

Effects of low and high red to far-red light ratio on tomato plant morphology and performance of four arthropod herbivores

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ABSTRACT

Changing the spectral composition of light has numerous advantages for the production and quality of horticultural crops. However, changing the light spectrum to stimulate growth can have negative consequences for plant responses to biotic stress. Especially changes in the ratio between red and far-red light (R:FR) have an important effect on plant-herbivore interactions. A low R:FR is indicative of shading and competition for light and induces strong growth responses which are known as shade avoidance responses, including stem elongation and leaf hyponasty. Exposure to low R:FR also inhibits plant defensive responses against biotic agents and increases the performance of pests and pathogens. In this study we tested whether an increase in R:FR, through the supplementation of red light LEDs can be used to reduce the performance of arthropod herbivores. Tomato plants (*Solanum lycopersicum*) were exposed to three different R:FR ratios; 0.5 (shading), 1.2 (sunlight) and 5.2 (artificial) and infested with either caterpillars (*Manduca sexta*), spider mites (*Tetranychus urticae*), aphids (*Myzus persicae*) or whiteflies (*Trialeurodes vaporariorum*). Plants exposed to a low R:FR showed clear stem elongation and leaf hyponasty consistent with the shade-avoidance responses, while plants exposed to high R:FR showed reduced stem length and reduced hyponasty. The performance of all four herbivore species was significantly increased after exposure to low R:FR, although the strength of this effect varied between phloem feeding and tissue feeding herbivores. Increasing the R:FR only reduced the performance of the caterpillars and did not significantly affect the other herbivore species. These results indicate that herbivore species with different feeding strategies respond differently to changes in light quality. These findings have implications for the use of LEDs in greenhouse horticulture.

1. Introduction

The use of light-emitting diodes (LEDs) in horticulture has led to great improvements in crop production, owing largely to their ability to precisely control the spectral composition of light. Many physiological processes in plants are affected by specific wavelengths of light (de Wit et al., 2016) and can, therefore, be influenced by altering light quality in greenhouses (Lazzarin et al., 2021). Using LEDs, growers are now able to achieve higher crop yields and higher-quality crops by influencing crop morphology, flowering and nutrient composition (Davis and Burns, 2016; Bantis et al., 2018). However, light quality is also known to influence plant immune responses to pests and pathogens (Ballaré, 2014). As predicted by the growth-defence trade-off (Zust and Agrawal, 2017), the use of specific wavelengths of light to stimulate plant growth can negatively impact plant resistance to biotic stress (Cargnel et al., 2014;

Ji et al., 2019). So far, only few studies have addressed the possible consequences of altered light spectral composition on the balance between plant growth and defence in horticultural crops (e.g. Douma et al., 2019; Rechner et al., 2017). Most of these studies involve changes in the red to far-red light ratio (R:FR) and indicate that spectral manipulation can have both negative and positive effects on pests and pest management (Ballaré, 2014; Shibuya et al., 2010; Cortés et al., 2016).

In natural canopies, a reduction in R:FR, caused by absorption of R light for photosynthesis and the reflection of FR light from vegetative tissue, serves as a signal of shading and light competition from neighbouring plants. In response to low R:FR, plants express a range of morphological and physiological changes that increase their light-capturing ability. These changes are collectively known as the shade-avoidance syndrome (SAS) and include stem elongation, leaf hyponasty and early flowering (Roig-Villanova et al., 2019). Differences in R:

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FR are perceived by the phytochrome B (phyB) photoreceptor. During high R light intensity, phyB is activated and inhibits plant growth responses, while under high FR light, phyB is deactivated leading to SAS responses.

Expression of SAS is also associated with reduced immune responses to biotic stress (Ballaré, 2014; Courbier and Pierik, 2019). Exposure to low R:FR leads to downregulation of both jasmonic acid (JA) and salicylic acid (SA) signalling, the two principle phytohormones orchestrating immune responses to herbivores and pathogens (Ballaré, 2014). JA is primarily induced by mechanical wounding and is involved in defensive responses against herbivores and necrotrophic pathogens, while SA is mainly involved in defence against biotrophic pathogens and phloem-feeding herbivores. The JA and SA signalling pathways are mutually antagonistic (Li et al., 2019; Yang et al., 2019), allowing the plant to fine-tune its response depending on the attacker. By inhibiting both JA and SA signalling during shading, plants prioritise shade avoidance responses over defence responses and shift the growth-defence balance towards growth (Ballaré and Austin, 2019). Consequently, plants exposed to low R:FR might grow faster but are also more susceptible to herbivory and support higher herbivore growth rates (Ballaré, 2014; Cortés et al., 2016).

So far, studies on the effects of shade avoidance on plant-herbivore interactions have mainly focused on caterpillars (Izzaguirre et al., 2006; Moreno et al., 2009; Agrawal et al., 2012; Cortés et al., 2016), and little is known on how changes in R:FR influence herbivores of other taxonomic groups. Arthropod herbivores can be divided into different feeding guilds and can induce different defensive responses depending on their feeding strategy. Tissue-feeding herbivores such as caterpillars primarily induce JA responses due to mechanical wounding, while cell-content feeders such as spider mites that damage cell walls to suck out cell contents can induce both JA and SA responses (Zhang et al., 2020). Several species of phloem-feeding arthropods, such as aphids and whiteflies, which pierce the plant's vasculature to suck out phloem sap, are known to actively induce SA-mediated defence responses to suppress the more efficient JA defences (Zarate et al., 2007; Elzinga et al., 2014). To what extent herbivores of different feeding guilds are affected by low R:FR remains to be studied.

Furthermore, contrary to the effects of FR light, little is known on how the R light component mediates plant-herbivore interactions and herbivore performance. Exposure to high R:FR through supplementation with R light has been shown to oppose some of the classical phenotypic features associated with SAS. For example, elongation growth was inhibited and flowering time was delayed in ornamentals when exposed to artificially high R:FR (Kurepin et al., 2007; Yamada et al., 2009). There are also indications that supplemental R light decreases the proliferation of biotrophic pathogens through stimulation of SA and JA signalling in the plants (Wang et al., 2010; Shibuya et al., 2011; Yang et al., 2015). Whether the supplementation of R light also affects the performance of arthropod herbivores has not yet been studied.

In this study we investigate (1) how high R:FR influences plant morphology in comparison to SAS morphology and (2) how changes in R:FR influence the performance of multiple arthropod herbivores belonging to different feeding guilds. We expect to find the classical SAS characteristics of stem elongation and leaf hyponasty in plants exposed to low R:FR, accompanied with increased performance of herbivores. We further expect that exposure to high R:FR induces opposite phenotypes and decreases the performance of the herbivores.

2. Materials and methods

2.1. Plant material and growing conditions

Tomato seeds (*Solanum lycopersicum* cv. Moneymaker) were sown in rockwool blocks (7.5 × 7.5 cm) soaked in Tomato 2.0 nutrient solution (Unifarm, Wageningen, the Netherlands). Two weeks after germination, plants were transferred to a climate-controlled growth chamber (25/

18°C, 70% RH, 16 h/8 h L/D and 150 µmol/m²/s photosynthetic active radiation [PAR]) for use in the experiments. Plants were divided into three groups and each group was exposed to one of three light-quality treatments (supplementary Figure 1): white light provided by fluorescent tubes (Philips Master TL-D 36 W/840, Eindhoven, the Netherlands) supplemented with high intensity FR light (730 nm; Philips Green Power LEDs, Eindhoven, the Netherlands) (+FR; R:FR=0.5), white light with low intensity FR light (C; R:FR=1.2) acting as control treatment or white light supplemented with red light (650 nm; Philips Green Power LEDs, Eindhoven, the Netherlands) (+R; R:FR=8.2). The lamps in the +R treatment were covered with thin shading cloth, which caused a slight attenuation of the broad spectrum fluorescent tubes (supplementary Figure 1) that was required to equalize PAR across treatments. The different treatments were present in the same climate chamber and were separated from each other using white reflective plastic to prevent light contamination of other treatments.

2.2. Herbivores

Two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) and green peach aphids, *Myzus persicae* (Hemiptera: Aphididae) were obtained from the stock colonies at the Laboratory of Entomology (Wageningen University, the Netherlands). The *T. urticae* strain is adapted to tomato and has been maintained on tomato plants for at least five years. *M. persicae* was reared on radish plants. Greenhouse whiteflies, *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae) were obtained from the stock colony of the Laboratory of Plant Breeding (Wageningen University, the Netherlands) and were reared on tomato plants. Tobacco hornworm eggs, *Manduca sexta* (Lepidoptera: Sphingidae) were obtained from the stock colony at the Max Planck Institute (Jena, Germany), which is maintained on tomato plants.

2.3. Plant morphology assessment

When plants were two weeks old, they were exposed to the three light-quality treatments for either 5, 7, 10 or 14 days. At each time point, 16 plants per treatment were removed to assess the morphological adaptations to the light environment in terms of plant height and leaf angle. Leaf angle measurements were always taken between 09:00 and 10:00 because time of day can influence the leaf angle. Leaf angle was determined for the first true leaf as the angle of the petiole (leaf base to first leaf segment) to the horizontal.

2.4. Herbivore performance essays

A different set of plants was similarly transferred to the experimental set-up at two weeks of age and were exposed to the different light conditions for 7 days before being used for herbivore performance essays.

Manduca sexta eggs were stored in Petri dishes under the same climatic conditions as the experimental set-up. Freshly hatched caterpillars were placed on the youngest fully expanded leaf (one larva per leaf). The caterpillars were allowed to feed and move freely on the plant for five days after which their body weight was measured. For each light treatment, fifty plants were infested.

Tetranychus urticae females (five adults of one to four days old) were taken from the stock colony and placed on the youngest fully expanded leaf. The spider mites were constrained to the infested leaf by placing cotton wool around the petiole. Spider mites were allowed to feed for four days, after which the number of eggs produced was counted. Fifty plants were infested per light treatment.

Apterous adult *M. persicae* aphids were taken from the stock colony for use in the experiment. Five adult aphids were placed on the youngest fully expanded leaf and were allowed to feed and move freely on the plant for seven days, after which the total number of nymphs produced was counted. For each light treatment, fifty plants were infested.

Adult *T. vaporariorum* females (three to five days after adult moult) were collected from the stock colony. Five adult whiteflies were placed on the oldest fully expanded leaf and were contained using clip cages. Due to the plant's stretching response to FR light, constraining younger leaves would cause growth deformations of the leaf and unwanted stress to the plants. Clip cages were supported by wooden clothes-pins attached to bamboo sticks to prevent mechanical stress caused by the weight of the clip cages. Whiteflies were allowed to feed on the plant for five days, after which the number of eggs produced was counted. Fifty plants per light treatment were infested.

2.5. Statistical analysis

Stem length was analysed using a two-way ANOVA after log-transformation of the data. Leaf angle was analysed using a two-way ANOVA after BoxCox transformation. Herbivore performance of *M. sexta*, *T. urticae* and *T. vaporariorum* was analysed using Generalized Least Squares. The performance of *M. persicae* was analysed using a Generalized Linear Model with a Negative Binomial distribution. When a significant difference was observed a Tukey HSD post-hoc test was performed to identify differences between treatments. All data analysis was performed in R (version 3.6.3).

3. Results

3.1. Plant morphology

We studied the effects of different R:FR ratios on plant morphology to determine if a supplementation of R light would oppose the classical symptoms of SAS induced by FR light. There was a significant effect of both light ($F(2)=1420.21, p<0.001$) and time ($F(4)=2255.09, p<0.001$) on the total stem length. As expected, +FR significantly increased the total stem length compared to the control at all time points (Fig. 1). +R reduced stem height compared to the control at all time points (Fig. 1). There is a significant interaction effect ($F(8225)=13.02, p<0.001$) leading to increasing differences over time.

After seven days of exposure, leaf angles in +FR were significantly increased compared to controls, indicating a more upward position of the leaves. In contrast, +R significantly reduced leaf angles compared to the control (Fig. 2). Similar responses were observed after 10 and 14 days of exposure, although differences between treatments and control

were not significant at these time points (Fig. 2). Leaf angles were always significantly higher in +FR when compared to +R. There was a significant interaction effect ($F(4, 128)=2.66, p=0.035$) indicating that differences in leaf angle diminished over time.

3.2. Herbivore performance

As predicted, supplementation of FR light significantly increased the performance of all four herbivore species included in this study compared to the control treatment (Fig. 3). This effect appears to be stronger in phloem feeders than in tissue feeders. Treatment +R significantly decreased the weight of *M. sexta* caterpillars. +R also lowered the number of eggs laid by *T. urticae*, although this difference was not significant compared to the control ($p=0.169$). No effect of +R was observed on the performance of *M. persicae* or *T. vaporariorum* (Fig. 3).

4. Discussion

The role of FR light in shaping the growth-defence trade-off through modulation of JA and SA signalling has been well established (Ballaré and Pierik, 2017; Fernandez-Milmanda et al., 2020). High levels of JA and SA are associated with growth inhibition and both phytohormones play an important role in growth-defence dynamics (Wasternack and Feussner, 2018; van Butselaar and van den Ackerveken, 2020). By downregulating JA and SA during plant competition, growth inhibition is alleviated and the growth-defence balance is tipped towards growth (Ballaré and Austin, 2020). In contrast to the well-described effects of FR light, little information is available on the effect of supplemental R light on the growth-defence balance.

Our results show that exposure to low R:FR induces the SAS phenotype in young tomato plants and increases the performance of four species of arthropod herbivores belonging to different feeding guilds. These results are in agreement with previous experiments in which exposure to (simulated) shade resulted in increased performance of caterpillars (Izzaguirre et al., 2006; Moreno et al., 2009; Cortés et al., 2016), and provide additional information by the observation that the strength of these effects depend on the feeding guild. The increase in performance after exposure to +FR appears to be larger in phloem feeders than in tissue feeders. We further show that exposure to high R:FR, through supplementation of R light, induces opposite morphological changes such as reduced stem height and smaller leaf angles. However,

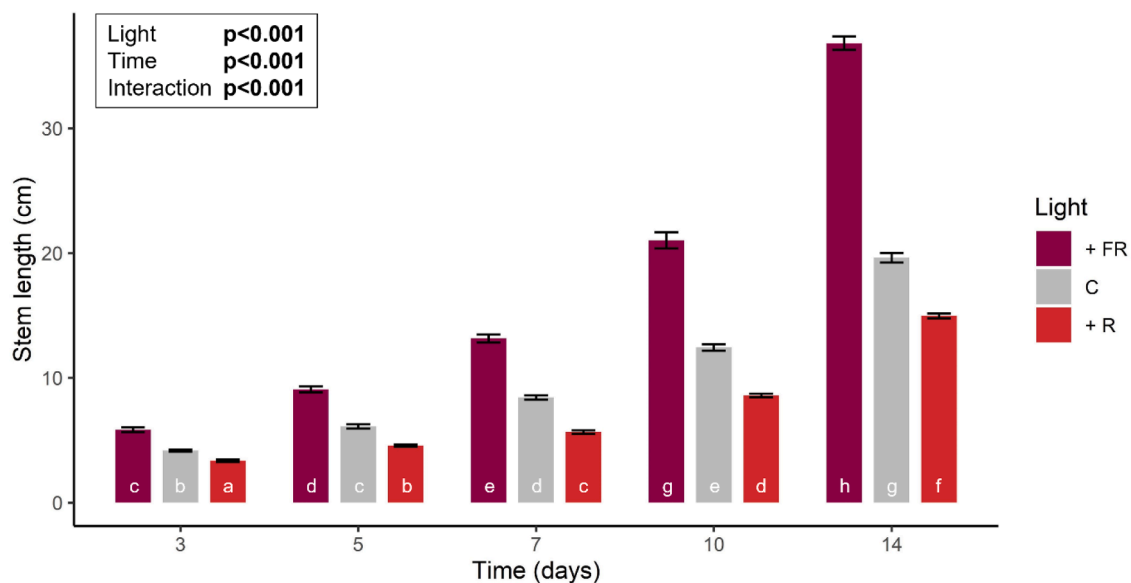


Fig. 1. Stem length (mean \pm SE) of plants exposed to supplemental far-red (+FR), control (C) or supplemental red (+R) for 3, 5, 7, 10 or 14 days. Different letters at the bottom of the bar indicate significant differences between means (Tukey HSD post-hoc test). For each bar $n=16$ plants.

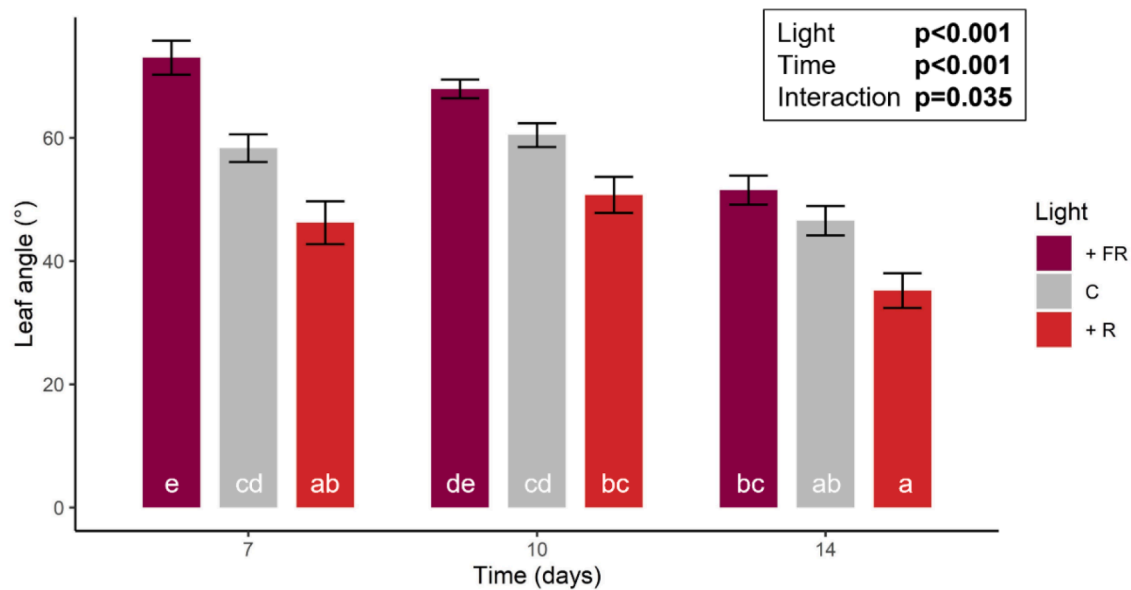


Fig. 2. Leaf angle (mean \pm SE) of the first true leaf of plants exposed to supplemental far-red (+FR), control (C) or supplemental red (+R) for 7, 10 or 14 days. Different letters at the bottom of the bar indicate significant differences between means (Tukey HSD post-hoc test). For each bar $n = 16$ plants.

+R did not affect herbivore performance except for *M. sexta* caterpillars, which showed a significantly reduced biomass gain on plants exposed to high R:FR.

It should be noted that the use of shading cloth in the +R treatment slightly attenuated blue light compared to the other treatments (supplemental Figure 1). Although blue light influences plant morphogenesis, the attenuation of blue light is commonly associated with the expression of shade avoidance symptoms, including stem elongation and leaf hyponasty (Keuskamp et al., 2012; Gonz  lez et al., 2019). The +R treatment does not lead to that phenotype. It is therefore unlikely that the observed effects of +R are affected by the slight attenuation of blue light in this treatment.

Other studies complement our findings that an increase in R:FR has an opposite effect on plants compared to the shade avoidance symptoms, by delaying flowering time and reducing elongation growth (Kurepin et al., 2007; Yamada et al., 2009; Craig and Runkle, 2013). Both observed morphological changes in response to low R:FR (leaf hyponasty and the elongation of stems) are predominantly mediated by the growth hormone auxin. Inactivation of phyB leads to increased biosynthesis and transport of auxin to its target cells (Tao et al., 2008; Sasidharan et al., 2014) where it induces stem elongation and leaf hyponasty. Conversely, active phyB can directly interact with and stabilize AUX/IAA proteins, which are known inhibitors of auxin response factors (ARFs), thereby inhibiting auxin signalling and downstream gene expression (Xu et al., 2018). Binding of phyB to AUX/IAA increases with increasing R light intensity (Xu et al., 2018) and might therefore explain the reduced stem height and leaf hyponasty in plants exposed to +R in our study.

Several studies have also reported that R light can enhance plant resistance against biotic stress. These studies found that monochromatic R light can reduce the proliferation of biotrophic pathogens through increased SA levels and SA-related gene-expression in *Arabidopsis* (Islam et al., 2008), cucumber (Wang et al., 2010) and tomato (Yang et al., 2015). Similarly, Yang et al. (2018) showed increased resistance of watermelon plants against the root-knot nematode *Meloidogyne incognita* after exposure to monochromatic R light, associated with increased JA and SA levels. In contrast, amongst the four arthropod herbivores tested in this study only the tissue feeder showed a significantly reduced performance when feeding on plants exposed to +R. It should be noted, however, that the effects of monochromatic R light can differ from the use of R light as a supplement in a white light background, as we applied

in our current experiment. Whether supplemental R light influences JA- and SA-dependant defences remains to be studied.

The differences in effects of +R on the performance of arthropod herbivores may be explained by the differences in infestation pressure posed by these herbivores. Infestation with tissue-feeding caterpillars results in far more extensive and prolonged leaf damage than the leaf damage inflicted by the other three herbivores that were tested. Therefore, the difference in herbivore performance in response to +R may be linked to a difference in the level and duration of the induced JA signal in plants. Indeed, while minor compared to cell damage inflicted by caterpillars, the cell damage caused by spider mite feeding is more extensive than the more subtle phloem feeding of aphids and whiteflies. Although the performance of spider mites was not significantly reduced under +R, it does show a trend towards lower egg production (Fig. 3B), which is not observed for aphids and whiteflies (Fig. 3C, D). Therefore, we cannot exclude that an effect of the +R treatment on the performance of whiteflies, aphids or spider mites may emerge when infestation pressure of these herbivores is increased.

Furthermore, the different plant defence responses induced by the different feeding styles of the herbivores might contribute to the observed differences in herbivore performance in the +R treatment. *Manduca sexta* is a tissue feeder that primarily induces JA-dependant defence responses and shows a significant reduction in performance when feeding on plants exposed to +R. The spider mite *T. urticae* is classified as a cell-content feeder that induces both JA- and SA-dependant defensive responses (Zhang et al., 2020), but *T. urticae* strains that are adapted to their host plants (as used in this study) are also known to suppress plant defences through oral secretions (Blaazer et al., 2018). Aphids and whiteflies are both phloem feeders that are also known to manipulate host-plant defences through oral secretions. They actively induce SA-dependant responses that result in suppression of the more effective JA-dependant defence responses (Zarate et al., 2007; Elzinga et al., 2014; Xu et al., 2019). Therefore, the already much more subtle and local wound signalling induced by spider mite, aphid and whitefly feeding may still be effectively suppressed by effectors in oral secretions, resulting in the reduced or absent effects of +R on their performance.

Alternatively, supplementation of R light may not affect herbivore performance through defence signalling but can also influence plant resilience through other physiological or morphological adaptations. Exposure to FR light is known to decrease the production and

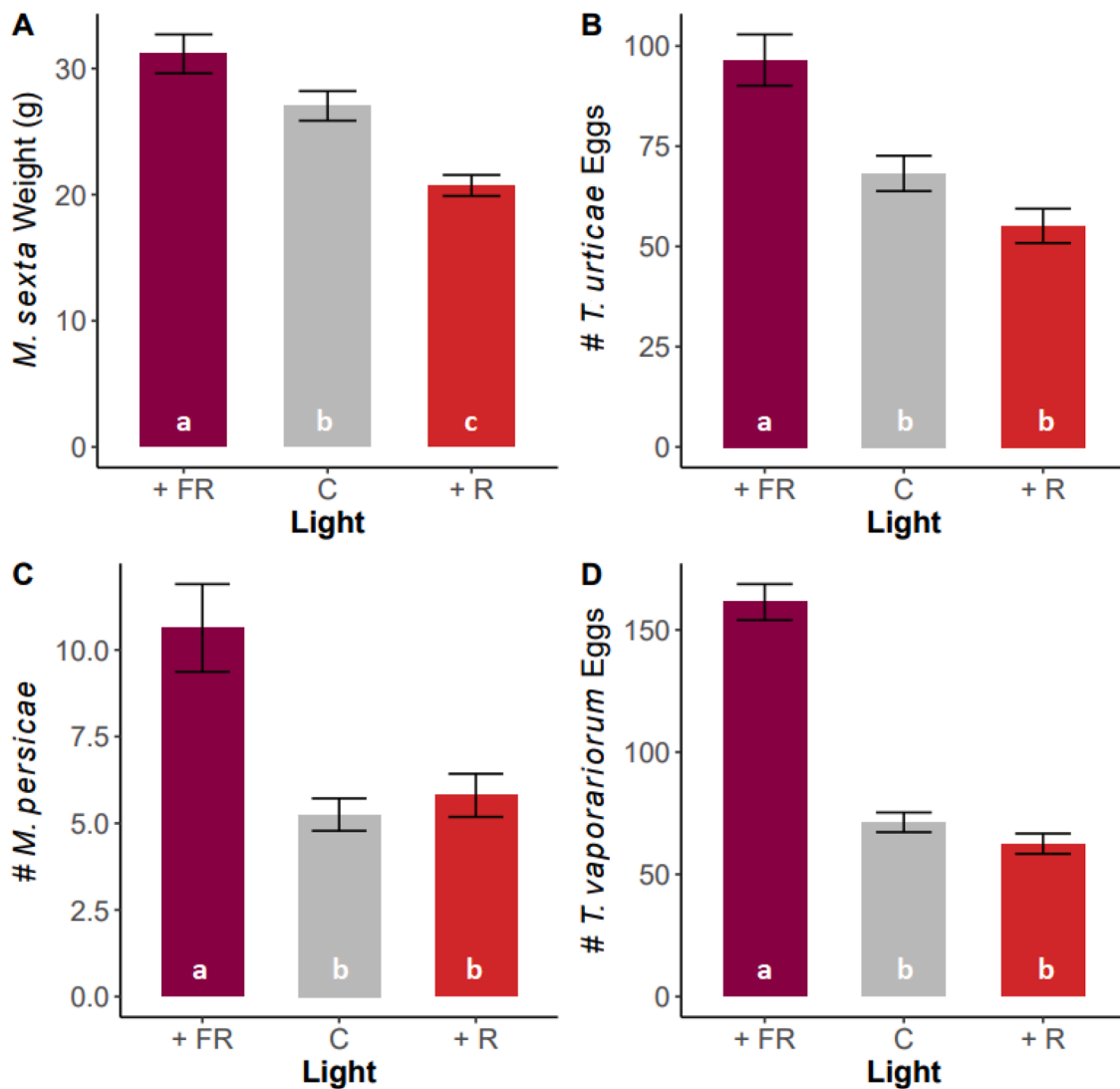


Fig. 3. Herbivore performance parameters (mean \pm SE) of *Manduca sexta* caterpillars (A), *Tetranychus urticae* spider mites (B), *Myzus persicae* aphids (C) and *Trialeurodes vaporariorum* whiteflies (D) exposed to supplemental far-red (+FR), control (C) or supplemental red (+R) light. Different letters at the bottom of the bars indicate significant differences (Tukey post-hoc test). For each bar $N = 50$ plants.

accumulation of many defensive compounds, thereby increasing plant susceptibility to biotic stress (Ballaré, 2014). However, in tomato leaves, FR-induced susceptibility to a fungal pathogen has also been associated with increased soluble sugar content (Courbier et al., 2020), indicating that changes in susceptibility are not solely mediated by defence metabolism. In cucumber, the increased resistance to powdery mildew (*Sphaerotheca cucurbitae*) in plants exposed to high R:FR conditions was attributed to changes in leaf thickness rather than defence signalling (Shibuya et al., 2011). Such changes in leaf morphology can also have important impacts on plant-herbivore interactions. For example, whiteflies preferred plants grown under low R:FR (1.2) compared to plants grown under high R:FR (7.0), which was attributed to the darker green colour and thicker leaves of high R:FR grown plants (Shibuya et al., 2010). Changes in leaf physiology and morphology are expected to differentially affect herbivores with different feeding styles and this might contribute to the observed differences between the tissue-feeding *M. sexta* caterpillars and the other herbivores on plants exposed to +R.

5. Conclusion

Our data confirm the important role of low R:FR-induced signalling on the growth-defence balance by showing a clear induction of SAS

morphology and increased performance of four herbivore species with different feeding styles. Our results indicate that the effects of high R:FR on growth-defence dynamics are complex and do not appear to favour one over the other. In natural canopies, a decrease in R:FR light is an ecological signal of plant-plant competition that plants respond to. However, increasing the R:FR to above sunlight levels (1.2) creates an artificial environment without ecological precedent, which makes it difficult to interpret plant responses to supplemental R light. Our results show that the supplementation of R light has the potential to reduce the performance of arthropod herbivores. However, a more detailed understanding of the molecular signalling and metabolic changes in response to R light is required to properly assess whether R light can be used to enhance plant resistance in greenhouse settings. Understanding how supplemental FR and R light influence not only plant growth and morphology but also resistance to arthropod pests is important for the implementation of LEDs in horticulture.

Author contribution statement

Davy Meijer: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft. **Mara Meisenburg:** Conceptualization, Formal analysis, Visualization, Writing - Review and Editing.

Joop van Loon: Conceptualization, Supervision, Writing – Review and Editing. **Marcel Dicke:** Conceptualization, Project administration, Funding acquisition, Supervision, Writing – Review and 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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Supplementary materials

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