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Effects of far-red light on the behaviour and reproduction of the zoophytophagous predator *Macrolophus pygmaeus* and its interaction with a whitefly herbivore

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Abstract

Plants can detect neighbouring plants through a reduction in the ratio between red and far-red light (R:FR). This provides a signal of plant–plant competition and induces rapid plant growth while inhibiting defence against biotic stress, two interlinked responses designated as the shade avoidance syndrome (SAS). Consequently, the SAS can influence plant–herbivore interactions that could cascade to higher trophic levels. However, little is known about how the expression of the SAS can influence tritrophic interactions. We investigated whether changes in R:FR affect the emission of herbivore-induced plant volatiles (HIPVs), and whether these changes influence the attraction of the zoophytophagous predator *Macrolophus pygmaeus*. We also studied how the expression of the SAS and subsequent inhibition of plant defences affects the reproduction of *M. pygmaeus* in both the presence and absence of the greenhouse whitefly (WF) (*Trialeurodes vaporariorum*) as arthropod prey. The results show that changes in R:FR have little effect on HIPV emissions and predator attraction. However, a reduction in R:FR leads to increased reproduction of both the predator and the WFs. We discuss that shade avoidance responses can increase the population development of *M. pygmaeus* through a combination of reduced plant defences and increased herbivore densities.

KEYWORDS

arthropod performance, predator–prey interactions, shade avoidance, *Trialeurodes vaporariorum*, tritrophic interactions, volatiles

1 | INTRODUCTION

Plants possess elaborate mechanisms to sense and respond to changes in their dynamic environment. These mechanisms help plants to differentially allocate their resources to many physiological and developmental processes to adequately respond to the risks and challenges posed by their environment. These allocation patterns often come down to trade-offs between growth and defence (Zust & Agrawal, 2017). An example of such a trade-off is the shade avoidance syndrome (SAS). The SAS is aimed at avoiding shade and light competition from neighbouring plants and consists of morphological and physiological adaptations that stimulate growth and reproduction

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(Casal, 2012; Kalaitzoglou et al., 2019), but it is also associated with reduced defensive responses towards biotic stress (Ballaré, 2014). Over the past decades, there has been increasing interest in understanding how plants perceive and respond to shading by neighbouring plants (Ballaré & Pierik, 2017; Fernández-Milmanda & Ballaré, 2021), and how these responses interact with responses to other biotic and abiotic stresses (Courbier & Pierik, 2019; Lazzarin et al., 2021). These studies have resulted in valuable insights into how plants balance responses between different stressors, and thereby provide opportunities to improve plant resilience in agricultural settings.

Shade avoidance depends on the detection of far-red (FR) light, which is reflected from vegetative plant tissue and therefore provides a signal of plant density and the degree of competition for light (Ballaré et al., 1990). Reflection of FR light lowers the ratio between red (R) and FR, which is detected by the phytochrome B (phyB) photoreceptor. Red light activates phyB, which is then transported to the nucleus and inhibits SAS responses. With increasing FR light, the R:FR drops and phyB is inactivated, allowing for the expression of SAS (Ballaré & Pierik, 2017). The SAS is characterized by morphological adaptations such as stem elongation, upward leaf movement, and reduced branching, which serve to increase light capture in crowded canopies (Casal, 2012). These adaptations are mediated through FR-induced stimulation of the growth-promoting phytohormones auxin and gibberellin (Ballaré & Pierik, 2017). At the same time, the inactivation of phyB inhibits the signalling of jasmonic acid (JA) and salicylic acid (SA), the two principal phytohormones involved in defence against biotic stress (Ballaré, 2014; Fernández-Milmanda & Ballaré, 2021). Consequently, plants exposed to FR light are more susceptible to biotic stress, leading to the increased performance of arthropod herbivores (Cortés et al., 2016; Izaguirre et al., 2006; Meijer et al., 2022; Moreno et al., 2009).

Both JA and SA are known to inhibit the signalling of growth-promoting phytohormones (Van Butselaar & van den Ackerveken, 2020; Wasternack & Feussner, 2018). Downregulation of defensive signalling is therefore required for the full and rapid expression of SAS and serves to prioritize SAS responses over defensive responses when experiencing competition for light (Ballaré & Austin, 2019). There are also indications that plants can compensate for the reduced direct defences against arthropod herbivores by stimulating interactions with the natural enemies of the herbivores (Cortés et al., 2016). Plants that are attacked by herbivores emit herbivore-induced plant volatiles (HIPVs), a blend of volatile organic compounds (VOCs) that attract the natural enemies of the attacking herbivores (Dicke & Baldwin, 2010). These volatile blends are highly specific and can contain information on the herbivore species, density and the abiotic conditions of the plant (Aartsma et al., 2017; Cabedo-López et al., 2019). Exposure to FR light can influence VOC emissions, with consequences for plant–arthropod interactions (Cortés et al., 2016; Kegge et al., 2013). Plants treated with methyl jasmonate (MeJA), a volatile form of the stress hormone JA commonly used to induce antiherbivore defences, became more attractive to the predatory bug *Macrolophus pygmaeus* after exposure to FR light (Cortés et al., 2016). These results indicate that plants might balance their direct and indirect defences in response to signals of competition.

M. pygmaeus is a generalist predator that can feed on a broad range of herbivore species (Bouagga et al., 2018; El Kenway et al., 2022; Leman et al., 2020; Messelink et al., 2011). However, *M. pygmaeus* is a zoophytophagous predator, meaning that it is also able to sustain itself on plant material in the absence of arthropod prey. At higher densities, *M. pygmaeus* can itself cause plant damage (Castañé et al., 2011; Sanchez et al., 2018). The extent of plant-feeding by *M. pygmaeus* is dependent on the availability of arthropod prey and on the defensive status of the plants. In the absence of prey, the induction of plant defences by a nonpathogenic strain of *Fusarium oxysporum* reduced *M. pygmaeus* reproduction (Eschweiler et al., 2019). In the presence of arthropod prey, inoculation with *F. oxysporum* did not affect *M. pygmaeus* reproduction but did lead to decreased prey abundance compared to non-inoculated plants, while prey abundance was not influenced by *F. oxysporum* inoculation alone (Eschweiler et al., 2019). Together, these results indicate a shift toward more prey consumption after the induction of plant defences. Reversely, reduced plant defences in low R:FR conditions might make the plant a more readily available food source for *M. pygmaeus* and might cause a shift toward more plant feeding.

In this study, we further investigated the effects of changes in R:FR on the attraction and feeding behaviour of *M. pygmaeus*. Cortés et al. (2016) tested the effects of FR light on the VOC emission and attractiveness of plants treated with MeJA. Although MeJA application can induce antiherbivore responses, there are no actual herbivores present. The results reported by Eschweiler et al. (2019) highlight the importance of prey availability for the interaction between plants and *M. pygmaeus*. We, therefore, studied the effect of R:FR on the HIPV emission of plants infested with the greenhouse whitefly (WF) (*Trialeurodes vaporariorum*), and how this influences the attraction of *M. pygmaeus*. We tested both an increase and decrease in R:FR compared to sunlight levels, as previous work indicated that both changes in R:FR could influence plant–WF interactions (Meijer et al., 2022; Shibuya et al., 2010), with possible consequences for plant-predator interactions. We also investigated how supplemental FR light influenced the reproduction of *M. pygmaeus* in both the presence and absence of *T. vaporariorum* as prey. We expect that a reduction in R:FR influences the emission of HIPVs and increases the attraction of *M. pygmaeus* to WF-infested plants. An increase in R:FR is expected to have little or no effect, as an increase in R:FR also did not influence the performance of *T. vaporariorum* (Meijer et al., 2022). We further expect that supplemental FR light increases *M. pygmaeus* reproduction, related to reduced plant defences in low R:FR conditions.

2 | MATERIALS AND METHODS

2.1 | Plants and arthropods

Tomato plants (*Solanum lycopersicum* cv. Moneymaker) were used in all experiments. Greenhouse WFs, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodide), were obtained from the stock colony of the Laboratory of Plant Breeding (Wageningen University, The Netherlands). The *T. vaporariorum* colony is maintained on tomato (Moneymaker) at 21°C/17°C, 60% relative humidity (RH) and 16/8 h L/D. The predatory bugs, *M. pygmaeus* (Hemiptera: Miridae), were obtained from a commercial strain of Biobest Biological Systems. The predators were kept in climate cabinets (25°C, 60% RH and 16/8 h L/D) on tomato plants supplemented with Artemac (Biobest Biological Systems) and reared for one generation to control the age of the predators used in the experiments.

2.2 | Experimental design

Laboratory experiments were performed to investigate the effects of R:FR on tomato HIPV emissions and the attraction of the predatory bug *M. pygmaeus*. Tomato seeds were sown in rockwool blocks (7.5 × 7.5 cm) soaked in Tomato 2.0 nutrient solution (Unifarm). Two weeks after germination, the plants were transferred to a climate-controlled growth chamber (25°C/18°C day/night, 70 ± 3% RH and 16/8 h L/D) and divided over three separate compartments with different light treatments. Each treatment consisted of 150 µmol/m^2/s white light (5700 K) supplemented with 60 (+FR), 30 (control light [CL]) or 0 (−FR) µmol/m^2/s of FR light (735 nm). The CL treatment was set at an R:FR of 1.2, which is equivalent to sunlight, and was reduced or increased to 0.6 (+FR) and 8.2 (−FR), respectively. These light treatments differentially affect the expression of SAS in young tomato plants (Meijer et al., 2022; Supporting Information: Picture S1). Both white and FR light were provided by Dyna light-emitting diode (LED) modules (Heliospectra). The different compartments were separated with white reflective plastic to prevent light contamination between treatments. Plants were exposed to the light treatments for 1 week before being exposed to *T. vaporariorum* WFs. Plants were individually covered with mesh bags, and tightly fastened at the base of the rockwool cube. One hundred adult WFs of mixed age and sex were released inside the mesh bags and left to feed freely for 5 days before plants were used in further experiments. Other plants remained uninfested (U) for 5 days under the same conditions, resulting in six treatment combinations (+FR$_{WF}$, +FR$_U$, CL$_{WF}$, CL$_U$, −FR$_{WF}$ and −FR$_U$).

2.3 | Y-tube olfactometer

The response of *M. pygmaeus* to plant volatiles was observed in a two-choice Y-tube olfactometer as described previously (Lins et al., 2014). A Y-shaped Pyrex tube, formed by an entry arm (20 cm) and two side arms (13 cm, 80° angle), was positioned vertically. The two side arms were each connected to 15 L glass jars containing tomato plants as odour sources. Compressed air was passed through the jars at a regulated flow of 2.5 L/min to carry the plant volatiles into the arms of the Y-tube. Before reaching the jars, the air was filtered by passing it through active charcoal. The glass jars were isolated in light-tight cabinets, equipped with a Dyna LED module, to provide plants with their respective light treatment throughout the choice assays while preventing visual detection of the plants by the predators. A single plant was introduced in each glass jar. The rockwool base of the plants was wrapped in aluminium foil before placement into the jar and the plants were left to acclimate for 15 min before starting choice assays. Individual predators were released at the downwind arm of the Y-tube, and their choice for either odour source was recorded when they passed at least 10 cm into one of the side arms, or no choice was recorded if they did not pass this mark within 10 min after their release. Pair-wise comparisons were made between WF-infested plants from the three light treatments (+FR$_{WF}$, CL$_{WF}$ and −FR$_{WF}$). Because *M. pygmaeus* is known to prefer WF-infested plants over undamaged plants (Ingegno et al., 2011; Leman et al., 2020), choice assays between uninfested and infested plants of the control-light treatment (CL$_U$ and CL$_{WF}$) were added as a positive control. For each pair-wise comparison, the response of 10 female *M. pygmaeus* predators 7–10 days old was tested daily for a total of 13 days (130 predators per comparison). After each set of five predators, the position of the odour sources was switched between the left and right side arms to prevent positional bias. After every 10 predators, the plants were removed and the Y-tube system was flushed with clean air for 10 min before introducing new plants.

2.4 | Collection of headspace VOCs

Volatiles were collected from plants of all six treatment combinations. The rockwool base of plants was wrapped in aluminium foil before plants were placed in 15 L glass jars. They were left to acclimate for 15 min before starting the headspace collection. Air was filtered through active charcoal before reaching the jars, and volatiles were collected by drawing air with a suction pump through a stainless steel cartridge containing 200 mg of Tenax TA (20/35 mesh, CAMSCO) at 150 mL/min for 2 h. During volatile collection, plants remained exposed to their respective light treatments. Samples were collected from 11 to 14 plants per treatment. Volatile samples of empty rockwool blocks soaked with Tomato 2.0 nutrient solution and wrapped in aluminium foil were also collected to correct for background odours. The Tenax cartridges with VOC samples were dry purged under a stream of helium (50 mL/min) for 15 min to remove excess moisture.

The collected volatiles were thermally released from the Tenax TA adsorbent using an Ultra 50:50 thermal desorption unit (Markes) at 250°C for 10 min under a 20 mL/min helium flow, while the volatiles were simultaneously recollected in a thermally cooled universal solvent trap: Unity (Markes) at 0°C. When desorption was completed, the volatile compounds were released from the cold trap by ballistic heating at 40°C/s to 280°C, which was then kept for 10 min, while all the volatiles were transferred to a ZB-5 MS analytical column (30 m × 0.25 mm ID × 1 mm FT with 10 m built-in guard column (Phenomenex), placed inside the oven of a Thermo Trace GC Ultra (Thermo Fisher Scientific) for further separation of the plant volatiles. The gas chromatograph (GC) oven temperature was initially held at 40°C for 2 min and was then raised at 6°C/min to a final temperature of 280°C, where it was kept for 4 min under a constant helium flow of 1 mL/min. A Thermo Trace DSQ quadrupole mass spectrometer (Thermo Fisher Scientific) coupled to the GC was operated in an electron impact ionization mode at 70 eV in a full scan with a mass range of 35–400 amu at 4.70 scans/s. The mass spectrometer (MS) transfer line and ion source were set at 275°C and 250°C, respectively. Automated baseline correction, peak selection (signal/noise > 3) and alignments of all extracted mass signals of the raw data were processed following an untargeted metabolomic workflow using MetAlign software, producing detailed information on the relative abundance of mass signals representing the available metabolites (Lommen, 2009). This is followed by the reconstruction of the extracted mass features into potential compounds using the MSClust software through data reduction by means of unsupervised clustering and extraction of putative metabolite mass spectra (Tikunov et al., 2012). Tentative identification of volatile metabolites was based on a comparison of the reconstructed mass spectra with those in the NIST 2008 and Wageningen Mass Spectral Database of Natural Products MS libraries, as well as experimentally obtained linear retention indices.

2.5 | *M. pygmaeus* reproduction

A greenhouse experiment was conducted to study the effects of supplemental FR light on the reproduction of *M. pygmaeus*, in both the absence and presence of *T. vaporariorum* as prey. Tomato seeds were sown in rockwool blocks as described above and transported to a greenhouse compartment (22°C/18°C, 70% RH and 16/8 h L/D) 3 weeks after germination. Plants were individually placed in mesh cages (60 × 40 × 40 cm; BugDorm) and divided over two tables, both illuminated with 150 μmol/m^2/s broad-spectrum white light provided by VYPR series LEDs (model VR-3X-BW4; Fluence) as a supplement to natural daylight. One table was further supplemented with 60 μmol/m^2/s FR light (730 nm; Philips Greenpower LEDs), creating an R:FR of 0.8 (+FR) compared to 1.6 in the control (CL). Ten plants were placed on either side of the greenhouse and were exposed to the light conditions for 1 week. After 4 weeks, 100 adult WFs of mixed age and sex were introduced to half of the cages, five in either light treatment, creating four treatments based on the supplementation of FR light and the presence of WFs (CL/−WF, CL/+WF, +FR/−WF and +FR/+WF). The introduction of 100 adult WFs occurred weekly to maintain a viable population and food source for *M. pygmaeus* throughout the experiment. At 6 weeks, 12 adult *M. pygmaeus* of approximately 5–10 days old (six males and six females) were introduced to each cage. After 25 days, all *M. pygmaeus* were collected and counted per cage. The experiment was repeated three times between April and September 2022, resulting in 15 replicates per treatment. During the second and third run, leaflets from the sixth and ninth leaf in the C/+WF and +FR/+WF treatments (10 plants per treatment) were collected to provide estimates of the WF population within the cage. Leaf discs of 2.5 cm^2 were excised from the three most terminal leaflets per leaf (30 leaf discs per leaf per treatment) and the number of WF eggs and nymphs was counted. The ninth leaf was the youngest fully developed leaf.

2.6 | Statistical analysis

Choice responses of *M. pygmaeus* in the two-choice Y-tube experiment were analysed with a two-sided binominal test with $\alpha = 0.05$, for each pair-wise comparison separately. Data are presented as the total number of *M. pygmaeus* choosing either odour source in each pair-wise comparison.

The volatile emission data, expressed as peak heights, were imported into SIMCA-P 17 statistical software (Umetrics), followed by log transformation, mean-centreing and unit-variance scaling before being subjected to multivariate data analysis. Unsupervised principal component analysis (PCA) and/or supervised partial least squares-discriminant analysis (PLS-DA), and its extension orthogonal partial least squares-discriminant analysis (OPLS-DA) were used as tools to compare and correlate treatment groups. The results of the analysis are visualized in score plots, which reveal the sample structure according to model components, and in loading plots, which display the contribution of the variables (individual VOCs) to these components as well as the relationships among the variables. R^2 and Q^2 metrics are provided for PLS-DA or OPLS-DA analysis. These metrics describe the explained variation within the data set and the predictability of the model, respectively, and were calculated based on the averages of the sevenfold cross-validation. R^2 and Q^2 values range between 0 and 1, and the closer these metrics are to 1, the higher the variance explained by the model and the more reliable the predictive power of the model. Significant differences in the total emission of individual VOCs between light treatments of either infested or uninfested plants were analysed using Kruskal-Wallis analysis. Pair-wise comparisons, as performed in the Y-tube choice assays, were analysed using Mann–Whitney *U* analyses for comparisons showing significant separation in multivariate data analysis.

M. pygmaeus reproduction, expressed as the total number of nymphs produced per six females, was analysed using a generalized linear mixed model with a negative binomial distribution, with light treatment and WF presence as fixed factors and random effects for the experimental repetition in time and for table withing the experimental repetition. WF numbers are expressed as the total number of eggs, crawlers (first instar nymphs) and nymphs per leaf disc. A separation between first instar nymphs and older stages is made because crawlers are more easily distinguished from other nymphal stages. Data were analysed using multivariate GLM with light treatment and leaf number as fixed factors, and plant ID and the experimental replicates as random factors.

3 | RESULTS

3.1 | Y-tube choice assays

In the positive control, *M. pygmaeus* significantly preferred WF-infested plants over uninfested plants (Figure 1). No preference was observed when *M. pygmaeus* were offered the choice between WF-infested plants exposed to different R:FR light ratios in pair-wise

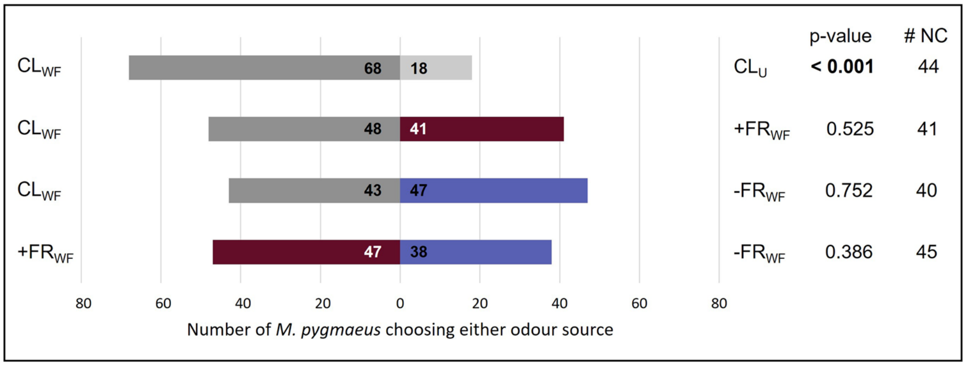

FIGURE 1 Total number of *Macrolophus pygmaeus* choosing either odour source in pair-wise comparisons between plants exposed to different R:FR light ratios (+FR = 0.6, CL = 1.2 and −FR = 8.2) and either infested with *T. vaporariorum* whiteflies (WFs) or uninfested (U). Different colours of the bars correspond to the treatments indicated on either side of the graph. *p* values in bold indicate a significant preference for either odour source (two-sided binominal test). For each pair-wise comparison, 130 predators were tested. CL, control light; NC, no choice; R:FR, red and far-red. [Color figure can be viewed at wileyonlinelibrary.com]

comparisons. This indicates that changes in R:FR did not influence the attraction of *M. pygmaeus* to WF-infested plants.

3.2 | Headspace VOC emissions

We identified 70 VOCs across the six different treatment combinations (Supporting Information: Table S1). These compounds were detected in at least 50% of the samples from at least one of the treatment combinations. Multivariate analysis (OPLS-DA) comparing the volatile blends from uninfested plants of all three light treatments ($+\text{FR}_{\text{U}}$, CL_{U} and $-\text{FR}_{\text{U}}$) did not result in a significant separation between volatile blends (permutation test: $R^2 = 0.287$, $Q^2 = 0.024$; $p_{\text{cv-ANOVA}} = 1.000$), indicating that changes in R:FR did not influence the composition of constitutive volatile blends (Figure 2a,b). Similarly, OPLS-DA including the WF-infested plants of all three light treatments ($+\text{FR}_{\text{WF}}$, CL_{WF} and $-\text{FR}_{\text{WF}}$) also did not result in significant separation (permutation test: $R^2 = 0.320$, $Q^2 = 0.056$; $p_{\text{cv-ANOVA}} = 0.998$), indicating that HIPV emission is also not affected by changes in R:FR (Figure 2c,d). In uninfested plants, nine VOCs were emitted in significantly different quantities by plants exposed to different R:FR ratios, all showing a gradient from highest emission in +FR to lowest in −FR, with the exception of (*Z*)-3-hexen-1-ol (Supporting Information: Table S1). In WF-infested plants, only four VOCs showed significant differences, following the same gradient from +FR to −FR, with the exception of 2-methylbutanal-O-methyloxime (Supporting Information: Table S1).

We also compared volatile blends pair-wise following the pair-wise comparisons performed in the Y-tube choice essays. Surprisingly, multivariate analysis (PCA) did not show a separation between the volatile blends of CL_{U} and CL_{WF} (Supporting Information: Figure S1). Similarly, no separation was observed between the volatile blends of CL_{WF} and $+\text{FR}_{\text{WF}}$, or between VOC blends of CL_{WF} and $-\text{FR}_{\text{WF}}$ (Supporting Information: S2). We did observe significant separation between the blends of $+\text{FR}_{\text{WF}}$ and $-\text{FR}_{\text{WF}}$ using PLS-DA analysis (permutation test: $R^2 = 0.967$, $Q^2 = 0.731$; $p_{\text{cv-ANOVA}} = 0.011$) (Supporting Information: S3). Twenty-three compounds contributed most to the separation, with five VOCs showing significantly higher emission in $+\text{FR}_{\text{WF}}$ and one compound showing significantly lower emission in $+\text{FR}_{\text{WF}}$ (Supporting Information: Table S2).

3.3 | *M. pygmaeus* reproduction

The total number of *M. pygmaeus* nymphs collected after the 25-day period was significantly higher in the presence of WF prey compared to when no prey was available (~600% increase) (Figure 3). Furthermore, the number of nymphs was significantly higher in plants exposed to +FR compared to CL treatments, although the effect size is lower compared to the effect of prey availability (~30% increase). No significant interaction between the presence of prey and the light treatments was found.

3.4 | *Trialeurodes vaporariorum* density estimate

Both light treatment and leaf number had a significant effect on the number of WFs of all three life stages (Figure 4). +FR significantly increased WF numbers compared to CL. The effect of leaf number was related to the leaf age; younger leaves (ninth leaf) contained more eggs and crawlers while older leaves (sixth leaf) had more nymphs. A significant interaction between light treatment and leaf number was only observed for nymphs (Figure 4).

4 | DISCUSSION

Shade avoidance responses are part of a complex network of ecological interactions within the canopy that together shape the growth-defence dynamics in plants (De Vries et al., 2017). The prioritization of shade avoidance responses over defensive responses

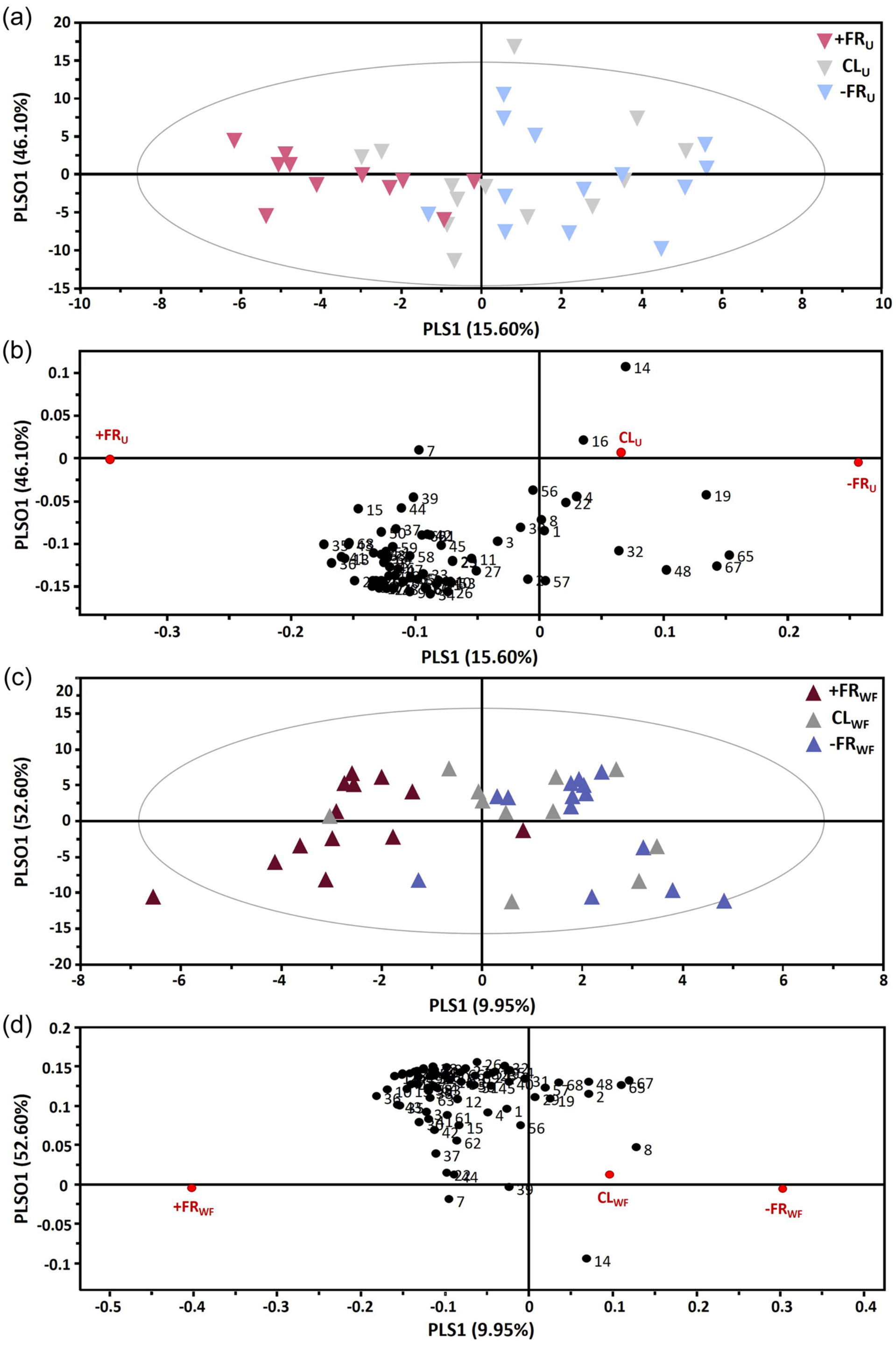

FIGURE 2 Effects of exposure to different R:FR light ratios on the blend of volatile organic compounds (VOCs) collected from either uninfested or whitefly (WF)-infested tomato (*Solanum lycopersicum* cv Moneymaker) plants. (a) Multivariate comparison using orthogonal projection to latent structures-discriminant analysis between uninfested plants exposed to different R:FR light ratios ($+FR_U = 0.6$, $n = 11$; $CL_U = 1.2$, $n = 13$; $-FR_U = 8.2$, $n = 13$), displayed in a two-dimensional score plot. (b) Loading plot indicating the contribution of each VOC to the separation between uninfested plants exposed to different R:FR light ratios. (c) The same analysis as described for (a) but now comparing plants infested with *Trialeurodes vaporariorum* whiteflies and exposed to different R:FR light ratios ($+FR_{WF}$ $n = 13$; CL_{WF} $n = 11$; $-FR_{WF}$ $n = 14$). (d) Loading plot indicating the contribution of each VOC to the separation between WF-infested plants exposed to different R:FR light ratios. For VOC identification: the numbers in the loading plots correspond to the numbers in Supporting Information: Table S1. CL, control light; PLS, partial least squares; R:FR, red and far-red. [Color figure can be viewed at wileyonlinelibrary.com]

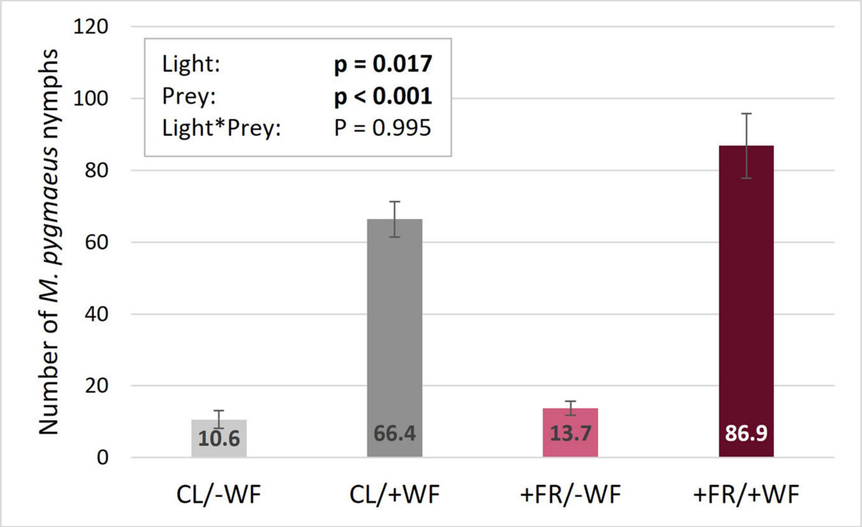

FIGURE 3 Average number of nymphs (±SE) produced by 12 *Macrolophus pygmaeus* (six males and six females) in the presence (+WF) or absence (−WF) of whitefly prey on tomato plants grown under control light (CL) conditions or CL with supplemental far-red light (+FR) during 25 days. There was a significant effect of both the presence of prey ($\chi^2(1) = 249.20$, $p > 0.001$) and the light treatment ($\chi^2(1) = 5.65$, $p = 0.017$) on the total number of nymphs produced. There was no interaction effect between prey presence and light treatment ($\chi^2(1) > 0.01$, $p = 0.995$). The numbers in the bars represent the averages. CL/−WF $n = 15$, CL/+WF $n = 15$, +FR/−WF $n = 15$, +FR/+WF $n = 13$. WF, whitefly. [Color figure can be viewed at wileyonlinelibrary.com]

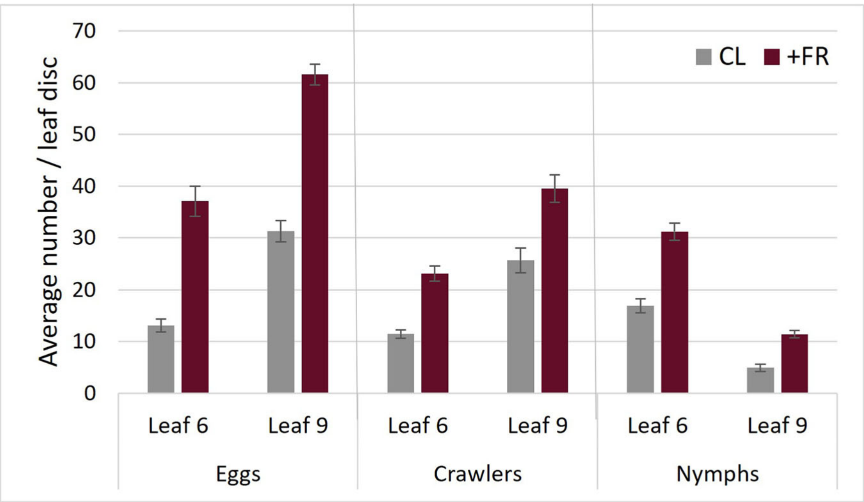

FIGURE 4 Average number of whitefly eggs, crawlers or nymphs (±SE) counted on leaf discs from the sixthth or ninth leaf of tomato plants grown under control light (CL) conditions or CL with supplemental far-red light (+FR). Whitefly numbers in all three life stages were significantly affected by light treatment (eggs: $F(1) = 38.44$, $p < 0.001$; crawlers: $F(1) = 11.72$, $p < 0.001$; nymphs: $F(1) = 14.41$, $p < 0.001$) and leaf number (eggs: $F(1) = 97.70$, $p < 0.001$; crawlers: $F(1) = 86.01$, $p < 0.001$; nymphs: $F(1) = 172.78$, $p < 0.001$). A significant interaction between light treatment and leaf number was only observed for nymphs (eggs: $F(1) = 2.15$, $p = 0.146$; crawlers: $F(1) = 0.16$, $p = 0.690$; nymphs: $F(1) = 10.46$, $p = 0.002$). Results were not affected by the experimental replicates (eggs: $F(1) = 0.02$, $p = 0.880$; crawlers: $F(1) = 0.53$, $p = 0.470$; nymphs: $F(1) = 0.04$, $p = 0.835$) or plant ID (eggs: $F(1) = 0.01$, $p = 0.933$; crawlers: $F(1) = 0.14$, $p = 0.706$; nymphs: $F(1) = 0.22$, $p = 0.63$). Leaf 6: CL $n = 30$, +FR $n = 30$; leaf 9: CL $n = 30$, +FR $n = 27$. [Color figure can be viewed at wileyonlinelibrary.com]

leads to changes in plant–arthropod interactions that span across trophic levels (Lazzarin et al., 2021). Previous work indicated that plants experiencing competition might trade direct defences for indirect defences by showing that plants expressing the SAS are more attractive to the predatory bug *M. pygmaeus* (Cortés et al., 2016). In this paper, we further examined the effects of shade avoidance on the interaction between *M. pygmaeus* and tomato plants, thereby taking into account the zoophytophagous nature of this predator. We show that the volatile-mediated attraction of this predator to WF-infested plants is not affected by changes in R:FR, but that FR light does influence the reproduction of *M. pygmaeus* and WF.

Our results indicate that changes in R:FR do not strongly affect the emission of tomato volatiles and also do not influence the attraction of *M. pygmaeus* to WF-infested plants. Cortés et al. (2016) previously reported that exposure to FR light increased the attraction of this predator to MeJA-treated tomato plants. WFs are known to induce SA-dependent defences in plants (Elzinga et al., 2014; Xu et al., 2019). SA- and MeJA-induced volatiles can be differentially affected by changes in R:FR, resulting in differences in predator behaviour in response to these volatiles. However, previous work showed that the attraction of predatory mites to plants infested with JA-inducing spider mites (*Tetranychus urticae*) was also not affected by changes in R:FR (Meijer et al., 2023), indicating that changes in R:FR do not influence the emission of both SA- and JA-induced HIPVs. The observed results by Cortés et al. (2016) might therefore result from the use of MeJA instead of actual herbivory. Although application of MeJA is an effective method to induce antiherbivore responses in plants, there are differences in the responses induced by MeJA application and true herbivory (Dicke et al., 1999; Kappers et al., 2010; Lortzing et al., 2017; Papazian et al., 2019), which can affect predator preference behaviour. For example, volatiles emitted by spider mite-infested plants were more attractive to a predatory mite than volatiles from JA-treated plants (Dicke et al., 1999). VOC blends emitted by hormone-induced plants are missing the specific information pertaining to herbivore identity and density and might therefore provide a more general stress signal (Kappers et al., 2010). Generalist predators are proposed to be more sensitive to general stress indicators compared to specific HIPVs (Silva et al., 2021). Due to the zoophytophagous nature of *M. pygmaeus*, it is also possible that the presence or absence of actual herbivores can change the informational value of the volatile blends. FR light might alter the information provided by MeJA-induced volatile blends as it provides information on the defensive status of the plant and the accessibility of plant material, while changes in R:FR might not change the attractiveness of herbivore-infested plants as the presence of prey is the overriding element. It would be interesting to perform comparative studies between MeJA-treated and herbivore-infested plants to determine whether the presence of prey is a determining factor for the attraction of predators in plants experiencing competition.

The lack of preference between WF-infested plants exposed to different R:FR light ratios largely corresponds with the lack of differences in volatile blend composition, with the exception of the pair-wise comparison between $+\mathrm{FR}_{\mathrm{WF}}$ and $-\mathrm{FR}_{\mathrm{WF}}$. A significant separation between the volatile blends of these treatments was observed, although *M. pygmaeus* did not show a preference for plants exposed to either $+\mathrm{FR}_{\mathrm{FW}}$ or $-\mathrm{FR}_{\mathrm{WF}}$. Reversely, we did not find a significant separation between volatile blends of WF-infested or uninfested plants grown under CL conditions ($\mathrm{CL}_{\mathrm{WF}}$ and CL_{U}), while *M. pygmaeus* showed a clear preference for $\mathrm{CL}_{\mathrm{WF}}$ plants. A possible explanation is that compounds emitted by WF-infested tomato plants that are relevant for attracting *M. pygmaeus* were emitted at levels below the detection ability of the analytical instruments used. The volatiles detected in the headspace of tomato plants in this study primarily consisted of terpenoids (60 out of 70 compounds), which play a minor role in the attraction of mirid predators (Silva et al., 2021). Feeding by *T. vaporariorum* is also known to induce the emission of the ester methyl salicylate (MeSA) by tomato plants (Ángeles López et al., 2012; Conboy et al., 2020), which was not detected in the headspace analysis of the current study. MeSA is an important compound for the attraction of mirids (Silva et al., 2021), and its emission can be modulated after exposure to FR light (Cortés et al., 2016).

The results of this study also show that exposure to supplemental FR light increases the reproduction of *M. pygmaeus*. This effect could be two-sided. The downregulation of plant defences under supplemental FR light (Fernández-Milmanda & Ballaré, 2021) could directly increase plant quality for the zoophytophagous predator, but can also indirectly benefit *M. pygmaeus* by supporting higher prey abundance (Meijer et al., 2023). Indeed, along with the increased reproduction of *M. pygmaeus*, we also found increased numbers of *T. vaporariorum* in the +FR treatment, which corresponds with previous findings (Meijer et al., 2022). In previous studies, supplemental FR light increased the population growth of spider mites (*T. urticae*), allowing a more rapid population growth of the predatory mite *Phytoseiulus persimilis* and leading to a stronger suppression of the herbivore (Meijer et al., 2023). Unfortunately, the time frame of the current study was too short to study population development in *M. pygmaeus* and to make a proper assessment of the effectiveness of WF control by *M. pygmaeus*. Furthermore, because no significant interaction between the effects of light treatment and WF presence on the number of *M. pygmaeus* nymphs was found, it is difficult to ascribe the increased reproduction of *M. pygmaeus* to either direct or indirect effects alone, and further study is required to disentangle both aspects. However, the results observed in our study provide promising opportunities for the combined use of FR light and *M. pygmaeus* as biological control agents in greenhouses.

The use of FR LEDs is an application in horticulture to manipulate plant morphology and reproductive development and thereby increase crop yield (Demotes-Mainard et al., 2016), but at the same time, it can lead to an increased pest pressure (e.g., Meijer et al., 2022). Cortés et al. (2016) suggested that FR light might have a role in biological control by increasing the attraction of natural enemies. Although our current results indicate that changes in R:FR neither enhance nor interfere with the attraction of the predatory bug *M. pygmaeus*, supplemental FR light might still stimulate biological control by allowing a more rapid build-up of the predator population. *M. pygmaeus* is often used in preventative release strategies by maintaining predator populations on banker plants, but its successful establishment depends on the species of banker plant, the crop and the availability of supplemental food (Bresch et al., 2014; Messelink et al., 2015; Sanchez et al., 2021). Supplemental FR light might contribute to increased establishment of *M. pygmaeus* during preventative release.

We conclude that changes in predator performance and predator–prey dynamics could mitigate the increased pest pressure occurring after plant exposure to low R:FR conditions. However, the tritrophic interactions between plants, arthropod herbivores and *M. pygmaeus* are complex, and more research is required to understand how FR light shapes the ecological interactions between trophic levels. For example, plant feeding by mirid predators can induce plant defences and increase resistance to herbivores (Bouagga et al., 2020; Pappas et al., 2015; Pérez-Hedo et al., 2022; Silva et al., 2022). Herbivores also avoid plants that have been exposed to *M. pygmaeus* (Zhang et al., 2019). On the other hand, too high densities of *M. pygmaeus* can cause plant damage through direct feeding or the transmission of viruses (Castañé et al., 2011; Moerkens et al., 2016, 2017; Sanchez et al., 2018). As FR light exerts strong effects on plant defensive signalling (Fernández-Milmanda & Ballaré, 2021), it has the potential to influence both direct and indirect interactions between all three trophic levels. A proper understanding of how these interactions are affected by changes in R:FR is required to adequately assess the efficiency of supplemental FR light to stimulate biological control.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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