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Research

Seasonal Dynamics of *Spissistilus festinus* (Hemiptera: Membracidae) in a Californian Vineyard

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Abstract

The three-cornered alfalfa hopper, *Spissistilus festinus* (Say) was shown to transmit *Grapevine red blotch virus* (GRBV) in a greenhouse study. GRBV is the causal agent of Grapevine Red Blotch Disease, which reduces the quality of wine produced from infected grapes. Due to the general lack of prior concern regarding *S. festinus* on grapevines, the biology of this species in vineyards has been largely unknown. A 2-yr study with weekly sampling was conducted in a Californian vineyard to increase the knowledge of *S. festinus* seasonal dynamics and distribution. The overwintering *S. festinus* adults were first captured in the vineyard before bud break. Detection of late-instar *S. festinus* nymphs, the first in-field adult generation, and grape anthesis occurred concurrently in 2016 and 2017. Two in-field *S. festinus* generations were documented by peaks in sweep net sampling of vineyard groundcover in 2016, whereas only one generation was observed in 2017. There appears to be an inverse relationship between the number of *S. festinus* adults sampled on ground cover and the number of girdles in the grapevine canopy. *Spissistilus festinus* exhibited an aggregated distribution in the vineyard and a significant edge effect. Results from this study will contribute to the development of sampling and management guidelines and determine timing of control measures to reduce populations of *S. festinus* within vineyards to minimize the virus spread.

Key words: *Spissistilus festinus*, three-cornered alfalfa hopper, seasonal dynamics, *Grapevine red blotch virus* (GRBV), SADIE

Spissistilus festinus (Say) has primarily been studied in the southern United States as a pest on alfalfa, peanuts, and soybeans (Wildermuth 1915, Beyer et al. 2017). In addition to crop hosts, *S. festinus* feeds and reproduces on a variety of alternative hosts that include resident weeds (Osborn 1911, Wildermuth 1915, Moore and Mueller 1976, Mitchell and Newsom 1984, Preto et al. 2018a). *Spissistilus festinus* undergoes hemimetabolous development and progresses through four to six instars during development, although five instars are the most common (Wildermuth 1915, Moore and Mueller 1976). These treehoppers are capable of producing one to four generations per annum, determined by the availability of host plants and weather (Wildermuth 1915, Mitchell and Newsom 1984). *Spissistilus festinus* are known for their distinctive feeding pattern that causes necrotic tissue to form around petioles and young shoots resulting in a girdle (Wildermuth 1915).

Spissistilus festinus had previously been referred to as an occasional pest on grapevines due to girdles resulting from their feeding (Smith 2013). However, its perceived pest status increased considerably when it was discovered to be a vector of *Grapevine red blotch virus* (GRBV) in grapes in a greenhouse study (Bahder et al. 2016). GRBV is the causal agent of Grapevine red blotch disease (GRBD) (Al Rwahnih et al. 2013, Varsani et al. 2017, Yepes et al. 2018). GRBD is responsible for reducing sugar accumulation in berries and delaying grape maturity resulting in negative impacts on aroma, flavor, and color in wine produced from infected grapes (Calvi 2011, Wallis and Sudarshana 2016, Blanco-Ulate et al. 2017). In attempting to limit the spread of new GRBV infections, the wine industry became eager to learn about *S. festinus* biology, behavior, and seasonal dynamics in relation to grapevines.

The primary objective of this study was to assess the abundance and distribution of *S. festinus* in vineyards and surrounding vegetation in Northern California. Results from this study can serve as a baseline for future ecological studies but also provide valuable insight into the biology of *S. festinus*, so growers can better implement management strategies. By knowing when peak abundance occurs throughout the year and where in vineyards *S. festinus* is

most prevalent, growers can implement cost-effective management decisions to provide the most significant level of control in order to reduce the spread of GRBV.

Materials and Methods

Vineyard Description

The study was conducted in a research vineyard located at the University of California Oakville Research Station, Napa County, CA (38° 25′ 46.0884″ N, 122° 24′ 31.1724″ W, elevation 57 m). The vineyard block consisted of 51 rows of 30 spur-pruned bilateral cordon vines on vertical shoot position trellising. Grapevines were Cabernet Sauvignon (FPMS clone 8) vines grafted onto 420A, 101-14Mgt, and 110R rootstocks planted in 1994. Vine spacing was 1.8 m by 2.4 m within and between rows, respectively with a west to east orientation. The north, west, and south ends of the vineyard block were in close proximity to other vineyard blocks whereas the east edge of the vineyard was ~7.6 m from an irrigation ditch that paralleled that border. Grapevines were watered by drip irrigation.

Fifty-two ground rows were each located between adjacent grapevine rows. Vegetation was tilled under for odd numbered ground rows and resident vegetation remained in even numbered ground rows, which is standard practice for most California growers. Native vegetation varied throughout the vineyard but included the following known reproductive hosts: *Acmispon americanus* (Spanish clover), *Convolvulus arvensis* (field bindweed), *Medicago polymorpha* (bur clover), *Senecio vulgaris* (common groundsel), *Taraxacum officinale* (dandelion), and *Vicia* spp. (vetch) (Wildermuth 1915, Mueller and Dumas 1987, Preto et al. 2018a).

Sampling

Sampling by sweep net was chosen based upon previous research that determined sweep nets to be effective at assessing adult populations of *S. festinus* (Kogan and Herzog 1980, Rahman et al. 2007). Three weeks after *S. festinus* was announced as a vector of GRBV in grapes (Bahder 2016), sweep net samples commenced and were taken every week from 16 March 2016 until 19 March 2018. The vineyard block was removed after the last sample date due to extensive GRBV infection. Even numbered ground rows were sampled using bidirectional sweeps of ground vegetation with an aerial sweep net (#7318NA, BioQuip Products, Rancho Dominguez, CA) every week in three sections denoted by A: the distance of the first six vines on the west side, B: the distance of the middle eighteen vines, and C: the distance of the last six vines on the east side. Additionally, the ground cover immediately adjacent to the west and east sides of the block were sampled, as well as the ground cover located near the four cardinal points of an irrigation pond located approximately 85 m north of the vineyard. The number of *S. festinus* nymphs and adults and sex of the adults were recorded for each sample location. Ultimately, only fourth and fifth instar nymphs were successfully detected in our sweep net samples. In addition to the *S. festinus* sampled, our collection also documented the presence of another adult treehopper found in the vineyard, *Tortistilus* spp. (Hemiptera: Membracidae).

In 2016, yellow sticky cards (7.6 × 12.7 cm) were suspended between vines from both the cordon and irrigation wires in five of the sampling locations. Sticky cards suspended from the irrigation wires were approximately 30.5 cm from the soil surface which, according to Johnson and Mueller (1989), is within the optimal height range of 0–33 cm for sticky card placement for trapping *S. festinus* in soybean. The placement of yellow sticky cards in the vineyard was not repeated in 2017/2018 due to the lack of treehoppers collected using this method. Wistrom et al. (2010) showed few adult *S. festinus* collected on sticky cards in comparison to the active sampling method of beat-sweeps and Cieniewicz et al. (2018) also suggested that sticky cards may not give an accurate estimate of insect populations in comparison to sweep nets.

Girdle Counts

In 2017, girdle counts commenced 3 wk after bud break on April 27 and continued until the sample date prior to leaf drop on November 30. Girdles were counted and removed every 2 wk from six rows containing five vines each located within the same vineyard. Girdles were documented as being located on the apical shoot or leaf petiole and counted only if necrosis extended around the entire petiole or shoot. Girdle counts were not repeated in 2018 as the vineyard block was removed before bud break.

Data Analysis

Spatial data were analyzed using R Statistical Software version 1.0.143 (R Development Core Team 2016). A Spatial Analysis by Distance IndicEs (SADIE) analysis was used to determine if the yearly distribution of *S. festinus* was random, uniform, or aggregated (Perry 1995, 1998; Holland et al. 1999; Li et al. 2012). A SADIE Red-Blue method was used to determine location and significance of *S. festinus* aggregation gaps and clusters (Perry et al. 1999) using the 'sadie' function in the 'epiphy' package (Gigot 2018). To determine if there was a significant edge effect, a one-way ANOVA was used to compare treehopper densities found on the edges of the vineyard (sections A, C) versus the center (section B). Treehopper density was standardized by section length and calculated as the count of insects divided by the distance of the given section with distance being a fixed effect. Assumptions of the one-way ANOVA were independence, homoscedasticity, and normality.

Results

Seasonal Dynamics

In 2016, adult *S. festinus* were already present in the vineyard on the first sample date (March 16; Fig. 1). The first detection of overwintering adult *S. festinus* in the vineyard occurred on February 15 and February 1 in 2017 and 2018, respectively. In all 3 yr, the overwintering *S. festinus* adults were detected in the vineyard before bud break (Fig. 1). Bud break was documented on March 23 and April 6 of 2016 and 2017, respectively (noted by arrows in Fig. 1). The vineyard was removed in 2018 prior to bud break, which occurred sometime after our last sample on March 19 (Fig. 1). The first detection of nymphs, representing the first seasonal in-field generation as confirmed by a dramatic increase in *S. festinus* adult densities that followed, and grapevine anthesis occurred concurrently on the May 17 and May 23 in 2016 and 2017, respectively (Fig. 1). Two in-field generations appeared to occur based on sweep net sampling in 2016 whereas only one in-field generation was observed based on sweep net sampling in 2017 (Fig. 1). Resident vegetation was noted to be drying on August 3 and August 10 in 2016 and 2017, respectively with the adult population notably decreasing during this time (Fig. 1). Major fires occurred in Napa Valley and neighboring areas between October 8 and 31 of 2017 that obscured the sun by smoke, and mandatory evacuations of the area delayed our sampling by 1 wk during this time. The male to female ratio fluctuated throughout the 2-yr sampling period but both males and females were present throughout the duration and also

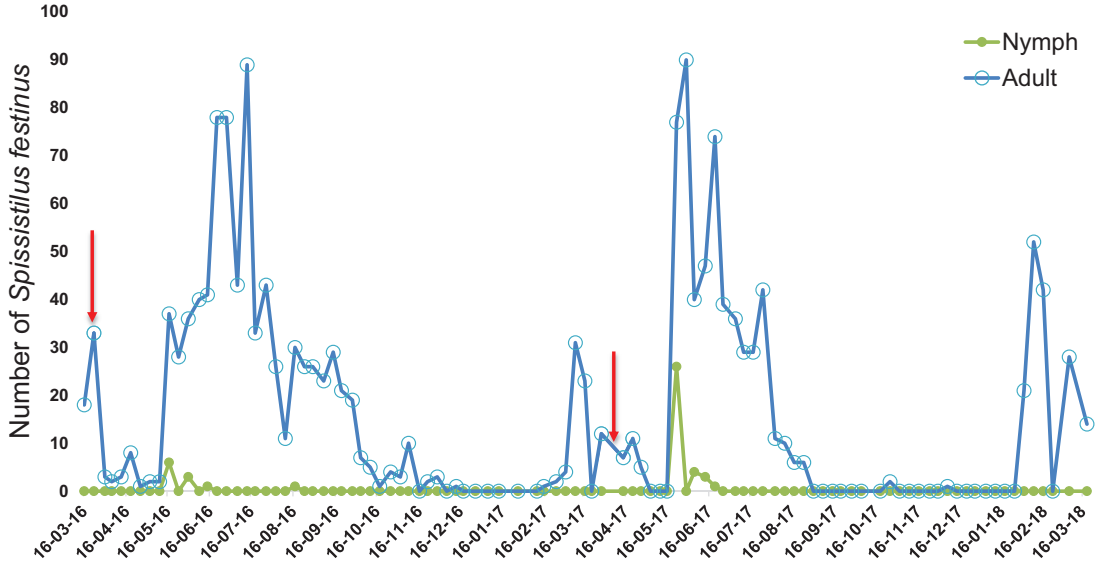

Fig. 1. *Spissistilus festinus* adults and nymphs collected from resident vegetation in a Cabernet Sauvignon vineyard, Oakville, CA from March 2016 until March 2018.

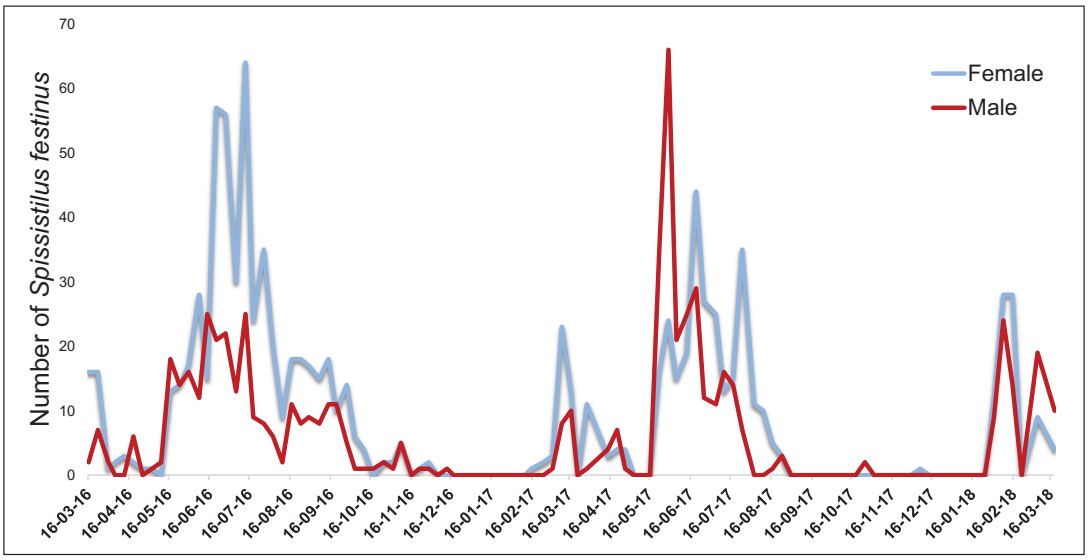

Fig. 2. Total number of male and female *Spissistilus festinus* adults collected during weekly sampling in a Cabernet Sauvignon vineyard, Oakville, CA from March 2016 until March 2018.

in the overwintering generation that was first detected in the vineyard each year (Fig. 2).

Girdle Counts

In 2017, girdles were counted and removed every 2 wk from April 27 to November 30 with the exception of the October 12 sample that was postponed 1 wk due to major fires mentioned previously (Figs. 3 and 4). Girdle counts trended higher overall throughout the season with the exception of the October 19 sample date, which reflected a sizeable reduction in the number of girdles (Fig. 3). The subsequent sampling date of November 2 and those samples taken thereafter reflected a sharp increase in the number of girdles (Figs. 3 and 4). There appears to be a negative relationship between the number of adult *S. festinus* collected while sampling resident vegetation and the number of girdles found in the grapevine canopy (Fig. 3). The relative number of petiole and apical shoot girdles documented on grapevines changed throughout the growing season, although proportionately more were found on petioles earlier (June/July) and later season (November/December) while proportionately more were found on apical shoots when they occurred during the intervening period (Fig. 4). Two *Tortistilus* spp. were collected in June of 2016 and five *Tortistilus* spp. were collected in May and June of 2017, representing 0.2 and 0.8% of the total treehoppers collected for each year, respectively. Therefore, the contribution of this species to the total girdles counts in the vineyard where the study conducted was likely negligible.

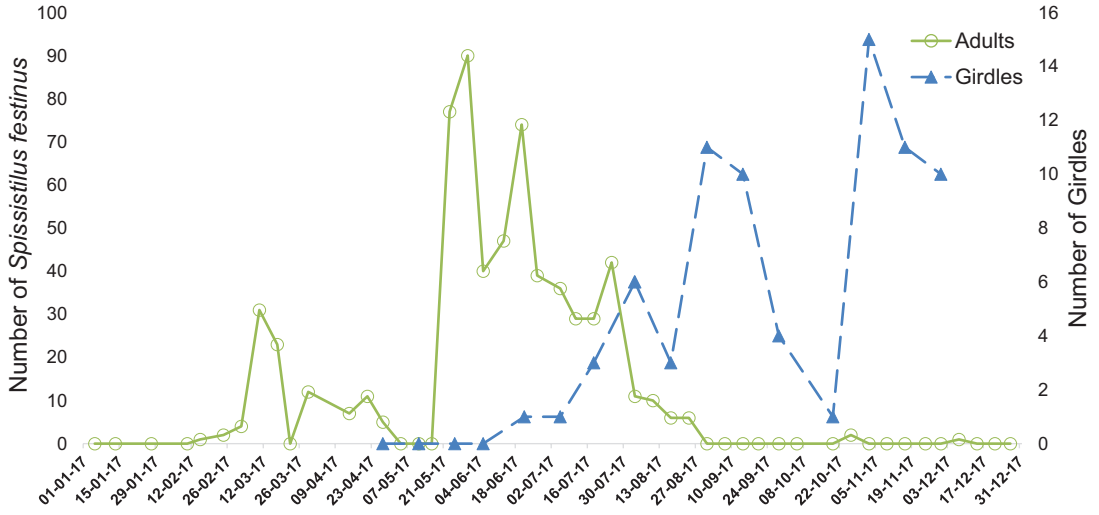

Fig. 3. Total number of adult *Spissistilus festinus* collected from weekly sweep net samples in 2017 and total number of girdles counted from a subset of 30 grapevines in 2017.

Spatial Analysis

The results of the SADIE analysis for 2016 and 2017 showed that

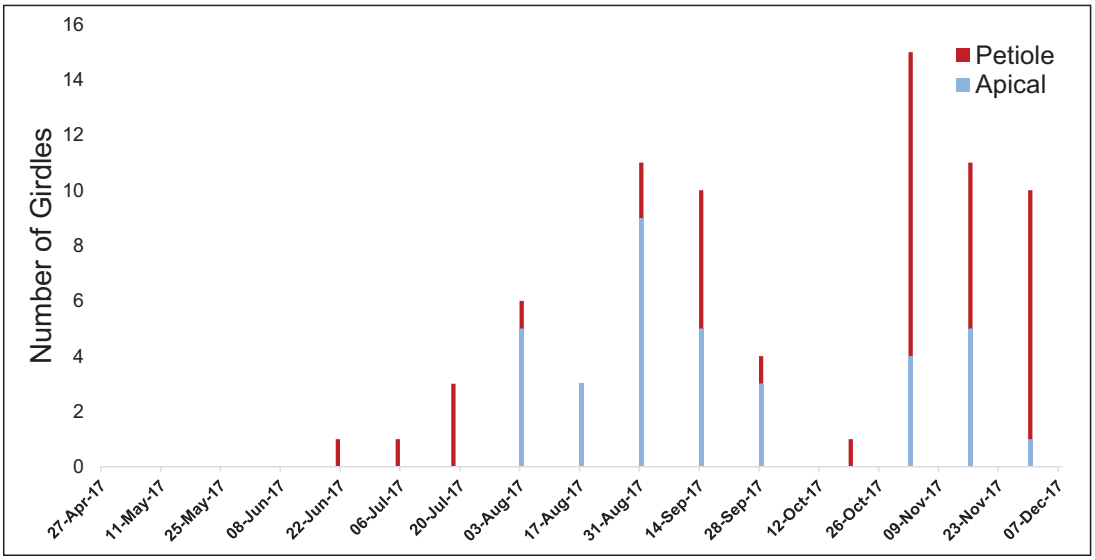

Fig. 4. Total number of *Spissistilus festinus* feeding girdles located on apical shoots and leaf petioles in 2017.

Table 1. Vineyard Spatial Analysis by Distance IndicEs (SADIE) calculated from cumulative *S. festinus* counts per annum

Year	I_p [a]	I_a [b]	P_a [c]	Distribution type
2016	2.1381	2.0378	0.03	Aggregated
2017	1.6829	1.7086	0.04	Aggregated

SADIE indices (I_a and I_p) equal to 1 indicates random arranged counts whereas > 1 indicates aggregation of observed counts; degree of aggregation significant at $P_a < 0.05$.

[a]Index of aggregation.

[b]Index of aggregation for Red-Blue mapping estimation method (Fig. 5).

[c]Probability observed counts are arranged randomly.

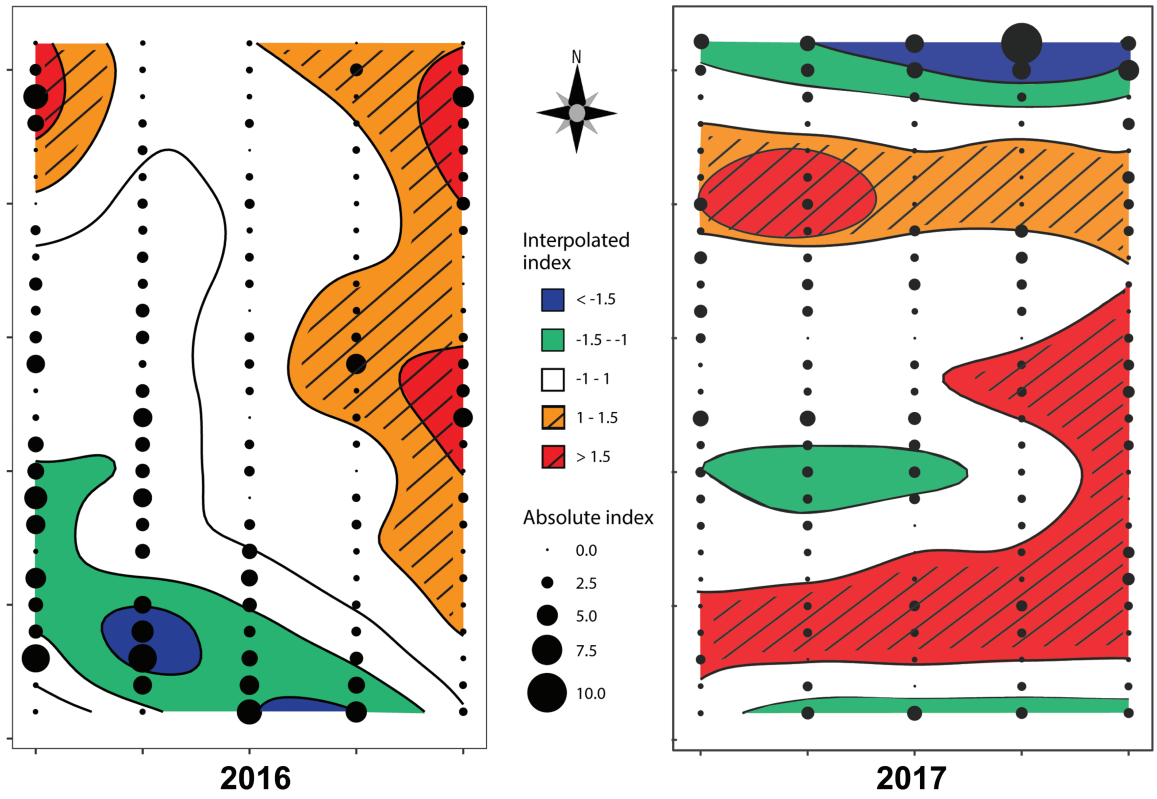

Fig. 5. SADIE red-blue interpolated plots of absolute indices of *Spissistilus festinus* density in 2016 and 2017.

adult *S. festinus* were significantly aggregated in the vineyard (Perry 1995; Table 1). Aggregations occurred primarily on the field edges, and especially on the eastern border (Fig. 5). Treehopper counts from the edge of the vineyard (sections A, C) differed significantly from insects counts from the middle of the vineyard (section B) ($F = 17.7$; df = 2, 15,897; $P = 2.09e{-}08$).

Discussion

Spissistilus festinus overwintering adults were first detected in the vineyard in late winter, as ambient temperatures started to warm, but prior to bud break for all 3 yr (Fig. 1). Although *S. festinus* are known to feed on and girdle leaf petioles and green shoots of grapevines (Smith 2013, Preto et al. 2018b), Preto et al. (2018b) showed that *S. festinus* do not survive on dormant wood. Therefore, we posit that *S. festinus* appearance in the vineyard before bud break indicates that the treehoppers are initially attracted into the vineyard by other feeding and breeding hosts which were present in this study.

Previous research indicated that *S. festinus* population overwinters as unmated adults that migrate from their overwintering host to leguminous plants such as vetch and clovers in early spring (Newsom et al. 1983). Our results support these findings in that live adults were occasionally found in samples during the winter (Fig. 1) and males are reported as dying shortly after mating (Wildermuth 1915, Mitchell and Newsom 1984), yet males were present in the overwintering generation that was sampled in the vineyard in early Spring (Fig. 2). Newsom et al. (1983) indicated the colonizing spring *S. festinus* populations on clover and vetch were strongly skewed towards females, although our 2 yr of observations in a California vineyard did not support their findings (Fig. 2).

After the adults of the overwintering *S. festinus* generation were captured in the vineyard, a depression in the adult population occurred in 2016 and 2017, followed several weeks later by a notable increase in the adult population (Fig. 1). This population increase coincided with the phenological marker of anthesis in the vineyard in both years (anthesis was not documented in 2018 due to removal of the vineyard) and the first collected *S. festinus* fourth and fifth instar nymphs. We posit that adults of the *S. festinus* overwintering generation arrive in the vineyard to feed, mate, lay their eggs in resident vegetation and/or cover crops that serve as hosts, and proceed to die-off, similar to what was described in other systems by Mitchell and Newsom (1984) and Wildermuth (1915). The depression seen in the adult population following the initial influx represents the period in which nymphs are emerging from eggs laid in resident vegetation in the vineyard and developing from the first through third instar that are not effectively sampled and recorded with sweep nets. The earlier developmental stages of *S. festinus* nymphs are difficult to detect in sweep net samples in the field due to their small size (1.4–3.0 mm) and being straw-colored (Wildermuth 1915). The fourth and fifth instar *S. festinus* are larger (3.5–5.0 mm), darker, and therefore, more easily identified in sweep net samples. We believe that this explains our first detection of later-instar *S. festinus* nymphs simultaneously with the substantial increase in the adult population.

The finding that the grape phenological marker of anthesis and the first in-field adult generation of *S. festinus* occurred concurrently suggests the potential for timing control measures in regions of similar climate and cultivar such as tilling under resident vegetation and/or cover crops in advance of anthesis to reduce nymphal abundance. Mowing could also be effective if it kills the vegetation instead of simply reducing the plant's size and vigor. The majority of *S. festinus* nymphs have been found to feed on the hypocotyl (Trichilo et al.

1993); therefore, mowing without allowing time for the vegetation to be killed and consequently starving the immature stages might not be expected to help in control of the populations. This cultural control measure would allow for the overwintering generation of adults to lay their eggs and die-off while the nymphs that emerge would not be capable of completing their life cycle in the absence of a viable feeding host. An early season reduction in the *S. festinus* population can contribute to reducing the secondary spread of GRBV in the vineyard.

In addition, it would be beneficial to apply cultural practices to leguminous weeds outside of the vineyard rows, such as the perimeter of the vineyard blocks and areas in close proximity to the grapevines. Since tilling under is unlikely to be feasible for these regions of the vineyard, spot removal or spot application of an herbicide to kill leguminous and reproductive weeds (Mueller and Dumas 1987, Preto et al. 2018a) timed before the emergence of the first in-field adult *S. festinus* generation in spring would contribute to an overall plan to reduce the population numbers and attractiveness of the vineyard to *S. festinus*.

Our sampling suggests that two in-field generations occurred on vineyard groundcover in 2016 with peak adult captures occurring in late June and early July and again in late August, whereas only one adult peak was documented in 2017, again in late June to early July. According to the literature, the number of *S. festinus* generations that occur per annum can vary due to local environmental conditions and the availability of host plants (Wildermuth 1915, Mitchell and Newsom 1984, Beyer et al. 2017). While the reason that only one *S. festinus* in-field adult peak was indicated by our sampling of vineyard groundcover in 2017 is not known, it is plausible that at this time *S. festinus* left the ground cover to move up into the grapevine canopy to feed, left the vineyard for a more favorable feeding/reproductive host, or were negatively impacted by some unknown factor that reduced the population. The vineyard had not been treated with an insecticide prior to the population decline.

In 2017, we observed that resident vegetation began declining in the vineyard on August 10 and this event coincided with the reduction in the adult *S. festinus* population sampled on ground cover and an increase in girdles counted in the grapevine canopy (Fig. 3). We believe that when feeding hosts become scarce in the vineyard, *S. festinus* migrate into the grapevine canopy to feed and may acquire GRBV from infected vines. Cieniewicz et al. (2018) showed adult *S. festinus* started to test positive for GRBV in a Napa County vineyard in June of 2015 and 2016, which coincided with the same month that grapevine girdles were first counted in our current study (Fig. 3).

Preto et al. (2018b) showed that *S. festinus* is capable of using *Vitis vinifera* as a reproductive host, but we did not measure whether reproduction occurred in the canopy in this study. Further research to determine the relationship between presence of *S. festinus* on grapevines and the status of groundcover host vegetation is needed for confirmation.

Spissistilus festinus adults exhibited a clustered distribution in the vineyard for 2016 and 2017 (Table 1; Fig. 5). These findings are consistent with previous research in other host crops (Sparks and Boethel 1987, Trichilo et al. 1993). *Spissistilus festinus* adults tended to be significantly more concentrated at the vineyard margins than in the center of the vineyard (Fig. 5). The presence of an edge effect implies that *S. festinus* adults overwinter outside the vineyard and aggregate at the vineyard's edge when returning from their overwintering habitat. A higher incidence of aggregation was seen on the vineyard's eastern border in 2016 and 2017, which was also the only side of the vineyard in close proximity to a water source (Fig. 5). Whether this pattern implies that *S. festinus* tend to aggregate more readily near water sources or whether resident vegetation that serves as feeding and reproductive hosts for *S. festinus* tend to be in greater abundance near water sources could not be determined from this study. However, investigating the relationship between *S. festinus* populations and water sources could be a fruitful topic for future research and could provide useful management implications.

The results presented in this paper provide a baseline of information on the seasonal occurrence and distribution of *S. festinus* in a California vineyard that would serve as a foundation for future research on this species. It also suggests preliminary cultural management approaches that could help mitigate future spread of GRBV.

Acknowledgments

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