PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2024.016 PHOTOSYNTHETICA 62 (2): 180-186, 2024

Influence of additional far-red light on the photosynthetic and growth parameters of lettuce plants and the resistance of the photosynthetic apparatus to high irradiance

A. SHMAREV*, M. VERESHAGIN**, P. PASHKOVSKIY**, V.D. KRESLAVSKI*,
and S.I. ALLAKHVERDIEV*,**,***,+

*Institute of Basic Biological Problems, Russian Academy of Sciences, Institutskaya Street 2, 142290 Pushchino, Russia****
*K.A. Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, Botanicheskaya Street 35, 127276 Moscow, Russia***
*Faculty of Engineering and Natural Sciences, Bahçeşehir University, Istanbul, Turkey****

Abstract

The effects of additional far-red light (FRL) on the photosynthetic and growth parameters of *Lactuca sativa* plants grown for 30 d and on the photosynthetic activity of the plants under high irradiance [4 h; 1,500 μmol(photon) m^{-2} s^{-1}] were studied. The plants were grown under coloured light-emitting diodes at a ratio of red light (RL): blue light (BL): green light (GL): far-red light (FRL) = 0.7:1:0.3:0.4 or RL:BL:GL:FRL = 0.7:1:0.3:0.8 (test, T). Additional FRL led to an increase in plant biomass, height, and leaf area but to a decrease in photosynthesis and respiration rates. However, PSII activity was greater in plants with additional FRL. It is suggested that the increase in biomass occurred mainly due to an increase in leaf area but not in photosynthesis. In addition, PSII in the experiment was less resistant to high irradiance. The possible direct and indirect influences of the FRL on growth and photosynthesis were considered.

Keywords: chlorophyll *a* fluorescence; far-red light; growth; *Lactuca sativa*; photosynthesis; red light.

Introduction

In modern intensive plant cultivation systems, effective crop lighting is paramount for optimal growth and ontogenesis and for enhancing the biological quality of cultivated crops (Berkovich *et al.* 2017, Liu *et al.* 2020). The ratio of RL to FRL (RL/FRL) is a well-known aspect of light quality that is linked to many light effects on plant photomorphogenesis, growth, and metabolic processes (Franklin 2008, Franklin and Quail 2010, Voitsekhovskaja 2019, Liu *et al.* 2020, Tan *et al.* 2022). Some studies have shown that adjusting this ratio by providing plants with additional FRL led to pronounced positive effects (Cao *et al.* 2018, Zhen and Bugbee 2020a,b; Legendre and van Iersel 2021, Tan *et al.* 2022).

Notably, many studies suggest that phytochromes (PHYs) (Cao *et al.* 2018) participate in these processes regulated by the RL/FRL ratio. PHYs are photoreceptors

Highlights

- Additional far-red light increased plant biomass, height, and leaf area in lettuce plants
- The addition of far-red light decreased PSII resistance to high irradiance
- A decrease in the RL/FRL ratio reduced photosynthesis in lettuce plants

Received 28 December 2023
Accepted 25 March 2024

+Corresponding author
e-mail: suleyman.allakhverdiev@gmail.com

Abbreviations: BL – blue light; Chl – chlorophyll; DM – dry mass; FM – fresh mass; F_m – the maximum fluorescence; FRL – far-red light; F_v – the variable fluorescence; F_v/F_m – PSII maximum quantum yield; GL – green light; LEDs – light-emitting diodes; Pfr – far-red light-absorbing active form of phytochrome; PHYs – phytochromes; PI_{ABS} – PSII performance index; P_N – net photosynthetic rate; Pr – red light-absorbing inactive form of phytochrome; R_D – respiration rate; RL – red light.

Acknowledgements: This research was funded by financial support from the Ministry of Science and Higher Education of the Russian Federation (themes: 122042700044-6, 122041100071-1, and 122050400128-1).

Conflict of interest: The authors declare that they have no conflict of interest.

that help plants respond to RL and FRL and regulate plant photomorphogenesis and development. PHY exists in two photoconvertible forms, Pr (a red light-absorbing form of phytochrome) and Pfr (a far-red light-absorbing form of phytochrome), which are in dynamic equilibrium (Kreslavski *et al.* 2009, Franklin and Quail 2010, Voitsekhovskaja 2019). The Pr form has an absorption maximum of approximately 660 nm, whereas Pfr has an absorption maximum of 730 nm. RL transforms PHYs to the active Pfr form, whereas FRL drives PHYs to the initial Pr form. The RL/FRL ratio, which is equal to approximately 1.15 under direct sunlight but can decrease to 0.2 under a canopy, regulates the Pfr/(Pr+Pfr) ratio (Heraut-Bron *et al.* 2000), which is a fraction of the active phytochrome form. The reason is the predominance of the FRL (700–750 nm) under the foliage canopy, and at the same time, the red region (600–700 nm) of the light spectrum is absorbed by the pigments, which reduces the RL/FRL ratio. Consequently, too much FRL can induce shade avoidance (Franklin 2008). During these experiments, noticeable variations in the growth patterns, leaf morphology, and colouration of lettuce leaves exposed to different RL/FRL ratios were observed. Usually, plants exposed to higher FRLs have longer internodes and larger, more expanded leaves, suggesting a potential 'shade avoidance' response (Middleton 2001). Moreover, plants subjected to relatively high RL exhibited relatively little growth with more green leaves, indicating increased chlorophyll (Chl) content (Allakhverdiev *et al.* 2016). It is suggested that increasing plant growth in lettuce by FRL is linked to an increase in leaf area (LA) and canopy size to absorb more light to boost photosynthesis (Legendre and van Iersel 2021). Similarly, in another study, under FRL, the biomass increased (Jin *et al.* 2021), and this increase was mainly due to the increase in the leaf area.

However, there is contradictory information on the influence of added FRL on the stress resistance of the photosynthetic apparatus. Thus, an increase in the net photosynthetic rate was demonstrated for both single leaves and the foliage canopy of 14 diverse crop species (Zhen and Bugbee 2020a). On the other hand, the addition of FRL significantly reduced leaf photosynthesis and leaf mass but increased resistance to CO_2 diffusion in tomato plants grown under low light conditions (Wassenaar *et al.* 2022). However, under high light, these effects were slight.

It has been proposed that FRL can induce not only photomorphogenetic processes but also photochemical processes of photosynthesis in photosystems by capturing FRL with PSI (Gobets and van Grondelle 2001, Pettai *et al.* 2005, Zhen *et al.* 2019). Under certain conditions, this enhancement can lead to an increase in photosynthetic electron transport, increasing the photosynthetic rate. For example, Yang *et al.* (2013) explored how varying ratios of RL/FRL influenced photosynthetic parameters and Chl fluorescence in *Chrysanthemum*. These findings highlighted that certain RL/FRL ratios promote enhanced photosynthesis and Chl production. However, no deep understanding of how these ratios influence the underlying mechanisms, especially about the phytochrome system, was achieved. In another study, Zhen and Bugbee (2020a,b) investigated the effects of FRL on both isolated leaves and photosynthesis within the plant canopy. Their data underscored the fact that adding a significant fraction of FRL (to 35% of all photon flux density) can increase photosynthetic rates. Thus, the enhancement of growth and photosynthesis depends on two processes regulated by PHY (likely PHYB) and photochemical photosynthetic processes responding to additional FRL. In addition, background light intensity and FRL intensity can also affect plant responses.

Changes in the RL/FRL ratio can also affect plant stress resistance. For example, altering the RL/FRL ratio by the addition of FRL (with RL/FRL ratios of 7.4, 1.2, and 0.8) was found to affect the resistance of tomato plants to salt stress (Cao *et al.* 2018). Under salt stress, biomass accumulation was greatest at an RL/FRL ratio equal to 1.2 but did not depend on this ratio in the *phyb1* mutant. It was concluded that exposure to the lowest RL/FRL ratio was the most effective at improving tomato's tolerance to salt stress (Cao *et al.* 2018). Additionally, the authors suggested that the RL/FRL ratio affects stress resistance most likely by regulating antioxidant enzyme activity and the content of low-molecular-mass antioxidants and that phytochrome B1 plays an important role in these processes.

However, there is still a knowledge gap regarding the role of additional FRL in plant growth and photosynthesis under both normal and stressful conditions, as plant responses to FRL can vary depending on the species, variety, and developmental stage. Given this context, our research aimed to explore the impact of the addition of FRL on the photosynthetic and growth parameters of young lettuce plants and photosynthetic apparatus stress resistance caused by high irradiance (HI).

Materials and methods

Plant material and growth parameters: Plants (*Lactuca sativa* L.) were grown for 30 d in a thermostatically controlled chamber at the K.A. Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, Botanicheskaya Street 35, Moscow, with a 12-h photoperiod at a temperature of 23 ± 1°C during the day and night. The light intensity was 300 ± 10 μmol(photon) m^{-2} s^{-1}. The plants were watered with a 2-fold diluted Hoagland nutrient solution.

The light source (Fig. 1) was constructed on the basis of blue (BL, maximum 460 nm), green (GL, maximum 540 nm), red (RL, maximum 660 nm), and far-red (FRL, maximum 730 nm) LEDs (*Epistar*, Taiwan). The spectral characteristics of the light sources were determined using an *AvaSpecULS2048CL-EVO* spectrometer (*Avantes B.V. Oude Apeldoornseweg*, Apeldoorn, The Netherlands) (Fig. 1). Two options for LEDs were used for comparison: the matrix of LEDs with an RL:BL:GL:FRL = 0.7:1:0.3:0.4, where the RL/FRL ratio was 1.75 (further in the text 'control'), and the matrix with an RL:BL:GL:FRL ratio = 0.7:1:0.3:0.8, where the RL/FRL ratio was 0.875 (hereinafter referred to as the 'test'). Subsequently, some plants were transferred to a separate phytotron chamber and irradiated at the onset of the photoperiod for 4 h by

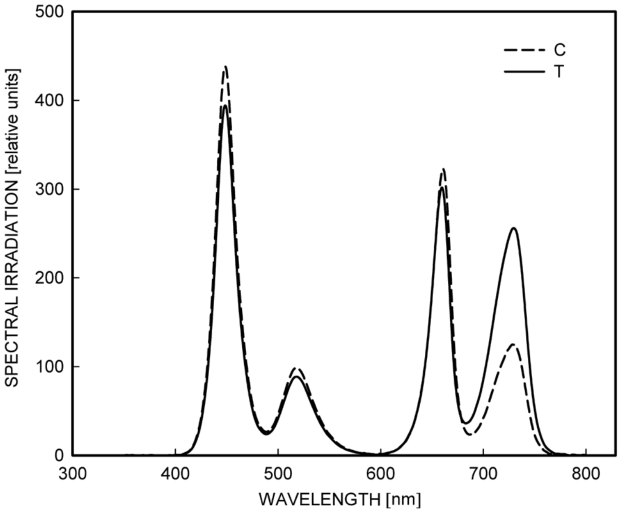

Fig. 1. Emission spectra of the control (C) (RL:BL:GL:FRL ratio = 0.7:1:0.3:0.4) and test (T) (RL:BL:GL:FRL ratio = 0.7:1:0.3: 0.8) LED (light-emitting diode) matrices. RL – red light, BL – blue light, GL – green light; FRL – far-red light.

high-intensity light [1,500 µmol(photon) m^{-2} s^{-1}]. This high irradiance (HI) was provided by white LEDs (*Epistar*, Taiwan).

Experimental design: In the experiments, 144 plants were distributed across 12 vessels and grown for 10, 16, or 30 d. To assess the morphological and growth parameters during development (biomass, leaf area, height) of the lettuce plants, we studied them after the 10, 16, and 30 d, starting from the day of planting the seeds. These time points were selected because seed germination was observed on the 5th day, the seedlings had the minimum biomass needed for measurements on the 10th day, and on the 16th day, a fully developed true first leaf had formed. On the 30th day, the appearance of 3–4 fully developed true leaves was observed. The leaf area was assessed by scanning the leaves using an *Epson V600* scanner and subsequently quantifying the area using *Adobe Photoshop 6.0.*

The influence of additional FRL on the maximum quantum yield of PSII (F_v/F_m) and the PSII performance index (PI_{ABS}) was evaluated in 30-d-old plants after 4-h irradiation with HI.

Photosynthetic activity and photosynthetic and respiration rates: PSII photosynthetic activity was assessed using the JIP test. Before the measurements, the leaves were fixed inside the measuring cell and kept in the dark for 15 min. The induction curves of OJIP transitions (increase in Chl *a* fluorescence yield from minimum to maximum value) were recorded using a fluorometer described earlier (Kreslavski *et al.* 2014). Based on the induction curves of fast Chl fluorescence, the following fluorescence parameters were calculated: minimum fluorescence level (F_0), maximum fluorescence level (F_m), and variable fluorescence (F_v), defined as the difference between F_m and F_0; the PSII maximum quantum yield (F_v/F_m); and the PSII performance index (PI_{ABS}) (Stirbet and Govindjee 2011, Goltsev *et al.* 2016). The following formula was used to calculate the PI_{ABS}: $PI_{ABS} = (F_v/F_m)/(M_0/V_J) \times (F_v/F_0) \times (1 - V_J)/V_J$. Here, $M_0 = 4 \times (F_{300\mu s} - F_0)/(F_m - F_0)$ is the average value of the initial slope of the relative Chl *a* fluorescence variable, reflecting the rate of closing of PSII reaction centers, and $V_J = (F_{2ms} - F_0)/(F_m - F_0)$ is the relative level of fluorescence in phase J after 2 min. Additionally, the influence of additional FRL on the F_v/F_m and the PI_{ABS} of 30-d-old plants after 4-h irradiation was evaluated.

CO_2 gas exchange: The rates of photosynthesis and respiration were determined using a portable *LCPro+* gas-exchange system (*ADC BioScientific Ltd.*, UK) in an open system at a temperature of 22 ± 0.5°C, a CO_2 concentration of 410 ± 10 µmol m^{-2} s^{-1}, and a relative humidity of 70–80%. The measurements were carried out at a saturating light intensity of 800 µmol(photon) m^{-2} s^{-1}. Here, P_N and R_D are net photosynthetic and respiration rates, respectively.

Pigment content: The contents of Chl *a* and *b*, as well as carotenoids, were measured in ethanol extracts using known absorption coefficients (Lichtenthaler 1987). The content of photosynthetic pigment was determined as µg g^{-1}(FM).

UV-absorbing pigments (UAPs, mainly flavonoids) were isolated from fresh leaves by a previously described method (Mirecki and Teramura 1984). Leaf cuts were kept for 24 h in acidic ethanol (ethanol:water:HCl, 78:20:2) at 4°C. Then, the optical density was determined on a *Genesis 10 UV* device (*Spectronic Unicam*, USA) at 327 nm and recalculated per 1 g of fresh mass (FM).

Statistics: Growth parameters were measured for at least ten lettuce plants in each treatment group. The rates of P_N and R_D and the leaf area values were measured for 5–10 plants of each variant. Fluorescence parameters were measured using no less than eight leaf discs with a diameter of 1 cm. Statistical data processing and plotting were performed using *SigmaPlot 12.0.* The results are presented as the means of three biological and 5–10 analytical replicates with standard errors. A statistically significant difference in the results between each experimental and control point was assessed using *Student*'s *t*-test at $p<0.05$. The values presented in the table and figures are the arithmetic means ± standard errors.

Results

During the early stages of our experiments, lettuce plants with relatively higher FRL fractions exhibited accelerated vertical growth, with elongated internodes and expanded foliage.

Thus, on the 10th day, the plants did not differ from one another in terms of FM, height, leaf area, or rate of photosynthesis and respiration (Figs. 2, 3). However, the value of the PI_{ABS} increased by 30% with the addition of the FRL. On the 16th day (the time of formation of the first true leaf), the addition of the FRL to the spectrum

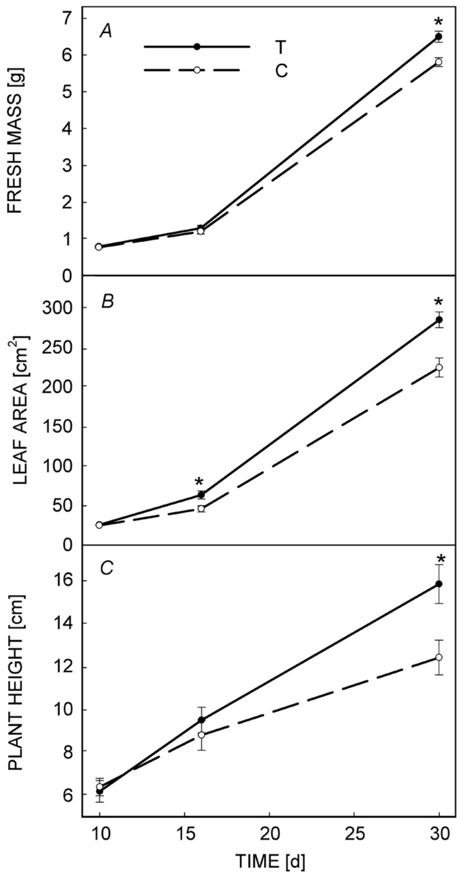

Fig. 2. Dynamics of the growth parameters of lettuce plants grown in the control matrix with an RL/FRL ratio = 1.75 (control, C) and in the experimental matrix with an RL/FRL ratio = 0.875 (test, T): fresh mass of the plants (*A*), leaf area (*B*), and plant height (*C*). The data are presented as the means ± SE. The values between the 'control' and 'test' curves marked with an asterisk differ at the $p<0.05$ level, $n = 10$. RL – red light, FRL – far-red light.

led to an increase in the leaf area, maximal quantum yield (F_v/F_m) and performance index (PI_{ABS}) but a reduction in the UAP content (Table 1).

By the 30th day (formation of fully developed 3–4 true leaves), at an RL/FRL ratio of 0.875 (test), the FM of the upper part of the plants, the leaf area value and the height of the plants increased by 12, 27, and 27%, respectively (Fig. 2). Moreover, the average FM of fully developed leaves did not significantly differ: 1.21 ± 0.07 g in the control treatment group and 1.34 ± 0.06 g in the experimental group; moreover, the DM was 87 ± 5 mg in the control group and 73 ± 4 mg in the experimental group and was reliably lower than that in the control group.

On the 30th day, the photosynthetic and respiration rates were lower in the experiment than in the control by 26 and 25%, respectively (Fig. 3). Additionally, the UAP content decreased during the experiment (by 32%) (Table 1). On the 30th day, the contents of Chl *a*, *b*, and carotenoids were essentially equal: 844 ± 12, 383 ± 9, and 262 ± 11, respectively, in the control plants and 816 ± 10, 375 ± 11, and 256 ± 12, respectively, in the experimental plants (Table 1). On the 30th day, the values of PSII activity, such as the F_v/F_m and PI_{ABS}, were different between the experimental and control plants. Thus, the values of F_v/F_m in the control and the experiment with added FRL were 0.78 ± 0.01 and 0.81 ± 0.01, respectively, and the values of PI_{ABS} in the control and the experiment were 31.9 ± 3.4 and 43.4 ± 4.3, respectively (Fig. 4); that is, in the experiment, these parameters were greater than those in the control.

After 4 h of irradiation, the F_v/F_m and PI_{ABS} decreased (Fig. 3), *i.e.*, PSII activity decreased both in the control and experimental plants. However, at the same time, in the control plants, the values of F_v/F_m and the PI_{ABS} decreased less than the values of these parameters in the experimental plants enriched with FRL (Fig. 4).

Discussion

It is known that RL and FRL have an impact on the growth and development of plants (Tan *et al.* 2022). In particular, FRL regulates leaf angle and can increase plant height and leaf area by inducing the expression of associated genes. This leads to the appearance of an increased leaf area, allowing the capture of more light (Tan *et al.* 2022). The emphasis of the study was placed on the use of two RL/FRL ratios, which cause changes in the PHY system. At noon, with a cloudless sky, the ratio of the RL to the FRL in solar radiation is usually approximately 1–1.3 (Legendre and van Iersel 2021). Therefore, we used two such RL/FRL ratios: 0.875 and 1.75. According to our data, accelerated vertical growth with elongated internodes and expanded foliage was observed under irradiation enriched with FRL (Fig. 2). This 'shade-avoidance' behaviour, commonly termed 'shade avoidance', is theorized to be a plant's natural reaction to competing for sunlight in dense foliage canopies, which is following available data (Franklin and Whitelam 2005, Franklin 2008).

One of the sensors involved in the plant response to RL or FRL (inducing a high or low RL/FRL ratio, respectively) is the PHY system, in which RL converts the original inactive form of PHY into an active form (Franklin and Quail 2010). It is assumed that both the RL and FRL and the RL/FRL ratio affect the photosynthetic apparatus through the PHY system (Carvalho *et al.* 2011, Kreslavski *et al.* 2018), primarily through the PHYB, as follows from Cao *et al.* (2018): fresh and dry mass of leaves and other plant organs, seedling height, photosynthesis, and antioxidant enzyme activity depend on the RL/FRL ratio. This effect was especially noticeable under stress conditions and was shown in tomato plants subjected to salt stress. However, a change in the RL/FRL ratio did not affect these parameters in the case of PHYB1 deficiency in the *phyb1* mutant (Cao *et al.* 2018). We found that in 10-d-old plants grown with a low RL/FRL ratio, PSII activity was greater than that in plants grown with a higher RL/FRL ratio (Fig. 3). These results agree with the data of other authors (Pettai *et al.* 2005, Zhen and van Iersel 2017, Tan *et al.* 2022). Thus, Pettai *et al.* (2005) showed that FRL short-term irradiation up to 780 nm supports oxygen evolution from the leaves of sunflowers and beans.

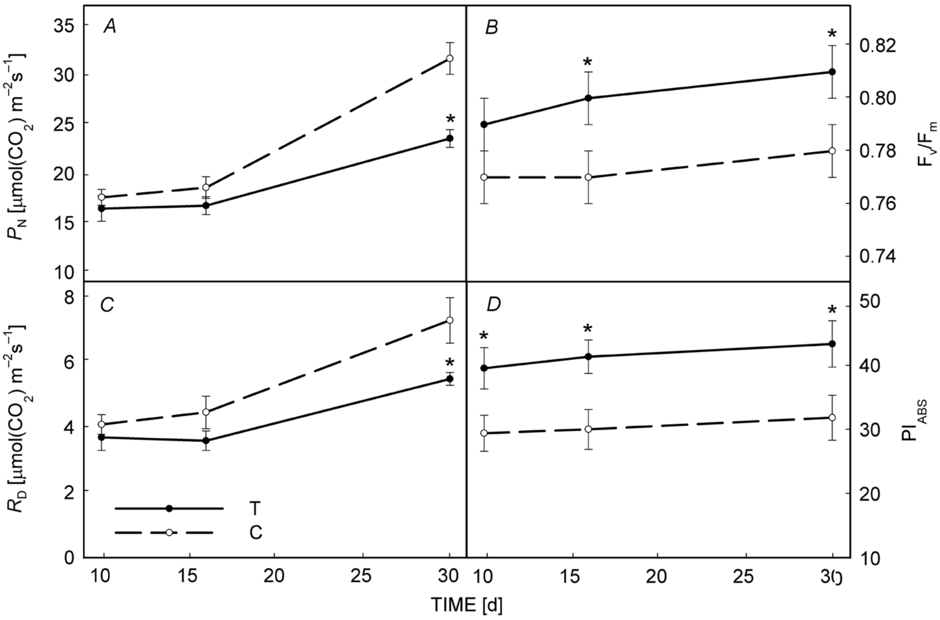

Fig. 3. Dynamics of photosynthetic parameters and respiration in lettuce plants grown in the control matrix with an RL/FRL ratio = 1.75 (control, C) and in the experimental matrix with an RL/FRL ratio = 0.875 (test, T). Data are presented as the means ± SE. The values between the 'control' and 'test' curves marked with an asterisk differ at the $p<0.05$ level. Here, F_v/F_m is the PSII maximal quantum yield, PI_{ABS} is the PSII performance index, and P_N and R_D are the photosynthesis and respiration rates, respectively, $n = 8$. RL – red light, FRL – far-red light; P_N – net photosynthetic rate; R_D – respiration rate.

Table 1. Dynamics of the pigment contents of lettuce plants grown in the control matrix with an RL/FRL of 1.75 (control, C) and in the experimental matrix with an RL/FRL of 0.875 (test, T). UAPs – absorbing pigments (mainly flavonoids). The data are presented as the means ± SE. The values between the 'control' and 'test' curves marked with an asterisk differ at the $p<0.05$ level ($n = 10$).

Day	Chlorophyll *a* [μg g^{-1}(FM)]		Chlorophyll *b* [μg g^{-1}(FM)]		Carotenoids [μg g^{-1}(FM)]		UAPs [relative units g^{-1}(FM)]	
	test	control	test	control	test	control	test	control
10	254 ± 12	261 ± 9	122 ± 6	125 ± 4	81 ± 4	83 ± 3	17.0 ± 3.5	25.0 ± 3.5
16	402 ± 16	430 ± 13	176 ± 8	170 ± 5	116 ± 5	132 ± 7	31.2 ± 3.8	48.5 ± 4.9*
30	816 ± 10	844 ± 12	375 ± 11	383 ± 9	246 ± 12	262 ± 11	58.1 ± 4.1	85.5 ± 7.0*

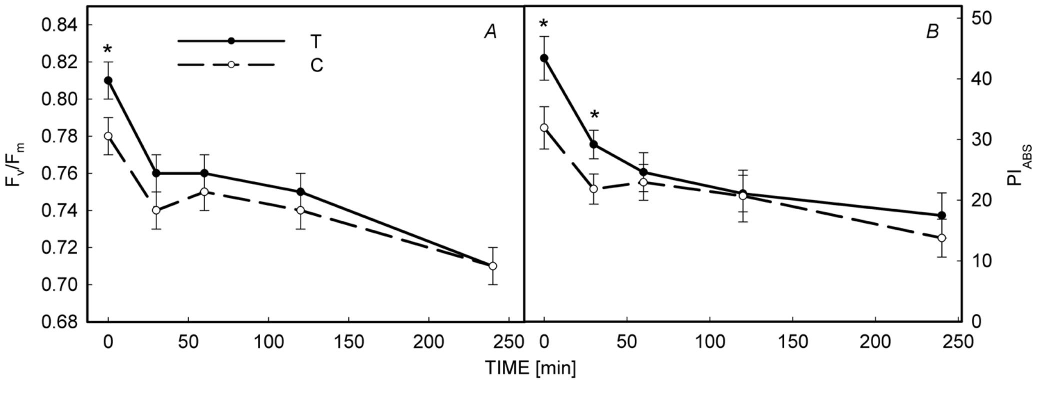

Fig. 4. Influence of additional FRL on the maximum quantum yield of PSII (F_v/F_m) and the PSII performance index (PI_{ABS}) of 30-d-old lettuce plants exposed to 4-h high light intensity [1,500 μmol(photon) m^{-2} s^{-1}]. Control (C), RL/FRL ratio = 0.875. Test (T), RL/FRL ratio = 1.75. The data are presented as the means ± SE. The values between the 'control' and 'test' curves marked with an asterisk differ at the $p<0.05$ level, $n = 6$. RL – red light, FRL – far-red light.

These authors tried to explain this effect by the presence of longwave aggregates absorbing FRL (Pettai *et al.* 2005), which seems unlikely.

One would expect that, in plants grown at a relatively high fraction of FRL, photosynthesis can be enhanced. However, the enrichment of the light spectrum with FRL led to lower photosynthetic and respiration rates per unit area but also to greater leaf FM and area, as well as to the development of taller plants. These data are not consistent with the results of Zhen and Bugbee (2020a), who indicated that the addition of FRL (up to 35% of all photon flux density) increased the photosynthesis of 14 diverse agronomic and horticultural crop species in the canopy, and this effect was similar to that of adding the same PAR photon flux. Additionally, Elkins and van Iersel (2020) suggested that adding FRL increased the growth of *Digitalis purpurea* plants by increasing the photosynthetic rate rather than through shade avoidance associated with acclimation responses. On the other hand, Jin *et al.* (2021) did not detect any changes in P_N, but leaf area and lettuce plant biomass increased with the addition of FRL; therefore, they explained the increase in biomass as an increase in leaf area. One of the reasons for the absence of a positive effect on the photosynthetic rate might be the high plant density in our study (approximately 100 plants per m^2), which significantly affects growth (Jin *et al.* 2021) and photosynthetic parameters. In the last experiments (Jin *et al.* 2021), at a high plant density of 51 plants per m^2, the positive effects of FRL on plant biomass and the leaf area were the lowest.

Li and Kubota (2009) demonstrated that in lettuce plants, the added far-red light can decrease the content of vital pigments such as anthocyanins, carotenoids, and Chl. However, there were no significant differences in the photosynthetic pigments under our conditions (Table 1), likely because of the small difference in two RL/FRL ratios in the light treatments with and without the FRL added to the original spectrum. However, there was a significant difference in UAPs. Low-molecular-mass substances such as UAPs are likely more sensitive to changes in the RL/FRL ratio.

We assumed that, in our case, a change in the RL/FRL ratio affects the studied parameters through the PHYB. First, Boccalandro *et al.* (2009) studied the stomatal density and water-holding capacity of the leaves of *Arabidopsis thaliana phyb* mutants and superproducers of PHYB and suggested that the active form of PHYB enhances the photosynthetic rate at the expense of water-use efficiency. With an increase in the proportion of FRL, the content of the active form of PHYB decreases (Kreslavski *et al.* 2018). In this case, the density of the stomata decreases, and the amount of water retained should increase. This is consistent with the greater FM and lower DM in the leaves of the plants in the FRL treatment group. Low stomatal density can also explain the decrease in CO_2 entering chloroplasts and reduced photosynthesis.

Other reasons for decreased photosynthesis can include a reduction in the efficiency of the primary photochemical processes of photosynthesis and a decrease in the activity of the enzymes involved in the CO_2 fixation cycle (Lawlor and Tezara 2009). A reduction in the activity of the enzymes of the Calvin cycle is possible. However, we did not observe a decrease in F_v/F_m value (Fig. 3).

In addition, the leaf area content in the experiment was greater than that in the control. Hence, the photosynthesis calculated for a plant was probably approximately equal in both cases. In addition to regulating photomorphogenesis, the PHY system also affects the adaptive capacity of plants and their photosynthetic apparatus (Carvalho *et al.* 2011, Franklin and Quail 2010). Thus, the added FRL reduced the resistance of PSII to high irradiance in our experiments (Fig. 4).

Phytochromes are key regulators of plant responses under stress conditions (Kreslavski *et al.* 2009, 2018; Gavassi *et al.* 2017), and their regulation depends on the RL/FRL ratio. We observed worse adaptation of lettuce plants grown in the experiment with the added FRL compared to the control without the addition of FRL (Fig. 4). We suggest that this difference is linked to the lower content of low-molecular-mass antioxidants in plants with added FRL (Table 1). Considering the earlier published data (Kreslavski *et al.* 2018), we assumed that lettuce plants grown with significant additional FRL would be less resistant not only to high irradiance but also to UV radiation.

Note that the influence of the RL/FRL ratio through a change in the content of the active form of PHY on the activity of the photosynthetic apparatus was revealed not only under physiological conditions but also under high irradiance conditions. However, the role of the FRL in the adaptation of photosynthetic apparatus under stress conditions is largely unclear, and further research is needed.

Conclusion: Our study indicates that incorporating FRL into the light spectrum in greenhouses significantly influences PSII activity, enhances photosynthesis, and promotes growth in the lettuce plant. This effect is evident in the improved PSII performance index and FM, suggesting a positive impact on lettuces' overall biomass and nutritional quality. We attribute these benefits primarily to the action of FRL on the PHY system, which appears to optimize leaf area and architecture. These morphological changes are likely instrumental in enhancing biomass production in lettuce. However, it is crucial to note that the response to FRL can vary based on factors like plant density, the intensity of FRL, and the specific lettuce variety. Understanding these notes is essential for optimizing greenhouse cultivation conditions for lettuce, potentially leading to significant economic benefits.

References

Allakhverdiev S.I., Kreslavski V.D., Zharmukhamedov S.K. *et al.*: Chlorophylls *d* and *f* and their role in primary photosynthetic processes of cyanobacteria. – Biochemistry-Moscow **81**: 201-212, 2016.

Berkovich Yu.A., Konovalova I.O., Smolyanina S.O. *et al.*: LED crop illumination inside space greenhouses. – Reach **6**: 11-24, 2017.

Boccalandro H.E., Rugnone M.L., Moreno J.E. *et al.*: Phytochrome B enhances photosynthesis at the expense of water-use efficiency in *Arabidopsis*. – Plant Physiol. **150**: 1083-1092, 2009.

Cao K., Yu J., Xu D. *et al.*: Exposure to lower red to far-red light ratios improve tomato tolerance to salt stress. – BMC Plant Biol. **18**: 92, 2018.

Carvalho R.F., Campos M.L., Azevedo R.A.: The role of phytochromes in stress tolerance. – J. Integr. Plant Biol. **53**: 920-929, 2011.

Elkins C., van Iersel M.W.: Supplemental far-red light-emitting diode light increases growth of foxglove seedlings under sole-source lighting. – HortTechnology **30**: 564-569, 2020.

Franklin K.A.: Shade avoidance. – New Phytol. **179**: 930-944, 2008.

Franklin K.A., Quail P.H.: Phytochrome functions in *Arabidopsis* development. – J. Exp. Bot. **61**: 11-24, 2010.

Franklin K.A., Whitelam G.C.: Phytochromes and shade-avoidance responses in plants. – Ann. Bot.-London **96**: 169-175, 2005.

Gavassi M.A., Monteiro C.C., Campos M.L. *et al*.: Phytochromes are key regulators of abiotic stress responses in tomato. – Sci. Hortic.-Amsterdam **222**: 126-135, 2017.

Gobets B., van Grondelle R.: Energy transfer and trapping in photosystem I. – BBA-Bioenergetics **1507**: 80-99, 2001.

Goltsev V.N., Kalaji H.M., Paunov M. *et al.*: Variable chlorophyll fluorescence and its use for assessing physiological condition of plant photosynthetic apparatus. – Russ. J. Plant Physiol. **63**: 869-893, 2016.

Heraut-Bron V., Robin C., Varlet-Grancher C. *et al.*: Light quality (red:far-red ratio): does it affect photosynthetic activity, net CO_2 assimilation, and morphology of young white clover leaves? – Can. J. Bot. **77**: 1425-1431, 2000.

Jin W., Urbina J.L., Heuvelink E., Marcelis L.F.M.: Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. – Front. Plant Sci. **11**: 609977, 2021.

Kreslavski V.D., Carpentier R., Klimov V.V., Allakhverdiev S.I.: Transduction mechanisms of photoreceptor signals in plant cells. – J. Photoch. Photobio. C **10**: 63-80, 2009.

Kreslavski V.D., Lankin A.V., Vasilyeva G.K. *et al.*: Effects of polyaromatic hydrocarbons on photosystem II activity in pea leaves. – Plant Physiol. Biochem. **81**: 135-142, 2014.

Kreslavski V.D., Los D.A., Schmitt F.-J. *et al.*: The impact of the phytochromes on photosynthetic processes. – BBA-Bioenergetics **1859**: 400-408, 2018.

Lawlor D.W., Tezara W.: Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. – Ann. Bot.-London **103**: 561-579, 2009.

Legendre R., van Iersel M.W.: Supplemental far-red light stimulates lettuce growth: disentangling morphological and physiological effects. – Plants-Basel **10**: 166, 2021.

Li Q., Kubota C.: Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. – Environ. Exp. Bot. **67**: 59-64, 2009.

Lichtenthaler H.K.: Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. –Method. Enzymol. 148: **350**-382, 1987.

Liu M., Pan T., Allakhverdiev S.I. *et al.*: Crop halophytism: an environmentally sustainable solution for global food security. – Trends Plant Sci. **25**: 630-634, 2020.

Middleton L.: Shade-tolerant flowering plants: adaptations and horticultural implications. – Acta Hortic. **552**: 95-102, 2001.

Mirecki R.M., Teramura A.H.: Effects of ultraviolet-B irradiance on soybean: V. The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. – Plant Physiol. **74**: 475-480, 1984.

Pettai H., Oja V., Freiberg A., Laisk A.: Photosynthetic activity of far-red light in green plants. – BBA-Bioenergetics **1708**: 311-321, 2005.

Stirbet A., Govindjee: On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and Photosystem II: Basics and applications of the OJIP fluorescence transient. – J. Photoch. Photobio. B **104**: 236-257, 2011.

Tan T., Li S., Fan Y. *et al.*: Far-red light: A regulator of plant morphology and photosynthetic capacity. – Crop J. **10**: 300-309, 2022.

Voitsekhovskaja O.V.: Phytochromes and other (photo)receptors of information in plants. – Russ. J. Plant Physiol. **66**: 351-364, 2019.

Wassenaar M.L.J., van Ieperen W., Driever S.M.: Low red to far-red ratio increases resistance to CO_2 diffusion and reduces photosynthetic efficiency in low light grown tomato plants. – Environ. Exp. Bot. **200**: 104918, 2022.

Yang Z.Q., Li Y.X., Zhang J.B. *et al.*: Effects of the red:far-red light ratio on photosynthetic characteristics of greenhouse cut *Chrysanthemum*. – Hortic. Sci. **40**: 40-43, 2013.

Zhen S., Bugbee B.: Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. – Plant Cell Environ. **43**: 1259-1272, 2020a.

Zhen S., Bugbee B.: Substituting far-red for traditionally defined photosynthetic photons results in equal canopy quantum yield for CO_2 fixation and increased photon capture during long-term studies: Implications for re-defining PAR. – Front. Plant Sci. **11**: 581156, 2020b.

Zhen S., Haidekker M., van Iersel M.W.: Far-red light enhances photochemical efficiency in a wavelength-dependent manner. – Physiol. Plantarum **167**: 21-33, 2019.

Zhen S., van Iersel M.W.: Far-red light is needed for efficient photochemistry and photosynthesis. – J. Plant Physiol. **209**: 115-122, 2017.