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UV light attracts *Diaphorina citri* and its parasitoid

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HIGHLIGHTS

- *Diaphorina citri* is attracted by UV.
- Some other colors become more attractive when combined with UV.
- UV was more attractive than other colors and color combinations.
- UV also attracted *Tamarixia radiata*, a parasitoid of *D. citri.*
- UV can improve attractiveness of sticky traps for *D. citri* and *T. radiata.*

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ABSTRACT

Diaphorina citri Kuwayama (Hemiptera: Psyllidae) transmits the bacteria associated with Huanglongbing, an incurable and lethal disease affecting citrus productivity and fruit quality worldwide. This vector is prominently phototactic and uses visual cues to find host plants. Yellow sticky traps are used for its monitoring, but their efficiency is limited, especially at low population densities. *Diaphorina citri* can be captured at night when light is provided and it is attracted to UV light. One way to increase the attraction of *D. citri* is therefore combining sticky traps with LEDs of specific colors at night, but more information about attractiveness of UV and colors combined with UV is needed. Moreover, information on the attraction of the main parasitoid of *D. citri*, *Tamarixia radiata* Waterson (Hymenoptera: Eulophidae) to UV and other light colors is lacking. We examined the attraction of males and females of *D. citri* to LED lights of different colors but comparable intensities separately or combined with ultraviolet (UV). The non-UV colors alone did not differ in attractiveness, whereas green, light blue and red light became more attractive when combined with UV. However, none of these color combinations were more attractive than UV alone. The parasitoid *T. radiata* was also attracted to UV LEDs. Female parasitoids were equally attracted to UV during day and night, but males were more attracted at night. These results suggest that the effectiveness of the commonly used yellow sticky traps can be increased by combining them with UV LEDs at night, and the parasitoid of *D. citri* may also be attracted. On the one hand, attraction of parasitoids to the traps may help monitoring their presence, but on the other hand, it may affect biological control by this natural enemy.

1. Introduction

Diaphorina citri Kuwayama (Hemiptera: Psyllidae), the Asian citrus psyllid, is a vector of Huanglongbing (HLB), the most devastating disease of citrus worldwide (Bové, 2006). The causal agents of HLB are *Candidatus* Liberibacter spp. which are gram-negative bacteria that colonize plant phloem (Garnier et al., 1984; Halbert and Manjunath, 2004; Li et al., 2006). *Diaphorina citri* acquires the bacteria when feeding on the phloem of an infected tree and they transmit it by subsequently feeding on the phloem of an uninfected plant (Halbert and Manjunath,

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2004). To date, HLB is incurable (Ramadugu et al., 2016; Pandey and Wang, 2019), affecting all known commercial citrus cultivars (Zou et al., 2019) and causing losses in yield and fruit quality (Bové, 2006). Nowadays, the disease is present in the main citrus producing countries, such as Brazil, the United States and China (Wang, 2019).

In affected areas, symptomatic plants are eradicated to remove the inoculum (Bassanezi et al., 2013; Grafton-Cardwell et al., 2013). Studies on HLB-resistant genotypes are advancing (Alquézar et al., 2021), however, the main management measure to date is chemical control of the vector with foliar and systemic insecticides (Grafton-Cardwell et al., 2013; Miranda et al., 2018). Excessive pesticide applications may result in undesirable consequences such as secondary pest outbreaks (Miranda et al., 2018), development of insecticide resistance (Kanga et al., 2016; Chen and Stelinski, 2017), and effects on non-target organisms, such as natural enemies (Monzo et al., 2014) and pollinators (Chen et al., 2017). Moreover, chemical control is not always effective when natural enemies are present (Janssen and van Rijn, 2021). Excessive use of pesticides can also result in pesticide residues on fruits (Ortelli et al., 2005), pollution of the environment (Li et al., 2019) and increases of production costs (Tansey et al., 2017). Therefore, effective monitoring is necessary to optimize control measures and HLB management in a sustainable way (Stelinski, 2019).

Even with the rapid spread of HLB in citrus-producing countries, there are still areas free of HLB. For example, *D. citri* has been registered in Brazil since the 1940s (Costa Lima, 1942) and HLB was reported in the state of São Paulo in 2004 (Coletta-Filho et al., 2004), and then spread rapidly to other citrus-producing states such as Minas Gerais, Paraná, and Mato Grosso do Sul (Bassanezi et al., 2020), but states such as Bahia, which is the third largest citrus-producing state of the country, are still HLB free (Abreu et al., 2020). Hence, the arrival of the disease in these states is considered an imminent risk. The main strategy against HLB in disease-free areas is prevention through monitoring (Monzo and Stansly, 2017; Abreu et al., 2020). Methods that can effectively detect the presence of the vector even at very low population densities are required, because one infected individual already constitutes a threat and needs to be controlled (Miranda et al., 2018).

In this context, the monitoring of *D. citri* populations is crucial for early detection and to mitigate disease spread (Keremane et al., 2015; Monzo et al., 2015). Monitoring *D. citri* not only in citrus groves, but also outside them is considered essential for greening management because of the risk of dispersion (Hernández-Landa et al., 2018), and *D. citri* occurs also in urban areas (Godfrey et al., 2013; Hernández-Landa et al., 2018). Psyllids use visual stimuli for orientation and selection of host plants (Farnier et al., 2015; Ben-Yakir and Fereres, 2016). *Diaphorina citri* is no exception to this: it showed difficulties in finding host plants when olfactory cues were provided without visual cues (Wenninger et al., 2009a; Patt et al., 2011, 2014). The most effective monitoring method to detect *D. citri* when present at low densities is with yellow sticky traps, which are also used to quantify densities (Sétamou et al., 2014; Miranda et al., 2018). Although yellow sticky traps are known to catch more insects than traps of other colors (Hall et al., 2010; Sétamou et al., 2014), they are still not effective enough to detect the very low densities of *D. citri* that are required for efficient management (Hall et al., 2010; Monzo et al., 2015). Knowledge of the specific visual stimuli that attract *D. citri* can therefore be used to increase the capture efficiency of traps (Sétamou et al., 2014). *Diaphorina citri* shows positive phototaxis (Yasuda et al., 2005; Stelinski, 2019), wavelength-specific behavior toward UV, and is attracted by green and yellow LEDs (Paris et al., 2015). Hence, traps may be made more attractive by combining them with UV LEDs and lights of other colors, especially at night.

The use of LEDs is a promising method to increase trap effectiveness for several insect species (Duehl et al., 2011; Sonoda et al., 2014; Park and Lee, 2017). For example, the addition of UV increased the attractiveness of traps for the tomato-potato psyllid, *Bactericera cockerelli* Sulc (Hemiptera Psylloidea), black fungus gnats *Bradysia difformis* Frey (Diptera: Sciaridae); the cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae); the spiralling whitefly, *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae); and *Culex* spp. mosquitoes (Zheng et al., 2014; Stukenberg et al., 2018; Peck et al., 2018; Hodge et al., 2019; Pan et al., 2020). Although *D. citri* is a diurnal insect and its movements are reduced at night (Wenninger and Hall, 2007), it can respond to light provided at night (Sétamou et al., 2012). Indeed, in the dark, traps with white LEDs attracted 5-fold more *D. citri* than traps without LEDs (Mangan and Chapa, 2013). It is therefore expected that traps with specific color LEDs could further increase catching efficiency (Bellows et al., 1988; Sétamou et al., 2012).

Hence, addition of specific-colored LEDs to the current yellow sticky traps would also allow catching *D. citri* at night. It has been reported that green or yellow lights plus UV attracted more *D. citri* than without UV (Paris et al., 2017b), and substances with UV reflective properties applied to the surface of yellow sticky traps increased the attraction of this pest (George et al., 2020a). However, it is not known whether *D. citri* is more attracted to colors combined with UV compared to only UV. Here, our objective was to verify which LED colors are more attractive when combined with UV LEDs and whether colors combined with UV are more attractive to *D. citri* than UV alone. If so, these LEDs can be combined with yellow sticky traps, thus also attracting *D. citri* at night.

Besides pests, light traps may attract and kill non-target organisms such as natural enemies (Ogino et al., 2016; Bian et al., 2018). Pests and natural enemies may show different preferences for particular wavelengths and the light provided with sticky traps needs to be as specific as possible to attract the pest and limit the capture of beneficial organisms (Bian et al., 2018), unless the presence of these natural enemies also needs to be monitored. Therefore, knowledge of the phototactic behavior of *Tamarixia radiata* Waterson (Hymenoptera: Eulophidae), the main parasitoid of *D. citri*, is also of importance for the development of an effective trapping method. This natural enemy is an ectoparasitoid from Asia that parasitizes the last nymphal instars of *D. citri* (Chen and Stansly, 2014). It has already been caught on yellow sticky traps used in citrus orchards and in orange jasmine plants, *Murraya paniculata* (L.) Jack (Rutaceae), in urban areas (Schapovaloff et al., 2019). In Brazil, the parasitoid is released especially outside citrus orchards managed with pesticides, such as organic and abandoned groves, and in urban areas (Gomez-Marco et al. 2019; Diniz et al., 2020). In these areas, monitoring of the densities of *D. citri* is necessary as decision tool (Shrestha et al. 2021). It is known that males and females of this parasitoid show positive phototactic behavior (Mann et al., 2010). Therefore, the attraction of *T. radiata* to colored LEDs should also be investigated, on the one hand, to design selective monitoring traps to increase the capture of *D. citri*, but not the capture of *T. radiata*, at night, to avoid possible negative effects on the densities of this natural enemy. On the other hand, if traps can also attract *T. radiata*, these traps can be used to more accurately monitor both pest and natural enemy populations in integrated pest management programs.

2. Materials and methods

2.1. Insects

Diaphorina citri were aspirated from orange jasmine plants (*Murraya paniculata*) into plastic vials (7 cm long × 1 cm wide) in the Brazilian states of Bahia (12°20′04″ S, 38°97′19″ W and 12°40′39″ S, 39°06′23″ W) and in the municipality of Viçosa, Minas Gerais (20° 45′ 37″ S 42° 52′ 04″ W), which are still considered HLB free-areas in Brazil. The experiments on attraction of *D. citri* to UV and other colors and color combinations were carried out at the Feira de Santana State University, Bahia, whereas the preference experiments were carried out at the Federal University of Viçosa, Minas Gerais. Because the aim of this study was to investigate the possibility to use light as an additional method of monitoring field populations of *D. citri*, it was essential to use field-collected individuals for experiments, consisting of a natural mix of individuals of different age, sex and physiological conditions. After being collected, the insects were taken to the laboratory, where the abdominal color was classified as gray/brown, green/blue or orange/yellow (Wenninger and Hall, 2008). These morphs are thought to be related to specific characteristics, for example, individuals with orange/yellow abdomens are assumed to be more sensible to insecticides (Tiwari et al., 2013); blue/green abdomens are thought to be related to dispersing morphs which acquire and transmit HLB less frequently (Wenninger et al., 2009b; Martini et al., 2014a; Hosseinzadeh et al., 2019; Ibanez et al., 2019), and gray/brown morphs were reported to have lower body mass, females have lower reproductive output, and males seem to fertilize fewer eggs in their matings (Wenninger and Hall, 2008; Wenninger et al., 2009b).The individuals were sexed and the same numbers of males and females were used in each experiment.

Individuals of *T. radiata* were collected as parasitized *D. citri* nymphs (4th and 5th instars) on the campus of the Federal University of Viçosa. Orange jasmine plants were searched for parasitized nymphs, and branches of orange jasmine plants (about 10 cm long) were cut and taken to the laboratory. The base of the branches was wrapped with wet cotton wool and placed in plastic seedling trays (128 cell trays, 4.8 × 28 × 54.5 cm; Nutriplan®, Cascavel-PR, Brazil) inside a BugDorm-4F insect cage (0.5 × 0.5 × 1.0 m) until emergence of adult *T. radiata*. Individuals were collected, sexed and tested. Thus, all individuals tested were approximately the same age and because copulation occurs about 2–3 d after emergence (Étienne et al., 2001), all individuals tested were probably virgin.

2.2. Tubular arena with LEDs

A transparent acrylic tubular arena (30 cm long × 5 cm diameter) was developed to evaluate attraction of *D. citri* by different light colors (Fig. 1). The tubular arena was equipped on both sides with commercially available LEDs (Kento, Hubei Kento Electronic Co. Ltd., Guangdong Province, China) that produced UV, green, yellow, blue, red, light blue or white light. The parts to fit the LEDs on each side (Fig. S1) of the tube were made using a 3D printer (Prusa i3 MK3S, Prusa Research). Each side of the tube was equipped with seven LEDs: three of the UV type with peak emissions at 400 nm and four Red/Green/Blue (RGB) types with peak emissions at 635, 515 and 470 nm, respectively. The UV had one chip LED and RGB had three chip LEDs. Other colors (yellow, white and light blue) were obtained by combining RGB LEDs, superposing their spectra. Together, this allowed us to investigate the full spectrum of colors from UV to red. The LEDs circuit was powered with an electric potential difference of 9 V and the current was limited by resistors of 1200Ω (one resistor per color). The current through the diodes was approximately 3 mA and it was calibrated to obtain similar light intensity peaks. LEDs on each side of the tube could be switched on independently. Each side of the tube had a hole (4 mm) for insect insertion close to the part with the LEDs. A central hole (4 mm, Fig. 1), was made later, to introduce insects in the choice tests.

2.3. Attraction of psyllids to UV and other colors

After having been sexed, the insects were taken to a dark room without artificial light and no direct daylight, but with enough light to carry out the experiments. Each insect was introduced in a pipette tip (1000 μL), which was fitted in one of the holes at each side of the arena. The psyllids were released through one of these holes, on the side of the tube opposite the light source that would be turned on at the other side of the tube. The arena was marked five cm from each light source and individuals were assumed to have made a choice if they crossed the line opposite the side where they were released. Individuals were assumed not to have made a choice when they did not move or did not cross the line on the opposite side within 1 min. For psyllids that showed positive phototactic behavior, the response time was recorded. The side with light was alternated between individuals to eliminate positional bias. The experiment was designed to assess the attraction to UV and one of 6 light colors: blue, light blue, green, red, white or yellow. Sixty males and 60 females were individually exposed to UV for 1 min and to one of the other 6 light colors for another minute. The order of testing UV or the other color was alternated, hence, half of psyllids were exposed to UV first, the other half to the other color first. When an individual had walked to the first light, it was turned off and the light of the other side was turned on. When the individual did not walk to the first light provided, the tube was rotated 180° horizontally and then the second light was turned on. If the insect took>1 min to reach the other side, we waited until it walked to the other side to turn on the second light. Exposure to non-UV colors followed a fixed sequence, so if the first insect was exposed to red, this color would only be tested again after all other colors were tested. Pilot tests showed that males did not respond any longer after several other males had been tested in the tube, but that the response was restored after cleaning the tube, so apparently, the males left behind some cue that affected the behavior of subsequent males. Therefore, individuals of the same sex were tested sequentially and the tubular arena was cleaned with neutral detergent and water after 5 insets were tested. All assays were conducted under controlled conditions (temperature: 27 ± 1 °C and relative humidity: 70 ± 10%), between 10:00–18:00 h, which is when *D. citri* is most active (Paris et al., 2015). Data consisted of series of zeros and ones and were tested with a generalized linear model with a quasi-binomial error distribution. Because there were no sufficient observations per combination to include all interactions among factors, abdomen color was not included. We included sex, the order of offering UV and the alternative color and their pairwise interactions as factors in the first model. This model was subsequently simplified by removing non-significant interactions and factors. The response times of those psyllids that did respond were compared with GLM using a Gaussian error distribution with sex, color and order as factors. The package emmeans with a Tukey correction for multiple comparisons (Lenth et al., 2020) was used to assess contrasts among treatments. We also tested the independence of response to UV and to the alternative color with GLM with a binomial error distribution,

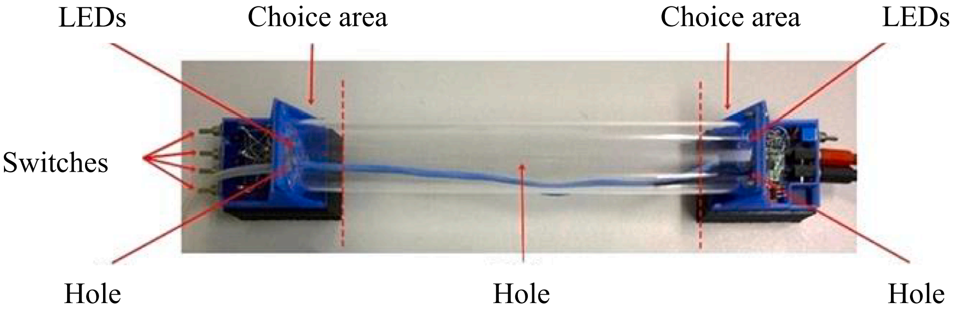

Fig. 1. Experimental arena used for evaluating attraction of adults of *Diaphorina citri* and *Tamarixia radiata* to light of different colors. UV lights and LEDs of different colors can be switched on and off independently at each end of the tube. There were 7 LEDs on each side: 3 UV and 4 RGB. On each side of the tube, the areas starting from 5 cm until the LEDs were considered as areas of choice. The holes indicated in the picture were used to introduce the insects.

with order and response to UV as factors. All statistical analyses were done using R version 3.5.3 (R Core Team, 2020).

2.4. Attraction of psyllids to UV combined with other colors

This experiment was designed to assess if UV combined with other colors was more attractive than UV alone. Psyllids (60 males and 60 females) were individually exposed to UV and to one of the six other colors combined with UV. Further methodology and statistics were as described above (Section 2.3).

2.5. Psyllid preference

This experiment was designed to assess whether psyllids were more attracted to UV light or to other colors combined with UV, when both were provided simultaneously. The preference experiment was conducted in a completely dark room and a red LED light (OuroLux™ SuperLed S30 3 W, spectrum in Fig. S1) outside the tube was used to enable observations by the researchers. In this experiment, the insects were introduced through a hole (4 mm) that was drilled in the center of the tubular arena, in the middle between the two light sources. The hole was made at the underside of the tube because *D. citri* shows negative geotaxis (Yasuda et al., 2005), so would move up into the tube when introduced. Each insect was placed in a transparent pipette tip (200 μL), which was cut at the narrow end to an opening large enough for *D. citri* to pass through. As soon as the tip with the insect was inserted into the hole, the lights in the arena above were switched on and the external red light was switched off. Recording of the time started when the insect came out of the pipette tip and reached the arena. An individual was considered to show a preference when it reached one of the areas of choice (as above) within 1 min after entering the tube. Two UV LEDs were switched on one side and one UV LED and one LED with another color (light blue, green or red) on the other side. Only these three combinations were tested because they were the most attractive in the previous experiment. Forty-five males and 46 females were used, of which three males and six females did not make a choice, resulting in 15 males and females for the combination UV with light blue, 14 males and 12 females for UV with red and 13 males and 13 females for UV with green. The predominant abdominal color of psyllids was gray, and it was not possible to verify if there was a difference in preference among psyllids with different abdominal colors. The other procedures were as described above (Sections 2.3 and 2.4). Per combination of sex and color, we first calculated the probability of obtaining the observed result with a binomial test with the expectation that the individuals would choose for each of the alternatives with probability 0.5 (Siegel and Castellan, 1988). Subsequently, we compared responses among color combinations, between sexes and between sides of the tube (to detect any unforeseen directionality in the response) with a GLM and interactions were included as above.

2.6. Attraction of *Tamarixia radiata* to UV

This experiment was designed to verify whether the parasitoid *T. radiata* is attracted to UV, because this stimulus alone was the most attractive to *D. citri* in all previous experiments. We individually tested attraction of males and females in a dark room during the day, simulating dark conditions as with *D. citri*. Because it is unknown, to our best knowledge, whether *T. radiata* responds to light at night, we also tested its attraction to UV from 8 pm onwards. Eighty-four individuals were tested, 20 females and 20 males during the day in a dark room and 24 females and 20 males at night. The individuals were released through the hole in the center of the tube using a tip as described above (Section 2.5). UV was provided on one side of the tube; the other side was dark. Light colors were changed from one side of the tube to the other to eliminate possible bias. We considered individuals responsive when they walked towards the UV light or the opposite side of the tube within 1 min during the day and 3 min at night, considering that diurnal insects may have reduced activity at night (Helfrich-Förster, 2018). The results were analyzed in two ways. First the responsiveness of males and females was analyzed (comparing the numbers of individuals that either made a choice for either side of the tube or not) with a GLM with a Poisson error distribution with gender, period (day or night) and response (no response vs a choice for one of the sides of the tube) as factors. Second, we tested for the significance of the preference of males and females for UV light during the day and night separately with a binomial test as above.

3. Results

3.1. Attraction of psyllids to UV and other colors

In agreement with earlier research (Paris et al., 2015), we observed that *D. citri* was strongly attracted to UV light: 77.5% of *D. citri* was attracted by UV. Other colors were much less attractive; about 37.5% was attracted to them. The 6 non-UV colors did not differ in attractiveness (GLM: $F_{5,113} = 1.12$, $p = 0.35$; Fig. 2), and the order of presenting the colors, and the sex of the psyllids did not significantly affect the attraction (GLM, all $p > 0.094$). The response time was neither affected by light color (GLM, $F_{5,41} = 0.48$, $p = 0.79$), by the order in which the lights were presented nor by the sex of the psyllids (GLM, all $p > 0.21$). Besides, the responses to UV and to other colors were independent (GLM, deviance = 2.54, d.f. = 1, p = 0.11). Of the 120 insects tested, 7 females and 5 males were attracted to another color and not to UV (blue 2; light blue 2; red 2; white 4; yellow 2) and 26 females and 34 males were attracted to UV but not to another color. This is confirmation that UV is more attractive than the other colors for most *D. citri*.

3.2. Attraction of psyllids to UV combined with other colors

We observed that 82.5% of the psyllids responded to UV alone and 76% responded to UV combined with the other colors. The attraction of psyllids differed significantly among color combinations (GLM, $F_{5,114} = 2.45$, $p = 0.038$; Fig. 3). They were more attracted to light blue, green, red and blue combined with UV than to yellow and white combined with UV. Sex of psyllids and order in which the color with UV and UV alone were provided did not affect the response (GLM, all $p > 0.29$). The response time did not differ among colors (GLM, $F_{5,72} = 0.92$, $p = 0.47$), and was not affected by order or sex of psyllids (GLM, all $p > 0.2$). Besides, the responses to UV and to colors combined with UV were independent (GLM, deviance = 1.19, d.f. = 1, p = 0.28). Of the 120 insects tested, only 1 male responded to a color combined with UV (green) but

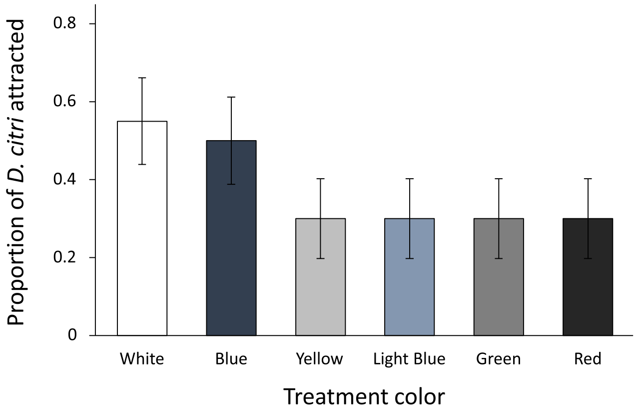

Fig. 2. Proportions of adults of *Diaphorina citri* attracted to different colors (white, blue, yellow, light blue, green and red). 120 insects were tested, 10 males and 10 females per color. Each individual was tested separately in the tube (Fig. 1). Error bars represent the standard error. In total, 78.3% of the insects were responsive.

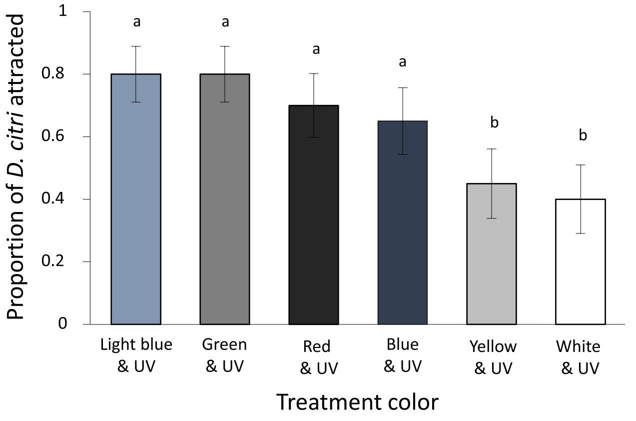

Fig. 3. Proportion of adults of *Diaphorina citri* attracted to different colors (light blue, green, red, blue, yellow and white) combined with UV. Each individual was tested separately in the tube (Fig. 1), 120 insects were tested, 10 males and 10 females per color. Letters above bars indicate significant differences among combinations (contrasts after GLM, $p < 0.001$). Error bars represent the standard error. In total, 82.5% were responsive to UV alone and 76% were responsive to UV combined with the other colors.

not to UV and 9 females and 15 males responded to UV but not to a combination.

3.3. *Psyllid preference*

UV alone was more attractive than UV combined with light blue, green or red (binomial test, all $p < 0.001$, Fig. 4). There was a significant difference in attraction among colors (GLM, deviance = 7.77, d.f. = 2, p = 0.02). Green and red combined with UV were more attractive than light blue with UV (Fig. 4). The two sexes were similarly attracted to the different colors and there was no significant preference of the psyllids for one direction (left- or right-hand side of the tube). The response time did not differ between sexes or colors. In conclusion, psyllids were always significantly more attracted to UV alone than to UV combined with other colors. In this experiment, 97 insects were tested and 3 females and 3 males did not respond to any color.

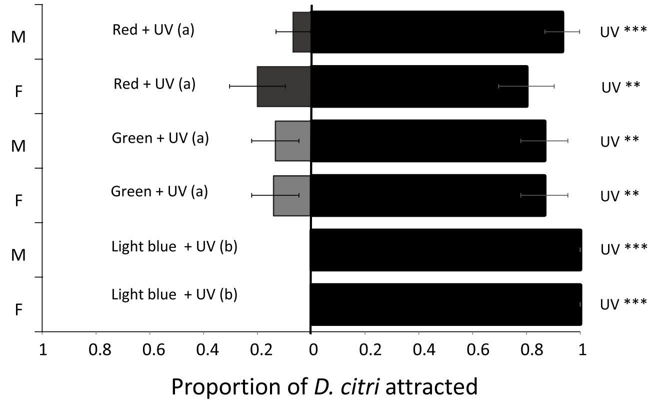

Fig. 4. Preference of males (M) and females (F) of *Diaphorina citri* when offered a choice between red, green and light blue combined with UV and UV (400 nm) alone. Red + UV: red combined with UV, Green + UV: green combined with UV and Light blue + UV: light blue combined with UV. Asterisks indicate significant difference in attraction to colors combined with UV and UV alone per sex (binomial test, **: $p < 0.01$; ***: $p < 0.001$). Lowercase letters indicate differences in attraction to UV among the different color combinations. The attraction of males and females did not differ. Error bars represent standard errors and 94% of the insects were responsive.

3.4. *Attraction of Tamarixia radiata to UV*

Responsiveness of the parasitoid differed significantly between sexes (GLM, interaction of sex and response: deviance = 6.22, d.f. = 1, p = 0.0126) and between day and night (interaction of period with response: deviance = 3.97, d.f. = 1, p = 0.0464). The response of females and males differed significantly during the day (GLM, interaction of sex with response: deviance = 9.09, d.f. = 1, p = 0.0025) but not at night (deviance = 0.81, d.f. = 1, p = 0.776). This was because males of *T. radiata* were less responsive during the day than during the night, but females were equally responsive during the day and at night (Fig. 5). At night, males and females were equally responsive. Females of *T. radiata* were attracted to UV during the day and at night (binomial test, both $p < 0.001$). Males were only significantly attracted to UV at night (binomial test, $p < 0.001$), not during the day (binomial test: p = 0.145, Fig. 5). The response time did not differ between sexes (GLM, deviance = 0.64; d.f. = 1; p = 0.28) or period (GLM, deviance = 34.2; d.f. = 1; p = 0.07).

4. Discussion

We show that adult *D. citri* were more attracted to UV (400 nm) than to light of other colors or to UV combined with these colors. Adult females of *T. radiata*, a parasitoid of *D. citri* were also attracted to UV during the day and at night, but males were only attracted at night. Possibly, *D. citri* is attracted to UV because it uses it to find suitable host plants. New flushes with a thin layer of epidermis reflect more UV than older leaves (Gausman et al., 1975; Paris et al., 2017a), and *D. citri* depends on these flushes for oviposition, feeding and development (Catling, 1970). In turn, parasitoids may use UV light for host location and spatial orientation (Chiel et al. 2006).

In previous studies, the attraction of *D. citri* to UV and other colors was also observed, as well as an increased attraction to yellow and green when combined with UV (Paris et al., 2015; Paris et al., 2017b). These results indicate that the behavior of *D. citri* was affected by light of different colors and that this effect is more pronounced for some specific wavelengths. In this previous study, the attractiveness of UV did not differ from that of green, yellow or blue (Paris et al., 2015). In the present study, all non-UV colors alone did not differ significantly in attractiveness (Fig. 2), and combining green, red and light blue light with UV increased their attractiveness (Fig. 3), but no combination was more attractive than UV alone in the dark (Fig. 4). Remarkably, colors that attracted proportionally fewer individuals of *D. citri* on their own

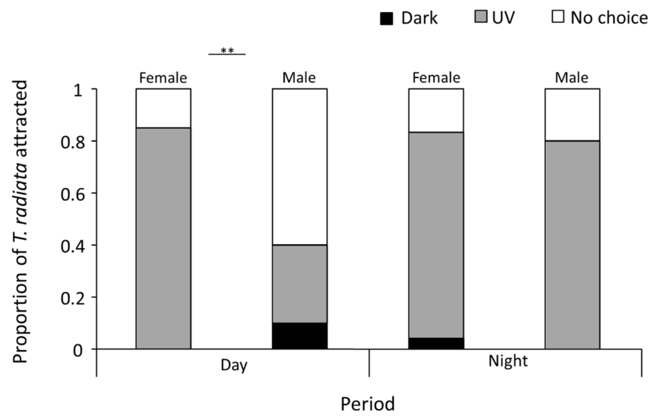

Fig. 5. Proportion of males and females of *Tamarixia radiata* attracted to UV during the day and at night. Each individual was tested individually in the tube (Fig. 1), 20 females and 20 males were tested during the day and 24 females and 20 males at night. Asterisks above bar indicate significant differences between males and females during the day. Error bars represent standard errors. About 84% of the females were responsive during the day and night, whereas 40% of the males were responsive during the day and 80% at night.

(light blue, green and red, Fig. 2) became most attractive when combined with UV (Fig. 3), whereas white light attracted more individuals of *D. citri* on its own (Fig. 2) and became proportionally the least attractive when combined with UV. Hence, it appears that offering a combination of two attractive colors (white and UV) interferes with the attraction to each of these colors. We do not have an explanation for this at present.

A factor that may explain the difference between our results and those of Paris et al. (2015) is a difference in methodology. The proportion of responsive psyllids observed in our experiments (about 80%) was higher than in previous reports (Paris et al., 2015; Paris et al., 2017b). There are several possible causes for this difference in attraction. Here, we tested each insect separately, whereas Paris et al. (2015, 2017b) tested groups of *D. citri*. Individuals may affect the response of others: females may release pheromones that attract males (Zanardi et al., 2018) and females are known to avoid cues of other females (Martini et al., 2014b). Moreover, we observed that males that were tested after several other males had been tested in the tube did not respond well, and periodical cleaning of the tube restored male response, suggesting that males leave behind some cue. This is the first evidence that males of *D. citri* may repel other males, but this has been recorded for another psyllid (Guédot et al., 2009). Another difference between the current study and previous studies is that we observed the response in real time, and were thus capable of observing the first response of each individual. This is important because insects may learn after some time that the light is not associated with a reward (i.e., a host plant), or may show habituation to the light, resulting in a reduction of the attraction and arrestment. Besides, differences observed among the current and previous studies may be explained by the wavelengths of LEDS used.

In the first two experiments, about 80% of individuals responded to UV, while only about 5.4 % of the individuals that did not respond to UV responded to other colors. Psyllids that did not respond within one minute were included in our analysis as non-responsive; these individuals may not have responded in the established time because they differed from the individuals considered responsive, for example, in physiological conditions. Paris et al. (2017a) found that the age of *D. citri* did not influence the phototactic response, except for 4–7-day-old psyllids, which responded slower to green light. We did not observe differences in time of attraction among the responsive psyllids, but they were collected from the field and probably consisted of a mixture of ages and states. So there may have been females and males at the end of their reproductive period, and they do not need to find plants to oviposit or partners to copulate anymore. This may explain why about 20% of psyllids were unresponsive. Additionally, we did not observe significant differences in responses of males and females to light colors.

It can be argued that the attraction tests with single colors and with non-UV colors combined with UV are based on the response of few individuals per color. Many tests of the response of animals use cues of biological origin, which are inherently variable, requiring testing several individuals and several different cue sources. Here, we used light cues that were constant, thus eliminating one source of variation. Another source of variation is that among individuals. We tested all individuals for their response to UV, and this response was high, showing that the vast majority of the individuals tested were responsive in our set-up, so there was also not much variation in responsiveness among individuals. Nevertheless, we could probably have shown significant differences in attractiveness among non-UV colors (Fig. 2) by testing more individuals, but we were mainly interested in finding more, and not less, attraction and the non-UV colors were all much less attractive than UV alone. We therefore decided to test these colors in combination with UV (Fig. 3) to select the three most attractive color combinations for the choice test.

Males and females of parasitoid wasps may differ in attraction and sensitivity to perception of specific wavelengths (Romeis et al., 1998; Hoelmer and Simmons, 2008; Chen and Stansly, 2014; Cochard et al., 2017). We found here that females of *T. radiata* were equally attracted to UV at night and day (about 80% of individuals), but males were less attracted during the day. As far as we know, this is the first report of a response to light stimuli that is affected by period and sex in a diurnal parasitoid wasp. Sticky traps can be used to monitor the presence, capacity of dispersion and population trends of natural enemies to support decision-making in integrated pest management programs (Dowell and Cherry, 1981; Romeis et al., 1998; Mills et al., 2006; Böckmann and Meyhöfer, 2017). On the one hand, a trap that is attractive for the pest and its natural enemy may be used to monitor both simultaneously in a more cost-efficient and easy way (El-Wakeil and Volkmar, 2013; Böckmann and Meyhöfer, 2017). On the other hand, highly attractive traps for natural enemies may reduce their densities and hinder their conservation in crops (Böckmann and Meyhöfer, 2017). Future research needs to quantify the effect of light traps on the biological control by *T. radiata*. Knowing what specific UV wavelength and intensity is best for triggering attraction behavior of *D. citri* with minimal negative effects on its natural enemies also deserves further investigation. An alternative for the use of these sticky traps is the use of biological control agents that do not use visual stimuli or fly, such as predatory mites of *D. citri* (Juan-Blasco et al., 2012; Fang et al., 2013; Kalile et al., 2021).

Information on wavelengths that attract target insects that exhibit positive phototactic behavior may enhance the attractiveness of traps used for monitoring and physical control (Cohnstaedt et al., 2018). UV is known to affect the behavior of various insects such as whiteflies, flies, psocids and thrips (Pickens and Thimijan, 1986; Antignus et al., 2001; Shimoda and Honda, 2013; Diaz-Montano et al., 2018; Liu et al., 2019) and is known to be used to orient flight activity toward the sky (Bellows et al., 1988; Chyzik et al., 2003; Stukenberg et al., 2015; Ben-Yakir and Fereres, 2016). UV-deficient environments can negatively affect pest behavior such as dispersion. For example, the use of UV-reflective metalized polyethylene mulch in citrus orchards resulted in lower *D. citri* infestations (Croxton and Stansly, 2014; Kigathi and Poehling, 2012; Miranda et al., 2015). In turn, effects of UV on parasitoids are ambiguous: they may or may not be affected by UV-absorbing plastic sheets (Chiel et al., 2006; Legarrea et al., 2014).

The sensitivity of yellow traps used to monitor *D. citri* may be enhanced by using UV LEDs at night. Further studies should evaluate how many LEDs are sufficient to increase attractiveness of *D. citri* to be economically viable. Besides increasing the attractiveness at night, the use of substances that increment the UV reflectance, such as magnesium oxide, also improve the attractiveness of yellow traps (George et al. 2020a). Moreover, traps that reflect solar radiation in the yellow and UV wave length have to compete with attractive cues from the environment (plant cues, pheromones, sound emitted by potential sexual partners and so on). However, in periods when the intensity of the solar light is not so strong, UV LEDs powered by a photovoltaic system jointly with yellow supports are a promising way for psyllid detection. More promising yet is the possibility to use phosphorescent substances that charge themselves during the day with solar light. A suggested substance that meets these requirements is strontium aluminate, which deserves to be investigated. In this way, traps can reflect yellow light during the day and UV at night without the need for a power supply.

It is known that the whitefly *Bemisia tabaci* is commonly attracted to green LEDs and that this attraction is increased when this pest is infected with the virus that causes tomato yellow leaf curl virus (Jahan et al., 2014). Here we did not investigate how infection of *D. citri* with *Candidatus* Liberibacter spp. affects its attraction to UV, but if it is increased, this is beneficial for physical control of *D. citri* with UV-yellow traps. Recently, formic acid was found to be attractive to *D. citri* (George et al., 2019), opening the possibility to design traps that emit multiple attractive cues, possibly resulting in improved capture of this pest (George et al., 2020b). Obviously, the attractiveness of such traps to natural enemies also needs to be studied.

5. Conclusions

UV light is attractive to *D. citri* and UV LEDs may therefore be used to increase the attraction of yellow sticky traps at night. UV also attracted *T. radiata*, a parasitoid of *D. citri*, so traps with UV light can also be used to monitor the presence of this natural enemy. We propose that the efficiency, production costs and compatibility with biological control agents of traps with UV light should be confirmed. This may subsequently result in more effective and sustainable traps for this important pest and vector of a devastating citrus disease.

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CRediT authorship contribution statement

Milena O. Kalile: Conceptualization, Methodology, Formal analysis, Investigation, Writing. **Arne Janssen:** Conceptualization, Methodology, Formal analysis, Data curation, Writing. **Marilene Fancelli:** Conceptualization, Writing – review & editing. **Daniela G. Magalhães:** Investigation, Writing – review & editing. **André C. Cardoso:** Investigation, Formal analysis, Writing – review & editing. **Manuela S. Rosa:** Investigation, Writing – review & editing. **Carlos A.S. Ledo:** Conceptualization, Writing – review & editing. **Mirco Ragni:** Conceptualization, Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Compliance with Ethical Standards

The authors declare no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2022.104928.

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