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ORIGINAL PAPER

Blue and UV light-emitting diodes (LEDs) disturb the greenhouse whitefly (*Trialeurodes vaporariorum*) from its host

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Abstract

Push–pull strategy is a well-known and widely used technique for integrated pest management, leading to the reduction of insecticides. This strategy involves the use of mostly visual and chemical stimuli to repel pests from a valuable crop (push) and attract them to an appealing target, e.g., a trap, (pull). Based on former results, this study explored the effect of light-emitting diodes (LEDs) as repelling factors of whiteflies (push). Wavelengths of blue and ultraviolet (UV) were investigated in different light intensities and exposure times in no-choice experiments, under controlled conditions. Whiteflies were exposed directly to LEDs on the underside of tomato leaves and number of repelled insects was counted. The results showed that light intensity and insect repellency were positively related. Insect repellency increased up to tenfold with longer light exposure period. Wavelength of blue and combination of blue + UV repelled more than 87% of whiteflies in light conditions. In darkness, results were only slightly different. The results reveal the property of blue light to repel whiteflies from its host and that addition of UV to blue enhances this effect. They further demonstrate that whitefly vision is dependent on wavelength, light intensity and exposure period. The contribution of the results on understanding the visual behavior of whiteflies and their possible implementation on pest control strategies is discussed.

Keywords Visual behavior · Insect repellency · Light disturbance · Take-off behavior · Pest control

Key Message

- The effect of blue and UV light as deterrent stimuli on whiteflies settled on a host was studied.
- Blue light efficiently disturbed whiteflies from their host and addition of UV enhanced this effect.
- Whitefly take-off behavior increased with higher light intensity and exposure period.
- Insights on whitefly visual behavior can improve push-pull and mass-trapping strategies.

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Introduction

The greenhouse whitefly *T. vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) ranks among the most important pests, as it attacks a wide variety of crops, worldwide (Byrne and Bellows 2003; Mound and Halsey 1978) and is the major insect pest of greenhouse crops in Europe (Lenteren and Noldus 1990). It has considerable economic importance, reducing plant productivity and longevity by feeding on plant sap and damaging crops by the production of honeydew, which acts as a suitable growth medium for mold and fungi and as vector of plant viruses responsible for significant economic damage (Cohen and Antignus 1982; Duffus et al. 1996; Wisler et al. 1998; Wintermantel 2004).

Late detection of whitefly population in the crop, neglection of integrated pest management (IPM) techniques and action thresholds, as well as inefficient biocontrol by natural enemies can lead to the use of conventional chemical pesticides (George et al. 2015), to the most important of which, whiteflies have shown resistance (Wardlow et al. 1976; Gorman et al. 2002, 2007). Additionally, EU has introduced restrictions on development of new chemical pesticides (Hillocks 2012), urging the increased implementation of IPM, which relies on limiting pesticide use through the adoption of alternative control measures (Prokopy and Kogan 2009; Stenberg 2017; IOBC-WPRS, IBMA, PAN-Europe 2019). In our study, we approached a biocontrol method aiming to whitefly mass trapping. More specifically, we focused on dispersion of whiteflies from their host, with the intention of luring them toward traps and, consequently, control their population in the crop. Highly attractive light traps have already been studied and developed (Stukenberg 2018), but, to date, no research has been made on light cues able to repel whiteflies from their host.

Light-emitting diodes (LEDs), with narrow-banded wavelengths that can be combined and intensities that can be adjusted, are an advantageous tool to investigate insects' color sensitivity in detail and offer the possibility to use specifically regulated light devices for better implementation of IPM techniques, such as pest monitoring (Stukenberg 2018; Stukenberg and Rechner 2019; Otieno et al. 2018; Niemann and Poehling 2022). Additionally, LEDs emit low thermal radiation (Ieperen and Trouwborst 2007), which allows installation close to plants (Massa and Kim 2008), they operate with low voltage, ensuring safety in greenhouse applications and their long endurance along with low power consumption makes them a cost-effective tool.

Visual orientation is crucial for initial host plant detection, landing and take-off of *T. vaporariorum*, which is affected not only by the wavelength (wavelength-specific behavior) but also the light intensity (Vaishampayan et al. 1975; Coombe 1981; Stukenberg and Poehling 2019). Studies on visual orientation of *T. vaporariorum* showed a "settling" behavior on yellow-reflecting objects (Lloyd 1921; Vaishampayan et al. 1975) and led to the development and common use of yellow sticky traps for monitoring and control of whiteflies in greenhouse crops (Gillespie and Quiring 1987; Pinto-Zevallos and Vänninen 2013; Böckmann et al. 2015). Further studies revealed attractiveness to monochromatic green-yellow light with a spectral peak at 550 nm (MacDowall 1972; Coombe 1981, 1982; Mellor et al. 1997). Additional measurements of the spectral sensitivity of whiteflies showed a peak at 340 nm (ultraviolet region), revealing that ultraviolet (UV) radiation is used for orientation and elicits migratory/take-off behavior and maintenance of flight activity, which appears to be reduced in UV-deficient environments (Coombe 1982; Mellor et al. 1997; Antignus et al. 2001; Kumar and Poehling 2006; Gulidov and Poehling 2013). Mellor et al. (1997) demonstrated that the eyes of *T. vaporariorum* are divided in a dorsal part with 54–55 ommatidia and a ventral part with 29–31 ommatidia per eye, with the former one being more sensitive to UV, and that there was no difference in the spectral efficiency at UV and green region between male and female whitefly. Based on these findings, the visual system of *T. vaporariorum* was presumed to be dichromatic.

Additional studies by Stukenberg et al. (2015) and Stukenberg and Poehling (2019) suggested a trichromatic visual system for *T. vaporariorum,* with a blue-green opponent mechanism evidently responsible for its wavelength-specific behavior. They showed higher attractiveness of green LEDs compared to yellow sticky traps and an inhibition of green light attractiveness when simultaneously combined with blue light, providing evidence for the presence of a blue photoreceptor suppressing the "settling" signal of an adjacent green photoreceptor, a mechanism also known for other herbivorous insects (Döring and Röhrig 2016; Döring and Chittka 2007). Moreover, Stukenberg et al. (2015) showed that blue light was not attractive for whiteflies, supporting previous findings on the inhibiting action of blue wavelength on *T. vaporariorum* (Vaishampayan et al. 1975; Coombe 1981; Affeldt et al. 1983). In the same study, combination of UV and green showed higher attraction than green alone; they observed that the whiteflies, after initially flying toward the UV enlightened space in front of the trap, were attracted by the green color, supporting previous findings on the influence of UV radiation on flight initiation, orientation and dispersal (Coombe 1982; Mellor et al. 1997; Antignus et al. 2001; Mutwiwa et al. 2005; Kumar and Poehling 2006; Gulidov and Poehling 2013). Presence of white foil, with reflection in the spectral range of 400–490 nm, covering the soil of broccoli and lettuce plants, showed significantly smaller number of settled *T. vaporariorum* on the plants, compared to plants growing on bare soil (Niemann et al. 2021). Additionally, presence of blue LEDs below lettuce and poinsettia plants showed reduced settlement of *T. vaporariorum* on them compared to plants without blue LEDs (LUH patent DE 10 2018 208 424 B3), confirming the blue-green opponency in the visual system of whiteflies (Niemann and Poehling 2022). These findings were focused on the settling behavior of whiteflies and, therefore, can be implemented as a preventive measure to restrict their approach toward a crop. However, no studies could be found on the effect of disturbing light wavelengths on the behavior of whiteflies once they have settled and feed on a host plant. From an ecological point of view, after landing, whiteflies employ gustatory or other sensory and metabolic signals to assess host quality and determine whether or not to oviposit (Bleeker et al. 2011). They normally fly off their host when it no longer provides them with sufficient sources for feeding and oviposition, which could be attributed to the host's altered physiology and, therefore, lower quality, to competition between other pests and to presence of natural enemies (Sehgal et al. 2006). Using deterring light to disturb whiteflies from their host, may induce take off behavior and consequently increase the possibility of them landing on a trap, acting thus, as a key tool of mass trapping and a push–pull strategy, an important pest management technique, reducing insecticides (Cook et al. 2007). It involves a combination of repellent and attractive stimuli toward pests, in order to manipulate their distribution in the crop and, thus, protect it. The principle of push–pull strategy is to reduce pests by repelling or deterring them from the crop in question (push) and simultaneously attract them on a highly appealing target (pull), using behavior-modifying stimuli, which are mostly visual and chemical (Cook et al. 2007). Taking into account that a cue can be classified as repellent when it triggers an organism to move away from its host (Nordlund et al. 1981) and that disruption of feeding activity by deterrent stimuli can be a type of insect repellence (Deletre et al. 2016), we considered repellent a stimulus that pushes an insect away from its host before as well as after landing onto it. In our study, we focused on repellence of whiteflies from their host, with the aim to orient them toward traps and, therefore, mass trap them. This is the first investigation on the effect of deterrent LED qualities on the behavior of the greenhouse whitefly while settled on a host (push). Taking into consideration the color vision properties and disturbing mechanisms of *T. vaporariorum* revealed by previous findings, this study explored the influence of blue (465 nm), UV (365 nm) and their combination, by means of LEDs illuminating upwards, toward the underside of tomato leaves. More specifically, the influence of light intensity, exposure period and wavelength were investigated in a series of no-choice experiments, under controlled conditions.

Material and methods

Rearing of the greenhouse whiteflies

All greenhouse whiteflies (*T. vaporariorum*) used in this study were reared on tomato plants (*Solanum lycopersicum* L. cv. Brioso) in a gauze cage (90 × 60 × 60 cm) in a climate chamber at 23 ± 3 °C, 50% ± 5% relative humidity (RH) and light:dark 16:8, at the Institute of Horticultural Production Systems, Leibniz Universität Hannover, Germany. For each experimental trial, about 5 adult whiteflies, without further sex identification, were carefully collected with an aspirator from the underside of leaves into an Eppendorf tube (1.5 ml), which was then placed into the experimental arena. Tomato plants were grown in pots (*h* x *d* = 10 × 12 cm) under greenhouse conditions before introduction to the rearing or the experiments.

Technical LED setup

In order to study the visual behavior of *T. vaporariorum*, single chip LEDs (1.0 × 1.0 × 0.0 cm) were used (Luminotrix® LED-Technik GmbH, Hechingen, Germany) in blue (465 nm, 1 W, 3 V, Nichia NCSB219B-V1), UV (365 nm, 2 W, 4 V, Nichia NCSU275) and white color (400–700 nm, 2 W, 3 V, Nichia NVSL219CT),. Aluminum plates (5 × 5 × 0.1 cm) were constructed and two LEDs of the same color were fixed with thermal conductive double-sided adhesive tape (Ak-tt12-80, Akasa Ltd., Greenford, UK) in the center of each plate, with 2 cm distance between them.

The LEDs were measured in pairs by placing the sensor 5 cm above a plate, in between the 2 LEDs, in darkness. The intensity of blue and white LEDs (μmol/m^2/s) was measured with the LI 250 Light Meter and the LI 190 Quantum Sensor (LI-COR Biosciences GmbH, Bad Homburg, Germany), as this sensor is only suitable to measure broadband photosynthetic active radiation (PAR, 400–700 nm). The intensity of UV LEDs (W/m^2) was measured with the datalogger Almemo® 2390–5 in combination with the UV-A Sensor type 2.5 (Ahlborn GmbH, Bodenwerder, Germany). The intensity of UV LEDs in W/m^2 was converted into μmol/m^2/s using the LED spectra, Planck's constant and Avogadro's number.

General experimental design and procedure

Experiments were conducted in a climate chamber at 23 ± 3 °C and 50% ± 5% RH at the Institute of Horticultural Production Systems, Leibniz Universität Hannover, Germany. LEDs were placed 1.2 m below the light tubes of the chamber and parallel to them. The luminance of the fluorescent tubes in the chamber was 6500 ± 200 lx and was measured from 1.2 m distance (LEDs level) with the datalogger HOBO U12-012 (Datenlogger-Store, Eichstetten, Germany). A leaf from 7-week-old tomato plants (*Solanum lycopersicum* L. cv. Brioso) was cut with its petiole, at a height of 20–50 cm above the soil. The petiole was then inserted into a glass vial (*h* x *d* = 5 × 2.5 cm) filled with water, to keep the leaf fresh during the experiment. A pair of single chip LEDs were arranged 5 cm below the leaf, emitting radiation upwards, toward the underside of the leaf; the leaf's main vein was vertical to the 2 LEDs. A transparent plastic cylinder (*h* x *d* = 15 × 10 cm), with gauze-covered openings on the sides, was used to enclose the setup. About 5 greenhouse whiteflies were released from an Eppendorf tube (1.5 ml) inside the cylinder24 h before the LEDs were switched on to allow their settlement on the leaf, a procedure conducted under ambient light conditions. After this time, the whiteflies settled on the underside of the leaf were counted; none of them were found on the upper side of the leaf and whiteflies found on other surfaces were discarded. The Eppendorf tube was removed and the plastic cylinder was replaced by an identical one, which remained in place for 2 h and contained insect glue on the inside to trap the dispersed whiteflies. Additionally, a black cardstock paper (size A3) was placed around each cylinder, covering only the

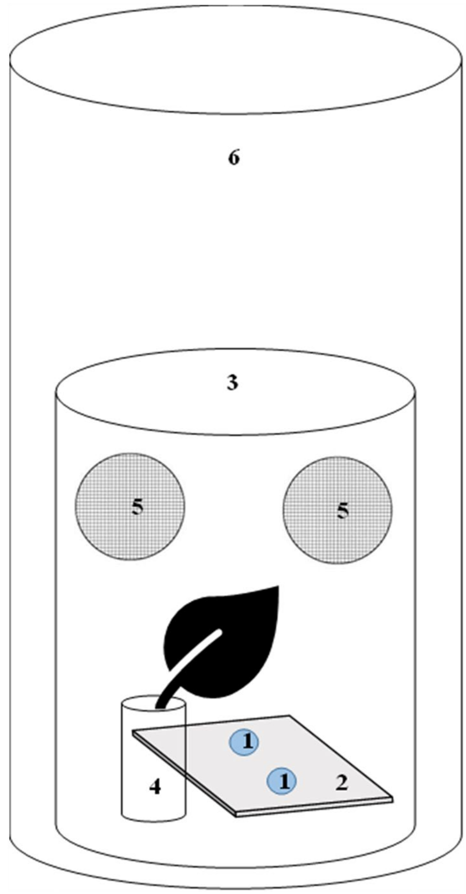

Fig. 1 Scheme of the experimental setup. 1: LEDs, 2: aluminum plate, 3: transparent plastic cylinder, 4: glass vial filled with water, 5: gauze-covered openings on the cylinder, 6: black cardstock paper (size A3). Before the LEDs were switched on, the plastic cylinder (3) was replaced by an identical one, which contained insect glue on the inside to trap the dispersed whiteflies, and a black cardstock paper (6) was placed around it leaving the top open

sides and not the top, to avoid interference from neighboring LEDs and allow exposure of the setup to the ambient light (Fig. 1). Each trial lasted 2 h and after this time, the remaining whiteflies on the underside of the leaf were counted. The whiteflies that left the underside of the leaf during a trial were considered disturbed and were found either glued on the plastic cylinder or on other surfaces within the cylinder area. After each trial, all surfaces were cleaned carefully and the insects and leaves were discarded. The same setup, without any LEDs, was included as control in all the experiments (mentioned as "control"). Trials were performed consecutively on a metal bench covered with black plastic mulching film. The position of LEDs was changed in a randomized block design every three replicates (trials).

Experimental classification

Three experiments were conducted to investigate *T. vaporariorum* visual disturbance using LEDs, in a stepwise manner. More specifically, the effect of light intensity, exposure period and wavelength were examined. Firstly, different intensities of blue and UV LEDs were tested under a fixed light exposure period, in ambient light conditions (chamber light switched on), to determine which intensity had the highest disturbing effect against *T. vaporariorum*. In the second experiment, the resultant optimal (most disturbing) luminance intensity of blue and UV was used to examine the repellent rate of *T. vaporariorum* at different light exposure periods, in ambient light conditions. Finally, the resultant optimal light exposure period was used in a wavelength dependence experiment, where optimal intensity of blue, UV, their combination (blue + UV) and white light, were compared both under ambient light and dark (chamber light switched off) conditions, A general overview of the experimental designs is given in Table 1. In the following paragraphs, the specifics of each experiment are described.

Effect of LED intensity on whitefly disturbance from the leaves: blue, UV and control (no LEDs)

Three different intensities of blue and UV and their effect on greenhouse whiteflies were compared in this experiment, in ambient light conditions. The three intensities of each color were equally distributed over the intensity range (33%, 66% and 100% of maximum intensity at 350 milliamperes (mA) operating current) resulting in 150 μmol m^{-2} s^{-1} (33%), 300 μmol m^{-2} s^{-1} (66%) and 450 μmol m^{-2} s^{-1} (100%) for blue LEDs and 40 μmol m^{-2} s^{-1} (33%), 80 μmol m^{-2} s^{-1} (66%) and 120 μmol m^{-2} s^{-1} (100%) for UV LEDs in 5 cm distance. Preliminary experiments showed that maximum intensity at 350 mA operating current of blue and UV LEDs induced disturbance of whiteflies after 7 min of continuous light exposure. Considering these observations and taking into account that minimum use of artificial light equals maximum cost effectiveness, it was decided to test the LED intensities for 7 min followed by a switch off for 13 min (7 min/13 min on/off). This corresponded to a total of 42 min light exposure in 2 h (approx. 33% of the total time). This experiment consisted of 28 replicates for every intensity and the control, as described in 2.3.

Effect of LED exposure period on whitefly disturbance from the leaves: blue, UV and control

The resulting optimal luminance intensity of blue and UV from the first experiment was used to examine the

Table 1 Overview of the design and characteristics of the experiments

Experiment	LED wavelength	LED intensity (μmol m^{-2} s^{-1})	LED exposure period intervals within 2 h and total time of LED switched on (min)	Trial duration (min)	Ambient light or dark conditions (chamber light switched on or off, respectively)	Replicates
(1) Effect of LED intensity on whitefly disturbance	Blue (465 nm)	(i) 150 (ii) 300 (iii) 450	7 on—13 off total: 42	120	Ambient light conditions	28
	UV (365 nm)	(i) 40 (ii) 80 (iii) 120				
	Control	No LEDs				
(2) Effect of LED exposure period on whitefly disturbance	Blue (465 nm) UV (365 nm) Control	450 120 No LEDs	i) 7 on—13 off total: 42 ii) 13 on—7 off total: 78 iii) 30 on—1 off total: 120	120	Ambient light conditions	24
(3) Effect of LED wavelength on whitefly disturbance	Blue (465 nm) UV (365 nm) Mix (Blue + UV) White (400–700 nm) Control	450 120 450 + 120 450 No LEDs	30 on—1 off total: 120	120	i) Ambient light conditions ii) Dark conditions	20

disturbance of *T. vaporariorum* at three different light exposure periods, in ambient light conditions. These were equally distributed over the total time (33%, 66% and 100%) of 2 h and the LEDs were switched on during the following periods: 7 min followed by a switch off for 13 min (7 min on—13 min off), 13 min followed by a switch off for 7 min (13 min on—7 min off) and 30 min followed by a switch off for 1 min (30 min on—1 min off), corresponding to 42 (33%), 78 (66%) and 120 (100%) min of total light exposure in 2 h, respectively. In order to expose the insects repeatedly to the LEDs throughout the 2 h trial, it was decided to switch on and off the LEDs at regular intervals instead of keeping them on continuously. In 120 min exposure period the LEDs were switched off for 1 min after 30 min and did not continuously stay on, in order to avoid extreme heating of the metallic plate and the surroundings. This experiment consisted of 24 replicates for every light exposure period and the control, as described in 2.3.

Effect of LED wavelength on whitefly disturbance from the leaves: blue, UV, white, blue + UV and control

In this experiment, *T. vaporariorum* wavelength-specific behavior was investigated in the resulting optimal exposure period from the second experiment. The optimal blue and UV intensities from the first experiment, along with white light as a second control, were compared to a treatment where the optimal blue and UV intensities were combined (blue + UV), by gluing a pair of blue and a pair of UV LEDs on the same plate, as described in 2.2 (Fig. 2). By combining those two colors, a potential disturbing blue–UV chromatic mechanism against *T. vaporariorum* was examined. The intensity of white light was adjusted to the same level of blue. This experiment consisted of 20 replicates for every LED color (blue, UV, blue + UV, white) and the control,

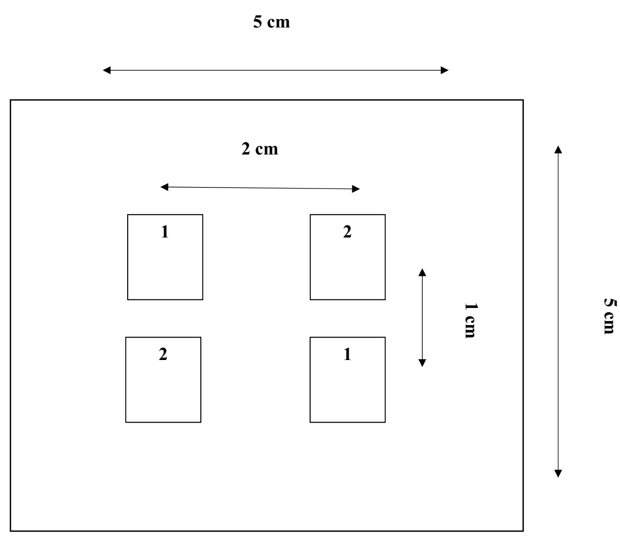

Fig. 2 Scheme of the combination blue + UV LEDs on an aluminum plate. 1: Blue LEDs, 2: UV LEDs

both in ambient light and dark conditions, as described in 2.3.

Statistical analysis

Data were statistically analyzed with R version 4.2.1 (R Core Team, 2019). The rate of disturbed whiteflies (response variable) for different LED intensities, exposure periods and wavelengths (explanatory variables), was analyzed using generalized linear model (GLM), assuming a quasibinomial distribution (count data with overdispersion) (McCullagh and Nelder 1989; Cox et al. 2019). A deviation analysis (*F*-test) running on the logit link were fitted to determine influences of the explanatory variables on the number of whiteflies settled on tomato leaves (McCullagh and Nelder 1989; Demétrio et al. 2014). Subsequent Tukey-type multiple pairwise comparisons at $\alpha = 0.05$ using the R-package "emmeans" (Lenth et al., 2019) were conducted to clarify which treatment differed from another (mean value differences) in each of the experiments. All figures showing results are boxplots and were made using *R* (version 4.2.1) and the ggplot2 package (Wickham 2016).

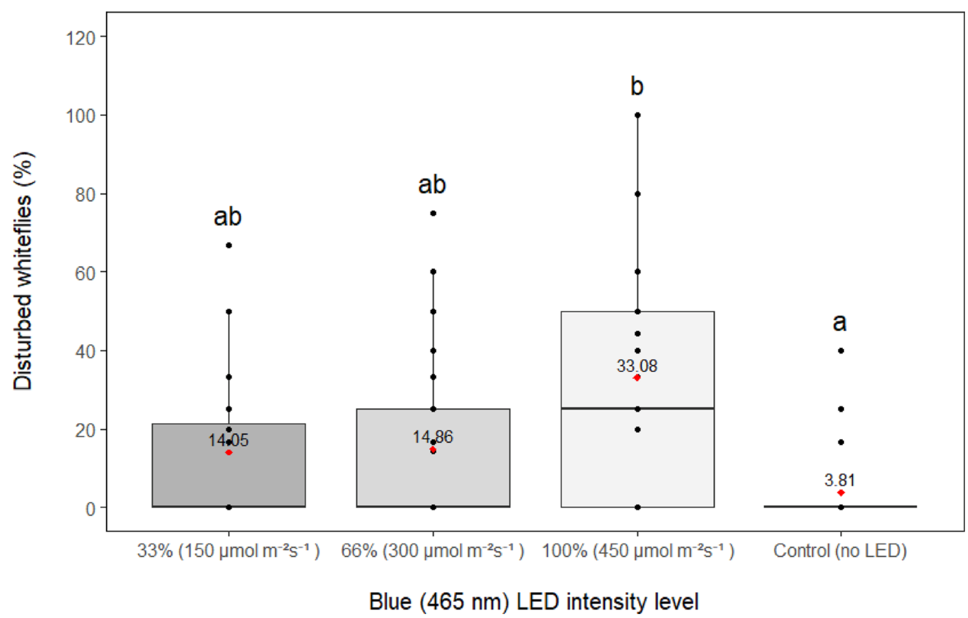

Fig. 3 Disturbed whiteflies that left the underside of the leaf in no-choice experiment under 3 different blue LED intensity levels, in 42 min of total light exposure period within 2 h, under ambient light conditions. Means are indicated with red dots and labeled with numbers. Significant differences between the effect of different intensities are represented by different letters (GLM, pairwise mean comparisons, $a = 0.05$)

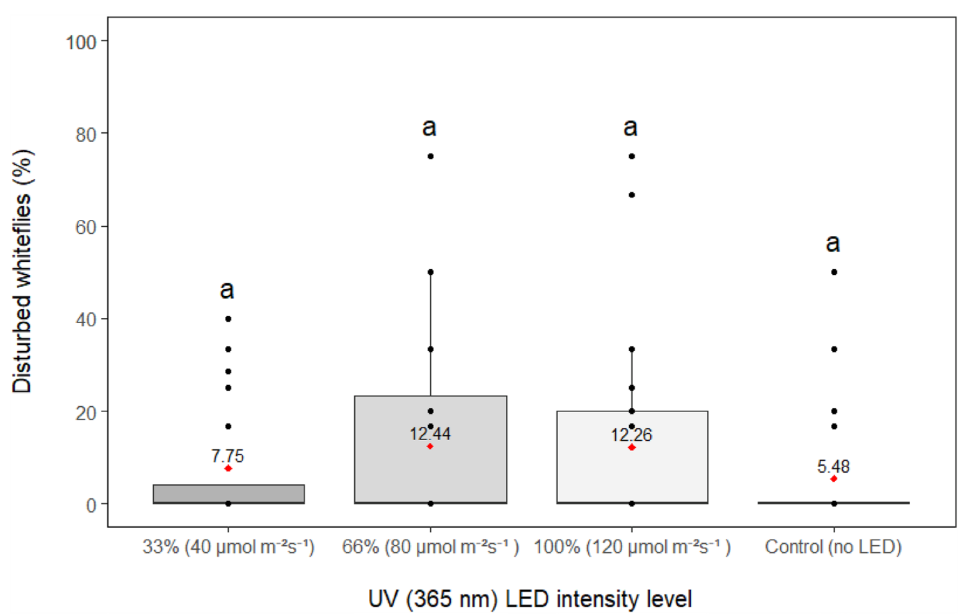

Fig. 4 Disturbed whiteflies that left the underside of the leaf in no-choice experiment under 3 different UV LED intensity levels, in 42 min of total light exposure period within 2 h, under ambient light conditions. Means are indicated with red dots and labeled with numbers. Differences between the effect of different intensities were not statistically significant, hence, represented by the same letters (GLM, $a = 0.05$)

Results

Effect of LED intensity on whitefly disturbance from the leaves

The percentage of disturbed whiteflies represents the percentage of *T. vaporariorum* that flew off the underside of the leaf. The results of this experiment showed that intensity of blue light, illuminating for a total of 42 min, had a significant effect on the disturbance of whiteflies ($F_{3,108} = 8.21$, $p < 0.001$), which increased with higher intensity. Minimum intensities (33 and 66%) disturbed 3.7 and 3.9 times more whiteflies, respectively, than the control, although these differences were not statistically significant. Increasing the intensity from 66 to 100% doubled the number of disturbed insects, while compared to the control, the numbers increased 8.7-fold in maximum intensity (100%) ($p < 0.001$) (Fig. 3). No significant repellent effect ($F_{3,108} = 0.85$, $p = 0.47$) of UV against whiteflies was observed, although maximum intensity disturbed 2.2 times more insects compared to the control, but minimum intensity only 1.4 times (Fig. 4).

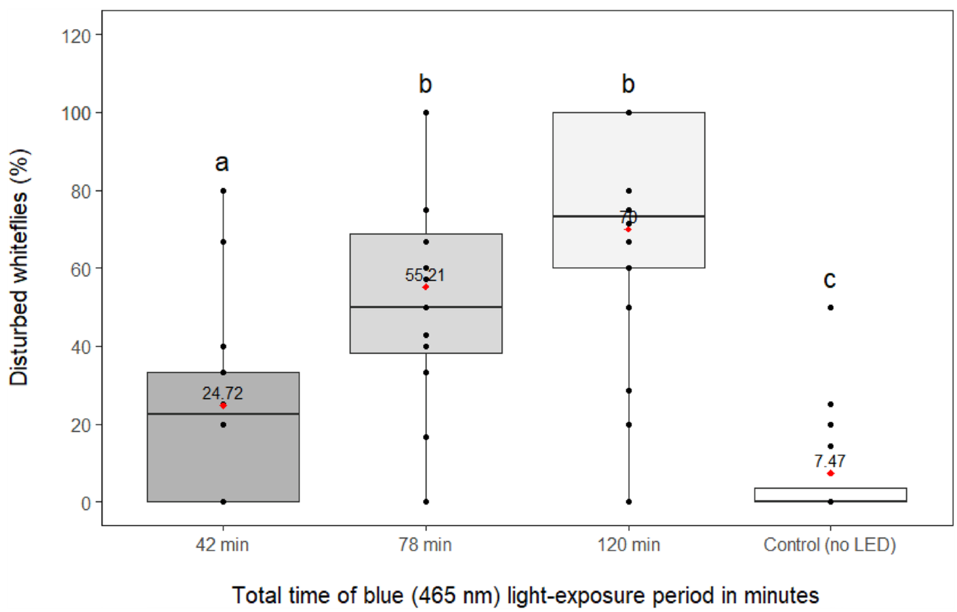

Fig. 5 Disturbed whiteflies that left the underside of the leaf in no-choice experiment under 3 different blue LED exposure periods, with blue intensity at 450 µmol m^{-2} s^{-1}, under ambient light conditions. Total exposure period of 42, 78 and 120 min, within 2 h, corresponds to light intervals of 7 min on—13 min off, 13 min on—7 min off and 30 min on—1 min off, respectively. Means are indicated with red dots and labeled with numbers. Significant differences between the effect of different light exposure periods are represented by different letters (GLM, pairwise mean comparisons, $a = 0.05$)

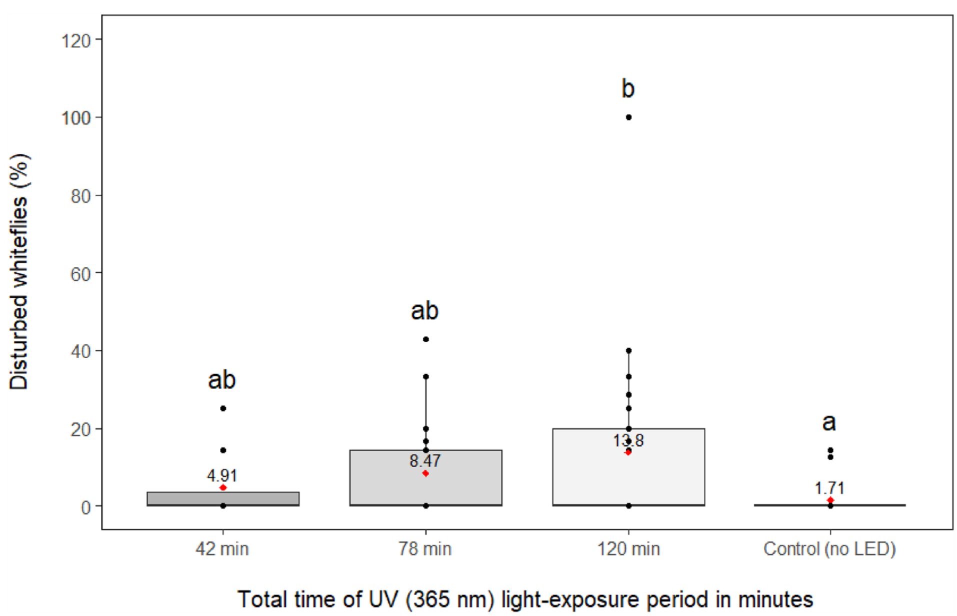

Fig. 6 Disturbed whiteflies that left the underside of the leaf in no-choice experiment under 3 different UV LED exposure periods, with UV intensity at 120 µmol m^{-2} s^{-1}, under ambient light conditions. Total exposure period of 42, 78 and 120 min, within 2 h, corresponds to light intervals of 7 min on—13 min off, 13 min on—7 min off and 30 min on—1 min off, respectively Means are indicated with red dots and labeled with numbers. Significant differences between the effect of different light exposure periods are represented by different letters (GLM, pairwise mean comparisons, $a = 0.05$)

Effect of LED exposure period on whitefly disturbance from the leaves

Increasing light exposure period, led to higher repellency rates for both colors. Blue light exposure period had a significant effect on the repellence of whiteflies ($F_{3,92}=31.23$, $p<0.001$); minimum exposure period (42 min) disturbed 3.3 times more whiteflies compared to the control ($p=0.003$). Disturbance increased nearly threefold from 42 to 120 min of exposure period ($p<0.001$) and 120 min of exposure period disturbed nearly 10 times more insects ($p<0.001$) compared to the control (Fig. 5). Maximal intensity of UV was chosen after considering the results of the first experiment (3.1), due to easier technical adjustment and considering possible LED power losses overtime, that might drop the intensity lower than 66%. UV light exposure period had a significant effect on the repellence of whiteflies ($F_{3,92}=3.92$, $p=0.01$). However, 120 min of UV illumination was the only significantly disturbing period compared to the control ($p=0.03$), repelling 8 times more insects (Fig. 6).

Effect of LED wavelength on whitefly disturbance from the leaves

Maximal intensity of blue and UV was chosen after considering the results of the first experiment (3.1), and light

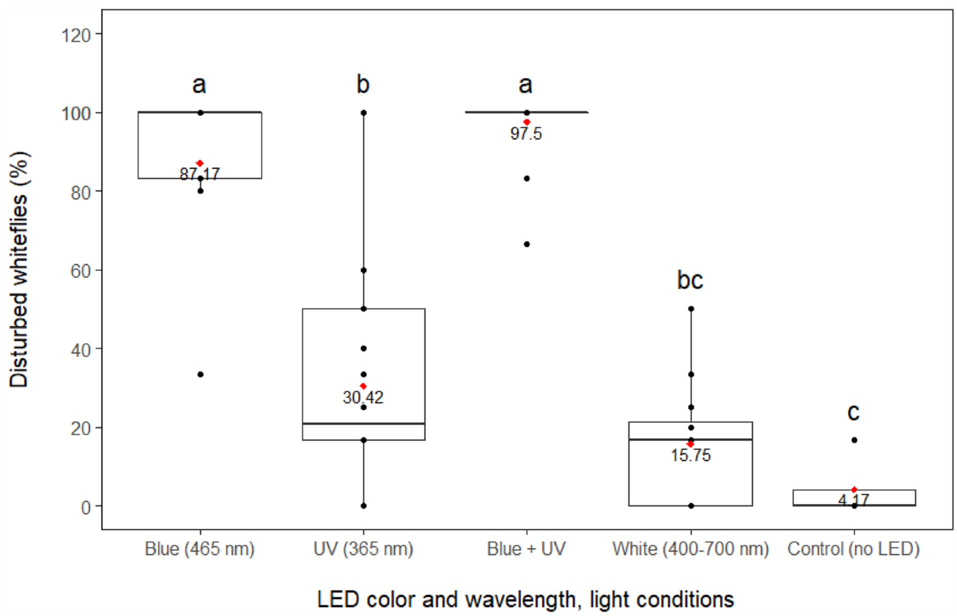

Fig. 7 Disturbed whiteflies that left the underside of the leaf in no-choice experiment, in ambient light conditions, under 4 different LED wavelengths, in 120 min of light exposure period in the following intensities: blue 450 µmol m^{-2} s^{-1}, UV 120 µmol m^{-2} s^{-1}, blue + UV 450 µmol m^{-2} s^{-1} + 120 µmol m^{-2} s^{-1}, white 450 µmol m^{-2} s^{-1}. Means are indicated with red dots and labeled with numbers. Significant differences between the effect of different wavelengths are represented by different letters (GLM, pairwise mean comparisons, $a=0.05$)

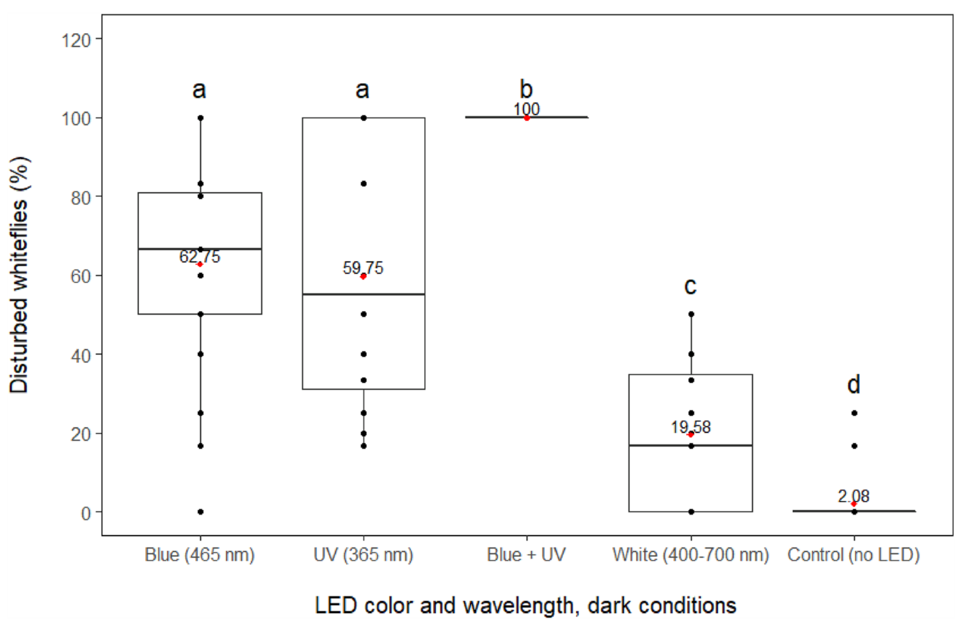

Fig. 8 Disturbed whiteflies that left the underside of the leaf in no-choice experiment, in dark conditions, under 4 different LED wavelengths, in 120 min of light exposure period in the following intensities: blue 450 µmol m^{-2} s^{-1}, UV 120 µmol m^{-2} s^{-1}, blue + UV 450 µmol m^{-2} s^{-1} + 120 µmol m^{-2} s^{-1}, white 450 µmol m^{-2} s^{-1}. Means are indicated with red dots and labeled with numbers. Significant differences between the effect of different wavelengths are represented by different letters (GLM, pairwise mean comparisons, $a=0.05$)

exposure period of 120 min after considering the results of the second (3.2). Maximal intensity of blue and UV was also chosen for the combined treatment blue + UV. Light wavelength had a significant effect on the repellence of whiteflies both in light and darkness ($F_{4,95} = 71.88$, $p < 0.001$ and $F_{4,95} = 73.23$, $p < 0.001$, respectively). Under light conditions, blue disturbed 21 times more insects compared to the control ($p < 0.001$) and with addition of UV, disturbance increased to 23 times higher than the control ($p < 0.001$). UV showed significantly lower repellency on whiteflies compared to blue + UV ($p < 0.001$) and blue ($p < 0.001$), but 7.3 times higher than the control ($p = 0.001$). White light and control had the lowest disturbing effect (Fig. 7). In darkness, disturbance by blue light increased 30-hold compared to the control ($p < 0.001$) and addition of UV resulted in an increase in 48-hold compared to the control ($p < 0.001$). UV showed nearly 29 times higher disturbing effect than the control ($p < 0.001$), but disturbed less whiteflies than blue ($p = 0.89$) and blue + UV ($p < 0.001$). White light and control showed significantly the lowest disturbing effect among the treatments (Fig. 8). Blue had 24.42% higher repellent effect in the light compared to dark ($F_{1,38} = 11.88$, $p = 0.001$) and UV 29.33% higher repellent effect in the dark compared to light ($F_{1,38} = 7.31$, $p = 0.01$). There was no effect of light and dark conditions on the rest of the treatments (all $p > 0.05$).

Discussion

The results of this study reveal evidence that blue LEDs have good potential to efficiently disturb *T. vaporariorum* from its host plant and that the addition of UV light to blue enhances the effect. They further demonstrate that whitefly behavior is not only dependent on wavelength, but also on light intensity and exposure period. Moreover, our results confirm the proposed presence of both a UV and a blue photoreceptor in the trichromatic visual system of whiteflies (Coombe 1981, 1982; Stukenberg et al. 2015; Stukenberg and Poehling 2019) and provide additional evidence that whiteflies have a broad visual field, since this system is functional not only when LEDs illuminate directly in front of them, as in the studies of Stukenberg et al. (2015) and Stukenberg and Poehling (2019), but also when they illuminate in their back (indirectly), as in our experiments.

When we tested the effect of LED intensity on whiteflies, the results showed that *T. vaporariorum* reacts in different intensities of the same wavelength, which corroborates with previous findings on the intensity dependence of whiteflies and other insects (Booth et al. 2004; Coombe 1981; Scherer and Kolb 1987). The number of disturbed whiteflies increased with higher intensity of both blue and UV light. According to Kelber et al. (2003), a wide range of animals is expected to have chromatic mechanisms independent of intensity. Many studies suggest that visual behaviors are exercised either solely chromatically or achromatically and it is frequently uncertain whether both features are engaged (Kelber and Osorio 2010). The results of this study, however, reveal that the proposed trichromatic mechanism has both chromatic and achromatic features, showing that wavelength and intensity are both important in the visual behavior of *T. vaporariorum*. Repellence of whiteflies was significantly higher compared to no LEDs under maximum blue intensity (450 µmol m^{-2} s^{-1}), revealing the quality of blue light to repel whiteflies from their host and, hence, expanding results of former studies showing its property to reduce whiteflies settlement on plants (Niemann and Poehling 2022). The two lower blue intensities were not adequately bright to considerably disturb the whiteflies and thus, not distinctive enough under the ambient light. In comparison with the light intensity of naturally reflecting surfaces, LEDs' consistent intensity is independent of the ambient light intensity and should look brighter or darker in comparison. In our case, the highest blue intensity appeared as the brightest one to the whiteflies, under the ambient light conditions in the climate chamber. Contrastingly, there was no significant disturbing effect of different UV intensities on the whitefly visual behavior. However, there was a correlation between rising UV intensity and percentage of repelled whiteflies. This result extends the findings of Stukenberg and Poehling (2019), who reported that rising of a UV LED trap's intensity caused lower rate of whitefly recapture. They demonstrated that the UV LED trap was moderately attractive to whiteflies; however, compared to their trials with different LED colors, they observed slow and weak orientation of whiteflies toward UV and low overall recapture rates. Stukenberg et al. (2015) found that whiteflies were more attracted to green and UV than green alone, while Vaishampayan et al. (1975) reported the same for the combination of yellow and UV. These results supported the proposed influence of UV radiation on the orientation of whiteflies toward the plant canopy, which reflect in the yellow–green range (Prokopy and Owens 1983; Antignus 2000; Mound 1962). In our experiment, since the whiteflies were already settled on fresh leaves before the UV light was switched on, it can be assumed that orientation toward another plant source was not induced, because their response to UV light during feeding or egg laying might be lower compared to other activities, such as host searching and orientation. Moreover, it can be suspected that exposure to UV light for this time period was insufficient to signal a take-off response.

Regarding our experiment using different LED exposure periods, the results provide evidence that there is an effect of light exposure period on the whitefly behavior. Photoreceptors modify their responses through a variety of mechanisms to adapt to the perceived light compared to the background light (Arshavsky 2003; Laughlin and Hardie 1978). This prevents photoreceptor saturation and serves as a method to sustain color constancy (Foster 2011; Kemp et al. 2015). According to our results, longer exposure period of blue and UV led to higher number of disturbed whiteflies, indicating that their photoreceptors could not adapt to a perceived blue and UV light longer than a certain period. A threshold of exposure period to blue and UV is therefore suggested, above which, these lights signal low host plant quality or even danger and lead to whitefly take-off response. According to our findings, the proposed thresholds are 42 min for blue and 120 min for UV light, since these were the exposure periods required to significantly disperse whiteflies compared to the control. Blue light exposure of 120 min disturbed about 63% more whiteflies than the control and 45% than exposure of 42 min. This shows that continuous blue illumination, with shorter light-off intervals, causes higher stimulation of the blue photoreceptor over the green one—responsible for the settling on the leaf—to the extent that the whitefly is forced to leave its valuable resource and search for an alternative one, independently of its current feeding or oviposition activity. In a natural environment, blue wavelength is only slightly present on the underside of a leaf, where whiteflies settle. It is, therefore, proposed that addition of blue light above a certain threshold period creates an unsuitable or even threatening environment for whiteflies, which leads to their behavioral response of fleeing a valuable source in order to ensure survival. Our results also suggest that lengthening of light exposure period may be an alternative to higher intensity, which in case of blue light, can have a negative effect on tomato plants, i.e., induce photoinhibition and reduce photosynthetic efficiency if used above a certain intensity level (Fan et al. 2013). Regarding UV light, only exposure of 120 min led to significantly higher disturbance compared to the control. This is aligned with the findings from Poushand et al. (2017), showing that prolonging the exposure period of UV on whiteflies settled on bean leaves increased their mortality 24 h later. Thus, it can be suggested that long exposure to UV rises a mortality risk to whiteflies, forcing them to disperse in order to survive. In our setup, UV light was directly applied on the underside of the leaf, meaning that whiteflies perceived UV and green − reflecting from the leaf − from opposite sides. This provides an important observation that while UV increased the attractivity of green when they were both emitted from the same side on a trap (Stukenberg et al. 2015), this scenario changed in our experiment, where the two wavelengths were emitted from opposite sides, since whiteflies abandoned the green leaves while exposed to UV. Contrastingly, blue showed the same inhibiting effect on whiteflies both when it was emitted from the same side with green on a trap (Stukenberg et al. 2015) and from opposite sides, as in our setup, supporting the proposed blue-green photoreceptor opponent mechanism.

The results of our experiment on the effect of different LED wavelengths on whiteflies revealed the property of blue light to repel whiteflies already settled on a host, an effect that was enhanced with addition of UV, indicating, thus, an interaction between the blue and UV photoreceptor. Contrastingly, whiteflies showed little response to white light, which was used as second control, revealing that has no effect on whitefly behavior. The high levels of disturbance induced by the combination of blue and UV can be attributed to a proposed quality of these lights to signal absence of food resources, by camouflaging the green tissue of the leaves. Considering that whiteflies rely on UV for immigration and dispersal (Coombe 1982; Mellor et al. 1997; Antignus et al. 2001; Mutwiwa et al. 2005; Kumar and Poehling 2006; Gulidov and Poehling 2013), it could be suggested that the effect of this combination resulted, on the one hand, from the influence of UV radiation on dispersal and, on the other hand, the disturbing property of blue light. Moreover, while the rest of the treatments consisted of 2 LEDs, the combination blue + UV consisted of 4 LEDs, meaning higher overall intensity compared to the other treatments. UV disturbed a significantly higher percentage of whiteflies compared to the control, but lower compared to blue. These results met our expectations considering the effectivity of exposure periods and confirmed the role of UV on flight initiation and dispersal of whiteflies. In a natural setting, high intensities of UV rays are related to skylight (Wehner 1982) and presumably help whiteflies find a path out of the plant canopy in order to initiate long distance dispersal. An important observation is that UV was almost two times more disturbing in darkness compared to ambient light, which could be attributed to the fact that the small percentage of UV emitted by the chamber's fluorescent light possibly competed with the UV emitted by the LEDs. In darkness UV light was perceived by the whiteflies directly and solely from the LEDs, which in absence of ambient light appeared presumably stronger and therefore more distinctive. In the same context, the light from the sun or the lamps in a greenhouse environment could compete with additional UV LEDs. According to our results, the UV photoreceptor showed sensitivity at 365 nm, supporting existing findings on the peak sensitivity of the UV photoreceptor lying between 340 and 370 nm (Stukenberg and Poehling 2019). In regards to the blue photoreceptor, a sensitivity peak at 465 nm was obvious in our experiments, adding an important insight on the proposed peak between 480 and 490 nm from Stukenberg and Poehling (2019), indicating a wider sensitivity of the blue photoreceptor between 465 and 490 nm.

Conclusion and outlook

This is the first study investigating the deterrent effect of LEDs on the behavior of whiteflies already settled on a host. Since our experiments were conducted under controlled conditions without any light fluctuations, the results provide a good understanding of photoreceptor interactions and sensitivities and can contribute to the improvement of technological approaches to push–pull strategies and development of mass trapping techniques. Since blue is one of the essential wavelengths required for optimal plant photosynthesis and regular growth and development (Hogewoning et al. 2010; McCree 1971), it could be implemented as a deterrent factor against whiteflies in agricultural crops, without endangering the plants. Future research should aim to investigate the disturbing effect of these light qualities on whitefly behavior on larger scale assays under controlled and greenhouse conditions. This will enhance the efficacy of the traps and contribute to the development of mass trapping systems, a crucial component of integrated pest control.

Author contribution

MA conceived, designed and conducted the experiments, analyzed data, wrote manuscript, did review and editing. RM provided resources, supervision, project administration, acquired funding, designed the experiments, did data supervision, review and editing. All of the authors read and approved the manuscript.

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Data availability The datasets generated and/or analyzed during the current study are available in the LUH Data Repository (Athanasiadou and Meyhöfer 2023), https://doi.org/10.25835/y071n4rn (accessed on 28 June 2023).

Declarations

Conflict of interest The authors declare that they have no relevant financial or non-financial interests to disclose.

Ethical approval This research was not reviewed by an institutional or governmental regulatory body as the work was performed on invertebrates.

Consent to participate Consent was given by all participants included in the study.

Consent for publication All authors consent to the publication of this study in Journal of Pest Science.

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