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Effects of light quality on growth, mineral compositions, and functional contents of green and red amaranths

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Summary

Amaranth (*Amaranthus tricolor* L.) is a highly nutritious leafy vegetable, and the varieties have bright light green (green amaranth) and red (red amaranth) leaves. Light quality control is an important factor for high vegetable productivity in plant factories; however, the effects of light quality on growth, mineral compositions, and functional contents of amaranth have not been investigated. In this experiment, green and red amaranth seedlings were transplanted 28 days after sowing to a plant factory, with three LED treatments with different red/blue ratios and the presence or absence of far-red light, and cultivated for 24 days. Results showed that the growth of red amaranth was enhanced by the white and far-red light with the lowest blue light ratio, whereas the betalain and β -carotene contents in green amaranth were considerably enhanced by the middle blue light ratio. The highest iron content in both varieties was obtained under the light condition with the highest blue light ratio. Our findings suggest that amaranth yield can be increased, and their carotenoid, betalain, and mineral contents can be controlled by adjusting far-red and blue light intensities. The results of this study will help in light quality control during amaranth production in plant factories.

Introduction

In recent years, due to the impact of climate change, population growth, and the need to strengthen food security, plant factories that systematically and stably produce food in an environment that is not affected by seasonal change and weather conditions are attracting attention (AVGOUSTAKI, 2020; CAROTTI, 2021). Plant factories provide countermeasures against risks such as food poisoning, shortage of clean water, and plant pathogen and pest (AVGOUSTAKI, 2020). Plant factories can be established anywhere, making them suitable for promoting local production, increasing local consumption, and addressing the rapid population growth in urban areas. However, the enormous energy required by plants in plant factories is a major challenge (AZAD, 2020), and high-value and high-yield crops are necessary for the cost-effective utilization of expensive land for agriculture in urban areas (CAROTTI, 2021). The main vegetable varieties currently produced in plant factories are ruffle lettuce, leaf lettuce, and baby leaf, and it is necessary to increase the number of vegetable varieties that can be produced in plant factories. Therefore, we conducted this research with an emphasis on effective cultivation methods and high added value in plant factories and concentrated on amaranth, a highly nutritious vegetable that increases the appeal of vegetable salads.

Amaranth (*Amaranthus tricolor* L.) is a C₄ plant of the Amaranthaceae family. Amaranth seedling is often used as a type of cereal grain, but it also has highly nutritious stems and leaves. Amaranth as a vegetable contains high levels of dietary fiber, calcium, vitamin C, and carotenoids (MIYAKE et al., 1997). In addition, it is known to contain free amino acids and free sugars at the same level as other

leafy greens, and because it has low oxalic acid content, it is simple to prepare and consume (MIYAKE et al., 1999). Amaranths contain betalains, which are plant pigments that give their leaves their distinctive green and red color. Betalains are broadly classified as betacyanin (red pigments) and betaxanthin (yellow pigments) (KHAN and GIRIDHAR, 2015) and are known to have radical scavenging, antioxidant, and antitumor properties. The antioxidant capacity of betacyanin is approximately one and a half, two, and three times more than that of rutin, catechin, and ascorbic acid, respectively (KAWAKAMI and ARIGA, 2016). The cultivation of amaranth in a plant factory and the probable year-round supply of nutrient-enriched amaranth could contribute to countermeasures against food crises and promote people's health.

Environmental factors, such as temperature, relative humidity, gas conditions, nutrient solution constituents, and light conditions, can be controlled in plant factories using artificial light. Plant development and growth responses to environmental conditions are species-specific (WONG, 2020). Although various environmental factors are known to have different effects on the growth and secondary metabolites of amaranth (WITTAYATHANARATTANA et al., 2022a, 2022b; SARKER and OBA, 2018), only a few studies have examined the effects of light quality in amaranth. Previous studies showed that far-red (FR) light irradiation promoted plant growth (MURAKAMI et al., 1992; HANYU et al., 1996; LI and KUBOTA, 2009), but some cultivars have been reported to be unaffected by FR light irradiation (MICKENS et al., 2019). Blue light irradiation typically enhances the accumulation of carotenoids and anthocyanins (LI and KUBOTA, 2009; OUZOUNIS et al., 2015), but studies have shown that the optimum red/blue ratio for anthocyanin production differs with plant species and growth stage (NICOLE et al., 2016). Moreover, the effects of FR light and red/blue ratio on the growth and functional components of amaranth have not been investigated, and the effect of light quality on the mineral compositions of plants is less studied (AMOOZGAR et al., 2017; PENNISI et al., 2019; BRAZAITYTE et al., 2020; DEGNI et al., 2021).

It is hypothesized that light quality will influence the yield, mineral compositions, and functional contents of amaranths. Therefore, the aim of this study was to investigate the effects of light quality on amaranth, particularly the effects of far-red and blue light on amaranth growth and betacyanin, betaxanthin, β -carotene, lutein, and mineral compositions. We investigated light irradiation technology for amaranth production to develop more efficient and high-value plant factory vegetables.

Materials and methods

Plant materials and growth conditions

Edible amaranth with green leaves, known as 'Green amaranth' (*Amaranthus tricolor* L. 'Amaranth' (black seed); Fujita Seed Co., Ltd., Japan), and the one with red leaves, known as 'Red amaranth' (*Amaranthus tricolor* L. 'Red amaranth' (scarlet red); Nakahara Seed Co., Ltd., Japan), were used as the test plants. Seeds were sown

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on a urethane sponge ($23 \times 23 \times 27$ mm) soaked in tap water, and seedlings were transplanted after 12 d into 10 L ($630 \times 405 \times 80$ mm) containers with a hydroponic system designed with a deep flow technique. Fifty seedlings of both green and red amaranth were grown. WFR LEDs (Fig. 1) were used as light sources during seedling cultivation, and OAT House Solution A (OAT Agrio Co., Ltd., Japan) was used as the nutrient solution in the hydroponic system. Electrical conductivity (EC) and pH were adjusted to 1.0 dS m^{-1} and 6.0, respectively. The seedlings were grown under the following environmental conditions: light period of 16 h d^{-1} , photosynthetic photon flux density (PPFD) of $180 \mu\text{mol m}^{-2} \text{ s}^{-1}$, air temperature of $23 \pm 2 \text{ }^\circ\text{C}$, relative humidity of $65 \pm 10\%$, and carbon dioxide concentration of $1,000 \mu\text{mol mol}^{-1}$.

Light treatments

Twenty-eight-day-old green and red amaranth seedlings with three true leaves were transplanted into a hydroponic culture apparatus of a nutrient film technique system, and seven plants each were cultivated under different light treatments. Three types of LEDs (Philips LED GreenPower Production Module, 2nd generation, Signify (also known as Philips, Netherlands) were used as light sources for cultivation: WFR, MB, and HB LEDs. The spectra for each light source are shown in Fig. 1. Cultivation environmental conditions during the light treatments were the same as during seedling growth. The PPFD values were measured with a photon sensor (LI-190SA, LI-COR, USA) and a dedicated display (LI-250A, LI-COR, USA). The light

wavelength was measured using a spectral irradiance meter (SIM-2 plus Spectral Irradiance Meter, Mettue, USA). All cultivation experiments were carried out at an indoor-type plant factory of Future Sci Tech Lab at Tamagawa University (Tokyo, Japan).

Measurements

Growth parameters

Plants under the three light treatments were harvested 24 days after cultivation. Top fresh weight, leaf fresh weight, plant height, and number of leaves were measured at harvest. To measure dry weight, fresh stems (excluding leaves) from seven plants and fresh leaves from three plants per treatment were dried to constant weight at $85 \text{ }^\circ\text{C}$ (WFO-520, EYELA, Japan). Moreover, fresh leaves from four plants per treatment were harvested and stored at $-30 \text{ }^\circ\text{C}$ for subsequent component analysis. These frozen leaves were then dried to a constant weight utilizing a lyophilizer (FDU-1110; Tokyo Rikakikai Co., Ltd., Japan). The dry weights of stems and leaves from the seven plants in each treatment were subsequently determined, and their sum yielded the top dry weight.

Pretreatment for component analysis

Leaves of four plants per treatments were stored at $-30 \text{ }^\circ\text{C}$ after harvest. The frozen leaves were dried using a lyophilizer, and the dried leaves were pulverized using a Wonder blender (WB-1; Osaka Chemical Co., Ltd., Japan).

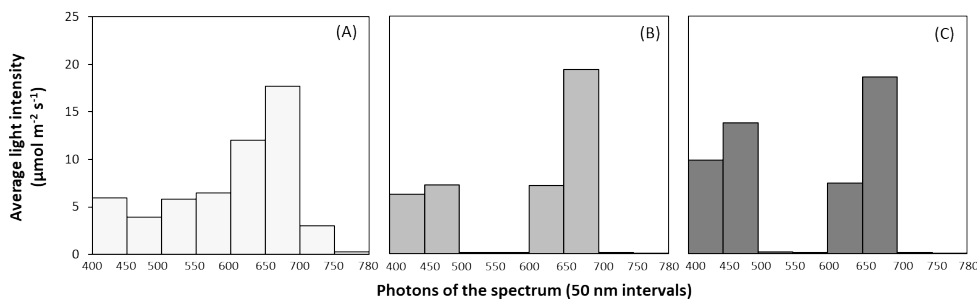


Fig. 1: Photons of the spectrum (50 nm intervals) of each LED lamp used in this experiment (A) WFR: DR/W/FR_LB (DR: deep red, W: white, FR: far-red, LB: low blue) LEDs, (B) MB: DR/B_MB (DR: deep red, B: blue, MB: medium blue) LEDs, (C) HB: DR/B_HB (DR: deep red, B: blue, HB: high blue) LEDs

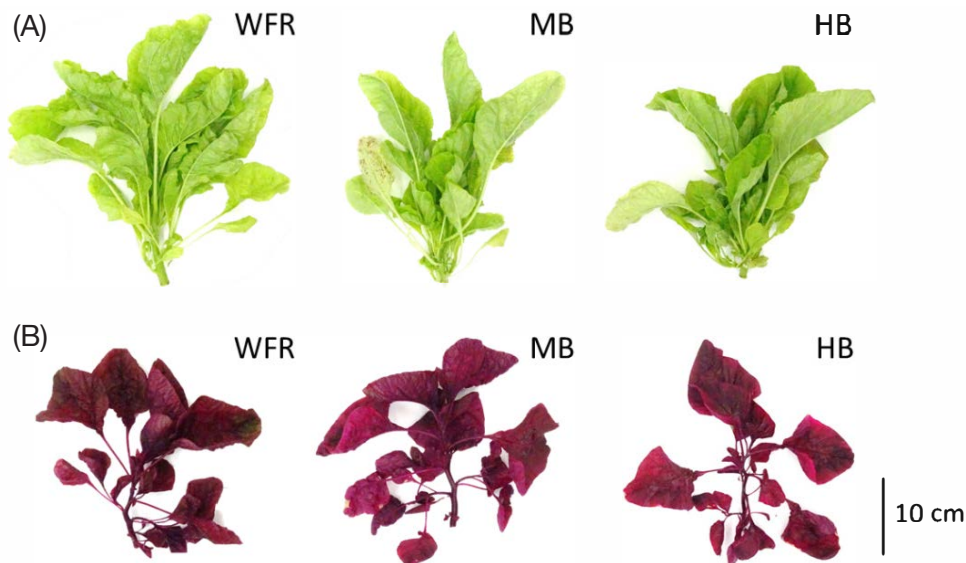


Fig. 2: Green (A) and red (B) amaranth plants after 24 days of cultivation under different light conditions (WFR: DR/W/FR_LB LEDs, MB: DR/B_MB LEDs, HB: DR/B_HB LEDs)

Determination of betaxanthin and betacyanin contents

Powdered amaranth leaves were used for betaxanthin and betacyanin analyses, according to the method described by RAVICHANDRAN et al. (2013), with some modifications. A 30-mg sample was accurately weighed and transferred to a 2-mL tube containing 1 mL of 50% aqueous ethanol solution and agitated for 10 seconds. Thereafter, the homogenate was centrifuged at $20,400 \times g$ for 5 min with an MX-305 centrifuge (Tomy Seiko Co., Ltd., Japan), and the supernatant was collected from the extract. This extraction procedure was repeated five times, and the supernatants were collected. Furthermore, 4 mL of ethanol was added to 5 mL of the extract to make a total volume of 9 mL and mixed using Vortex® (Vortex-Genie 2; M&S Instruments Inc., Japan). This extract was used to quantify the betalains.

The contents of betaxanthin and betacyanin in the extracts were measured using a spectrometer (UH5300, HITACHI, Japan) at 538 and 480 nm, respectively according to the method described by STINTZING et al. (2003). Absorbance readings were used to calculate the betalain content (BC) in each sample using the following formula:

$$BC \text{ (mg/g D.W.)} = ((A \times DF \times MW) / (e \times l \times S))$$

where, 'A' is the absorption of betacyanin and betaxanthin at 538 and 480 nm, respectively; 'DF' is the dilution factor; 'l' is the path length of the 1 cm cuvette. 'S' is the sample weight. 'MW' and 'e' are the molecular weights and extinction coefficients of the representative compounds betacyanin ($MW=550 \text{ g mol}^{-1}$; $e=60,000 \text{ L mol}^{-1} \text{ cm}^{-1}$ in H_2O) and betaxanthin ($MW=308 \text{ g mol}^{-1}$; $e=48,000 \text{ L mol}^{-1} \text{ cm}^{-1}$ in H_2O), respectively.

Determination of β -carotene and lutein contents

β -carotene and lutein in amaranth leaves were determined using high performance liquid chromatography (HPLC) according to the method of TOMARI et al. (2021). A 30-mg sample was accurately weighed and transferred to a 2-mL tube containing 1 mL of tetrahydrofuran. The mixture was ultrasonically extracted for 15 min using a sonicator (Sine Sonic 100; Kokusai Electric Semiconductor Service Inc., Japan) and centrifuged (5 min, $4 \text{ }^\circ\text{C}$, $204,00 \times g$) with an MX-305 centrifuge (Tomy Seiko Co., Ltd., Japan); the supernatant was collected from the extract. This extraction procedure was repeated three times, and 3 mL of the total supernatant was collected and mixed using a Vortex® (Vortex-Genie 2; M&S Instruments Inc., Japan). The extract, filtered with a $0.45\text{-}\mu\text{m}$ membrane filter, was used as a test solution for HPLC analysis. Measurements of β -carotene and lutein were performed using a Chromaster HPLC system (Hitachi High-Tech Science Corp., Japan). The HPLC conditions for β -carotene and lutein were CAPCELL PAK C18 MGIIS-5 ($\phi 5 \mu\text{m}$, $4.6 \times 150 \text{ mm}$, Osaka Soda Co., Ltd., Japan); temperature, $30 \text{ }^\circ\text{C}$; flow rate, 1.0 mL min^{-1} ; run time, 18 min; and injection volume, $10 \mu\text{L}$. A gradient elution program was conducted for chromatographic separation with mobile phase A [water:methanol (10:90)] and mobile phase B (ethyl acetate) as follows: 0 min (100% A), 7 min (100% B), 12 min (100% B), 12.5 min (100% A), and ending at 5.5 min. β -carotene and lutein were detected by measuring the absorbance at 450 nm. The retention times of β -carotene and lutein were 8.8 min and 6.0 min, respectively. Quantitation was conducted using the absolute calibration curve method. Standard curve was made with a diluted solution of β -carotene standard reagent (Fujifilm Wako Pure Chemical Corp., Ltd., Japan) and lutein standard reagent (Funakoshi, Ltd., Japan) with tetrahydrofuran.

Mineral compositions analysis

Dry amaranth leaves (50 mg) were completely digested with 25% HNO_3 and 30% H_2O_2 using a microwave pretreatment system

(ETHOS UP, Milestone General, Japan). Mineralized samples were diluted to 10 mL using ultrapure water. Elemental profile was analyzed using inductively coupled plasma atomic emission spectroscopy (ICP-AES, 710 ICP-AES, Agilent Technologies Japan, Ltd., Japan). The analytical wavelengths chosen were: 213.618 nm (P), 766.491 nm (K), 315.887 nm (Ca), 285.213 nm (Mg), 238.204 nm (Fe), 213.857 nm (Zn), 259.372 nm (Mn), 204.598 nm (Mo), 396.152 nm (Al), and 589.592 nm (Na). Calibration curves were prepared using ICP-AES standard reagents (K, P, Ca, Fe, Mg, Mn, Mo, Zn, Na, and Al (Fujifilm Wako Pure Chemical Corp.)) diluted in 5% HNO_3 to determine the content of mineral compositions.

Statistical analysis

The plant sampling in this study followed the principle of random sampling. We analyzed the functional content and mineral composition of four out of the seven green and red amaranth plants subjected to each light treatment. The entire experiment, from cultivation to all the tests, was repeated twice to ensure reproducibility. Data obtained were analyzed using the statistical analysis software JMP14 (SAS Institute, Japan). Tukey-Kramer's test was used at $P < 0.05$ to investigate significant differences between each light treatment in plant growth and contents.

Results and discussion

Plant growth

Top fresh weight and leaf fresh weight of green amaranth under the three light treatments were not different (Fig. 3 (A), (B)). The top fresh weight and leaf weight of red amaranth in the WFR treatment were significantly higher than those in the MB and HB treatments (Fig. 3 (A), (B)). This effect tended to be suppressed as the percentage of blue light increased. Top dry weight and leaf dry weight showed similar trends to fresh weights (Fig. 3 (C), (D)). The plant height of green amaranth in the WFR treatment was significantly higher than that in the HB treatment. The plant height of red amaranth in the WFR treatment was significantly higher than that in the MB and HB treatments (Fig. 3 (E)). The number of leaves of green amaranth under the three light treatments was not different; however, the number of leaves of red amaranth in the WFR treatment was significantly higher than that in the HB treatment, probably because of the high rate of blue light (Fig. 3 (F)).

Previous studies have shown that supplemental FR light promotes plant growth (LEE et al., 2016; MICKENS et al., 2018; JIN et al., 2021). FR light promotes the photosynthetic activity of photosystem II (THAPPER et al., 2009) and enhances the photosynthetic efficiency of short-wavelength light (ZHEN and VAN IERSEL, 2017). The light source used under WFR treatment in this experiment included FR light. In the present study, FR light irradiation had no significant effect on green amaranth; however, in red amaranth, the WFR treatment significantly increased the top fresh weight, leaf fresh weight, top dry weight, leaf dry weight, plant height, and the number of leaves, indicating that FR light irradiation had a positive effect on the growth of red amaranth. Although an increase in leaf area brought on the shade response induced by FR light irradiation of plants has been reported in previous studies, in this study, FR light irradiation did not only increase the leaf area of red amaranth but also increased the number of leaves. These results suggest that FR light irradiation may have promoted the photosynthetic response of red amaranth, thereby stimulating its growth. Moreover, the growth of amaranth tended to be suppressed as the ratio of blue light increased. In other vegetables, the higher the ratio of blue light, the greater the growth inhibitory effect (JOKKAN et al., 2010; KONG and NEMALI, 2021), and a similar trend was observed for red amaranth.

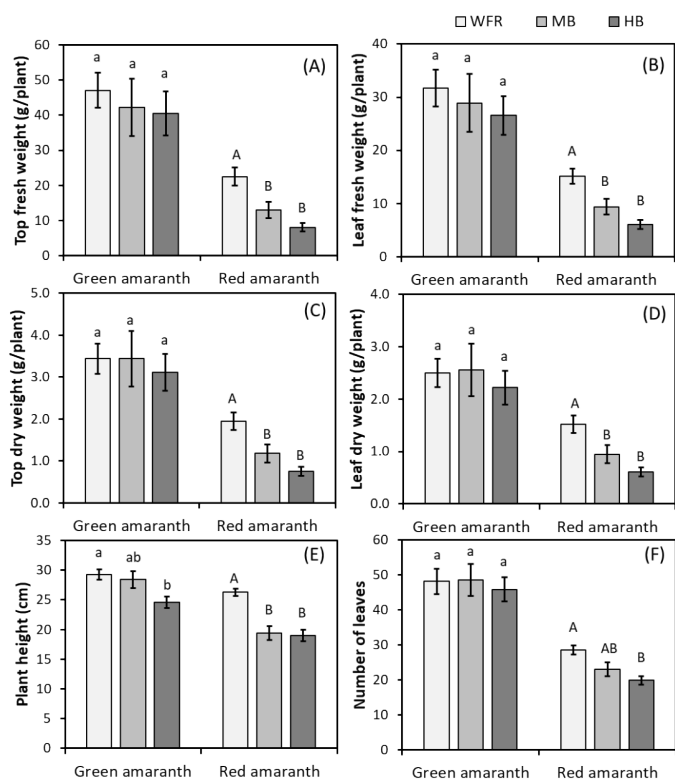


Fig. 3: Top fresh weight (A), leaf fresh weight (B), top dry weight (C), leaf dry weight (D), plant height (E), and number of leaves (F) in green and red amaranth plants after 24 days of cultivation under different light conditions. Vertical bars indicate mean \pm SE. Different letters indicate significant differences among the light conditions at $p < 0.05$ according to Tukey-Kramer's test ($n = 7$)
WFR: DR/W/FR_LB LEDs, MB: DR/B_MB LEDs, HB: DR/B_HB LEDs

Betaxanthin and betacyanin contents

The betacyanin content per 1 g dry weight in red amaranth was much higher than that in green amaranth (Fig. 4 (A)). The betacyanin and betaxanthin contents in the leaves of green amaranth in MB treatment were significantly higher than those in the WFR and HB treatments (Fig. 4 (A), (B)). The betacyanin and betaxanthin contents in the leaves of red amaranth were not different among the three light treatments but tended to be higher in the MB treatment (Fig. 4 (A), (B)).

Previous studies have shown that light stress increases the anthocyanin content in plants because of the short wavelength of blue light

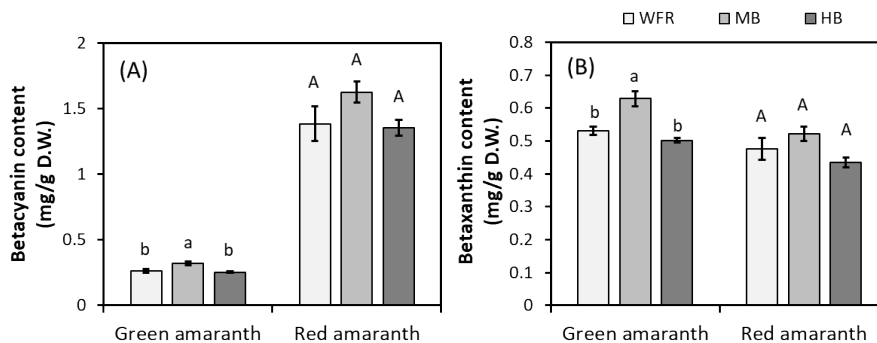


Fig. 4: Contents of betacyanin (A) and betaxanthin (B) in green and red amaranth plants after 24 days of cultivation under different light conditions. Vertical bars indicate mean \pm SE. Different letters indicate significant differences among the light conditions at $p < 0.05$ according to Tukey-Kramer's test ($n = 4$)
WFR: DR/W/FR_LB LEDs, MB: DR/B_MB LEDs, HB: DR/B_HB LEDs

(AZAD et al., 2020). Although the distribution of betacyanin and anthocyanins in the plant kingdom is mutually exclusive and their coexistence in the same species has not been reported, their localization in the plant body suggests functional similarity (STAFFORD, 1994), suggesting that blue light can affect betalain content. Results of this study showed that amaranth grown under MB treatment tended to have the highest betalain content, suggesting that the red/blue light ratio of MB treatment provided moderate stress, thereby resulting in higher betalain content.

β -carotene and lutein contents

The β -carotene and lutein contents per 1 g dry weight of leaves of red amaranth were higher than those of green amaranth (Fig. 5 (A), (B)). The β -carotene content in the leaves of green amaranth in the MB treatment was significantly higher than that in the WFR treatment (Fig. 5 (A)). The β -carotene content in the leaves of red amaranth in the WFR and MB treatments was significantly higher than that in the HB treatment (Fig. 5 (A)). Lutein content in both green and red amaranth leaves was not statistically different among the three light treatments (Fig. 5 (B)).

β -carotene content was affected by light quality in both green and red amaranth, but no significant difference was observed in lutein. This suggests that light treatment may affect the pathway downstream of lycopene, which is upstream of the synthetic pathway of both components (FREDE et al., 2019). The addition of blue light with red or white light usually leads to an enhanced accumulation of pigments, such as carotenoids (LI and KUBOTA, 2009; JOHKAN et al., 2010). However, high blue light irradiation in combination with red light had little effect on lutein in green and red amaranth, and HB treatment (the highest blue light ratio) on red amaranth showed a negative effect on β -carotene.

Mineral compositions

Fig. 6 shows the mineral compositions per 1 g dry weight of green and red amaranth leaves for each light treatment. The Fe contents in the leaves of green and red amaranth in the HB treatment were significantly higher than those in the MB treatment. There was no notable difference in the contents of K, Mg, Na, Mn, Zn, Mo, and Al in green and red amaranth leaves under the three light treatments. The red amaranth leaves in the HB treatment contained a higher P content and lower Ca content than the red amaranth leaves in the WFR and MB treatments. The mineral compositions in red amaranth was higher than those in green amaranth by 43% for Mg, 60% for Mn, 62% for Fe, 55% for Zn, and 30% for Mo across all the treatments.

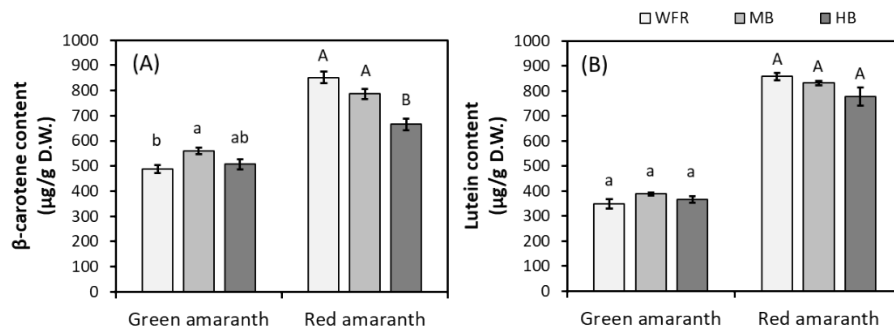


Fig. 5: Contents of β -carotene (A) and lutein (B) in green and red amaranth plants after 24 days of cultivation under different light conditions. Vertical bars indicate mean \pm SE. Different letters indicate significant differences among the light conditions at $p < 0.05$ according to Tukey-Kramer's test ($n = 4$) WFR: DR/W/FR_LB LEDs, MB: DR/B_MB LEDs, HB: DR/B_HB LEDs

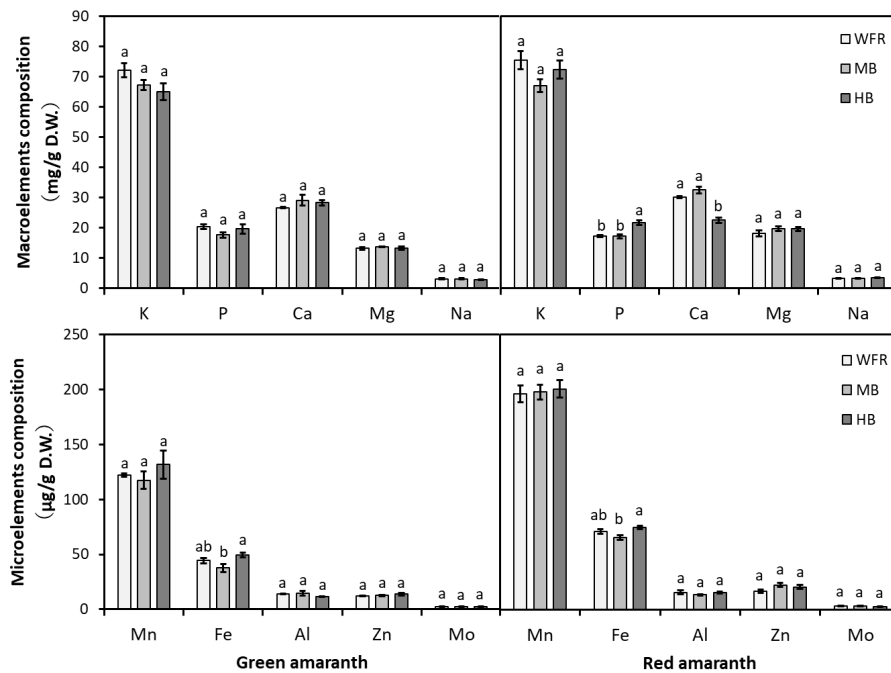


Fig. 6: Mineral composition in green and red amaranth plants after 24 days of cultivation under different light conditions. Vertical bars indicate mean \pm SE. Different letters indicate significant differences among the light conditions at $p < 0.05$ according to Tukey-Kramer's test ($n = 4$) WFR: DR/W/FR_LB LEDs, MB: DR/B_MB LEDs, HB: DR/B_HB LEDs

The highest Fe content was recorded in the HB treatment of both green and red amaranth. Further, in this treatment, red amaranth had the lowest Ca content. This indicates that the rate of blue light irradiation affected the absorption of mineral contents, especially in red amaranth. Additionally, no correlation was found between growth and mineral contents in amaranth, suggesting that light quality affects the absorption and accumulation of mineral contents, regardless of the growth. Previous studies on okra revealed that the Fe and Ca contents in okra under blue light treatment were higher and lower, respectively, than those in okra under red light treatment, and this is consistent with the results of this study, especially for red amaranth. The antagonism between Ca and Fe during ionic interactions may be responsible for the high Fe accumulation in plants grown under HB conditions, resulting in reduced Ca absorption and lower plant Ca contents (DEGNI et al., 2021). Blue light irradiation has been shown to positively affect the mineral content in broccoli microgreens, probably because of the effects of blue light on stomatal opening and membrane transport activity (KOPSELL et al., 2013). The results of these experiments suggest that the accumulation tendency of each element differs, suggesting that the elements are selectively absorbed according to the light quality in amaranth.

It is generally known that a trade-off relationship exists between plant growth and metabolites and that metabolite synthesis is suppressed when plant growth is promoted (FIGUEROA-MACÍAS, 2021). However, the amaranth in this study did not have a trade-off relationship. Based on the dry weight of the leaves and the functional and mineral contents obtained in this experiment, we calculated the amount of functional components obtained per plant under different light treatments for green amaranth and red amaranth. For green amaranth, MB treatment resulted in the highest value, whereas HB treatment resulted in the lowest value for all components of β -carotene, lutein, betacyanin, and betaxanthin. Furthermore, for green amaranth, the MB treatment had the highest values for Ca, Mg, Na, Al, and Zn, whereas all mineral components except Fe had the lowest values in the HB treatment. For red amaranth, WFR treatment resulted in the highest values for all components of β -carotene, lutein, betacyanin, betaxanthin, and mineral contents. In contrast, HB treatment resulted in the lowest values for β -carotene, lutein, betaxanthin, and mineral contents, with the exception of betacyanin. Therefore, green and red amaranths can be most effectively cultivated under MB and WFR treatments, respectively.

Conclusion

The results of this study indicate that it is possible to promote growth and control functional and mineral contents by controlling light quality when growing amaranth in plant factories. In addition, it was shown that the effects of light quality on green and red amaranths were different. When considering the weight per plant and the functional and mineral contents, both green amaranth and red amaranth can be most effectively cultivated through MB treatment and WFR treatment, respectively. For further efficient production of amaranth, it is expected that more energy-efficient and beneficial conditions would be revealed by investigating cultivations under more segmented light quality and light intensity conditions and adjusting light quality for each growth stage.

Acknowledgments

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Conflict of interest


No potential conflict of interest was reported by the authors. This work was financially supported by Signify: the company supplied the lighting systems and did not have any influence on the outcome of this study. Our study investigated the effect of different light spectra. The results are not specific to a certain product of Signify, but are a representative of any light source with similar light spectra.

References

- AZAD, M.O.K., KJAER, K.H., ADNAN, M., NAZIN, M.T., LIM, J.D., SUNG, I.J., PARK, C.H., LIM, Y.S., 2020: The evaluation of growth performance, photosynthetic capacity, and primary and secondary metabolite content of leaf lettuce grown under limited irradiation of blue and red led light in an urban plant factory. *Agriculture* 10(2), 28, 1-16. DOI: 10.3390/agriculture10020028
- AMOZGAR, A., MOHAMMADI, A., SABZALIAN, M.R., 2017: Impact of light-emitting diode irradiation on photosynthesis, phytochemical composition and mineral element content of lettuce cv. Grizzly. *Photosynthetica* 55 (1), 85-95. DOI: 10.1007/s11099-016-0216-8
- AVGOUSTAKI, D.D., XYDIS, G., 2020: Plant factories in the water-food-energy Nexus era: a systematic bibliographical review. *Food Security* 12, 253-268. DOI: 10.1007/s12571-019-01003-z
- BRAZAITYTĖ, A., VAŠTAKAITĖ-KAIRIENĖ, V., JANKAUSKIENĖ, J., VIRŠILĖ, A., SAMUOLIENĖ, G., SAKALAUŠKIENĖ, S., NOVIČKOVAS, A., MILIAUSKIENĖ, J., DUCHOVSKIS, P., 2020: Effect of blue light percentage on mineral elements content in Brassica microgreens. *Acta Hort.* 1271, 119-125. DOI: 10.17660/ActaHortic.2020.1271.17
- CAROTTI, L., GRAAMANS, L., PUKSIC, F., BUTTURINI, M., MEINEN, E., HEUVELINK, E., STANGHELLINI, C., 2021: Plant factories are heating up: Hunting for the best combination of light intensity, air temperature and root-zone temperature in lettuce production. *Front Plant Sci.* 28, 11:592171. DOI:10.3389/fpls.2020.592171
- DEGNI, B.F., HABA, C.T., DIBI, W.G., SORO, D., ZOUEU, J.T., 2021: Effect of light spectrum on growth, development, and mineral contents of okra (*Abelmoschus esculentus* L.). *Open Agriculture* 6, 276-285. DOI: 10.1515/opag-2021-0218
- FIGUEROA-MACÍAS, J.P., GARCÍA, Y., NÚÑEZ, M., DÍAZ, K., OLEA, A., ESPINOZA, L., 2021: Plant growth-defense trade-offs: Molecular processes leading to physiological changes. *Int. J. Mol. Sci.* 22(2), 693. DOI: 10.3390/ijms22ty020693
- FREDE, K., SCHREINER, M., BALDERMANN, S., 2019: Light quality-induced changes of carotenoid composition in pak choi *Brassica rapa* ssp. chinensis. *J. Photochem. Photobiol. B, Biol.* 193, 18-30. DOI: 10.1016/j.jphotobiol.2019.02.001
- HANYU, H., SHOJI, K., JI, S.B., 1996: Evaluation of light quality variation through supplement of far-red light and the difference in the effects on growth of a pole-type and a bush-type kidney bean, *Phaseolus vulgaris* L. *Environ. Control. Biol.* 34 (4), 267-275. DOI: 10.2525/ecb1963.34.267
- JIN, W., URBINA, J.L., HEUVELINK, E., MARCELIS, L.F.M., 2021: Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. *Front. Plant Sci.* 11, 1-9. DOI: 10.3389/fpls.2020.609977
- JOHKAN, M., SHOJI, K., GOTO, F., HASHIDA, S., YOSHIHARA, T., 2010: Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. *Hortscience* 45(12), 1809-1814. DOI: 10.21273/HORTSCI.45.12.1809
- KAWAKAMI, T., ARIGA, T., 2016: Foods and cosmetics containing betalains. JP2007143518A
- KHAN, M.I., GIRIDHAR, P., 2015: Plant betalains: chemistry and biochemistry. *Phytochemistry* 117, 267-295. DOI: 10.1016/j.phytochem.2015.06.008
- KONG, Y., NEMALI, K., 2021: Blue and far-red light affect area and number of individual leaves to influence vegetative growth and pigment synthesis in lettuce. *Front Plant Sci.* 12, 667407. DOI: 10.3389/fpls.2021.667407
- KOPSELL, D.A., SAMS, C.E., 2013: Increases in shoot tissue pigments, glucosinolates, and mineral elements in sprouting broccoli after exposure to short-duration blue light from light emitting diodes. *J. Am. Soc. Hortic. Sci.* 138(1), 31-37. DOI: 10.21273/JASHS.138.1.31
- LEE, M.J., SON, K.H., OH, M.M., 2016: Increase in biomass and bioactive compounds in lettuce under various ratios of red to far-red LED light supplemented with blue LED light. *Hortic. Environ. Biotechnol.* 57, 139-147. DOI: 10.1007/s13580-016-0133-6
- LI, Q., KUBOTA, C., 2009: Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. *Environ. Exp. Bot.* 67, 59-64. DOI: 10.1016/j.envexpbot.2009.06.011
- MICKENS, M.A., SKOOG, E.J., REESE L.E., BARNWELL, P.L., SPENCER, L.E., MASSA, G.D., WHEELER, R.M., 2018: A strategic approach for investigating light recipes for 'Outredgeous' red romaine lettuce using white and monochromatic LEDs. *Life Sciences in Space Research* 19, 53-62. DOI: 10.1016/j.lssr.2018.09.003
- MICKENS, M.A., TORRALBA, M., ROBINSON, S.A., SPENCER, L.E., ROMEYN, M.W., MASSA, G.D., WHEELER, R.M., 2019: Growth of red pak choi under red and blue, supplemented white, and artificial sunlight provided by LEDs. *Scientia Horticulturae* 245, 200-209. DOI: 10.1016/j.scienta.2018.10.023
- MIYAKE, T., NEGISHI, Y., OKUZAKI, M., SASAKI, H., SUGAHARA, T., 1999: Contents of free amino acids, free sugars, free alcohols and organic acids in selected amaranthus cultivars. *J. Integr. Stud. Diet. Habits.* 10, 57-62. DOI: 10.2740/jisdh.10.57
- MIYAKE, T., OKUZAKI, M., YAMAGUCHI, H., SUGAHARA, T., 1997: Chemical composition in vegetable amaranthus leaves. *J. Integr. Stud. Diet. Habits.* 8, 52-55. DOI: 10.2740/jisdh.8.2_52
- MURAKAMI, K., HORAGUCHI, K., MORITA, M., AIGA, I., 1992: Accelerating the growth of lettuce (*Lactuca sativa* L.) by additional far-red (FR) irradiation. *Environ. Control. Biol.* 30, 23-28. DOI: 10.2525/ecb1963.30.23
- NICOLE, C.C.S., CHARALAMBOUS, F., MARTINAKOS, S., VAN DE VOORT, S., LI, Z., VERHOOG, M., KRIJN, M., 2016: Lettuce growth and quality optimization in a plant-factory. *Acta Hort.* 1134, 231-238. DOI: 10.17660/ActaHortic.2016.1134.31
- OZOUNIS, T., ROSENQVIST, E., OTTOSEN, C.O., 2015: Spectral effects of artificial light on plant physiology and secondary. *HortScience* 50, 1128-1135. DOI: 10.21273/HORTSCI.50.8.1128
- PENNISI, G., BLASIOLI, S., CELLINI, A., MAIA, L., CREPALDI, A., BRASCHI, I., SPINELLI, F., NICOLA S., FERNANDEZ, J.A., STANGHELLINI, C., MARCELIS, L.F.M., ORSINI, F., GIANQUINTO, G., 2019: Unraveling the role of red:blue LED lights on resource use efficiency and nutritional properties of indoor grown sweet basil. *Front. Plant Sci.* 10:305. DOI: 10.3389/fpls.2019.00305

- RAVICHANDRAN, K., SAW, N.M.M.T, MOHDALY, A.A.A., GABR, A.M.M., KASTELL, A., RIEDEL, H., CAI, Z., KNORR, D., SMETANSKA, I., 2013: Impact of processing of red beet on betalain content and antioxidant activity. *Food Res. Int.* 50, 670-675. DOI: [10.1016/j.foodres.2011.07.002](https://doi.org/10.1016/j.foodres.2011.07.002)
- SARKER, U., OBA, S., 2018: Drought stress enhances nutritional and bioactive compounds, phenolic acids and antioxidant capacity of *Amaranthus* leafy vegetable. *BMC Plant Biol.* 18:258, 1-15. DOI: [10.1186/s12870-018-1484-1](https://doi.org/10.1186/s12870-018-1484-1)
- STAFFORD, H.A., 1994: Anthocyanins and betalains: evolution of the mutually exclusive pathways. *Plant Sci.* 101(2), 91-98. DOI: [10.1016/0168-9452\(94\)90244-5](https://doi.org/10.1016/0168-9452(94)90244-5)
- STINTZING, F. C., SCHIEBER, A., CARLE, R., 2003: Evaluation of colour properties and chemical quality parameters of cactus juices. *Eur. Food Res. Technol.* 216, 303-311. DOI: [10.1007/s00217-002-0657-0](https://doi.org/10.1007/s00217-002-0657-0)
- THAPPER, A., MAMEDOV, F., MOKVIST, F., HAMMARSTRÖM, L., STYRING, S., 2009: Defining the Far-Red Limit of Photosystem II in Spinach. *Plant Cell.* 21, 2391-2401. DOI: [10.1105/tpc.108.064154](https://doi.org/10.1105/tpc.108.064154)
- TOMARI, Y., MORI, N., WATANABE, H., 2021: Effects of supplemental irradiation of UV-A, blue, and far-red light with red light on the growth and functional components of *perilla frutescens*. *Eco-Engineering* 33. 3, 71-78. DOI: [10.11450/seitaikogaku.33.71](https://doi.org/10.11450/seitaikogaku.33.71)
- WITTAYATHANARATTANA, T., WANICHANANAN, P., SUPAIBULWATANA, K., GOTO, E., 2022a: Enhancement of bioactive compounds in baby leaf *Amaranthus tricolor* L. using short-term application of UV-B irradiation. *Plant Physiol. Biochem.* 182, 202-215. DOI: [10.1016/j.plaphy.2022.04.003](https://doi.org/10.1016/j.plaphy.2022.04.003)
- WITTAYATHANARATTANA, T., WANICHANANAN, P., SUPAIBULWATANA, K., GOTO, E., 2022b: A short-term cooling of root-zone temperature increases bioactive compounds in baby leaf *Amaranthus tricolor* L. *Front. Plant Sci.* 13:944716. DOI: [10.3389/fpls.2022.944716](https://doi.org/10.3389/fpls.2022.944716)
- WONG, C.E., TEO, Z.W.N., SHEN, L., YU, H., 2020: Seeing the lights for leafy greens in indoor vertical farming. *Trends Food Sci. Technol.* 106, 48-63. DOI: [10.1016/j.tifs.2020.09.031](https://doi.org/10.1016/j.tifs.2020.09.031)
- ZHEN, S., VAN IERSEL, M.W., 2017: Far-red light is needed for efficient photochemistry and photosynthesis. *J. Plant Physiol.* 209, 115-122. DOI: [10.1016/j.jplph.2016.12.004](https://doi.org/10.1016/j.jplph.2016.12.004)

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