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Use of yellow sticky traps to study daily flight activity and behaviour of sap-sucking insects inhabiting European vineyards

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Abstract

Yellow sticky traps are used to monitor sap-sucking insects in their roles as both pests and vectors across a broad range of crops including vineyards. They are also used to understand different aspects of insect biology, and for this purpose, a number of studies have been conducted to determine the daily flight activity of leafhoppers and thrips. In a vineyard in north-eastern Italy, the daily flight activities of leafhoppers [e.g. *Empoasca vitis* (Gothe), *Zygina rhamni* Ferrari, *Scaphoideus titanus* Ball], as well as the vine thrips *Drepanothrips reuteri* Uzel, were studied with yellow sticky traps during different monitoring days of the growing season. The traps were placed in both shady and sunny positions with respect to the grapevine foliage, and in inter-rows. They were routinely replaced every hour from the start of dawn to the end of dusk, while during the hours of darkness there was no replacement, except on one monitoring day. *E. vitis*, *S. titanus* and *D. reuteri* were mainly captured in sunny positions, while *Z. rhamni* was captured in shady positions. *E. vitis* exhibits bimodal daily flight activity with two peaks respectively at the dawn-sunrise and sunset-dusk. *Z. rhamni* prefers to fly around sunrise, when daily temperatures are lower, and *S. titanus* flies continuously from sunset to sunrise. The vine thrips flies only during sunshine hours. The daily hours with higher flight activity are mostly associated with changes in light intensity. The moderate light intensity that occurs immediately after sunrise and just before sunset inhibits the flight activity of leafhoppers outside the canopy but not inside. Knowing the daily flying activity and behaviour of leafhoppers and thrips can have important implications for establishing the optimal sampling time because in the hours of the highest flying activity counting adults can be more difficult.

Key words: leafhoppers, thrips, monitoring, sticky traps, daily flights, behaviour.

Introduction

Coloured sticky card traps capture herbivore insects by exploiting the visual stimuli in selecting host plant organs (Finch and Collier, 2000; Döring and Chittka, 2007; Brévault and Quilici, 2010; Schröder *et al*., 2017).

Yellow sticky traps have been widely used in European vineyards to monitor sap-sucking insects, both as pests and vectors of phytoplasmas, and to study their biology (e.g., number of generations, adult phenology, spatial distribution and dispersion). Among the pests, they have been used for leafhoppers (Hemiptera Cicadellidae) belonging to the Typhlocybinae [i.e., *Empoasca vitis* (Gothe), *Zygina rhamni* Ferrari and *Erasmoneura vulnerata* (Fitch) (Pavan *et al*., 1988; 2021; Bosco *et al*., 1996; Pavan, 2000; Decante and van Helden, 2006; 2008; Mazzoni *et al*., 2008; Duso *et al*., 2019; 2020)], the thrips *Drepanothrips reuteri* Uzel and *Thrips tabaci* Lindeman (Tysanoptera Thripidae) (Strapazzon, 1989; Strapazzon *et al*., 1990; Jenser *et al*., 2010; Pavan *et al*., 2021), and the grape filloxera *Viteus vitifoliae* (Fitch) (Hemiptera Phylloxeridae) (Stevenson and Jubb, 1976; Strapazzon, 1987). Among phytoplasma vectors, traps have been used for *Scaphoideus titanus* Ball and *Orientus ishidae* (Matsumura) (Hemiptera Cicadellidae Deltocephalinae), which are associated with Flavescence dorée (Pavan *et al*., 1987; 2012; 2021; Jermini *et al*., 1992; Lessio and Alma, 2004; Lessio *et al*., 2016), and *Hyalesthes obsoletus* Signoret (Hemiptera Cixiidae), associated with Bois noir (Bressan *et al*., 2007; Maixner and Reinert, 2000; Mori *et al*., 2016).

The study of the daily flight activity of pest and vector insects is important to understand in which positions of the plant they are during the day and when they disperse among plants of the same species or towards other plant species (Harker, 1973; Waloff, 1973; Saunders, 2002). For this purpose, yellow sticky traps have been used widely to study the daily flight activity of leafhoppers (Meyer and Colvin, 1985; Larsen and Whalon, 1987; Kersting and Bascedillapinar, 1995), planthoppers (Bressan *et al*., 2007) and thrips (Aliakbarpour and Rawi, 2010; Seal *et al*., 2010; Yan *et al*., 2017).

The daily flight activity of leafhoppers and planthoppers on herbaceous plants in the field has been also studied with other sampling methods, mostly suction traps, whose ability to intercept the activity of insects is not affected by light intensity as is the case of yellow sticky traps (Dysart, 1962; Ossiannilsson, 1966; Rose, 1978; Smith and Ellis, 1983; Taylor and Reling, 1986; Riley *et al*., 1987; Rodriguez *et al*., 1992; Taylor *et al*., 1993; Chancellor *et al*., 1997).

The studies mentioned above report that the factors involved in the increase or decrease in flight activity were not only changes in lighting levels but also in temperature in accordance with some reviews (Harker, 1973; Taylor, 1985; Saunders, 2002).

The main aim of this study was to acquire knowledge of the daily flight activity of the leafhoppers *E. vitis*, *Z. rhamni* and *S. titanus*, and the vine thrips *D. reuteri* by means of yellow sticky traps in vineyards. So far, only the daily flight activity of *S. titanus* has been studied (Lessio and Alma, 2004). More, based on the influence of trap positions with respect to the canopy (i.e., shady or sunny) (Pavan *et al*., 2021), the flight activity was studied for the first time by placing the traps in two different positions with respect to the canopy. Knowledge of the daily flight activity of leafhoppers and thrips and their positions relative to the canopy at different hours of the day can have important implications for adult sampling in relation to both the positions in the canopy where they are to be sampled and the risk that they will fly away before they can be counted. A second aim was to try to understand whether the effect of the shady positions of traps on captures was due to the different relationship with the vegetation or to the shadow itself.

Materials and methods

Vineyard and traps

The study was conducted in 1998 and 1999 in a one-hectare plain vineyard located in north-eastern Italy (Pasiano di Pordenone, Pordenone district, 45°50'40"N 12°39'22"E, 13 m a.s.l., cultivar Verduzzo Trevigiano). It had eight N50°W-S40°E oriented rows, with the grapevines trained to the Sylvoz system and planted at distances between and within rows of 4.0 and 2.0 m, respectively. In the vineyard, no insecticide was sprayed in the two years of the study and at least in the previous three years.

Yellow sticky traps were made with yellow plastic sheet (11 cm wide, 21 cm high and 0.1 cm thick) (Plastibor s.r.l., Ponte San Nicolò, Padova, Italy) smeared on both sides for 4/5 of the surface with colourless glue (Temo-O-Cid, Kollant Srl, Vigonovo VE, Italy).

Experiment 1 on daily flight activity

Table 1 provides the sampling scheme adopted for the study of the daily flight activity of *E. vitis*, *Z. rhamni*, *S. titanus* and *D. reuteri*. The late-June and early-August monitoring days were chosen to coincide with the peaks of *E. vitis* adults of the first or second generations (Pavan *et al*., 1987) and the latter day also for the peak of *S. titanus* adults of the single generation (Pavan *et al*., 1988). The late-September and early-October monitoring days were chosen to coincide with the dispersion of both *E. vitis* and *Z. rhamni* adults to overwintering host plants (Vidano, 1963; Pavan *et al*., 1987).

Times were expressed in Coordinate Universal Time (UTC). The average hourly temperature (°C), solar radiation (kJ/m^2), relative humidity and wind speed (km/h) recorded during monitoring days were obtained from a weather station (Agricultural Service of Pordenone district, Friuli Venezia Giulia region, Italy) approximately 4 km away. The moon phase was also reported.

Poles installed along the grapevine rows as part of the normal training support were used to string support wires perpendicularly across the rows at a height of 1.5 m from the ground. Yellow sticky traps were installed onto vertical wires attached to the horizontal support wires, with the traps positioned vertically to face the outer sides of the canopy, and parallel to the direction of the grapevine row. Traps were placed in two different positions, i.e. shady or sunny positions, with respect to the canopy. Traps in shady positions were immersed in the foliage of the canopy with their faces unobscured by leaves so that they could be visible looking from the inter-rows. Due to the presence of vegetation above them, the traps could only be hit by sun rays in the early morning (southeast-oriented side of the traps) and late afternoon (northwest-oriented side of the traps), i.e. for some hours after sunrise and before sunset. Traps in sunny positions were continuously exposed to direct sunlight during the day by removing the foliage above them. On the early-August monitoring day, to see when dispersive flight outside the grapevine canopy occurs, traps were placed also at the centre of the inter-row (i.e. about 2 m from the two contiguous rows), at the same height from the ground level as the traps on grapevines and with the two sides facing the two rows.

Three replicates, corresponding to three grapevine rows, were considered for each monitoring day and trap position.

For each monitoring day, the installation and replacement UTC hours of traps (sampling interval) are reported in supplemental material table S1 and are visible in the figures 1-10. For each monitoring day, the UTC hours corresponding to darkness, daylight, and two twilight periods, i.e. dawn (the first appearance of light in the sky before sunrise) and dusk (the time just after sunset when it is not yet dark) were calculated (http://www.internetsv.info/PhotoPeriodC.html). During the darkness, the traps were only replaced on the early-August monitoring day, while from dawn to dusk they were replaced every hour on the two summer monitoring days and every two hours on the two autumn monitoring days, when *E. vitis* adult population size was inferior. On the early-October monitoring day, sampling was not carried out during the

Table 1. Monitoring days in which the flight activity of the four sap-sucking pests was studied. The period in which the traps remained in the field (i.e., from the UTC hour of the first installation to the UTC hour of the last collection without replacement), the position of the traps with respect to the canopy (i.e., shady or sunny) and the species taken into consideration in each monitoring day are reported. E = *Empoasca vitis*, Z = *Zygina rhamni*, S = *Scaphoideus titanus*, D = *Drepanothrips reuteri*.

Monitoring days			Trap position			Species sampled			
	From	To	Shady	Sunny	Inter-row	E	Z	S	D
Late June	20:00 29/06	20:00 30/06	X	X		X	*		X
Early August	19:00 03/08	19:00 04/08**	X	X	X	X	X	X	X
Late September	16:30 30/09	16:30 01/10	X	X		X	X		
Early October	4:00 07/10	16:00 07/10	X	X		X	X		

(*) *Z. rhamni* was not considered because only a few individuals were captured.
(**) in sunny positions, the traps were maintained in the field up to 03:30 05/08.

hours of darkness because of the too-low captures in dark hours on the late-September monitoring day. The captures recorded at each sampling interval are expressed as a number per hour.

Experiment 2 on the influence of shading on captures

For this experiment, yellow sticky traps were individually hung within the grapevine canopy in the same manner described above, but this time, rectangular Plexiglas roofs (70 × 100 cm) were placed above the traps (supplemental material figures S1 and S2). Two types of Plexiglas roofs were compared: transparent and opaque (i.e., painted white).

The experiment was replicated in four weekly sampling intervals (21-28 June, 23-30 July, 5-12 August and 1-7 October), during which one trap per roof type was installed on each of the four grapevine rows. *S. titanus* was not captured in the first sampling interval, as the emergence of the adults of the only annual generation had not yet begun (Vidano, 1964; Pavan *et al*., 1987), whereas *D. reuteri* was not considered in the last sampling interval, as most of the adults of the last generation were already located in their overwintering sites (Strapazzon *et al*., 1990).

Identification and counting of insects in the laboratory

Traps were taken to the laboratory, where captured adults of *E. vitis*, *Z. rhamni*, *S. titanus* and *D. reuteri* were identified, using appropriate dichotomous keys (for leafhoppers: Vidano, 1958; 1959; 1963; 1964; for *D. reuteri*: Mound *et al*., 1976), and counted under a dissecting microscope. To see if the periods of flight activity varied between males and females, the sexes of the two most abundant species (i.e., *E. vitis* and *D. reuteri*) were also considered during the early-August monitoring day of experiment 1 on daily flight activity.

Data analysis

In experiment 1 on the flight activity of sap-sucking pests, the total daily adult captures on traps in shady and sunny positions were compared using a paired t-test. For early-August monitoring day and the two species that also had appreciable captures in inter-row positions, i.e. *E. vitis* and *D. reuteri*, three positions (shady, sunny, and inter-row) were compared using a repeated measures ANOVA and Tukey's post hoc test. For each monitoring day and trap position, a one-way ANOVA was performed to compare the captures recorded in the different sampling intervals. For both analyses, data were log (x + 1) transformed to meet the assumption of normality and homogeneity of variance. These statistical analyses were performed with GraphPad InStat version 3.0 (GraphPad Software Inc., San Diego, California). Ryan's test was used to compare the percentage of females of *E. vitis* and *D. reuteri* among the total captures on the traps placed in the three sampling positions (i.e., shady, sunny and inter-row).

In experiment 2 on the influence of shading on capture numbers, the data were submitted to a three-way ANOVA considering "Roof type", "Side orientation", "Sampling period" and their interactions as sources of variation. Data were checked for analysis assumptions and were log (x + 1) transformed prior to the analyses. Post hoc comparisons among sampling intervals were performed with a Tukey's test.

Results

Experiment 1 on daily flight activity

All meteorological data of the monitoring days are reported in supplemental material table S1. Temperatures and solar radiation were mostly considered in the results, because are the most important factors influencing the daily flight activity of insects (Saunders, 2002).

The wind speed dynamics were irregular and therefore not associated with specific times of the day. However, the monitoring days were not very windy.

The moon phase was "first quarter" on the late-June monitoring day, "three days before full moon" on the early-August monitoring day, "one day before last quarter" on the late-September monitoring day and "four days after the last quarter" on the early-October monitoring day.

E m p o a s c a   v i t i s

During the two summer monitoring days (i.e., late June and early August), the total captures of adults were respectively 2.6 and 2.0 times significantly higher on traps in sunny positions than on those in shady positions (late June: $t = 4.3$; df = 4; $P = 0.013$; early August: $t = 10.6$; df = 4; $P = 0.0004$) (figures 1 and 2; in supplemental materials table S2). The capture numbers varied significantly over the monitoring days (late June: shady, $F = 7.32$; df = 17, 36; $P < 0.0001$; sunny, $F = 28.81$; df = 17, 36; $P < 0.0001$; early August: shady, $F = 9.95$; df = 16, 34; $P < 0.0001$; sunny, $F = 24.71$; df = 16, 34; $P < 0.0001$). Although a few captures also occurred in both positions during the hours of darkness, they only became substantial at sunrise when a significant peak was recorded. Subsequently, the captures decreased and remained low for most of the daylight hours. In shady positions, there was a significant increase in captures from 16:00 to 17:00 UTC hours when temperatures started to drop and RH increased, and a daily peak was observed in the hour before sunset, with substantial captures also at dusk. In sunny positions, a significant increase in captures occurred only in the hour before sunset and a daily peak was observed at dusk. The absolute number of captures was continuously higher in shady positions than in sunny positions from 12:00 to 17:00 UTC hours. In both positions, the peak during the sunset period was significantly higher than during the sunrise period (late June: 3.8 and 2.8 times respectively for shady positions and for sunny positions; early August: 2.7 and 1.7 times respectively for shady positions and for sunny positions).

In sunny positions of the early-August monitoring day, when four sampling intervals were considered (three during darkness and one during dawn), the occurrence of the low number of captures during the hours of darkness and the significant increase in captures at dawn ($F = 153.9$; df = 3, 8; $P < 0.0001$) were confirmed (figure 2). The capture numbers did not vary among the early, mid and late periods of the night.

During early-August monitoring day, the adult captures on traps placed in inter-row positions were significantly lower than those on traps placed in sunny and shady positions (5.5 and 2.7 times lower, respectively) ($F = 49.62$; df = 2, 6; $P = 0.0002$) (figure 2). The capture numbers in inter-row positions varied significantly over the monitor-

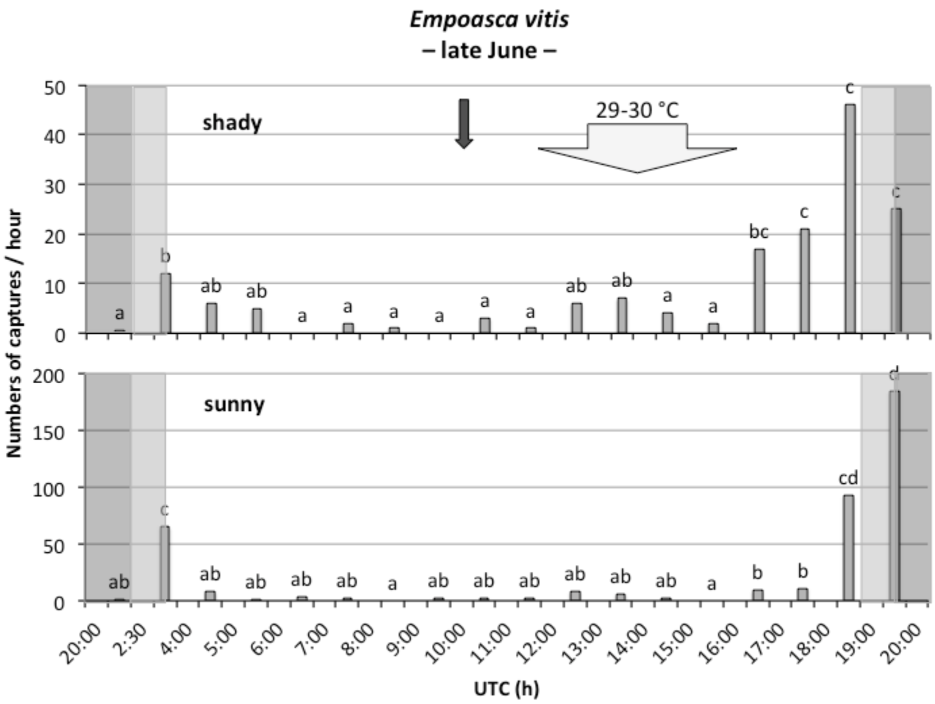

Figure 1. Captures of *E. vitis* adults recorded with three yellow sticky traps during a late-June monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

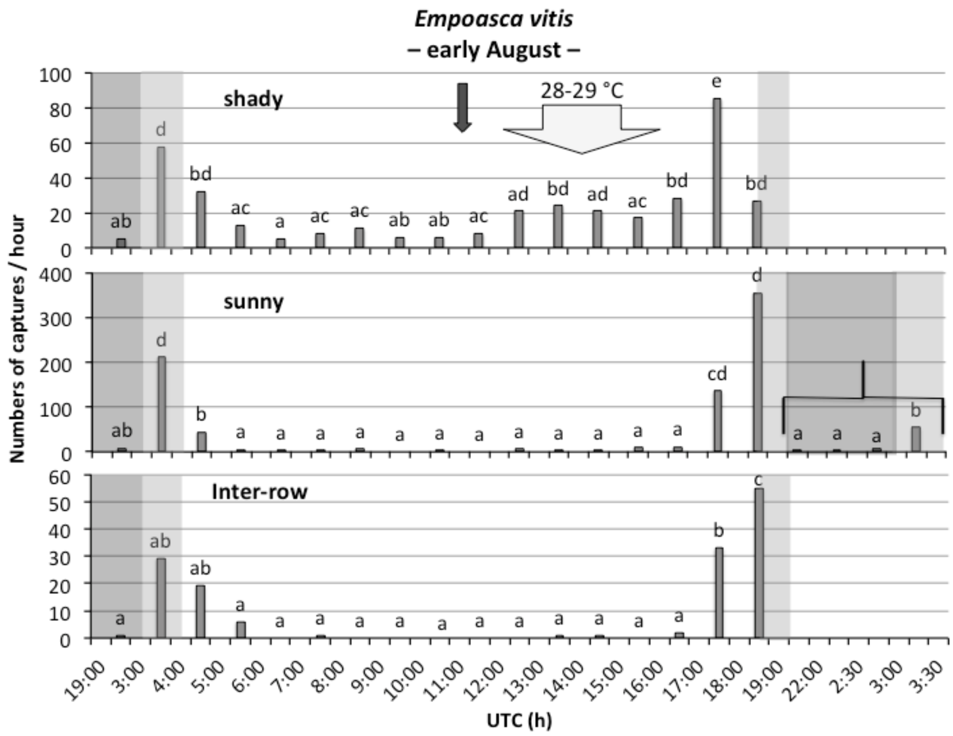

Figure 2. Captures of *E. vitis* adults recorded with three yellow sticky traps during an early-August monitoring day in shady (graph on the top), sunny (graph on the middle) and inter-row (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

ing day (F = 12.59; df = 16, 34; P < 0.0001) with a dynamic similar to that of the traps in sunny positions. During both the sunrise and sunset periods, the total captures in inter-row positions were significantly lower than in sunny positions and not different from those in shady positions (for sunrise: F = 13.45; df = 2, 6; P = 0.0061; for sunset: F = 197.31; df = 2, 6; P < 0.0001).

On the early-August monitoring day, females comprised 20% of total captured adults, but their proportion differed among the positions, resulting significantly lower in sunny positions (17.0%) than in shady (22.5%) and inter-row positions (30.4%) (P < 0.05 at Ryan's test). Considering the three sampling intervals with the highest captures, the percentage of females in the total captures was significantly different among the intervals with the lowest value at dawn (8.0%), the highest at dusk (28.1%) and mid-range in the hour before sunset (16.5%). At dawn, the percentage of females was not different among the three traps positions (8.0% in sunny, 7.0% in shady and 10.0% in inter-row), whereas it was significantly lower in sunny compared to the other positions both before sunset (5.9% in sunny, 29.4% in shady, 27.3% in inter-row) and at dusk (23.9% in sunny, 48.1% in shady, 45.6% in inter-row).

On the late-September and early-October monitoring days, total adult captures were respectively 12.6 and 25.0 times higher on traps in sunny positions than in shady positions (late September: t = 11.1; df = 4; P = 0.0004; early October: t = 11.5; df = 4; P = 0.0003) (figures 3 and 4). The capture numbers varied significantly over the monitoring day only in sunny positions in late September (shady: F = 1.90; df = 6, 14; P = 0.15; sunny: F = 57.75; df = 6, 14; P < 0.0001) and in both positions in early October (shady: F = 4.24; df = 5, 12; P = 0.019; sunny: F = 28.35; df = 5, 12; P < 0.0001). On the late-September monitoring day at dusk and in the hours of darkness, one individual was captured in shady positions and none in sunny positions. During both monitoring days, a significant peak in captures was observed at sunrise in sunny positions alone. In shady positions, captures occurred during the daylight hours on both monitoring days and it was only in early October that a significant peak in captures was recorded, coinciding with the peak of solar radiation. Captures in sunny positions during the daylight hours from 6:00 to 14:00 UTC occurred only on the early-October monitoring day, while a daily peak during the following two hours (those preceding sunset) was observed in both monitoring days. In sunny positions, the peaks just before sunset were higher than during sunrise (13.6 and 3.1 times respectively in late September and early October).

Zygina rhamni

On the early-August monitoring day, total adult captures were 3.2 times higher on traps in shady positions than in sunny positions (t = 3.2; df = 4; P = 0.033) (figure 5). The capture numbers varied significantly over the monitoring day (shady: F = 4.21; df = 16, 34; P = 0.0002; sunny: F = 10.10; df = 16, 34; P < 0.0001). In both positions, a few captures also occurred during the hours of darkness. In sunny positions, a peak of captures was observed at dawn,

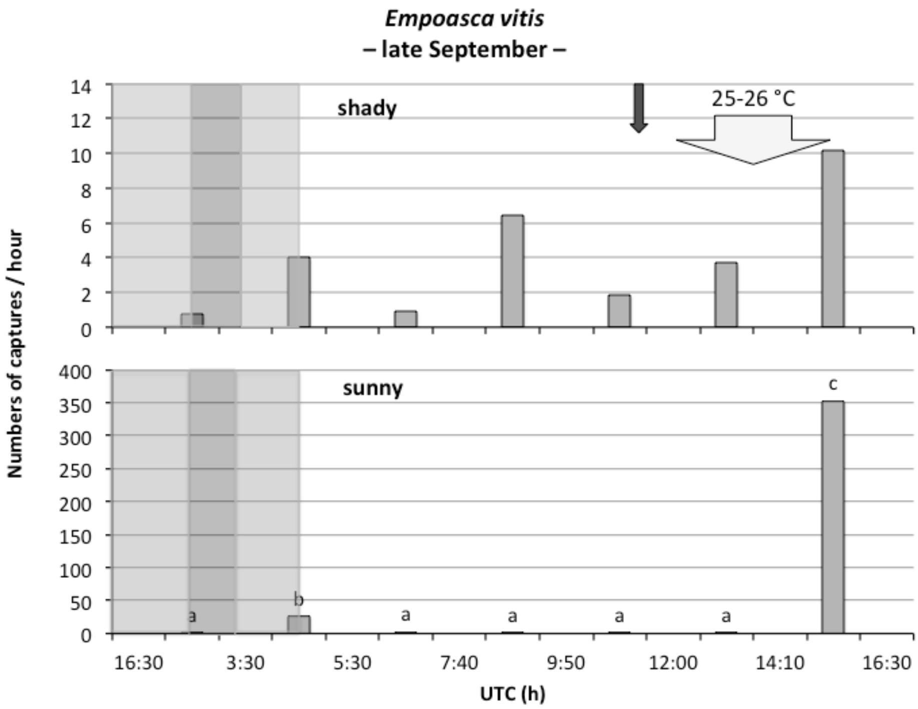

Figure 3. Captures of *E. vitis* adults recorded with three yellow sticky traps during a late-September monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

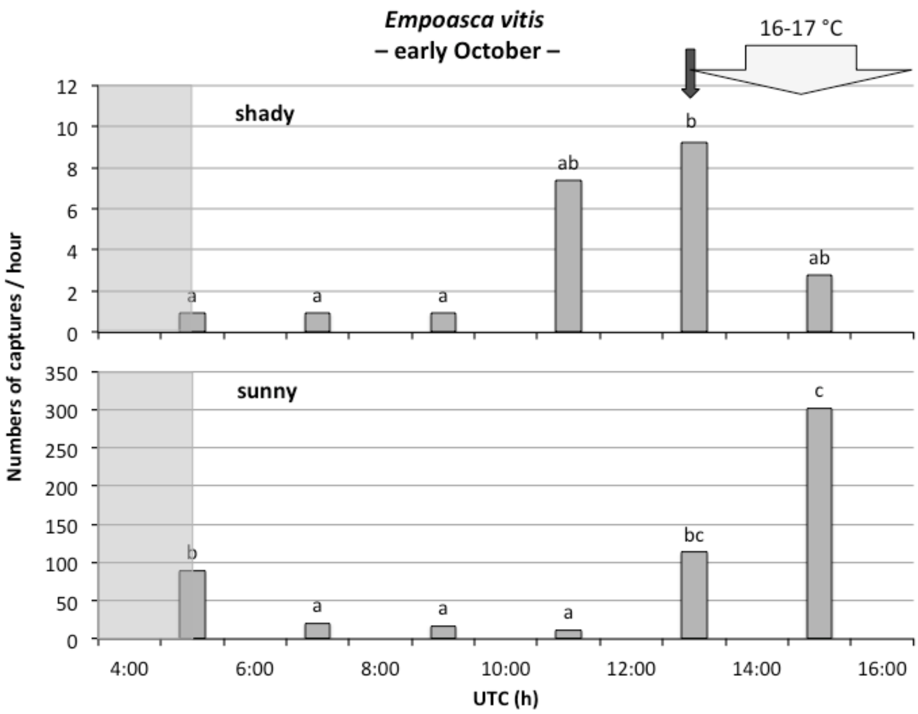

Figure 4. Captures of *E. vitis* adults recorded with three yellow sticky traps during an early-October monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The two different backgrounds of the graph (i.e., white and light grey) indicate the hours of sunshine and twilight hours, respectively. Sunset occurs at 16:00 UTC. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

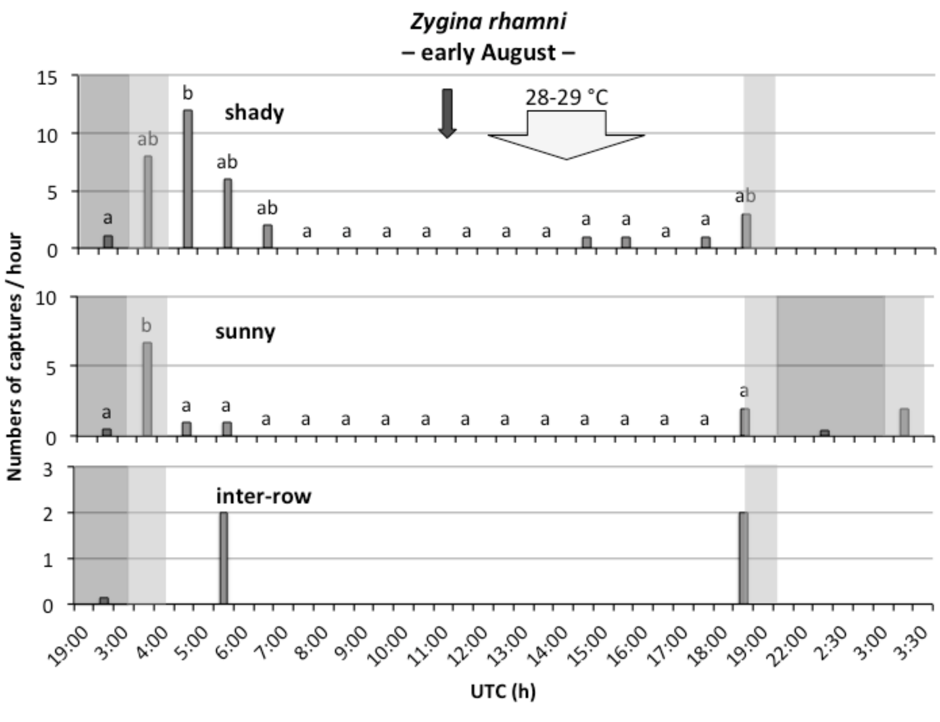

Figure 5. Captures of *Z. rhamni* adults recorded with three yellow sticky traps during an early-August monitoring day in shady (graph on the top), sunny (graph on the middle) and inter-row (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

after which the captures dramatically dropped. Even in shady positions, the captures increased at dawn, but the peak was delayed until just after sunrise and was followed by a gradual decrease in captures over the next two hours. In both positions, during the daylight hours the captures were nil or scarce, and it was only at sunset that a slight, but not significant, increase in captures was observed.

In sunny positions, when four sampling intervals were considered (three during darkness and one during dawn), the occurrence of low capture numbers during darkness followed by an increase in captures at dawn was confirmed (figure 5).

On traps placed in inter-row positions, two captures each were recorded during the early morning and at sunset and one capture during darkness (figure 5).

During the late-September and early-October monitoring days, adult captures were, respectively, 29.0 and 15.6 times on traps in shady positions than sunny positions, where few adults were captured over the two monitoring days (late September: t = 12.6; df = 4; P = 0.0002, early October: t = 12.4; df = 4; P = 0.0002) (figures 6 and 7). The capture numbers varied significantly over the monitoring days on traps in shady positions alone (late September, shady: F = 15.50; df = 6, 14; P < 0.00012; sunny: F = 0.63; df = 6, 14; P = 0.70; early October, shady: F = 7.81; df = 5, 12; P = 0.0018; sunny: F = 2.14; df = 5, 12; P = 0.12). On late-September monitoring day, when traps were also installed at dusk and during the hours of darkness, only a few captures were observed. In shady positions, a clear daily peak at dawn followed by low number of captures until sunset was recorded during both monitoring days.

Scaphoideus titanus

On the early-August monitoring day, adult captures were 5.3 times higher on traps in sunny positions than shady positions (t = 5.2; df = 4; P = 0.006) (figure 8). The capture numbers varied significantly over the monitoring day (shady: F = 2.69; df = 16, 34; P = 0.0076; sunny: F = 43.19; df = 16, 34; P < 0.0001). In shady positions, a few captures were observed during the hours of darkness, dawn and up to the second hour after sunrise, after which no captures were recorded until the hour before sunset, when capture numbers suddenly peaked and remained abundant at dusk. In sunny positions, there was a significant number of captures during the hours of darkness and, after declining at dawn, captures were absent until almost sunset when they suddenly reached the daily peak.

In sunny positions of the early-August monitoring day, when four sampling intervals were considered (three during darkness and one during dawn), the capture numbers were higher on the 19:00-22:00 UTC (23 captures on three traps) and 22:00-2:30 UTC (31 captures on three traps) sampling intervals than on 2:30-3:00 UTC (no captures) sampling interval (F = 153.9; df = 3, 8; P < 0.0001) (figure 8). Captures remained at low level also at dawn (one capture on three traps).

On traps placed in inter-row positions, only two captures were recorded during the hours of darkness.

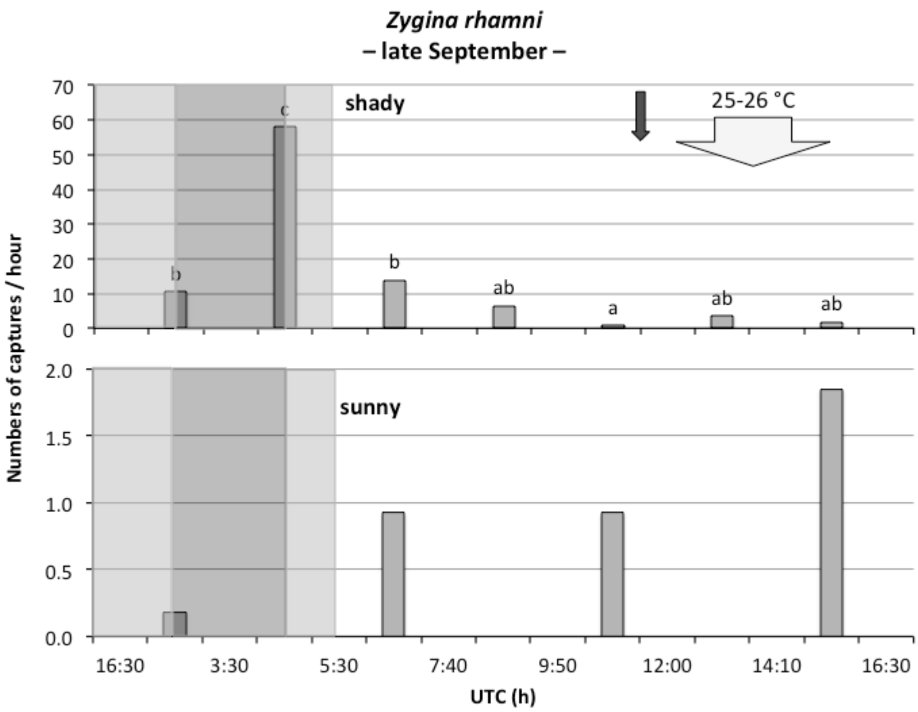

Figure 6. Captures of *Z. rhamni* adults recorded with three yellow sticky traps during a late-September monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

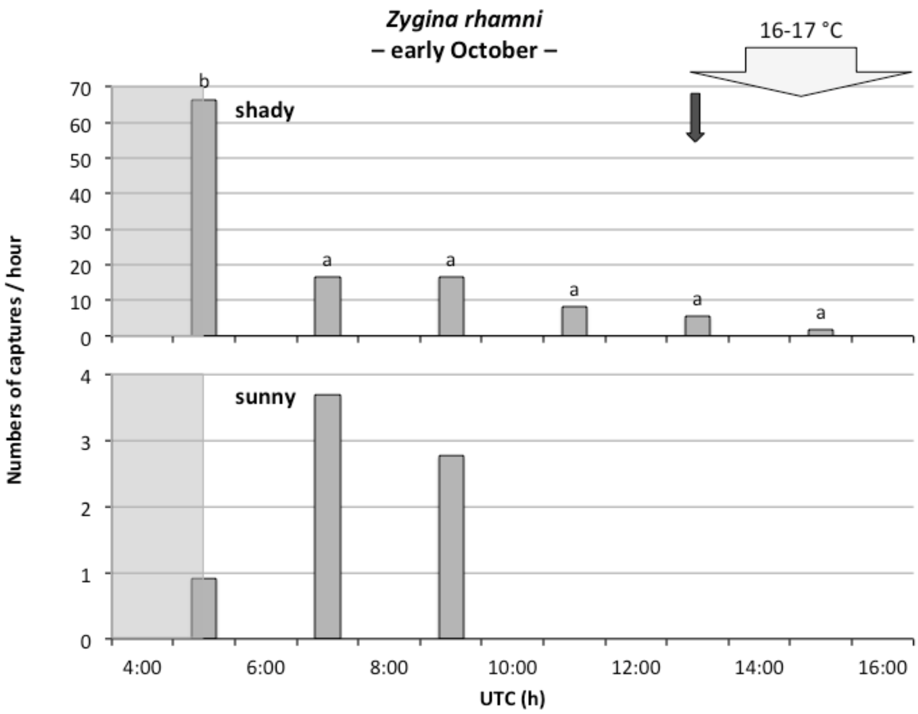

Figure 7. Captures of *Z. rhamni* adults recorded with three yellow sticky traps during an early-October monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The two different backgrounds of the graph (i.e., white and light grey) indicate the hours of sunshine and the hours of twilight, respectively. Sunset occurs at 16:00 UTC. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

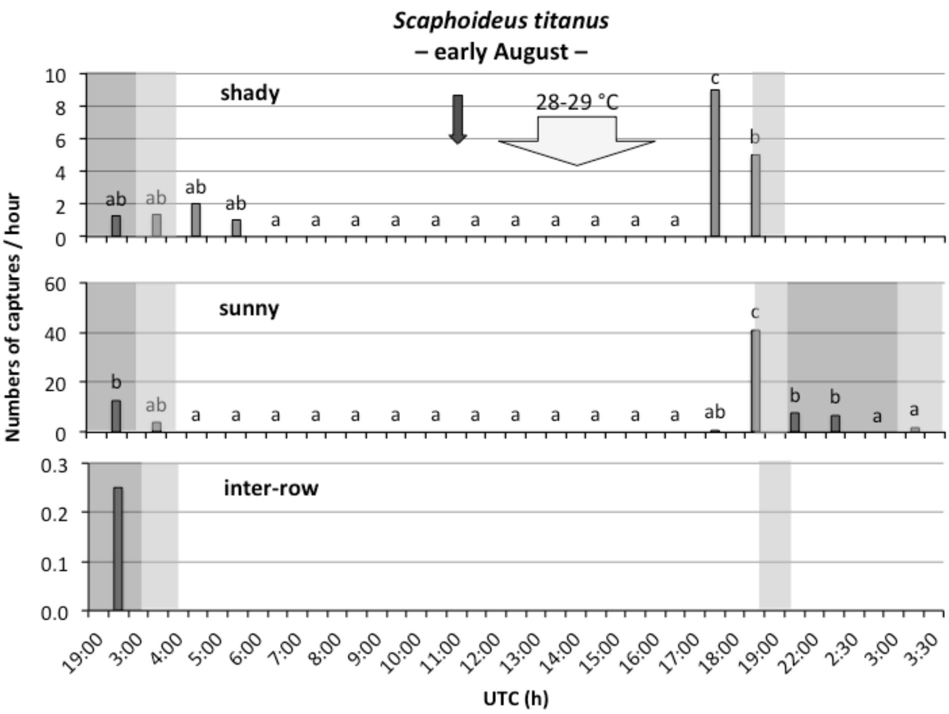

Figure 8. Captures of *S. titanus* adults recorded with three yellow sticky traps during an early-August monitoring day in shady (graph on the top), sunny (graph on the middle) and inter-row (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

Drepanothrips reuteri

On the late-June and early-August monitoring days, total adult captures were 6.4 and 9.8 times higher on traps in sunny positions than in shady positions, respectively (late June: t = 3.0; df = 4; P = 0.04; early August: t = 5.7; df = 4; P = 0.005) (figures 9 and 10). The capture numbers varied significantly over the monitoring day in sunny positions alone in late June (shady: F = 0.99; df = 17, 36; P = 0.48; sunny: F = 31.50; df = 17, 36; P < 0.0001) and in both positions in early August (shady: F = 2.58; df = 16, 34; P = 0.010; sunny: F = 25.24; df = 16, 34; P < 0.0001). On both monitoring days and positions, captures were observed only during the daylight hours and started three hours after sunrise. On the late-June monitoring day of both positions, the captures reached a peak three hours before the maximum of solar radiation, and then progressively decreased, reaching their lowest values three hours after the solar radiation maximum, and finally showed an oscillating trend until the hour preceding sunset. No sharp peak in capture numbers was observed on the early-August monitoring day, with similar numbers maintained from 7:00 to 15:00 UTC hours, and, unlike late June, no further captures were recorded in the two hours before sunset.

On the early-August monitoring day, captures on traps placed in inter-row positions were 13.0 and 1.3 times lower than those on traps placed in sunny and shady positions, respectively, but were only significantly different from the former (F = 27.07; df = 2, 6; P = 0.001). The capture numbers in inter-row positions varied significantly over the monitoring day (F = 6.04; df = 16, 34; P < 0.0001) with the highest daily captures in mid-morning coinciding with the early-morning increase in captures in sunny positions. However, adults also moved between the two rows at the same time as the peak in solar radiation, whereas only a few adults were captured during the hours when the maximum daily temperature was reached.

Females comprised 40% of the total captured adults, but the proportion of females significantly differed among the positions, resulting significantly lower in sunny positions (36.3%) than in shady (56.1%) and inter-row positions (62.5%) (P < 0.05 at Ryan's test).

Experiment 2 on the influence of shading on captures

For *E. vitis*, significant differences in the number of captures were observed for the sampling interval (F = 65.05; df = 3, 48; P < 0.0001), but not for the type of roof (F = 2.49, df = 1, 48; P = 0.12) or for the trap side orientation (F = 0.01; df = 1, 48; P = 0.94) (figure 11). The captures were significantly higher during 5-12 August (133.3 ± 6.3) than in the other sampling intervals (104.0 ± 12.7 on 23-30 July, 83.1 ± 8.4 on 21-28 June and 17.7 ± 1.5 on 1-7 October), all of which were significantly different from each other. None of the interactions was significant (sampling interval × roof type: F = 1.88; df = 3, 48; P = 0.15; sampling interval × trap side orientation: F = 0.03; df = 3, 48; P = 0.99; roof type × trap side orientation: F = 0.83; df = 1, 48; P = 0.37).

For *Z. rhamni*, significant differences in the number of

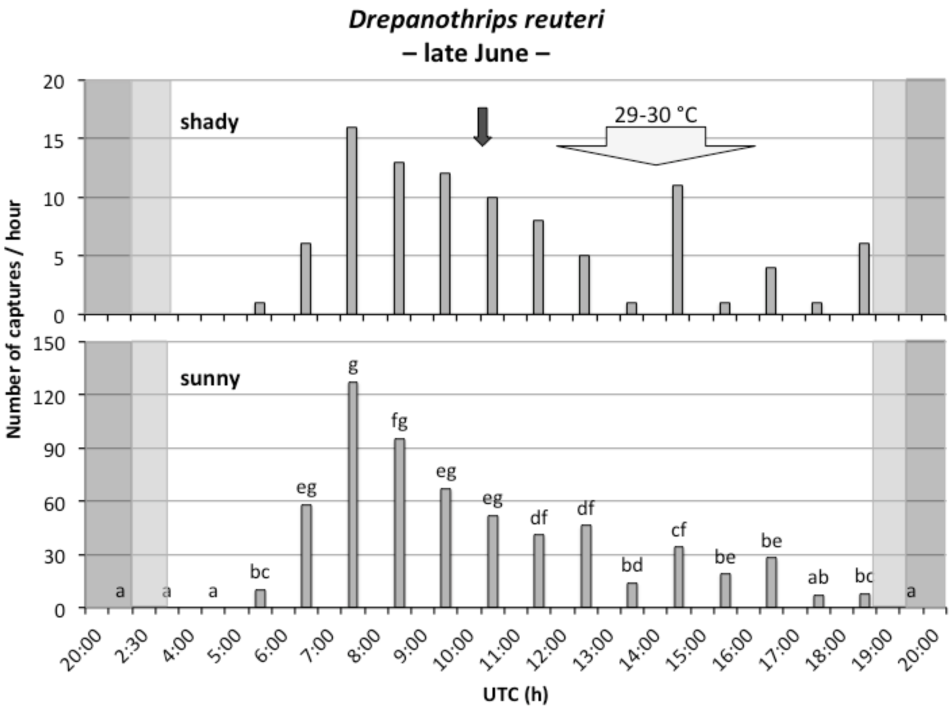

Figure 9. Captures of *D. reuteri* adults recorded with three yellow sticky traps during a late-June monitoring day in shady (graph on the top) and sunny (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

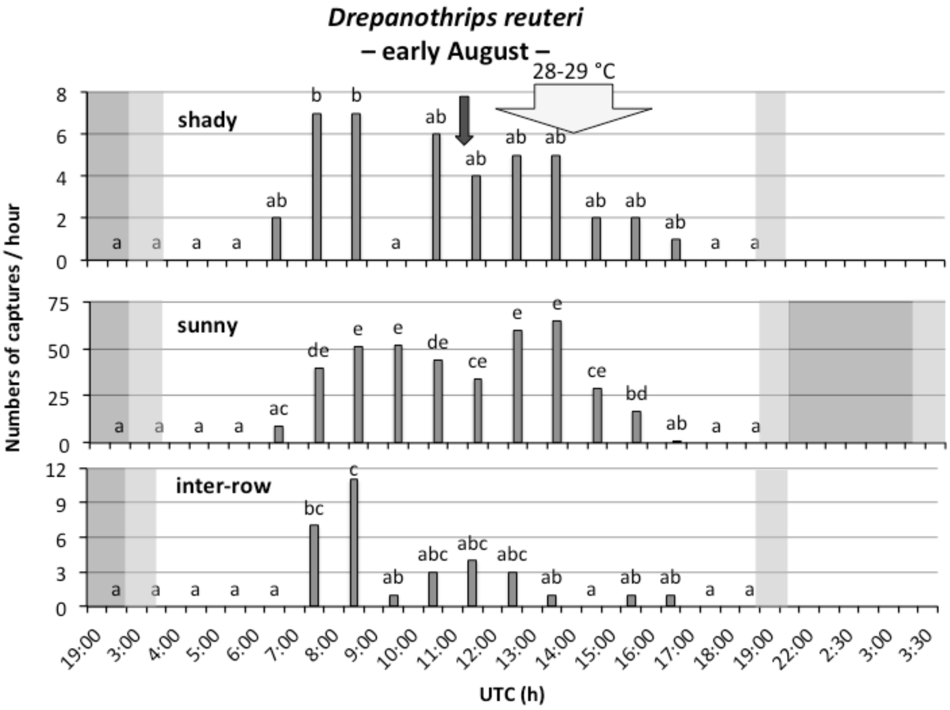

Figure 10. Captures of *D. reuteri* adults recorded with three yellow sticky traps during an early-August monitoring day in shady (graph on the top), sunny (graph on the middle) and inter-row (graph on the bottom) positions. The dark arrow indicates the peak hour of solar radiation, while the white arrow indicates the hours of maximum temperature. The three different backgrounds of the graph (i.e., white, light grey and dark grey) indicate the hours of sunshine, hours of twilight and hours of darkness, respectively. Different small letters above columns indicate significant differences among sampling intervals according to Tukey's test (α = 0.05).

captures were observed for the sampling interval (F = 28.56; df = 3, 48; P < 0.0001). The captures were significantly higher during 5-12 August (16.2 ± 1.6) than in 21-28 June (3.2.0 ± 0.5) or 23-30 July (10.2 ± 1.2), all of which were significantly different from each other. The 1-7 October sampling interval (13.4 ± 2.7) differed only from the 21-28 June sampling interval. The captures were significantly higher in traps under an opaque roof than under a transparent roof (F = 16.15; df = 1, 48; P < 0.0001) (figure 11). The trap side orientation did not influence the number of captures (F = 0.95; df = 1, 48; P = 0.33). The sampling interval × roof type interaction was significant (F = 3.73; df = 3, 48; P = 0.017) because the differences in the number of captures between the opaque and transparent roofs were higher on the early-October monitoring day (2.9 times) than on the three summer monitoring days (max 1.7 times). No significant differences were observed for the sampling interval × trap side orientation interaction (F = 0.40; df = 3, 48; P = 0.76) and the roof type × trap side orientation interaction (F = 1.83; df = 1, 48; P = 0.18).

For *S. titanus*, significant differences in the number of captures were observed for the sampling interval (F = 102.92; df = 2, 35; P < 0.0001). The captures were significantly higher during 5-12 August (10.88 ± 1.27) than in the other sampling intervals (5.1 ± 0.8 on 23-30 July and 0.3 ± 0.1 on 1-7 October), all of which were significantly different from each other. The captures were significantly higher under an opaque roof than under a transparent roof (F = 6.04; df = 1, 35; P = 0.019) (figure 11). The trap side orientation did not influence the number of captures (F = 0.01; df = 1, 35; P = 1.00). None of the interactions were significant (sampling interval × roof type: F = 0.94, df = 2, 35; P = 0.40; sampling interval × trap side orientation: F = 0.56; df = 2, 35; P = 0.58; roof type × trap side orientation: F = 0.28; df = 1, 35; P = 0.60).

For *D. reuteri*, significant differences in the number of captures were observed for the sampling interval (F = 10.57; df = 2, 35; P < 0.0001). The captures were significantly higher during 5-12 August (9.6 ± 2.0) than in the other sampling intervals (2.4 ± 0.6 on 21-28 June and 5.2 ± 1.0 on 23-30 July), all of which were significantly different from each other. The captures were significantly higher under a transparent roof than under an opaque roof (F = 4.78; df = 1, 35; P = 0.036) (figure 11). The trap side orientation did not influence the number of captures (F = 1.52; df = 1, 35; P = 0.23). No interactions were significant (sampling interval × roof type: F = 0.92; df = 2, 35; P = 0.41; sampling interval × trap side orientation: F = 0.12; df = 2, 35; P = 0.88; roof type × trap side orientation: F = 0.11; df = 1, 35; P = 0.74).

Discussion

Preference for sunny or shady positions

The captures of *E. vitis* were always higher on traps placed in sunny positions than in shady positions and the opposite occurred for *Z. rhamni*, which agrees with another study where the traps were left in the field for a

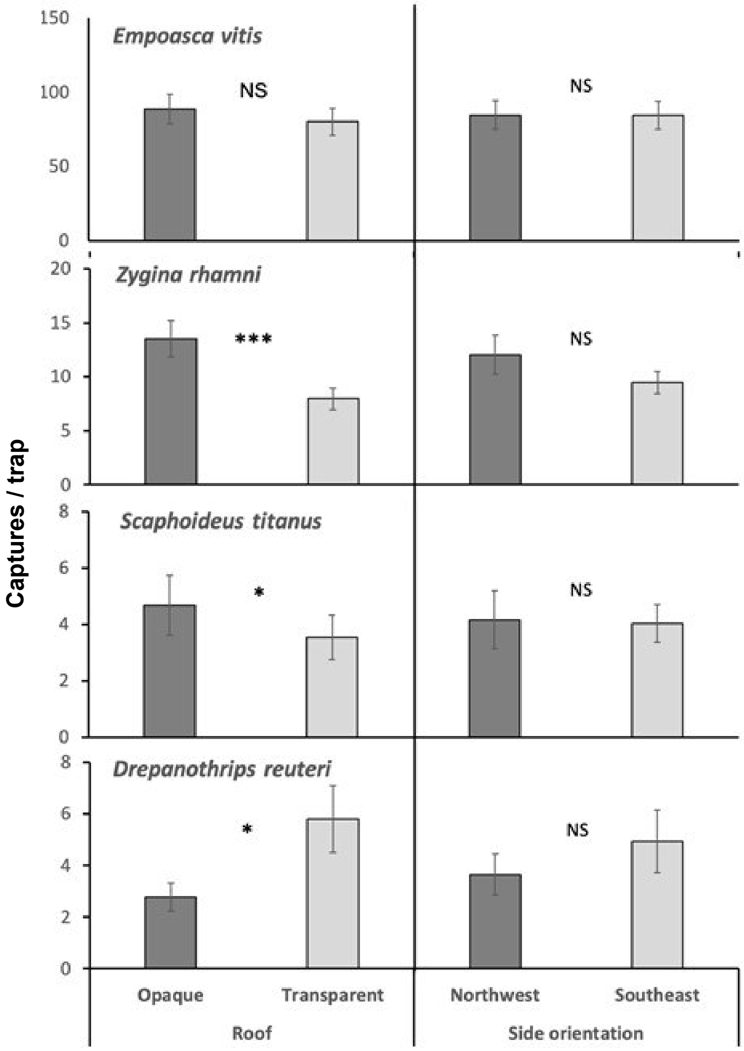

Figure 11. Captures of the four sap-sucking pests recorded with yellow sticky traps placed under opaque or transparent plastic roofs. The orientation of trap sides was also considered. NS = non-significant differences; *, *** = significant differences at 0.05 and 0.001 levels, respectively, using ANOVA.

week (Pavan *et al*., 2021).

The preference of *E. vitis* adults for sunny positions can be associated with a higher attractiveness of leaves not shaded by other leaves suggesting that its flights preferably take place among leaves located on the outside part of the canopy. However, since the captures were not reduced on traps under an opaque roof, it seems that the negative effect of shading is not due to shadow as such, but to the presence of vegetation above the traps. In fact, the greatest number of captures in the sunny-exposed traps occurred at dusk when the sun had already set and adults preferred flight outside the canopy, as evidenced also by both the peak of captures on traps placed in inter-row positions and the low capture numbers on traps placed in shady positions (2 times and 10 times lower than in inter-row positions and in sunny positions, respectively). It can be inferred that at sunset the leafhoppers are induced to disperse between the two walls of vegetation that are separated from each other, as occurred for both the sun-exposed traps placed along the row, above which the vegetation was removed, and for traps placed in inter-row positions.

The preference of *Z. rhamni* adults for shady positions can be associated with the fact that the leafhopper is hygrophilous and avoids direct solar radiation (Vidano, 1963). Because captures were reduced on traps under the opaque roof, it seems that this species preference for shady positions is not due to the presence of canopy above the traps but to the shade itself, confirming that the leafhopper is lucifugous.

The position preference of both *E. vitis* and *Z. rhamni* is even more marked in early autumn (> 10 times) than in early midsummer (2-3 times). For *E. vitis*, the even greater attractiveness of the sunny positions in early autumn could be explained by the increased flight activity outside the canopy favoured by the lower autumn temperatures (compare figures 1 and 2 with figures 3 and 4) and by the fact that the adults begin to disperse towards the overwintering hosts (Vidano, 1963).

Unlike *E. vitis*, the increase in the attraction of *Z. rhamni* for shady positions in early autumn with respect to early midsummer cannot be explained by the lower autumn temperatures. However, this increased preference for shady positions in early autumn does explain why the ratio between the number of adults captured on yellow sticky traps placed in shady positions and the adult density recorded on leaves is much greater than in early midsummer; i.e. in early autumn, the traps lead to a relative overestimation of the adult population (Pavan *et al*., 1988). In this period, *Z. rhamni* adults start to disperse towards overwintering hosts (Zanolli and Pavan, 2011), increasing their flight activity. If we suppose that the captures on traps placed in shady positions are due to the traps' attractiveness and that captures on traps placed in sunny positions are mostly random, an increased flight activity could be associated with even greater captures on traps in shady positions.

The captures of *S. titanus* were higher in sunny positions than in shady positions. In a previous study using differently coloured traps left in the field for seven consecutive days, shady positions were preferred (Pavan *et al*., 2021), but no differences were observed with the yellow traps used in the present study. Such differences in position preference could be due to the traps remaining in the field for only one or few hours in the current study, but seven days in the previous one. Perhaps the decline in trap efficiency over time in sunny positions was more rapid than in shady positions, and consequently this latter position was less preferred during the first exposure day but not after seven consecutive days of exposure. However, the captures of *S. titanus* were higher on traps shaded with the opaque roof, indicating this leafhopper's preference for artificially shaded traps.

The captures of *D. reuteri* were higher in sunny positions as previously reported in Pavan *et al*. (2021). The preference for traps exposed to sunlight aligns with the fact that other thrips species are mostly captured above the canopy of their host plants (Bian *et al*., 2014; Gharekhani *et al*., 2014). For *D. reuteri*, the preference for traps exposed all day to direct sunlight could be associated with their feeding preference for the apical part of the grapevine shoots. Since the captures were higher on traps under the transparent roof than under the opaque roof, it seems that the preference for sunny positions is due to the exposure to direct sunlight and not the absence of vegetation above the traps.

Daily flight activity

Empoasca vitis

During the early midsummer monitoring days, the daily capture pattern was two periods of higher capture numbers (i.e., dawn-sunrise and sunset-dusk), with the first being less important for females, separated by two long periods of lower capture numbers during the hours of sunshine and darkness.

The comparison between the captures on the traps located in the three different positions (i.e., shady, sunny and inter-row) highlighted that at dawn and dusk, the flight activity mainly occurs outside the canopy, while in the one-two hours after sunrise and before sunset the flight activity is relatively more important inside the canopy. Therefore, around sunrise and sunset, flight activity occurs mainly outside the canopy in the twilight periods and inside the canopy in the sunlight periods, suggesting that adult dispersal is favoured by diffused light.

Some captures were observed during the hours of darkness as well, and an underestimation of their numbers could occur due to the absence of solar light, even if on both monitoring days moonlight was present (the moon phase "first quarter" in last June and "three days before full moon" in early August). However, the absence of differences in captures during the hours of darkness between the traps in sunny and shady positions suggests that nocturnal captures occurred randomly.

On the early autumn monitoring days, and especially during the early-October one, which was characterized by lower temperatures and a cloudy sky, the daily flight activity of *E. vitis* showed some differences with respect to the summer monitoring days: the dawn peak was negligible, with captures being relatively abundant in the sunny hours and the daily peak of captures occurring before sunset in sunny positions as well. All these differences can be traced back to the lower temperatures that occurred in early autumn, which on one hand reduced flight activity after sunset and at dawn, and on the other hand even allowed the insects to fly during the daylight hours. On the early-October monitoring day, the fact that the sky was also cloudy may have favoured flight activity during the sunlight hours.

In summary, a bimodal daily flight activity for *E. vitis* can be surmised with peaks at sunrise and sunset, with the latter relatively more dominant, especially late in the season. On the basis of the present study, the lesser importance of the dawn peak is reinforced by the lower female mobility during these hours compared to the sunset-dusk. Using yellow sticky traps, a similar bimodal flight activity was reported for the leafhopper *Scaphytopius magdalensis* (Provancher) (Hemiptera Cicadellidae) (Mayer and Colvin, 1985). Moreover, on herbaceous plants, using a suction trap method for capture, which is not influenced by sunlight in the same way as coloured sticky traps, a bimodal daily flight activity with prevalence of a sunset peak was reported for the congeneric *Empoasca fabae* (Harris) (Dysart, 1962; Smith and Ellis, 1983; Taylor and Reling, 1986) as well as for other leafhoppers and planthoppers (Rodriguez *et al*., 1992; Chancellor *et al*., 1997). Moreover, the planthopper *Nilaparvata lugens* (Stal) (Hemiptera Delphacidae) and some Cicadellidae showed two peaks of flight activity at dusk and dawn using three sampling methods that differed from yellow sticky traps (Riley *et al*., 1987). Further, a laboratory simulation carried out on the leafhopper *Graminella nigrifrons* (Forbes) (Hemiptera Cicadellidae) revealed bimodal daily flight activity (Lopes *et al*., 1995). Therefore, because all flight detection methods concur with a bimodal activity for different leafhopper species, it can be assumed that *E. vitis* has two flight peaks, one during dawn-sunrise and one during sunset-dusk. The hypothesis of low temperatures to explain the fact that in early autumn the flight peak at dawn was even less important than in summer has already been reported for other leafhopper species of the genus *Dalbulus* (Hemiptera Cicadellidae) (Taylor *et al*., 1993).

Zygina rhamni

The flight activity of *Z. rhamni* occurred mostly from dawn to the first two to three hours after sunrise, even if a small increase in captures was recorded at sunset on the early-August monitoring day. Thus, this leafhopper prefers to fly when increased light intensity is associated with cooler daytime temperatures.

In midsummer, the peak of captures occurred at dawn in sunny positions and one hour after sunrise in shady positions. Some captures were also observed in the two to three hours after sunrise (the majority in shady positions), when adults were also detected on traps in inter-row positions, indicating the occurrence of flights between grapevine rows. In early autumn, the peak occurred in the two-hour interval around sunrise, substantially supporting the observations in early midsummer.

Since captures occurred mostly in shady positions in the two to three hours after sunrise during early-August monitoring day, it can be inferred that a high intensity of solar radiation inhibits flights. However, the fact that captures in early autumn occurred during the mid-sunlight hours, when daily solar radiation is the highest, suggests that a lower level of solar radiation or lower temperatures can reduce the inhibitory effect of solar radiation. In parallel, flights of *Cicadulina* spp. (Hemiptera Cicadellidae) have been reported as only occurring during the sunny hours in winter (Rose, 1978).

In summary, we observed that the daily flight activity of *Z. rhamni* comprises only one peak that occurs between dawn and the hour after sunrise. Moreover, even though single peaks of daily flight activity have been reported for other leafhoppers (Larsen and Whalon, 1987; Kersting and Bascedillapinar, 1995), these occur during the sunset-dusk period. To our knowledge, a single peak at dawn-sunrise has not been reported for other leafhoppers.

Scaphoideus titanus

In both sunny and shady positions, the peak of *S. titanus* captures occurred near sunset, but in shady positions, it was observed one hour before sunset, whereas in sunny positions it occurred at sunset and dusk. It can be assumed that, approaching sunset, the captures increased first in shady positions, suggesting greater mobility inside than outside the canopy, but at sunset captures increased in sunny positions, suggesting the emergence of greater flight activity in the outer part of the canopy. However, abundant captures of this species were also recorded during the hours of darkness. Nocturnal activity is supported by the fact that the captures in sunny positions, where the traps were illuminated by the moonlight, were 10 times higher than in shady positions and also the traps in inter-row positions captured some individuals. In contrast, captures were absent during the hours with high insolation, suggesting that adults did not fly in this period.

Therefore, the trend of captures suggests that this leafhopper has a peak of flight activity near sunset but that it also continues being mobile during the hours of darkness, at dawn and in the hours just after sunrise. However, in sunny positions the captures from the last sampling interval of the hours of darkness appear occasional indicating that at sunrise the flight activity outside the canopy is practically ended. Lessio and Alma (2004) reported that the flight activity of *S. titanus* occurred from sunset to sunrise, with a probable flight activity even immediately after sunrise. Nonetheless, the two authors suggest that *S. titanus* flight activity could also occur at dusk, or mostly at dusk, based on the behaviour of other Deltocephalinae species, e.g. *Paraphlepsius irroratus* (Say) (Larsen and Whalon, 1987), *Dalbulus* spp. (Taylor *et al*., 1993), *Circulifer haematoceps* (Mulsant et Rey) (Kersting and Bascedillapinar, 1995) and *G. nigrifrons* (Rodriguez *et al*., 1992). The present study confirmed that flight occurs from sunset to sunrise and showed that the hypothesis of Lessio and Alma (2004) on the daily peak of captures at dusk is true. Moreover, the present study highlighted that the leafhopper is very active and also disperses at night. Flight activity was also observed just after sunrise and just before sunset, but occurs only inside the canopy.

Since the phytoplasma associated with Flavescence dorée can also be inoculated into the grapevine by infectious adults of *S. titanus* colonizing vineyards from outside (Pavan *et al*., 2012; Lessio *et al*., 2015), it may be necessary to apply insecticides against adults. The efficacy of insecticides that acts against the leafhopper mainly by topical contact (e.g. pyrethroids) (Prazaru *et al*., 2023) could increase if they were applied around sunset because adults flying in the outer canopy are more exposed to the sprayed product than when they are immobile and hidden inside the canopy.

Drepanothrips reuteri

In contrast to the three leafhopper species, *D. reuteri* adults fly only in the daylight hours, with no captures even in the two-three hours just after sunrise on both monitoring days and in the late afternoon on the early-August monitoring day. This behaviour is coherent with the fact the vine thrips prefers to colonize the apical leaves of shoots that are sun-exposed.

Data collected in inter-row positions during the early-August monitoring day suggest that dispersal occurs preferably in mid-morning than in the afternoon, i.e. when the temperatures are lower. Moreover, the higher incidence of females on the traps in the inter-row compared to traps in the grapevine canopy suggests that the dispersion is more performed by females than by males.

The flight activity of *D. reuteri* agrees with the daylight-hour occurrence recorded for other thrips (Aliakbarpour and Rawi, 2010; Seal *et al*., 2010; Yan *et al*., 2017).

Conclusions

This study confirms that the studied grapevine leafhoppers have peaks of daily flight activity when there are abrupt changes in light intensity at dawn and dusk, as described for many insects belonging to different orders (Harker, 1973; Saunders, 2002). However, there were important differences among the three leafhoppers studied, as *E. vitis* exhibits bimodal flight with two peaks, *Z. rhamni* prefers to fly around sunrise, when daily temperatures are lower, and *S. titanus* flies continuously from sunset to sunrise. The placement of traps in two different positions of the grapevine canopy (i.e., sunny and shady) allows highlighting that, approaching sunset, the increase in flight activity of the leafhoppers starts earlier inside the canopy than outside and, after sunrise, the flight activity continues only inside the canopy.

In contrast, the flight activity of the vine thrips *D. reuteri* was inhibited during the hours of low light intensity occurring from a few hours before sunset to a few hours after sunrise.

Knowledge of the daily flying activity of leafhoppers and the variation of their behaviour over time with regard to preference for different parts of the canopy can have important implications for establishing the optimal sampling time. In the hours of maximum mobility of adult leafhoppers, the estimate of their population density per leaf may be less accurate because the adults, which live protected on the underside of the leaves and cannot be observed without touching the leaf to invert it, can escape before being identified and counted. For the same reason, adults captured with a beating tray may flee before counting or collecting.

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