<sup>-1</sup> in France (Grossman, 2012, personal communication), while other neurotoxins and growth regulators are used in Italy and Switzerland (Table 4).

In France, reducing the three mandatory insecticide applications was tested from 2000 to 2003, and since 2004 has been

**Table 4** Insecticides used against *S. titanus*

Chemical class	Chemical name	Mode of action	Country	References
Natural product	Pyrethrins	Neurotoxic	France, Italy, Switzerland	COSVIR XI 2013; E-phy 2013; OFAG 2013
Neonicotinoid	Thiamethoxam	Neurotoxic	Italy	COSVIR XI 2013
Organophosphorus	Chlorpyrifos	Neurotoxic	France, Italy, Switzerland	COSVIR XI 2013; E-phy 2013; OFAG 2013
Pyrethrinoid	Betacyfluthrin	Neurotoxic	France	E-phy 2013
	Cyfluthrin	Neurotoxic	France	E-phy 2013
	Cypermethrin	Neurotoxic	France, Italy	COSVIR XI 2013; E-phy 2013
	Deltamethrin	Neurotoxic	France, Italy	COSVIR XI 2013; E-phy 2013
	Esfenvalerate	Neurotoxic	France	E-phy 2013
	Cyhalothrin	Neurotoxic	France, Switzerland	E-phy 2013; OFAG 2013
	Tau-fluvalinate	Neurotoxic	France	E-phy 2013
	Acrinathrin	Neurotoxic	France, Italy	COSVIR XI 2013; E-phy 2013
Thiadiazin	Buprofezin	Growth regulator	Italy, Switzerland	COSVIR XI 2013; OFAG 2013
Blend				
Neonicotinoid+Anthranilic diamide	Thiamethoxam+Chlorantraniliprole	Neurotoxic	France	E-phy 2013
Organophosphorus	Dimethoate+Chlorpyrifos	Neurotoxic	France	E-phy 2013
Organophosphorus+Pyrethroid	Chlorpyrifos+Cypermethrin	Neurotoxic	France	E-phy 2013
	Chlorpyrifos+Deltamethrin	Neurotoxic	France, Italy	COSVIR XI 2013; E-phy 2013

increasingly applied (Decoin et al. 2005; Trespaille-Barrau and Grosman 2011; van Helden et al. 2011). Rules determining the number of treatments depend on regional settings. In the Saint Emilion vineyard (East of Bordeaux) plots situated 2–4 km from a Flavescence dorée focus received no larvicide treatments, while one or two treatments against nymphs are applied in those that are closer (Dufour et al. 2008). Treatment against adults is made if more than three adults are caught on yellow sticky traps during a week. In Bordeaux, 90 % of the vineyards received only two applications (Trespaille-Barrau and Grosman 2011). However, this insecticide reduction is costly (26 €ha<sup>-1</sup>) because of increased monitoring (Dufour et al. 2008), and the consequences of this reduction on the epidemic will be better known in the coming years. In the Piemonte region, the two treatments can be reduced to one if the *S. titanus* population level is under 0.02 nymphs per five leaves per plant and less than two adults are captured on three traps per season (Bosco and Mori 2013).

Treatment reductions cannot be used in vine nurseries. Indeed, all nurseries have to be treated from the first hatching of *S. titanus* to the adult instar (May to September) in France. The number of treatments performed depends on the persistence of the insecticide employed.

The mandatory control of *S. titanus* is problematic for organic production because organic growers can only use natural pyrethrins that are neither sufficiently efficient nor persistent, especially against adults, the most dispersive instar (Gusberty et al. 2008; Sivčev et al. 2010). It is also a problem for growers that decrease their insecticide use by practising pheromonal

mating disruption to control the pests *Lobesia botrana* and *Eupoecillia ambiguella* (Lepidoptera, Tortricidae). Mandatory treatments impede their sustainable approach to agriculture. However, mating disruption using synthetic moth sexual pheromones against grape moth are rather limited in European viticulture, about 25,000 and 20,000 ha in France and Italy, respectively, in 2012. Prophylactic measures can be used to reduce vector populations. The destruction of woody canes carrying eggs after pruning reduces *S. titanus* numbers and, thus, Flavescence dorée transmission. Pruning was cited as a partial explanation for the differences in density observed in the early 1960s between two southwestern areas, Armagnac and the Chalosse (long pruning, highest densities), and Bordeaux (short pruning, lowest densities) (Schvester 1962; Schvester et al. 1962b).

## 6.2 Use of healthy planting material

The prophylaxis of plant material has unfortunately been neglected for years, while the relation of the epidemic to vine trading activities now receives more attention. It is possible to ensure vineyard safety by destroying the phytoplasmas that may be harbored by grapevine seedlings, and the eggs of *S. titanus* laid under the bark, by immersion in hot water (Caudwell et al. 1990, 1997; Linder et al. 2010). A 45-min immersion in water at 50 °C eliminates microorganisms and eggs without causing the death of vines (Caudwell et al. 1997). Hot-water treatments are compulsory in Australia and New Zealand for multiplicative materials, in Canada for

imports from countries where phytoplasma diseases of grapevines occurs, are routinely used in France, and are being developed in certain other countries, like Italy and Switzerland (Bianco et al. 2000; Dupraz and Schaub 2007; Mannini 2007; Canadian Food Inspection Agency 2009).

### 6.3 The removal or control of Flavescence dorée and *S. titanus* reservoirs

The removal of diseased stocks and abandoned vines, as well as the new growth of wild vines, avoids the formation of disease reservoirs that might result in the contamination of nearby vineyards (Boudon-Padieu 2000). In addition, these areas can serve as refuges for the vector, therefore reducing the effectiveness of their control (Forte et al. 2009). In France, uprooting is mandatory for infected Flavescence dorée hosts, and when 20 % of diseased plants are detected, the whole plot must be removed (Boudon-Padieu 2002). In Italy, however, stocks with grapevine yellows symptoms are uprooted only in areas with Flavescence dorée outbreaks (Belli et al. 2010). In Lombardy, the control strategy is partially based on the destruction of uncultivated vineyards (Belli et al. 2010), and recommendations to growers in the Piemonte region involve the destruction of wild vegetation surrounding the vineyard by mechanical and chemical means (Bosco and Mori 2013). After pruning, the burning or burying of egg-carrying cut wood is preferred to grinding because it suppresses more eggs (Cazenove and Planas 1991; Boudon-Padieu 2000; Bosco and Mori 2013). Since the nymphal density is higher on suckers than in the canopy, the frequent removing of suckers can contribute to decreased *S. titanus* population levels in vineyards (Schvester et al. 1962b; Bernard and Du Fretay 1988; Cazenove and Planas 1991; Posenato et al. 2001; Cara et al. 2013).

### 6.4 Reducing the probability of vector survival by biological control agents

*S. titanus* population levels observed on *V. vinifera* in France are significantly higher than those in the USA (Maixner et al. 1993), which suggests that the native natural enemies, which are more efficient in the original area, were not introduced with the vector. However, natural enemy pressure against *S. titanus* is lower in both continents (Schvester et al. 1962b; Bernard and Du Fretay 1988; Malausa and Sentenac 2011) than for other grape pests. In Europe, for example, grapevine moth larvae can be parasitized up to between 50 and 80 % depending on the vineyard (Marchesini and Monta 1994; Thiéry et al. 2001; Bagnoli and Lucchi 2006; Xuéreb and Thiéry 2006). In North America, several species of parasitoids, Hymenoptera Dryinidae and Diptera Pipunculidae were observed on *S. titanus* (1.3 and 0.8 %, respectively) (Barnett 1976), and also Hymenoptera Mymaridae and

Trichogrammatidae, but not with quantified parasitism rates (Table 5) (Malausa et al. 2003). Interestingly, *S. titanus* seems to have a special relationship with the predatory bug *Malacocoris chlorizans* (Hemiptera: Miridae). This bug does not feed on *S. titanus* but can stimulate its honeydew production through contact between its antennae and the abdomen of the leafhopper when feeding on the liquid (Carle 1965), as is the case in aphid–ant interactions (Stadler and Dixon 2005). These are laboratory observations, but vineyard monitoring showed that populations of *M. chlorizans* are associated and synchronized with the occurrence of *S. titanus* (Carle 1965).

Biological control of *S. titanus* has been attempted, either by releasing natural enemies from their native habitat or by increasing local natural enemy populations; however, these two strategies have yielded poor results so far (Malausa and Sentenac 2011). In France, the release of *Gonatopus flavipes* (Hymenoptera: Dryinidae) was performed during three successive years in two experimental sites (Burgundy and Côtes du Rhône vineyards). In total, 368 adults were released and 46,000 *S. titanus* were collected and examined. The best parasitism rate was very low, <0.4 % (Malausa and Sentenac 2011). The apparently very low efficiency of this parasitoid is magnified by the difficulty of rearing it.

### 6.5 Vector monitoring

The monitoring of *S. titanus* can be achieved using four main techniques, counting the number (1) of nymphs on the underside of leaves, (2) after beating, (3) using a suction apparatus as, for example, D-vac, and (4) using sticky traps, with the last two techniques being preferential for adults, which are more mobile than larvae (Table 6). The accuracy of these techniques is variable; thus, they should be considered only as estimates. For example, after rainfalls, nymphs were not observed on leaf counts for a period of up to 3 days (Bernard et al. 1988), while they were still present on the plot. All monitoring methods are susceptible to variations in efficiency depending on the weather, the season, the vineyard management, and plant position in the vineyard (internal or bordering). The effectiveness of traps is the most dependent on weather conditions (temperature, wind, and rain) and population density, which poses the problem of trap reliability in agronomy and plant protection. With low population densities, it is necessary to enhance the catch number in the plot to obtain a reliable estimate of population size (Jermini et al. 1992). Capture samples do not account for the relative importance of males and females, as more males than females are captured (Bosco et al. 1997; Lessio et al. 2009b). In addition, the sex ratio of trapping varies with location and the particular season, with more males being caught at the beginning of adult emergence, and more females at the end of the season (Lessio et al. 2009b). This time variation occurs because the males emerge first and have shorter lives than females (Bressan et al. 2005a).

**Table 5** Natural enemies of *S. titanus*

Order	Family	Species	Kind of enemy	Target instar	Country	References		
Insects	<i>Diptera</i>	<i>Pipunculidae</i>	<i>Eudorylas</i> sp.	Parasitoid	Larvae; adults	France	Malause and Sentenac 2011	
		<i>Syrphidae</i>	–	Predator	Larvae	France	Schvester et al. 1962b	
	<i>Hemiptera</i>	<i>Reduviidae</i>	–	Predator	Larvae	France	Schvester et al. 1962b	
	<i>Hymenoptera</i>	<i>Dryinidae</i>	<i>Anteon masoni</i>	Parasitoid	Larvae; adults	USA	Malause et al. 2003	
			<i>Anteon pubicorne</i>	Parasitoid	Larvae; adults	France	Malause and Sentenac 2011	
			<i>Esagonatopus niger</i>	Parasitoid	Larvae; adults	USA	Malause et al. 2003	
			<i>Esagonatopus perdebilis</i>	Parasitoid	Larvae; adults	USA	Malause et al. 2003	
			<i>Gonatopus audax</i>	Parasitoid	Larvae; adults	France	Malause and Sentenac 2011	
			<i>Gonatopus clavipes</i>	Parasitoid	Larvae; adults	France	Malause and Sentenac 2011	
			<i>Gonatopus lunatus</i>	Parasitoid	Larvae; adults	France	Malause and Sentenac 2011	
			<i>Gonatopus peculiaris</i>	Parasitoid	Larvae; adults	USA	Malause et al. 2003	
			<i>Lonchodryinus flavus</i>	Parasitoid	Larvae; adults	USA	Malause et al. 2003	
			<i>Mymaridae</i>	<i>Polynema</i> sp.	Parasitoid	Eggs	USA	Malause et al. 2003
				–	Parasitoid	Eggs	Europe	Malause and Sentenac 2011
				<i>Trichogrammatidae</i>	<i>Oligosita</i> sp.	Parasitoid	Eggs	USA
Mites			<i>Acarina</i>	<i>Anystidae</i>	<i>Anystis baccarum</i>	Predator	Larvae	France
	<i>Bdellidae</i>	–		Predator	Larvae	France	Chuche, personal observation	
Spiders	<i>Araneae</i>	<i>Philodromidae</i>	–	Predator	Larvae	Italy	Chuche et al. 2011c	
		<i>Thomisidae</i>	–	Predator	Larvae	Italy	Chuche et al. 2011c	

Additionally, males are active before mating (Mazzoni et al. 2009c), while mated females must displace themselves to lay their eggs later in the season. The effect of color on trap efficiency is still controversial and not fully understood. A yellow color is mainly used and seems the most attractive to nymphs and adults in the field (Chuche et al. 2011a; Mazzoni et al. 2011), while a red color attracted females in a laboratory experiment (Mazzoni et al. 2011) and males in a vineyard study (Lessio and Alma 2004a). Globally, the use of yellow sticky traps seems to be an effective compromise for all stages and both sexes. The position of the traps in vineyards also has an effect. Indeed, horizontal positioning, either in the foliage or underneath the plants, allows more insects to be captured than vertical positioning (Jermini et al. 1992).

In an integrated pest management context, the use of control methods is dependent on monitoring. The presence and the population level of the vector are key factors in the decision to

trigger a control and the type of control, but also to assess its effectiveness. To overcome the imprecision of monitoring methods, monitoring plans were developed (Jermini et al. 1993; Lessio and Alma 2006; Rigamonti et al. 2013a).

Currently, the Flavescence dorée risk is limited by vector control, the use of healthy plant materials and the removal of potential phytoplasma reservoirs. To decrease pesticide use, a cross survey of the vector population and of the infected hosts triggers the mandatory treatments.

## 7 Future directions for research and management

### 7.1 Vector control

Knowledge of the phenology of *S. titanus* is crucial for a timely application of insecticides. A phenology model was

**Table 6** Monitoring methods of *S. titanus*

Method	Which instar?	Efficiency	Factors of variation	Use
Countings	Nymphs	Good	Rainfalls	Time consuming, needs skilled people able to recognize quickly <i>S. titanus</i>
Beating the canopy	Mainly nymphs	Good	Rainfalls	Catch many arthropods and needs sorting
Suction collect	All	Good	Rainfalls	Catch a lot of arthropods and plant material, Needs many sorting
Yellow sticky traps	Mainly adults	Poor	Male and females differentially attracted. Depends upon adults' displacement. Wind and rainfalls	Easy even if non selective



**Table 7** Summary of important key research topics for the management of *S. titanus*

Research topics	Possible application	Status	
Vector feeding behavior	Feeding deterrents/push-pull	To be evaluated	
	Cultivar selection	To be evaluated	
Symbionts characteristics	Reducing feeding behavior and fitness	In progress	
	Blocking pathogen transmission	In progress	
Field dispersion characteristics	Developing spatial models	To be urgently developed	
	Improving risk assessment and insecticide treatment decision	In progress	
	Adapting the vineyard architecture/pruning type	To be evaluated	
Relationships between the vector and the pathogen	Understanding how the phytoplasma can alter the behavior of the vector	To be urgently developed	
	Evaluating the ability to transmit other pathogens	To be evaluated	
Better knowledge of the FD host plant system	Characterizing the risky plant reservoirs	To be evaluated	
	Managing of the weed plants surrounding vineyard	In progress	
Phenology of the vector/population dynamic			
	1—Population dynamic	Adjusting the treatment periods of the year	In progress
	2—Voltinism	Developing temporal dynamic models	To be urgently developed
Mating disruption	Transferring semi-fields results to a larger scale	In progress	

designed by Rigamonti et al. (2011) to improve the timing of insect growth regulator applications. A population model was also developed and allowed to determine that *S. titanus* dynamics are generally more susceptible to variations in biological timing parameters than rates (Maggi et al. 2013). These models support decision makers in making pest management operations more sustainable while strongly reducing the risk of Flavescence dorée's spread. Similar studies are needed to improve vector population control. These should include the effect of temperature on the dynamics of hatching that, in turn, affects the dynamics of the successive instars (Chuche and Thiéry 2009). Since improved timing requires reliable indicators of the insect's presence, the development of more efficient monitoring strategies is crucial (Table 7). Additionally, the dispersal capacity and the effect of vineyard architecture on the vector's dispersion require more attention.

## 7.2 Breaking the phytoplasma cycle

To date, no resistance or tolerance to grapevine yellows has been detected in the *Vitis* species considered (Laimer et al. 2009), despite the use of phytoplasma resistance detection methods (Jarausch et al. 1999; Sinclair et al. 2000; Cardena et al. 2003). Since selection and breeding methods do not seem to be promising solutions over the short and medium term, the development of transgenic grapevines represents a perspective (Laimer et al. 2009). Conclusive tests have been conducted with *Paulownia* sp. expressing antibacterial peptides of the Lepidoptera *Hyalophora cecropia* (Du et al. 2005). However, tests conducted with transgenic tobacco plants targeting the stolbur phytoplasma have so far been unsuccessful (Malembic-Maher et al. 2005). While using genetically

modified vines may constitute a technical issue, the consumer acceptance of genetically modified organisms for high quality and expensive wines may represent a limiting factor.

Symbiosis is a key driver of much insect biology, especially in Hemiptera. Symbionts may confer several benefits, such as improving nutrition, countering the host's defenses, increasing protection against natural enemies, and improving development and reproduction (Wu et al. 2006; Oliver et al. 2010; Frago et al. 2012); however, they may also have adverse effects in some cases, such as lifespan shortening and fertility reduction (Alam et al. 2011; Nakamura et al. 2012; Schraiber et al. 2012). Since symbionts are essential to insect development and adaptation, innovative and exciting biological vector control methods attempt to use such symbiotic relationships in controlling populations of vector-borne diseases (Hurd 2003; Riehle and Jacobs-Lorena 2005). Among natural biological control agents, the use of endosymbionts, like *Wolbachia*, seems encouraging, especially those acting to shorten lifespans (Cook et al. 2008) or block pathogen transmission (Bian et al. 2013). Interestingly, symbiotic bacteria of the genus *Cardinium*, which are responsible for impaired reproduction and behavior, were found in natural populations of both *S. titanus* sexes with a high prevalence (>94 %) and in different organs (ovaries, fat body, midgut, and salivary glands) (Marzorati et al. 2006; Sacchi et al. 2008). Symbionts were also observed coexisting with "*Ca. Phytoplasma vitis*" in the same *S. titanus* organs, which raises questions about the possible role of this bacterium in the transmission of the phytoplasma (Marzorati et al. 2006). So-called "yeast-like" symbiotes belonging to the ascomycete lineage, which could play a metabolic role and could be transmitted vertically, have also been discovered (Sacchi et al. 2008). Finally, *S. titanus* can also host symbiotic bacteria of

the genus *Asaia*, transmitted vertically by the female as well as by the male during mating, that can equally be acquired horizontally during feeding (Marzorati et al. 2006; Crotti et al. 2009). Some authors already suggested using these symbionts to decrease the vector's capacity for *S. titanus* (Marzorati et al. 2006; Crotti et al. 2009). In coming years, this approach should receive further consideration (Table 7).

### 7.3 Integrated vector management

Integrated vector management is currently the most promising and feasible management technique for sustainable viticulture. Behavior modification is an interesting *S. titanus* population management model (Table 7). The two main methods are mating disruptions and push-pull strategies.

As discussed, *S. titanus* uses vibrations transmitted by the leaf to mate and, therefore, vibrational disturbances would cause mating disruptions. Sexual disruption was successful in the laboratory and the first field-scale experiments were also promising (Mazzoni et al. 2009b; Eriksson et al. 2012). The challenge is to transfer these results to a larger scale. A similar strategy could not be extended to larval behavior disturbances because the nymphs do not use communication based on vibrations (Chuche et al. 2011c).

“Push–pull” strategies involve manipulating insect behavior via the combined use of attractive and repulsive items, including lures or plants capable of drawing pests into an area where they will be destroyed (Cook et al. 2007). The use of this technique against vectors of phytoplasma in grapes has already shown promising results against *H. obsoletus* in Israel (Zahavi et al. 2007), and could be effective against *S. titanus*. Repellents could include kaolinite clay particles, which have been employed in field trials and seem good candidates against piercing–sucking insects. They are already used in North American vineyards (Daniel et al. 2005; Duval and Weill 2007; Tubajika et al. 2007; Marko et al. 2008). As mentioned above, American *Vitis* are more attractive than *V. vinifera*. Thus, we could combine less attractive harvested grapes after treatment, with kaolin particles for example, with vineyard borders of more attractive American *Vitis*. Leafhoppers would be pushed from the crop while simultaneously being pulled to the American *Vitis*. Growers could then control *S. titanus* populations by spotted insecticide applications or the application of mineral oils to bark (Caudwell et al. 1972).

The development of alternative sustainable methods or strategies is now required to reduce insecticide use and to increase the control efficiency (Table 7). In the short term, new models could support making pest management operations more sustainable. In the long term, innovative techniques involving symbionts, mating disruptions, and/or push–pull strategies could improve *S. titanus* and Flavescence dorée control with less impact on the environment.

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