Impacts of LED spectral quality on leafy vegetables: Productivity closely linked to photosynthetic performance or associated with leaf traits?

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Abstract: The success of growing vegetables indoors requires the most appropriate selection of lighting spectrum. This mini review discusses the impacts of LED spectral quality on different leafy vegetables with a focus on the studies of Chinese broccoli (*Brassica alboglabra*), ice plants (*Mesembryanthem crystallinum*) and lettuce (*Lactuca sativa* L. cv. Canasta). For each species, plants exposed to different spectral LED lights were all under the same light intensity and same photoperiod. Chinese broccoli grown under red(R):blue(B)-LED ratio of 84:16 (16B) had the highest light-saturated photosynthetic CO_2 assimilation rate (A_{sat}) and stomatal conductance ($g_{s\ sat}$) compared to plants grown under other R:B-LED ratios. It was also shown that 16B is the most appropriate selection for Chinese broccoli to achieve the highest shoot productivity with a rapid leaf number and leaf area development. The highest concentrations of photosynthetic pigments, soluble and Rubisco protein on a leaf area basis were also observed in 16B plants. The results conclusively affirmed that the highest productivity of Chinese broccoli grown under 16B is closely linked to the highest photosynthetic performance on a leaf area basis. For ice plants grown under R:B-LED ratios of 90:10 (10B), they had the highest shoot biomass with a faster leaf development compared to plants grown under other RB-LED combinations. However, there were no differences in A_{sat}, $g_{s\ sat}$, photosynthetic pigments, soluble and Rubisco proteins on a leaf area basis. In the case of lettuce plants, it was a surprise to observe that plants grown under 0B and 20G (20% green (G)-LED and 80% R-LED) had the highest shoot biomass, and largest total leaf area and light interception area but the lowest net maximal photosynthetic rate on a leaf area basis, compared to other plants. The combined RB-LED enhanced other photosynthetic parameters while 0B and 20G conditions had inhibitory effects on maximum quantum efficiency of PS II with lower photosynthetic pigments, total soluble protein and Rubisco protein. These results suggest that impacts of LED light quality on productivity of lettuce (*L. sativa* L. cv. Canasta) are closely linked to leaf traits not associated with photosynthetic performance on a leaf area basis.

Keywords: leafy vegetable, leaf traits, LED spectral quality, photosynthetic performance, productivity
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1 Introduction

The economic success of the vertical farming system depends on providing sufficient uniform lighting to the plants, to allow fast growth but with minimal energy utilization[1-4]. Light-emitting diodes (LED) lighting used in both the greenhouse and indoor crop production has received a greater deal of international effort in the past two decades[5,6]. LED allows the manipulation of the light spectra, thus enabling the most appropriate selection of lighting environment for the individual crop to enhance growth and productivity in a cost-effective manner[6-8].

The quality of light is especially important for plant growth when artificial light is used for indoor farming[8-11]. Compared to R-LED alone, combined RB-LED promotes growth in pepper[12,13], wheat[14], lettuce[15,16], spinach and radish[15], strawberry plantlet[17], rapeseed rosette leaves[18], cucumber seedling[19], common ice plant[20], Chinese broccoli[21,22] and rapeseed (*Brassica napus* L.) plantlets *in vitro*[23]. Although green wavelength (500 to 600 nm) is photosynthetically inefficient, it has been shown to have specific effect on various plant processes[24-28]. Enhanced lettuce growth when green light was supplemented to combined red and blue light was attributed to the better penetration of green light into the deeper canopy[24,27-29]. However, other researchers reported that monochromatic green light inhibited plant growth, especially at the seedling stage of lettuce[30] and tomato[31].

The blue and red light absorption by plants is as high as 90%[27], implying that plant development and photosynthetic process are strongly influenced by the combinations of blue and red lights[9,16,32-33]. For instance, red light supplemented with blue light could prevent elongation growth and leaf expansion[16,34,35]. Blue light affects the photosynthetic process directly by regulating stomatal movement[19,36], chloroplast development[13,37] and chlorophyll (Chl) synthesis[20,38]. For example, Schuerger et al.[13] examined the changes in leaf anatomy of pepper under different colour combinations of light. Their results indicated that leaf thickness and number of chloroplasts per cell depended much more

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on the level of blue light than other wavelengths. Blue light also increases photosynthetic light use efficiency through the regulation of PS II efficiency (ΦPSII) and electron transport rate (ETR)[20,33,36,39]. The expression of PSII-core monomer and PSII-core dimer[40] and *rbcS*, *rbcL*, *psbA*, *psbB* genes are also enhanced by blue light)[31]. Some researchers attributed the blue light effects on photosynthesis to a higher nitrogen and Rubisco content[20,40] and Rubisco activity[41]. Green light also affects various plant growth developmental and physiological processes such as stomata opening and photosynthesis[24,27,42]. For example, green light decreases stomatal conductance in lettuce[24], but increases plant biomass and Chl content in lettuce seedlings when combined with blue and red light[42]. However a high percentage of green light such as >50% reduces plant growth[9]. Klein[43] reviewed the impacts of green light on plants, and concluded that green light represses plant growth and development.

In Singapore, due to limited land, local farming currently accounts for only 10% of the leafy vegetables consumed in 2019. It has been projected that over the next ten years, the local supply of leafy vegetables must increase from 10% to 30% by developing high-tech urban farming. LED-integrated vertical farming systems have been developed by our research team for both indoors and greenhouse for different leafy vegetable production[1,2]. We have designed and optimized LED lightings for the cultivation of popular and high-valued leafy vegetables and herbs[1,2,16,20-22,44-47]. They are Chinese broccoli (*B. alboglabra*), Na Bai (*B. chinensis* L.), wild rocket (*Eruca sativa*), mizuna (*B. juncea var. japonica*), red and green leaves lettuce (*L. sativa*), ice plants (*M. crystallinum)*, red- and green-leaved Chinese Basil (*Perilla frutescens*), kale (*B. oleracea*, cvs. Curly kale; Kale Toscano and Borecole red); sweet basil (*Ocimum basilicum*), red and green Chinese Basil (*Perilla frutescens*). Generally (but not always) combined RB-LED is more effective than only R- or B-LED lighting in enhancing photosynthesis and thus productivity[20-22]. The optimal combinations of LED lightings are species-dependent. Different vegetable crops also have different requirements in durations[46] and light intensities[47]. Questions about what combinations of LED lighting should be selected for maximal productivity, are still open. The correlations between productivity and photosynthetic performance or morphological changes such as leaf traits are limited. This mini review discusses the impacts of LED quality on different leafy vegetables with a focus on our studies of Chinese broccoli (*B. alboglabra*), ice plants (*M. crystallinum*) and lettuce (*L. sativa* L. cv. Canasta).

2 Productivity is closely linked to both the photosynthetic performance and leaf development of Chinese broccoli (*B. alboglabra*) under the optimal combination of RB-LED

In addition to red light, many studies have manipulated the proportion of blue light necessary for normal plant growth[13,15,16,39,48]. Supplementing appropriate amount of blue light to red light results in dramatic effects on the morphology and anatomy structure[13,18,23,48-50], chloroplast structure[31,48,51,52] and photosynthetic performance[18,36,39,53-54]. In our study with Chinese broccoli, plants were exposed to different RB-LED ratios: 1) 100:0 (0B); 2) 92:8 (8B); 3) 84:16 (16B) and, 4) 76:24 (24B) under the same photosynthetic photon flux density (PPFD) of 210 μmol/m^2 s and same photoperiod of 12-h. Results presented in Table 1 show that Chinese broccoli grown under 16B had the highest A_{sat} and $g_{s\ sat}$ compared to plants grown 0B, 8B and 24B. The 16B is the most suitable combination of RB-LED for Chinese broccoli to achieve the most rapid leaf development with the highest leaf number, total leaf area and leaf mass per unit area (LMA) and greatest stomatal density (SD). Chinese broccoli grown under 16B also had the highest concentration of photosynthetic pigments, soluble and Rubisco proteins on a leaf area basis[21]. Thus, these results more conclusively affirm that 16B is the most suitable light source to achieve the highest photosynthetic capacities. The highest productivity (shoot fresh weight, FW and dry weight, DW) of Chinese broccoli grown under 16B is closely linked to the highest photosynthetic performance on a leaf area basis. Our studies with red- and green-leaved Chinese Basil (*P. frutescens*) and Na Bai (*B. chinensis* L.) also showed a similar correlation between photosynthetic performance and productivity under the optimal combination of RB-LED (unpublished data). In the study with cucumber (*Cucumis sativus*), Hogewoning et al.[39] reported that leaves grown at 7% blue light and 93% red light had the highest photosynthetic capacity (A_{max}) compared with 0% blue light and other combination of red and blue lights. The highest A_{max} associated with the highest LMA and Chl content per leaf area. In another study on cucumber (*C. sativus*), it was reported that blue light promotes maximal photosynthetic capacity associated with leaf development and plant water relations[53]. In the indoor plant cultivation of sweet basil (*Ocimum basilicum* cv. Superbo, Sais seeds, Cesena, Italy), Pennisi et al. (2019) also reported that the greatest biomass production was achieved with the correct combination of RB-LED lightings, which resulted in highest Chl content, water and energy use efficiency[54]. The fact that red light supplemented with blue light which increased productivity is linked to enhanced photosynthetic performance has also been reported in many other plant species. They are wheat plants (*Triticum aestivum* L.)[14], cucumber (*Cucumis sativus*) seedlings[19,49], different peppermint species (*Mentha piperita, M. spicata, M. longifolia)*[32]. In the study with lettuce plants (*Lactuca sativa* L.), blue light could promote photosynthetic performance or growth by stimulating morphological and physiological responses, yet there was no positive correlation between photosynthetic rate and shoot dry weight accumulation[36].

Goins et al.[55] examined the growth of *Arabidopsis* plants under different combinations of RB-LEDs. When grown under R-LED alone, *Arabidopsis* leaf morphology was abnormal with the downward curling of leaf margins. However, supplementing any level of B-LED restored normal leaf morphology[55]. Although the Chinese broccoli grown under 0B were smaller with lower shoot and root productivity, smaller leaf number and total leaf area (Table 1) compared to those grown under combined RB-LEDs, all plants look healthy with minimum overlap expanded leaves, which reflects the maximum light-interception per unit leaf area. Compared to R-LED alone (0B), all combined RB-LEDs promote leaf growth and development, dry matter accumulation and photosynthesis of Chinese broccoli (Figure 1 and Table 1). These results support the notion that for certain species any level of blue light regulates leaf development and photosynthetic performance[18,36]. In other words, blue light alleviate “red light syndrome” such as a low photosynthetic rate, low LMA, unresponsive stomatal conductance and impaired shoot and root growth[7,36,39, 51].

a. b.

Figure 1 Chinese broccoli (*B. alboglabra* Bailey) plants grown under different RB-LEDs for 15 d (a) and under 16B condition for 21 d (b) (unpublished data)

Table 1 Leaf traits (leaf number, leaf area, leaf matter accumulation, LMA, stomatal density, SD), shoot and root productivity and photosynthetic gas exchange of Chinese broccoli (*B. alboglabra*) grown under different combinations of RB-LEDs

Parameters	RB-LED light treatments			
	0B	8B	16B	24B
Leaf number	5.2±0.19^c	5.4±0.21^c	7.1 ±0.13^a	6.2 ±0.17^b
Leaf area/cm^2	89.8±11.6^d	122.5±12.8^c	198.3±25.1^a	162.4 ±19.2^b
LMA/(mg cm^{-2})	2.105±0.06^d	2.614±0.072^c	3.406±0.093^a	2.911±0.086^b
SD/(Stomata mm^{-2})	157.6±31.1^c	238.6±18.3^b	293.2±24.5^a	291.6±24.1^a
Shoot FW/g	10.12±0.74^d	13.54±1.09^c	22.17±0.88^a	16.73±0.92^b
Shoot DW/g	0.542± 0.031^d	0.873±0.048^c	1.678±0.062^a	1.179±0.051^b
Root FW/g	0.711±0.152^d	1.143±0.135^c	1.726±0.161^a	1.436±0.119^b
Root DW/g	0.073±0.011^d	0.121±0.017^c	0.179±0.020^a	0.147±0.018^b
A_{sat} /(μmol CO_2 m^{-2} s^{-1})	11.65±0.93^d	14.02±0.85^c	22.15±1.27^a	17.69±0.87^b
$g_{s\ sat}$/(mmol H_2O m^{-2} s^{-1})	325±12.1^c	372±10.3^b	448±10.9^a	436±11.6^a

Note: Parameters of productivity were measured after harvest (that was, 21 days after transplanting) whereas A_{sat} and g_s sat were determine 3 days before harvest. Means with different letters are statistically different (p<0.05; n = 7) as determined by Tukey's multiple comparison test (Partially modified from He et al. 2015[21]).

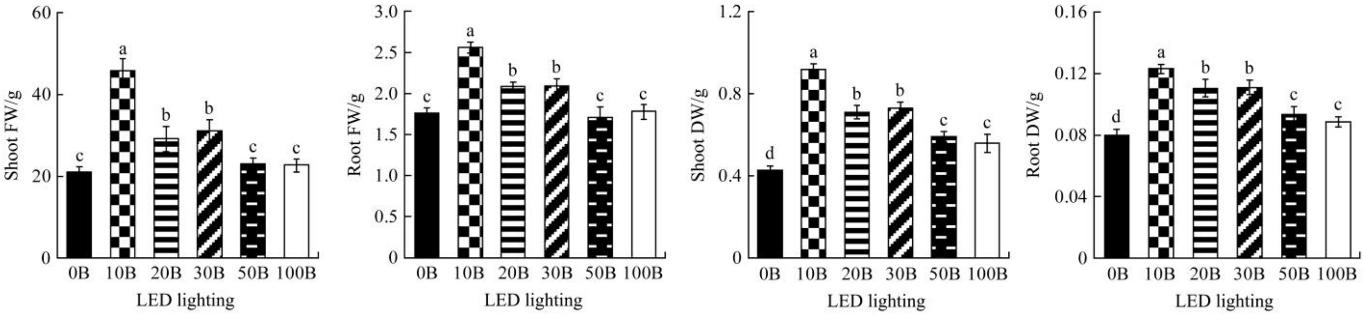
3 High B:R-LED ratios lead to the decline in productivity but do not affect the photosynthetic performance of ice plants (*M. crystallinum*)

It has long been known that the light absorption of photosynthetic pigments is greater in the blue and red regions of the photosynthetically active radiation spectral range[56]. However, the red light usually is the basal component to drive photosynthesis. Red light alone is sufficient for normal growth[8,57] because red wavelengths (600 to 700 nm) are efficiently absorbed by Chl[58]. Plants grown under blue light have higher total Chl content [20,21,39,42,53], higher Chl a/b ratio[32,59,60], greater cytochrome (Cyt)*f*[59], and Rubisco contents than plants grown under red light[20,31,59,60]. Furthermore, Hogewoning et al.[39] reported that the growth of cucumber in the absence of blue light, led to dysfunction of the photosynthetic machinery, in particular a loss of photochemical efficiency of PS II and the maximum photosynthetic capacity per leaf area. However, only 7% blue light was sufficient to prevent any overt dysfunction in photosynthesis[39]. Compared to 0% blue light, the A_{max} of cucumber grown at 7% blue light was two-fold higher and increased with increasing blue light up to 50%. On increasing blue light from 0 to 50% during growth, the increase in A_{max} *was* associated with a greater LMA, higher N and total Chl content per leaf area[39]. At 100% blue light, A_{max} was lower but maximal PS II efficiency was normal (i.e. F_v/F_m ratio >0.8). Our study with Chinese broccoli shows similar responses (Table 1) to increased blue light as cucumber leaves[39]. For instance, with increased blue light from 0 to 16% (16B), the increases in A_{sat} (=A_{max}) also associated with a greater leaf number, leaf area, LMA, SD, shoot and root biomass. However, plants grown under 16B and 24B had similar values of $g_{s\ sat}$ but lower A_{sat} was observed in plants grown under 24B (Table 1). These results imply that higher amounts of blue LED, for instance, 24B may cause some reversible damage on photosynthetic machinery as reflected by healthy Chl fluorescence F_v/F_m ratios of >0.8 (data not shown).

In our study with a facultative CAM ice plant (*M. crystallinum*)[39], impacts of different R:B-LED ratios on the photosynthetic performance and productivity differ from those of cucumber[39] and Chinese broccoli[21]. Figure 2a shows ice plants cultured aeroponically in a 16 h photoperiod at an equal photosynthetic photon flux density (PPFD) of 350 μmol/m^2 s under different RB-LED ratios: 1) 100:0 (0B); 2) 90:10 (10B); 3) 80:20 (20B), 4) 70:30 (30B), 5) 50:50 (50B) and 6) 0:100 (100B) for 14 d. Grown under 10B condition, ice plants had the highest shoot and root FW and DW compared to all other plants. No significant differences were observed in shoot and root FW and DW between 20B and 30B treatments. Plants grown under 0B, 50B and 100B conditions had similar lower values of shoot, root FW and DW (Figure 3). Our results of ice plants agree with the finding from many other studies that supplementing optimal amount of blue light to red light is necessary to achieve greater biomass accumulation[18,21,29,39,61,62]. However, similar to the 0B condition the stronger blue-LEDs such as 50B and 100B resulted in reduction of biomass accumulation in ice plant (Figure 3). In the study with lettuce, Wang et al.[36] studied how the different R:B-LED ratios affected photosynthetic performance. They reported that leaf photosynthetic capacity (A_{max}) and photosynthetic rate (P_n) were highest with R:B-LED ratio of 1 but increased with decreasing R:B-LED ratio (or increasing B-LED percentage). For ice plants, no differences in maximal photosynthetic O_2 evolution rate (Figure 4a), A_{sat}, (Figure 4b) and $g_{s\ sat}$ (Figure 4c) were observed among plants grown under different R:B-LED ratios although they were significantly higher than those of 0B plants. Statistically, ice plants grown under the different R:B-LED ratios had similar values of P_n, A_{sat} and $g_{s\ sat}$. In the study with rapeseed (*B. napus* L.), compared to 0% blue light, except for 100% B-LED, all other R:B-LED ratios (25%, 50% and 75%B) enhanced photosynthetic capacity (P_{max}). These results were similar to our results with ice plants (Figure 4a) except for that fact that rapeseed plants grown under 100% B-LED had similar lower P_{max} as 100% R-LED plants[18]. Rapeseed plants grown under 100% R-LED or 100% B-LED were stressed with a low photosynthetic maximum quantum yield (lower F_v/F_m ratio). However, in our study, all ice plants had F_v/F_m ratios of >0.8, indicating that no stress occurred in any plants[20].

a. b.

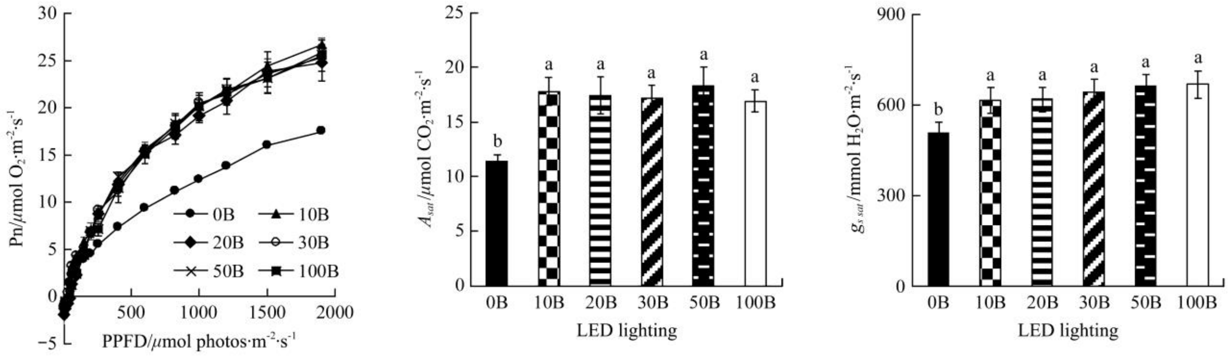
Figure 2 Ice plants (*M. crystallinum*) grown under different RB-LEDs (a) and under 10B condition for 18 d (b) (unpublished data)



a. b. c. d.

Note: Vertical bars represent the standard errors. Means with different letters are statistically different (p<0.05; n=6) as determined by Tukey's multiple comparison test (modified from He et al. 2017[20]). The same below.

Figure 3 Shoot FW and DW (a, c), root FW and DW (b, d) of ice plants (*M. crystallinum*) grown under different R:B-LED ratios for 21 d

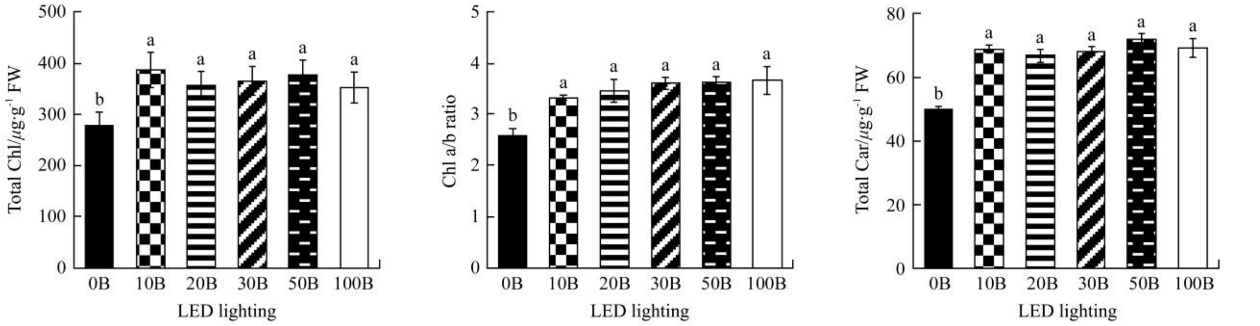


a. b. c.

Figure 4 Light response curves of photosynthetic O_2 evolution, P_n (a); A_{sat} (b) and $g_{s\ sat}$ (c) of ice plants (*M. crystallinum*) grown under different R:B-LED ratios for 21 d

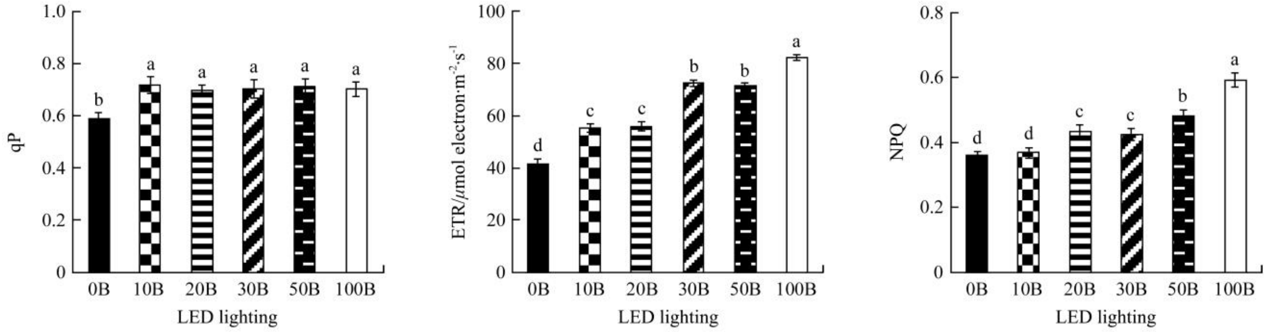
In rapeseed plants, it was also found that plants grown under different R:B-LED ratios and 100% B-LED had higher LMA, SD and total Chl content compared to those grown under 0% B-LED[18]. These results were similar to our studies with ice plants. Figure 5 shows that all R:B-LED ratios increased total Chl content, Chl a/b ratio and total carotenoids (Car) content to a similar higher level compared to those ice plants grown under 0B condition. However, there is no difference in Chl/Car ratio among ice plants grown under different R:B-LED ratios (data not shown). It was also reported that blue light affects Chl a/b-binding protein of PS II, and photosynthetic electron transport[36,59,63,64]. Chl or Car absorb blue light for the formation of 'sun-type' chloroplasts[59]. For ice plants, 10B was sufficient to stimulate 'sun-type' photosynthetic characteristic[65] at a rather low irradiance (red:blue LED; 315:35 μmol photon/m^2 s)[20]. Grown under R-LED alone (i.e. 0B), ice plants exhibited the characteristics of low-light-grown plants with lower P_n (Figure 4a) and A_{sat} (Figure 4b), less total soluble protein and Rubisco protein (data not shown)[20].

In the study with tomato (*Solanum lycopersicum*) seedlings, it was reported that the plant height was reduced under blue light, but the ΦPSII and ETR were enhanced[31]. In ice plants, photochemical quenching (qP, Figure 6a) and ETR (Figure 6b) measured under actinic light of 335 μmol photon/m^2 s that was close to the growth irradiance of all plants, were significantly higher in all plants grown under the different R:B-LED ratios compared to those grown under 0B condition[20]. Higher qP and ETR values of ice plants resulted from enhanced photosynthetic utilization of radiant energy due to the greater amount of total Chl contents and higher Chl a/b ratios (Figures 5a and 5b). Higher B-LEDs (20B, 30B, 50B and 100B) also resulted in higher NPQ in ice plants (Figure 6c). Higher level of blue light may damage PS II and ice plants increased NPQ to protect themselves against excess excitation energy through Car[66-69]. Recently, it was reported that cyclic electron flow (CEF) which generates a pH gradient (ΔpH) across thylakoid membrane triggers the protective process of NPQ under stress conditions[70]. The CEF around PSI is another mechanism for dissipating excess photon energy[71-75]. Higher ETR values of ice plants grown under higher levels B-LED (Figure 6b) could be partially due to CEF around PSI that is essential for protecting both PS I and PS II from the damage[73,74,76,77]. Red light alone inhibited electron transport from PS II donor side to PS I in cucumber[51] whereas decreased F_v/F_m ratio was observed in lettuce exposed to 100% B-LED[36]. However, all ice plants had F_v/F_m ratios of >0.8 regardless of R:B-LED ratios including 0B condition (data not shown). This result suggests that ice plants grown under higher levels of B-LED could had spent more energy to protect them from photodamage and/or recover from photodamage and thus decreased productivity (Figure 3).



a. b. c.

Figure 5 Total Chl content (a), Chl a/b ratio (b) and total Car content (c), of ice plants (*M. crystallinum*) grown under different R:B-LED



a. b. c.

Figures 6 qP (a), ETR (b) and NPQ measured at a PPFD of 335 μmol photon/m^2 s from ice plants (*M. crystallinum*) grown under different R:B-LED ratios for 21 d. Each bar is the mean of 20 measurements of 4 different leaves from 4 different plants

4 Productivity is closely associated with leaf traits not photosynthetic performance of lettuce (*L. sativa* L. cv. Canasta) grown under different qualities of LEDs

With a focus on our studies of Chinese broccoli and ice plants, this paper has discussed how different R:B-LED ratios affected photosynthesis and productivity in the previous sections. Although the optimal R:B-LED ratio is species-dependent, generally combined RB-LED is more effective than R-LED or B-LED alone in enhancing photosynthesis and thus productivity. This section discusses the impacts of R-LED, supplemented green (G)-LED to R-LED, and combined RB-LED on lettuce (*L. sativa* L. cv. Canasta).

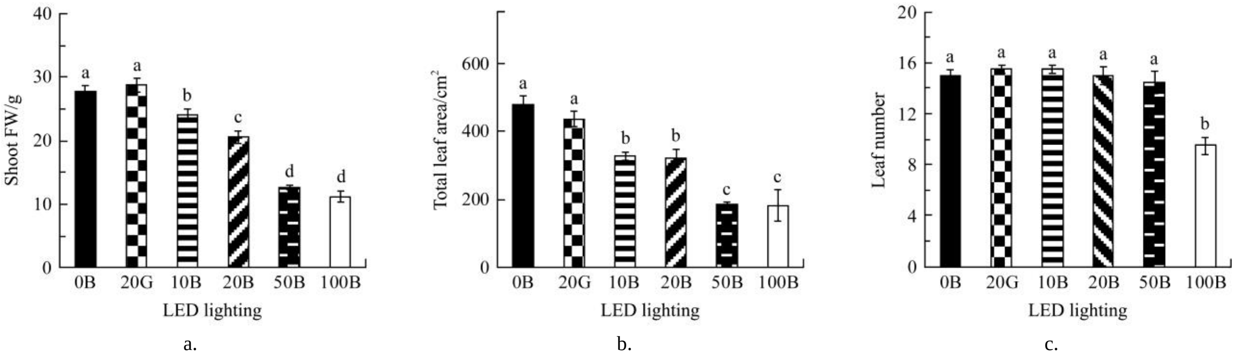
All lettuce plants were exposed to an equal PPFD of 230 μmol/m^2 s (16-h photoperiod) under each of the six combined LED ratios: 100% red (0B); 80% red and 20% green (20G); 90% red and 10% blue (10B); 80% red and 20% blue (20B); 50% red and 50% blue (50B); and 100% blue (100B). Figure 7 shows the lettuce plants grown under different LEDs for 21 d after transplanting. Compared to plants grown under 0B and 20G conditions, plants grown under different R:B-LED ratios were greener with some red pigment (Figure 7) but lower shoot FW (Figure 8a), smaller total leaf area (Figure 8b). However, all plants had similar leaf number except for those grown under 100B plants with smaller number of leaves (Figure 8c). These results indicate that B-LED inhibited leaf expansion but not leaf emergence of lettuce (*L. sativa* L. cv. Canasta). The results also agree with that red light supplemented with blue light could prevent elongation growth and leaf expansion reported in two different *Lactuca* recombinant inbred lines (RILs) by our research team[16], cucumber[34] and tomato seedlings[35]. However, in our studies with Chinese broccoli[21] and ice plants[20], it was found that the highest shoot productivity associated with a greater leaf number and a rapid leaf area development when 16% and 10% of B-LED was added to R-LED, respectively.

In a study with lettuce (*L. Sativa* 'Waldmann's Green'), Kim et al.[24] reported that green light enhanced growth when it was supplemented to combined red and blue light. Study with another lettuce variety (*L. sativa* L. var. youmaicai), Liu et al.[28,29] also reported that green light added to a wide spectral LED light increased shoot dry mass, total Chl content, light absorptance and CO_2 assimilation. However, other researchers reported that monochromic green light at low intensity inhibited plant growth, especially at the seedling stage of lettuce[30] and tomato[31]. Experiments with the seedling stage of red leaf lettuce (*L. sativa* L. cv Banchu Red Fire), different monochromic G-LEDs with different peak wavelengths such as 510 nm, 520 nm and 530 nm (named G510, G520, G530) were used at different photosynthetic photon flux (PPF) of 100, 200 and 300 μmol/m^2 s[30]. Compared with white fluorescence light, lettuce grown at low PPF 100, all G-LEDs decreased shoot growth. Shoot growth under 510 nm at PPF300 was the highest among all treatments. Leaf photosynthetic rate (P_n) of plants under G-LED at PPF 200 was significantly higher compared to those at PPF100. Plants grown with G510 had the highest P_n among all light sources. These results indicated that short wavelength of G510 at higher intensities increased the growth and P_n. With higher PPF the green light would penetrate into the leaves, be absorbed in chloroplast and drive the photosynthesis enough to growth[30]. Based on the above discussion, it seems that the impacts of G-LED on plant growth depend on not only the variety but also the wavelength, the intensity of G-LED and the other LED-spectra to which G-LED was supplemented. The effects of green light supplemented to combined red and blue light or green light alone on plant growth and physiology have been investigated and discussed above. However, there is no report of plants being cultivated under G-LED supplemented to R-LED only. Our study with lettuce (*L. sativa* L. cv. Canasta), grown under 20% G-LED (20G at wavelength 517 nm) and 80% R-LED had similar higher values of shoot FW and DW (data not shown), total leaf area as those plants grown under 100% R-LED (0B) compared to any combined R:B-LED ratio (Figure 8). These results indicate that lettuce plants absorbed the 20% G-LED for growth. However, lettuce (*L. sativa* L. cv. Canasta) grown under 0B and 20G had lower contents of total Chl (Figure 9a) and Car (data not shown), and lower net maximal photosynthetic rate (Net $P_{\max}$) on a leaf area basis measured under saturated light (Figure 9b) compared to those plants grown under all combined R:B-LED. The results also showed that combined RB-LEDs enhanced other photosynthetic performance while 0B and 20G conditions had inhibitory effects. For example, the maximum quantum efficiency of PS II (F_v/F_m ratio) was the lowest under 0B and 20G (Figure 9c). Cucumber[30] and tomato seedling leaves[31] developed under red light or green light alone was also shown lower F_v/F_m ratio. The concentrations of PS II, Cyt b_6f, total soluble protein and Rubisco protein, ETR and qP increased with increasing B-LED in those plants grown under different R:B-LED ratios while 0B and 20G plants had the lowest values (data not shown). It is well known that biomass accumulation and plant growth strongly depends on net photosynthesis and photosynthetic performance[14,32,36,49,78,79]. However, these correlations were not observed in lettuce (*L. sativa* L. cv. Canasta) grown under different LED qualities (Figures 8a, 9b and 9c).

It was reported that leaf growth determines light interception area which is an important parameter in determining plant productivity[80-82]. Figure 10a shows the light interception areas measured from the same plants that were used for the measurements of total leaf area (Figure 8b). Plants grown under 0B and 20G conditions had the largest light interception areas followed by those grown under 10B and 20B conditions. Lettuce plants grown under 50B and 100B conditions had the smallest light interception areas. By comparing the total leaf areas (Figure 8b) and light interception areas (Figure 10a), it was found that leaves grown under 0B and 20G had similar greatest values due to their large elongated and non self-shading expanded leaves (Figure 7). Those plants grown under 50B and 100B also had similar values of total leaf area and light interception area but due to their smallest non-self-shading leaves (Figure 7). However, due to some self-shading, plants grown under 10B and 20B, had light interception areas of 271 cm^2 and 286 cm^2, respectively (Figure 10a) and they were significant lower than the total leaf areas of 328 cm^2 and 322 cm^2 (Figure 8b). Light interception area could predict the whole plant carbon gain[80-82]. Figure 10c shows the photosynthetic capacities (PA) that were calculated from: PA = Gross $P_{\max}$ × total light interception area per plants × absorptance (Figure 10b). Although they had lower absorptance compared to those plants grown under RB-LEDs (Figure 10b), on a whole plant basis, 0B and 20G plants had the highest PA which was mainly due to the highest light interception area (Figure 10a). For plants grown under 10B and 20B, the higher values of PA resulted from both larger light interception area and higher absorptance. For those 50B and 100B plants, they had the smallest light interception area and thus the lowest PA. The above results indicate the importance of whole plant photosynthetic capacities instead of photosynthetic rate on a leaf area basis (Figure 9b), which is closely linked to the leaf traits in determining the final productivity.

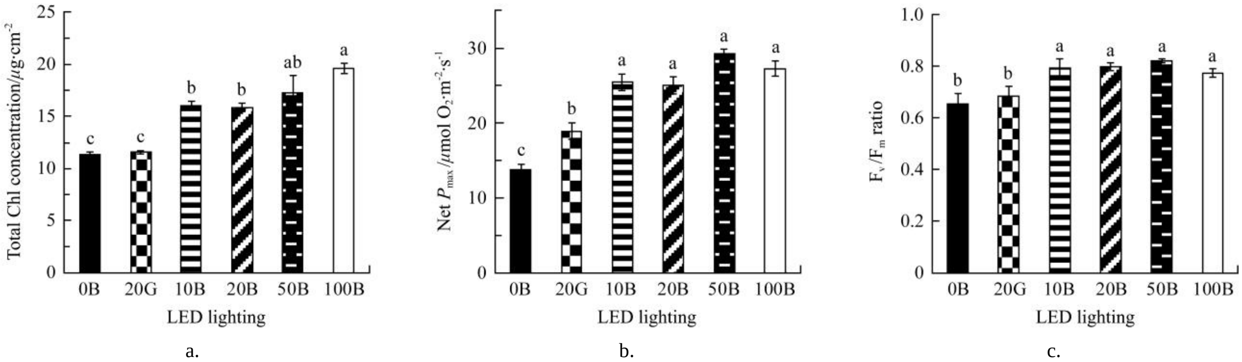
There are tremendous morphological variations such as leaf length, shape, size, color, and heading type in different types of lettuce[83]. Leaf anatomical structure that closely related to photosynthetic performance also varies greatly among and within plant species under different environmental conditions[84-86]. Different LED spectral qualities further modify the plant morphological and anatomical features of different types of lettuce[3,6,24,28,36,40,42,83]. Leaf functional traits including both morphological and anatomical traits determine not only the quantity of light interception but also the photosynthetic capacity and partitioning of photoassimilated carbon[87]. Engineering leaf functional traits to optimize light interception and to improve photosynthetic performance has been reported in rice[88] and wheat[89]. In a study with Eustoma, Roni et al.[86] reported that both quality and quantity of LEDs resulted in the changes of photosynthetic performance, and phenotypic variations of leaf morphology and anatomy. Using the loose-headed lettuce variety "United States greatly fast growing lettuce", Zhang et al.[90] reported that lettuce phenotype and nutritional quality were significantly changed under different LED lights. By controlling all other environmental conditions, it is feasible for a smart plant factory with artificial light (PFAL) to screen and to improve leaf functional traits in relation to their photosynthetic performance through manipulating LED conditions. Although it remains a challenge, using high-throughput plant phenotyping infrastructure corresponding principles for phenotype data analysis [91], the PFAL has a capability of phenotyping of leaf functional traits of different leafy vegetables to improve both productivity and quality on a large scale[92].

Figure 7 Lettuce (*L. sativa* L. cv. Canasta) grown under different combined LED lighting conditions for 21 d. 100% red (0B); 80% red and 20% green (20G); 90% red and 10% blue (10B); 80% red and 20% blue (20B); 50% red and 50% blue (50B); and 100% blue (100B) (unpublished data)



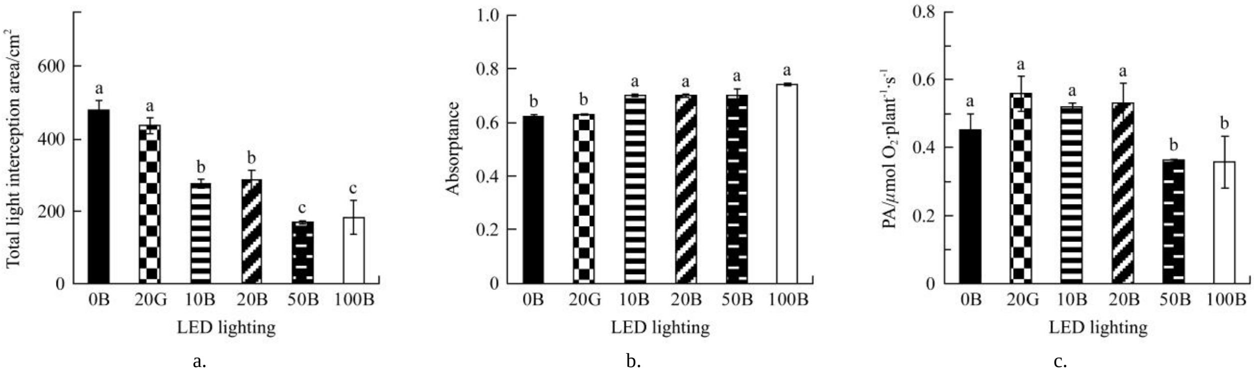
Note: Vertical bars represent the standard errors. Means with different letters are statistically different (unpublished data).

Figure 8 Shoot FW (a), total leaf area (b) and leaf number (c) of *L. sativa* (cv. Canasta) grown under different LED lightings for 21 d



Note: Vertical bars represent the standard errors. Means with different letters are statistically different (unpublished data).

Figure 9 Total Chl content (a), Net P_{max} (b) and F_v/F_m ratio (c) of lettuce (*L. sativa* L. cv. Canasta) grown under different LED lightings for 21 d



Note: Vertical bars represent the standard errors. Means with different letters are statistically different (unpublished data).

Figure 10 Light interception area (a), absorptance (b) and photosynthetic capacity, PA (c) of lettuce (*L. sativa* L. cv. Canasta) grown under different LED lightings for 21 d

5 Conclusions

Although the optimal R:B-LED ratio is species-dependent, generally, optimal combined RB-LED is more effective than R-LED or B-LED alone in enhancing photosynthesis and thus productivity. The impacts of G-LED on photosynthetic performance and productivity depend on not only plant species but also its wavelength, intensity and the combination of G-LED with other LED spectra. Productivity is closely linked to photosynthetic performance on a leaf area basis when plants have the maximum light-interception per unit leaf area. Otherwise, leaf traits such as light interception area and absorptance are important factors in determining the whole plant photosynthetic capability that is associated with productivity.

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