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Original article

Far-red illumination of the lower adult plant parts affects morphology and growth of the upper young plant parts in tomato

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Summary

Most of the studies on light spectrum do not consider effects of spectrum perceived by different plant parts. Local and long-distance plant responses to localized light spectrum have hardly been studied in large plants. This paper aims to investigate whether local supplementation of FR results in local or long-distance architectural and growth responses in full-grown tomato plants. Tomato plants grown in a climate chamber were separated horizontally with white plastic at 85 days after sowing (lower half was 50 cm and upper half 15 cm long). The lower half was already full-grown and did not elongate anymore. The following 17 days both halves received 123 µmol m^{-2} s^{-1} red/blue light. The lower, upper, or none of the plant halves received 94 µmol m^{-2} s^{-1} additional far-red radiation (FR). FR supplied to the upper half increased petiole and internode elongation as well as specific leaf area (SLA) in the upper half of the plant, while petiole angle decreased. Moreover, dry weights of leaf stem (petiole + rachis + petiolules) and stem increased while leaf (lamina) dry weight decreased. Leaf area was unaffected. When FR was supplied to the lower half of the plant SLA, stem length, and stem dry weight of the upper half also increased, but to a lesser extent than when FR was supplied to the upper half. However, FR supplied to the lower half of the plant did not significantly affect other parameters such as petiole length, petiole angle and leaf dry weight of the upper plant half. We conclude that locally supplied FR has long-distance effects on length and dry weight of the stem and on SLA, while some other parameters (petiole elongation, petiole angle, leaf weight) are only locally affected. Hence, morphology and growth of upper young developing plant tissue can be influenced by light spectrum perceived by lower adult plant parts.

Keywords

far-red, LED lighting, phytochrome, shade avoidance response, *Solanum lycopersicum*

Abbreviations

FR: far-red; PAR: photosynthetically active radiation; RB: red-blue; SAR: shade avoidance responses

Significance of this study

What is already known on this subject?

- Most of the studies on light spectrum in full-grown plants did not consider effects of spectrum perceived by different plant parts.

What are the new findings?

- Morphology and growth of young developing plant tissue is influenced by far-red light perceived by adult plant parts.

What is the expected impact on horticulture?

- When LED lighting is used in greenhouses and vertical farms, choices of positioning and spectrum of LEDs should consider the short- and long-distance effects of perceived signals by the plant organs.

Introduction

The link between a plant's site of light perception and the sites where morphological adaptations take place is a field of study with recent advancements but is still not fully understood (Küpers et al., 2018; Iglesias et al., 2017). Plants are modular organisms and are the product of build-up of individual organs connected to one big network through the xylem and phloem (Kroon et al., 2005). Each organ perceives its own light microclimate (light intensity and spectrum [Chelle, 2005]). Changes in morphology resulting from an individual organ's perceived light microclimate can be at the level of the organ itself (local) and at the plant level where it also affects other plant organs (long-distance). Local and long-distance morphological responses to the local light spectrum can be studied in relation to the photoreceptor phytochrome by lowering the ratio of red (R) to far-red (FR) light, mimicking shade, through application of FR. This lowered R to FR ratio induces shade avoidance responses (SAR) such as increased elongation of stems (Ballaré et al., 1991; Smith and Whitelam, 1997; Cole et al., 2011) and petioles (Kozuka et al., 2010) and reorientation of petioles (Whitelam and Johnson, 1982; Sasidharan et al., 2010; Pantazopoulou et al., 2017; Kalaitzoglou et al., 2019), in order for a plant to compete with its neighbours. There are plenty of reviews on the way SAR are thought to operate and on their functionality (Casal, 2013; De Wit et al., 2016; Fraser et al., 2016; Ballaré and Pierik, 2017; Viczián et al., 2017; Iglesias et al., 2017).

An increase in perception of FR upregulates the biosynthesis of auxin, a plant hormone strongly related to SAR (Tao

et al., 2008; Procko et al., 2014). Auxin is transported from cell to cell through polar auxin transport by auxin efflux carriers PIN-FORMED3 (PIN3), PIN4 and PIN7 (Keuskamp et al., 2010; Kohnen et al., 2016). Studies with (mutant) plants where auxin was limited in biosynthesis, conjugation, transport, downstream signaling or perception showed severely weakened SAR (Keuskamp et al., 2010, 2011; De Wit et al., 2015). The way this is thought to operate at the molecular level is that perception of FR inactivates phytochrome B, which results in a reduced phosphorylation and less degradation of the phytochrome-interacting factors (Ni et al., 2014; Shin et al., 2016). Phytochrome-interacting factors are basic helix-loop-helix transcription factors (Leivar and Quail, 2011) and promote elongation (Ni et al., 2014; Shin et al., 2016). Therefore, an increase in perceived FR increases the activity of phytochrome interacting factors, resulting in SAR.

Local versus long-distance responses to light spectrum are commonly studied in seedlings, where (de-etiolated) seedlings are used as study material, allowing for fast research (Küpers et al., 2018). These studies provide very useful information and have revealed that light spectrum perceived by an organ induces a wide range of morphological responses which can either be local or long-distance, depending on the type of organ receiving the light treatment and the morphological response looked at, as summarized by Küpers et al. (2018). Early work on cucumber (*Cucumis sativus* L.) (Black and Shuttleworth, 1974) and on white mustard (*Sinapsis alba* L.) (Casal and Smith, 1988, 1989) revealed that local illumination of the cotyledons by FR induced an increased extension growth of the first internode. This increased internode extension growth is fueled by and requires an increase in sucrose transport towards the internode (De Wit et al., 2018). Local illumination with FR on cotyledons of *Brassica rapus* seedlings induced hypocotyl elongation which was linked to an auxin gradient from the leaves towards the hypocotyl (Procko et al., 2014). A long-distance response was also found in *Arabidopsis thaliana*, where illumination with FR on the tip of a lamina induced a hyponastic response in the petiole of that particular leaf (Pantazopoulou et al., 2017; Michaud et al., 2017). Courbier et al. (2020) found that sugar content and botrytis increased in both the third and fourth formed leaf, when the fourth leaf of young tomato plants was illuminated by FR, but illumination of third leaf affected only the third leaf. Thus, using young plants as model plants has demonstrated that there is a variety of responses to local FR.

Extrapolation of results from studies on local lighting on de-etiolated seedlings, rosette plants, or very young plants to tall plants (e.g., longer than 1 m) is difficult if not impossible. Therefore, experiments should also be conducted with large adult plants (Küpers et al., 2018). That long-distance signaling is possible has been shown for root development and flowering, which are regulated by R:FR perception in the leaves (Chen et al., 2016; Endo et al., 2016; Van Gelderen et al., 2018).

According to the best of our knowledge, there has been no research in tall full-grown plants whether FR effects on growth and morphology are local or long-distance. Therefore, this paper aimed to investigate whether and to which extent local supplementation of FR results in local or long-distance architectural and growth responses in full-grown tomato plants. A climate room experiment was performed where tomato plants were horizontally separated by opaque white plastic in a lower and a upper half and FR was locally supplemented to either of the two halves.

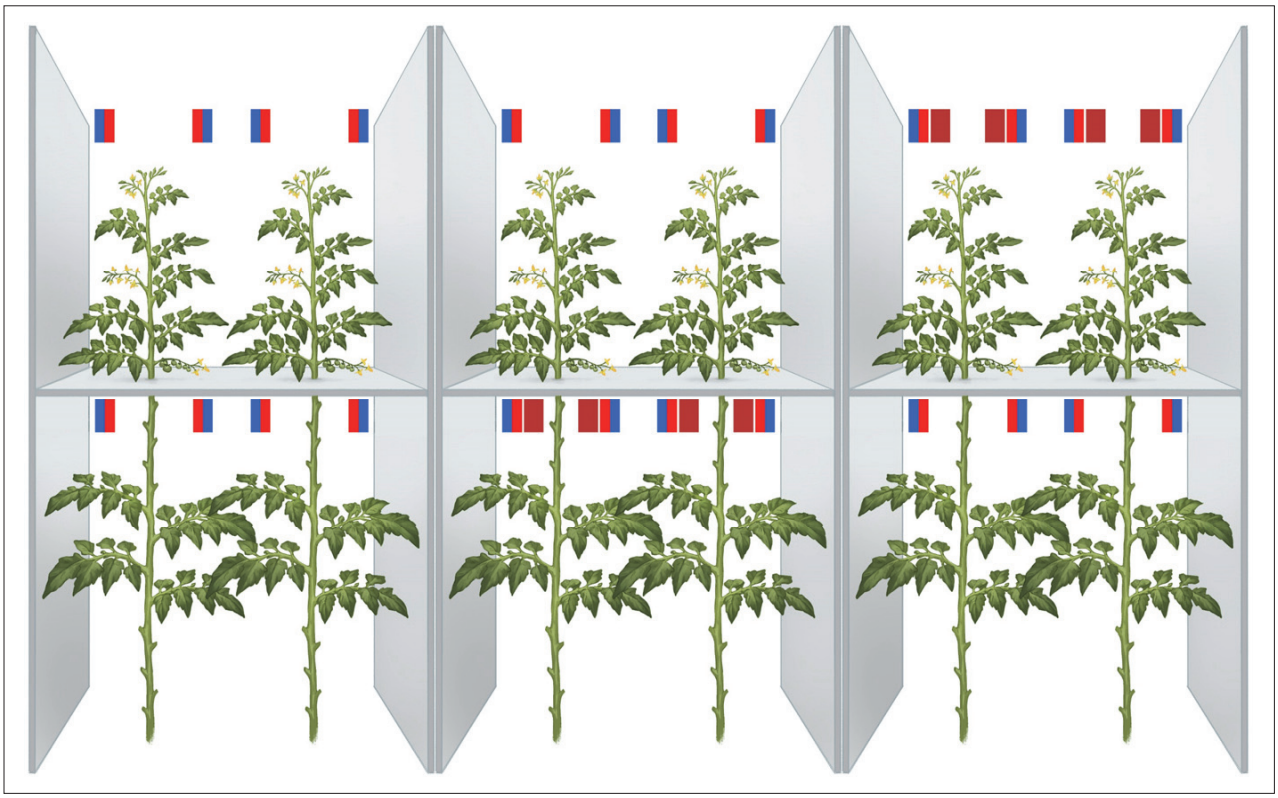

Figure 1. Tomato plants separated in lower and upper halves by use of two layers of white plastic. In each treatment both halves received R+B light by LED lighting (123 µmol m^{-2} s^{-1}) and received either no supplemental FR (left), supplemental FR (94 µmol m^{-2} s^{-1}) in the lower half of the plant (center) or supplemental FR (94 µmol m^{-2} s^{-1}) to the upper half of the plant (right).

Material and methods

Plant material and growth conditions

Tomato seeds (*Solanum lycopersicum*, cv. Cappricia) were sown in a tray with stonewool (Grodan, Roermond, The Netherlands) plugs in a climate chamber, irrigated with a tomato-specific nutrient solution (EC = 2.1 dS m^{-1} and pH = 5.5; Supplemental Table S1). Thirteen days since sowing, a total of 18 seedlings were transplanted onto stonewool blocks (10 cm × 10 cm × 6.5 cm) and placed onto 6 stonewool slabs (100 cm × 20 cm × 10 cm) placed in hard plastic gutters on the floor. Day length was 16 h with a light intensity of 123 µmol m^{-2} s^{-1} at the apex. Light was provided by red and blue (RB) LEDs (ratio 76:24; GreenPower RB production modules 150 cm, Philips, The Netherlands). The distance between light source and top of the plants was kept at a maximum of 40 cm and minimum of 30 cm by raising the height of the LEDs. Setpoint for relative humidity was 70%, and setpoints for day/night temperatures were 22/20°C. Temperature and relative humidity were continuously measured in one compartment with a Hoogendoorn Box (Hoogendoorn, The Netherlands). During both repetitions, measured day and night temperatures (°C) with standard deviations were 21.8 ± 0.5/ 19.9 ± 0.4 and 21.8 ± 0.4/ 19.8 ± 0.3. Measured relative humidity (%) was 70.0 ± 1.9 and 70.0 ± 1.4. Combined temperature and humidity loggers were placed in each compartment during several days to compare the local climate, with average differences between treatments of at most 4.5% relative humidity and 0.1°C (ML4106 Temperature and Humidity Data Logger: Hanwell, England; Supplemental Tables S2 and S3).

The plants were supported by a high wire once they reached 40 cm. The first truss (phytomere rank 12) was removed before anthesis to provide sufficient vegetative growth before the treatment began. Axillary bud outgrowths were removed at least every other day. To ensure pollination of the flowers a Vibri Vario (tomato pollinator; Royal Brinkman, The Netherlands) was used to vibrate each flowering truss 5 times a week. All trusses were pruned to 6 fruits per truss.

At 85 days since sowing the climate chamber was separated in three units by use of two layers of white/black double sided plastic (Figure 1). Each unit contained one of 3 treatments, randomly allocated, and was 1.2 m^2 in area with 6 plants, resulting in a planting density of 5 plants m^{-2}. Within each unit the plants themselves were divided into lower (up to phytomere rank 14) and upper plant (from phytomere rank 15) halves by use of two layers of white/black double sided plastic (white sides towards both the upper and lower half of the plants); the lower half was 50 cm long and the upper stem was 15 cm at start of the treatments. In addition to the already present RB LEDs above the apex, RB LEDs were installed in an identical way at the top of the lower plant part. In this way on each level there was 123 µmol m^{-2} s^{-1} RB light. Besides the additional RB LEDs, also FR LEDs (GreenPower LED production modules FR 120 cm, Philips, The Netherlands; λ: 710–760 nm; peak at 735 nm) were installed in two of the treatments, either at the lower or upper plant half, with an intensity of 94 µmol m^{-2} s^{-1}. The R:FR ratio with standard deviation was 1.30±0.12. The spectral distribution and photon flux density of the light was measured with a spectroradiometer (USB 2000 + UV-VIS, Ocean Optics, Duiven, The Netherlands). Leaves on phytomere ranks 10 to 14 were removed to make sufficient space between LEDs and the leaves. Also leaves on phytomere ranks 1 to 5 were removed due to some leaf senescence. The healthy leaves at rank 6 to 9 were kept. These were considered adult leaves since they had reached their final length and did not elongate during treatment (Supplemental Table S4). Supplemental FR lasted for 17 days.

Plant measurements

Non-destructive plant measurements were taken on the day of treatment initiation (day 85) and at the end of the experiment (day 102). These measurements were divided in measurements on the young (phytomere ranks ≥ 15) and on the adult part (phytomere ranks 6 to 14). Measurements on the young part included internode length (≥ 2 mm), leaf length (≥ 5 cm), and width as measured by protractor. Furthermore, pictures were taken to determine the petiole angle (upper angle between petiole and stem). At the end of the experiment (day 102), destructive measurements were performed on each individual phytomere, determining leaf area (LI-3100C, LI-COR, U.S.A.) and dry weights of internode, leaf lamina, leaf stem (this term is used here for the sum of petiole, rachis and petiolules), and fruit truss. Dry weight was determined after oven drying (ventilated oven, 70°C for 24 h, followed by 105°C for 24 h).

Statistical set-up and analysis

The experiment was conducted twice. In each experiment the three treatments were randomized over 3 plots. There were 6 replicate plants per plot in each experiment. As there was no systematic difference between replicate experiments for any of the parameters tested (data not shown), data were analyzed as randomized design by ANOVA, followed by mean separation with Student's Least Significant Difference (LSD) test. Normality and equal variances were assumed. Motivated by the small number of experimental units (n = 2), treatment effects were tested at the 10% instead of 5% probability level to avoid that likely treatment effects would be denied (Ott and Longnecker, 2010). Data collected on the adult plant parts before and after the treatments were compared using a paired samples t-test.

Results

Architecture

Supplying FR to the upper half of the plant (FR_{upper}) increased stem and petiole length and specific leaf area (SLA) in the upper half of the plant, while it decreased petiole angle (upper angle between petiole and stem), hence more upright leaves (Figure 2). Leaf area was not significantly influenced by supplemental FR. When FR was supplied to the lower plant half, stem length and SLA in the upper half of the plant also increased but to a lesser extent than when FR was supplied to the upper plant part (Figure 2). No significant differences were found between the control (no FR) and FR_{lower} (FR supplied to lower plant half) for petiole length, petiole angle, and leaf area in the upper half of the plant.

Biomass

FR, whether supplied to lower or upper half of the plant, increased stem dry weight of the upper plant half, though effects of FR_{upper} were larger than that of FR_{lower} (Figure 3). Dry weight of the leaf stem (petiole + rachis + petiolules) was significantly higher for FR_{upper} compared to the control FR_{lower} resulted in intermediate values of leaf stem weight that were not significantly different from either of the other two treatments. Leaf (lamina) dry weight was the same for control

and FR_{lower}, whereas this was significantly lower for FR_{upper}. Fruit dry weight seemed to increase from control to FR_{lower} to FR_{upper}, but the differences were not statistically significant due to a high variance. The treatments had no statistically significant effect on total dry weight of the upper plant half.

Discussion

Overall response to far-red radiation supplied to the upper plant half

The observed increases in petiole and internode length due to FR illumination of the upper half of the plant is in line with findings with FR illumination of whole plants (Ballaré et al., 1991; Kozuka et al., 2010; Cole et al., 2011; Holmes and Smith, 1975; Smith and Whitelam, 1997; Kalaitzoglou et al., 2019). The decrease in petiole angle (more upright leaves) is in line with findings on small balsam (*Impatiens parviflora*) (Whitelam and Johnson, 1982) and *Arabidopsis thaliana* (Sasidharan et al., 2010; Pantazopoulou et al., 2017), though Kalaitzoglou et al. (2019) found an increase in petiole angle when tomato plants were illuminated by additional FR.

Leaf (lamina) dry weight was significantly decreased in the upper half of the plant, while at the same time dry weights of leaf stem (petiole + rachis + petiolules) and stem increased when FR was supplied to the upper plant part (Figure 3). The observation that there was no statistically significant increase in the upper plant half total biomass might be explained by the short duration of the FR treatment. Kalaitzoglou et al. (2019) found that biomass increases with supplemental FR due to increased leaf area and hence light interception. Here, no differences were yet found for leaf area within the 17 days of treatment. The decrease in leaf dry weight while increase in dry weights of stem and leaf stem agrees with general effects of FR on dry matter partitioning (Ballaré et al., 1991; Smith and Whitelam, 1997; Cole et al., 2011; De Wit et al., 2018). Furthermore, the dry matter partitioning to fruits tended to increase (though not statistically significant), which is in line with Ji et al. (2019) when whole plants were illuminated by supplementary FR.

Local versus global response to far-red radiation

FR supplied to the upper half of the plant affected many variables of the upper plant half. Some of these variables such as petiole length, petiole angle, and leaf weight, were not affected by FR supplied to the lower plant part. Hence, FR had a local effect but not long-distance effect on these variables. In contrast, variables like stem length, specific leaf area and dry matter partitioning to stem and leaf stem (at the expense of leaves) were affected by both supplying FR to lower or upper half of the plant. However, these effects were

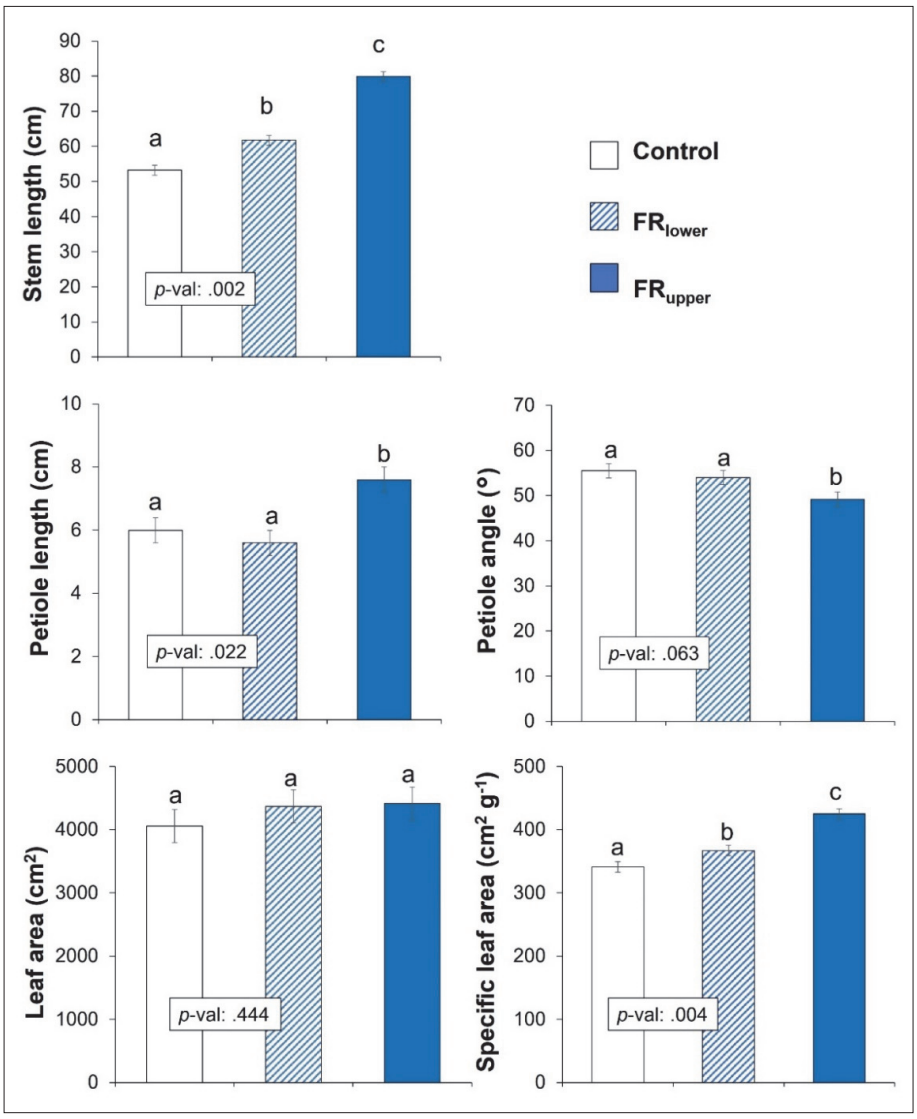

Figure 2. Architecture of the upper plant half when supplemental FR was applied to either no plant half (Control), the lower plant half (FR_{lower}) or the upper plant half (FR_{upper}). Different letters indicate significant differences ($P = 0.10$), based on the LSD test. Standard error of the mean was based on the common variance and *p*-values (F-test) are given in each panel.

stronger when FR was supplied to the upper half of the plant. This indicates that in relatively tall plants (1.3 m) FR has a long distance effect on these variables, though the FR effect is smaller for organs at a distance from the FR illuminated organs. An explanation for the weaker long-distance effects compared to local effects could be that the distance itself has a limiting effect on the transport of the signal, possibly through dilution, as seen with auxin transport (Goldsmith et al., 1974). Another explanation might be that local synthesis of a signal molecule is more important, as proposed for auxin (Zhao, 2018).

Conclusions

Morphological and growth responses occurred in the upper young part of tomato plants when FR was supplied to adult leaves of the lower half of the plants. The morphological and growth responses were weaker than those resulting from locally perceived FR at the upper young plant part. Still, morphology and growth of young developing plant tissue can be influenced by light spectrum perceived by adult plant parts. When LED lighting is used in greenhouses and vertical farms, choices of positioning and spectrum of LEDs should consider the short- and long-distance effects of perceived signals by the plant organs.

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Author contributions

M. van der Meer devised the project and the main conceptual ideas. M. van der Meer, P.H.B. de Visser, E. Heuvelink and L.F.M. Marcelis designed the experiment. M. van der Meer and G. Kim executed the experiment and processed the experimental data. All authors were involved in data analysis. M. van der Meer drafted the manuscript and designed the figures. All authors discussed the results and commented and edited the manuscript. L.F.M. Marcelis initiated the project and acquired the funding.

Conflict of interest statement

The authors declare no conflicts of interest.

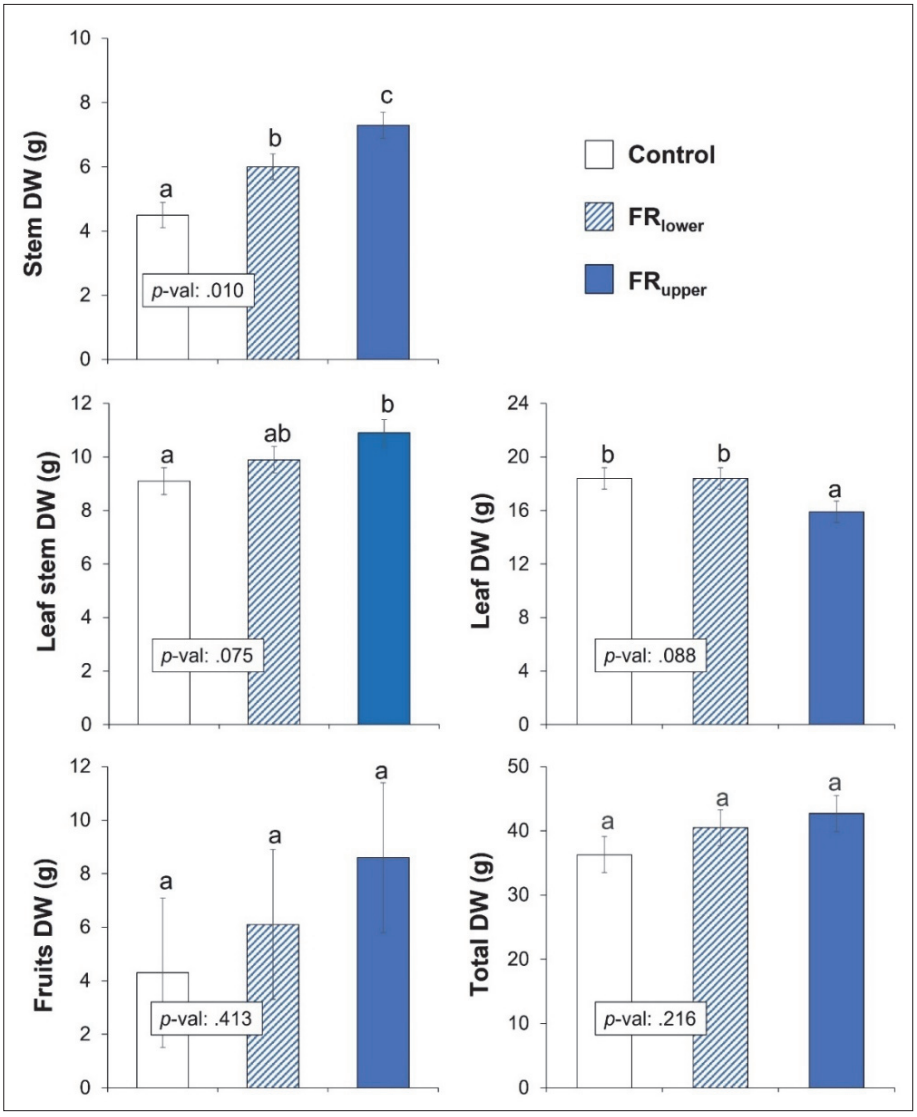

Figure 3. Dry weights of the plant organs and the total of all organs of the upper plant half when supplemental FR was applied to either no plant half (Control), the lower plant half (FR_{lower}) or the upper plant half (FR_{upper}). Leaf stem refers to sum of petiole, rachis and petiolules; leaf refers to the lamina of the leaf. Different letters indicate significant differences ($P = 0.10$), based on the LSD test. Standard error of the mean was based on the common variance and *p*-values (F-test) are given in each panel.

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Supplemental Information

Supplemental Information – Table S1. Composition of the nutrient solution used in the experiment. Solution EC: 2.1 and pH: 5.5.

Macro-nutrient	Concentration (mM)	Micro-nutrient	Concentration (µM)
NH_4	1.2	Si	0
K	7.2	Fe	35.0
Na	0	Mn	8.0
Ca	4.0	Zn	5.0
Mg	1.8	B	20.0
NO_3	12.4	Cu	0.5
SO_4	3.3	Mo	0.5
HCO_3	0	Cl	0
P	1.0		

Supplemental Information – Table S2. Temperature (°C) and relative humidity (%) (± st.dev.) measured during 4 consecutive days in each of the 3 compartments before start of treatments.

Period	Treatment	Temperature	Relative humidity
Day	Control	22.5 ± 0.5	67.2 ± 1.5
Day	FR_{lower}	22.5 ± 0.5	64.5 ± 1.3
Day	FR_{upper}	22.4 ± 0.5	68.7 ± 1.5
Night	Control	20.8 ± 0.2	66.2 ± 1.0
Night	FR_{lower}	20.8 ± 0.1	67.6 ± 1.0
Night	FR_{upper}	20.8 ± 0.1	63.1 ± 0.8

Supplemental Information – Table S3. Temperature (°C) and relative humidity (%) (± st.dev.) measured during 3 consecutive days in the lower and upper halves in each compartment during treatments.

Period	Treatment	Layer	Temperature	Relative humidity
Day	Control	Lower	21.3 ± 0.6	70.4 ± 2.7
Day	FR_{lower}	Lower	21.3 ± 0.6	69 ± 2.4
Day	FR_{upper}	Lower	21.3 ± 0.5	69.3 ± 2
Day	Control	Upper	21.4 ± 0.5	67.2 ± 1.9
Day	FR_{lower}	Upper	21.4 ± 0.4	67.5 ± 1.4
Day	FR_{upper}	Upper	21.3 ± 0.4	66 ± 0.7
Night	Control	Lower	19 ± 0.5	72.4 ± 4.2
Night	FR_{lower}	Lower	19 ± 0.5	71.9 ± 4.6
Night	FR_{upper}	Lower	18.9 ± 0.5	71.8 ± 4.5
Night	Control	Upper	19.5 ± 0.3	68.1 ± 1.5
Night	FR_{lower}	Upper	19.5 ± 0.2	67.8 ± 1
Night	FR_{upper}	Upper	19.4 ± 0.2	66.2 ± 0.8

Supplemental Information – Table S4. Paired samples *t*-tests reveal that there were no significant differences between stem length (phytomere ranks 6 to 14) and leaf length (phytomere ranks 6 to 9) at the moment the treatments started and the final day of the experiment.

Parameter	Treatment	Start of treatment	End of treatment	*P*-value
Stem length	Control	34.3	34.2	0.695
	FR_{lower}	34.6	34.9	0.215
	FR_{upper}	34.2	34.3	0.935
Leaf length	Control	36.6	36.6	1.000
	FR_{lower}	35.4	35.2	0.357
	FR_{upper}	35.6	35.4	0.407