



The Photosynthetic Performance of Red Leaf Lettuce under UV-A Irradiation

Giedre Samuoliene *[®], Akvile Virsile[®], Jurga Miliauskienė, Perttu Haimi, Kristina Laužikė, Julė Jankauskienė, Algirdas Novičkovas, Asta Kupčinskienė and Aušra Brazaitytė

Institute of Horticulture, Lithuanian Research Centre for Agriculture and Forestry, Kaunas str. 30, Kedainiai 58344, Lithuania; akvile.virsile@lammc.lt (A.V.); jurga.miliauskiene@lammc.lt (J.M.); perttu.haimi@lammc.lt (P.H.); kristina.lauzike@lammc.lt (K.L.); jule.jankauskiene@lammc.lt (J.J.); algirdas.novickovas@tmi.vu.lt (A.N.); asta.kupcinskiene@lammc.lt (A.K.); ausra.brazaityte@lammc.lt (A.B.)

* Correspondence: giedre.samuoliene@lammc.lt

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Abstract: The objective of this study was to evaluate how different UV-A wavelengths influence the morphology and photosynthetic behavior of red-leaf lettuce (*Lactuca sativa* L. cv. Maiko). In the experiments, the main photosynthetic photon flux consisted of red (R) and blue (B) light, supplemented with equal doses of different UV-A wavelengths (402, 387 and 367 nm). Treating the crops with low dosages of specific narrow-band UV-A radiation at key points in the life cycle initiated a cascade of responses in the above-ground biomass. According to the results, red-leaf lettuces acclimated to longer UV-A wavelengths by increasing biomass production, whereas different UV-A wavelengths had no significant effect on plant senescence reflectance, nor on the normalized difference vegetation index. A significant decrease in the maximum quantum yield of the PSII photochemistry of dark (Fv/Fm) and light (Φ_{PSII}) adapted plants was observed. A lack of significant changes in non-photochemical fluorescence quenching indicates that photo-inhibition occurred under RBUV367, whereas the photosynthetic response under RB, RBUV402, and RBUV387 suggests that there was no damage to PSII. The correlation of the photosynthetic rate (Pr) with the stomatal conductance (gs) indicated that the increase in the Pr of lettuce under supplemental UV-A radiation was due to the increase of gs, instead of the ratio of the intracellular to ambient CO₂ content (C_i/C_a) or stomatal limitations.

Keywords: controlled environment; morphology; photosynthesis

1. Introduction

The impact of different light indices, such as the wavelength and intensity, on plant photophysiological responses has been well described [1–3]. The understanding of the importance of controlling the light conditions in closed environment agricultural (CEA) systems is growing [1,4–7]. However, despite major research efforts focused on clarifying the impact of light quality and/or quantity on plants, there is still relatively little data concerning UV-A mediated responses. It has been established that plant responses to UV-A are mediated by blue-light photoreceptors, such as phototropins, cryptochromes (peak absorption at 370 and 450 nm) and Zeitlupe (ZTL) proteins [8,9]. In contrast to UVR8 photoreceptors, which absorb light between 280 and 315 nm [10], these systems act as photon counters within the range of 350–500 nm [11]. Generally, blue and red light are considered to be the most efficient wavelengths for driving photosynthesis in plants, and this has been a topical issue for several decades [12]. The perception of blue light through the aforementioned photoreceptors allows plants to sense the intensity of competition for light. Besides the morphogenetic effects, fluctuations in blue light involve changes in both energy balance components, and in gas exchange dynamics through stomatal functioning [13]. There is currently limited data concerning plant responses to UV-A.



However, some remarks can be drawn regarding the effects UV-A has on plants, as it affects both plant biomass accumulation and morphology [14,15], photosynthetic processes [16], and metabolic responses [17], although the direction of the responses depends on dose, duration [18,19], plants' genetic backgrounds [20], and the plant's organs [21].

The absorption, transmission or reflection of the electromagnetic spectrum by plant pigments can play a significant role in the monitoring of their response to environmental factors. Optical properties of plant species depend on plant physiology, morphology or anatomy, and thus variations in leaf structure, as well as pigment and water content, can result in changing reflectance properties [22]. The light reactions of photosynthesis regulate the conversion of electric light energy into biomass. However, not all photons are used to drive light reactions. Higher plants have developed a complex set of responses to excess light, which allows them to safely dissipate excess light energy as heat or as fluorescence [23]. The complex set of photo- and non-photochemical quenching reactions that have evolved in plants to mitigate photoinhibition has allowed them to thrive [24]. However, there is currently no common opinion concerning plant responses to UV-A. The objective of this study was to explore the physiological responses of red leaf lettuce to the UV-A spectrum, and to determine the effects of irradiation with different wavelengths of UV-A LEDs on biomass accumulation and photosynthetic behavior.

2. Materials and Methods

2.1. Plant Material and Growth Conditions

The experiments were performed in a walk-in controlled-environment growth chamber (4 × 6 m). Day/night temperatures of $21/17 \pm 2$ °C were established, with a 16 h photoperiod and relative humidity of 50–60%. Red leaf lettuce (*Lactuca sativa* L. cv. Maiko) was cultivated in a peat substrate (Profi 1, JSC Durpeta, Sepeta, Lithuania) (pH 6). The average amounts of nutrients (mg L⁻¹) in the substrate were as follows: N, 110; P₂O₅, 50; K₂O, 160. The microelements Fe, Mn, Cu, B, Mo and Zn were also present. Electrical conductivity (EC) varied between 2.0 and 2.5 m S/cm ± 0.03 m S/cm. Three seeds were seeded into a 120 ml vessel (58 × 55 × 70 mm); 28 vessels were used for each treatment. The plants were watered as needed to maintain an even soil moisture. Analyses were performed at the end of the lighting experiment in the maturity stage, at 49 according to the BBCH-scale, when typical above ground biomass was reached.

The plants were illuminated with a custom-made lighting system containing four separate modules for parallel growth runs. In order to achieve different spectra, desired values of PPFD, and the required light switch on/off regimes, each group of LEDs in each lighting module was independently controlled with the help of a remote computer. The surface area under each lighting module was 0.22 m². The distance between the canopy and light source was 25 cm. The main photosynthetic photon flux was provided by blue and deep-red LEDs, with peak wavelengths of 447 nm (LedEngin LZ1-00B200, Osram Sylvania, Wilmington, MA, USA) and 665 nm (Luxeon Rebel LXM3-PD01-0300, Philips Lumileds Lighting Co., San Jose, CA, USA), respectively. Three lighting modules were equipped with supplemental high-power UV-A LEDs emitting at 367 nm (LedEngin LZ4-04UV00, Osram Sylvania, Wilmington, MA, USA), or 402 nm (LedEngin LZ440UB00-U7, Osram Sylvania, Wilmington, MA, USA). The photosynthetic photon flux density (PPFD) of the blue and red components and photon flux densities (PFD) of the UV-A wavelengths are presented in Table 1. The PPFD was measured and regulated at the soil level using a photometer–radiometer (RF-100, Sonopan, Bialystok, Poland).

Treatment	R665 mol m ⁻² s ⁻¹	B447 mol m ⁻² s ⁻¹	UV402 mW cm ⁻²	UV387 mW cm ⁻²	UV367 mW cm ⁻²
RB	225	25			
RBUV402	225	25	2.2		
RBUV387	225	25		2.2	
RBUV367	225	25			2.2

Table 1. Experimental lighting conditions.

The emission spectra of the LEDs were measured using a photonic multichannel analyzer (Hamamatsu PMA- 12, Japan), and are presented in Figure 1. For the simultaneous measurement of emission spectra and irradiance level from UV LEDs, a calibrated spectrometer (Ocean Optics Flame-S-UV-VIS-ES, USA) with a cosine corrector (Ocean Optics CC-3-DA, USA) was used.



Figure 1. Emission spectra of the LEDs used in the lighting equipment. UV-A at 367, 387 and 402 nm is represented on the left axis as irradiance (mW cm⁻²); blue 447 nm and red 665 nm are represented on the right axis as photosynthetic photon flux density (PPFD) (μ mol m⁻² s⁻¹).

2.2. Leaf Gas Exchange Indices

The photosynthetic rate (Pr, μ mol CO₂ m⁻² s⁻¹), transpiration rate (Tr, mmol H₂O m⁻² s⁻¹), stomatal conductance (gs, mol H₂O m⁻² s⁻¹), intracellular CO₂ concentration (μ mol mol⁻¹), and ratio of intercellular to ambient CO₂ concentration (C_i/C_a) were measured on the third developed leaf, using a portable photosynthesis system (LI-COR 6400XT, USA). The leaf chamber conditions were set at 21 °C, a CO₂ concentration of 400 µmol mol⁻¹, and 60% relative humidity. Artificial irradiation in the leaf chamber was supplied from 665 and 470 nm LED sources (665 and 470 nm), PPFD ~1000 µmol m⁻² s⁻¹. Photosynthesis was measured from 9 to 12 am. Water usage efficiency (WUE, µmol CO₂ mmol⁻¹ H₂O) and light use efficiency (LUE, mol CO₂ mol⁻¹ photons) were also calculated.

2.3. Chlorophyll Fluorescence

Chlorophyll fluorescence was measured using red (660 nm) and blue (450 nm) excitation wavelengths as the measuring light, using a multi-mode chlorophyll fluorometer acquisition system (OS5p, Opti-Sciences, USA).

Measurements of light-adapted steady state chlorophyll fluorescence (F'), light-saturated chlorophyll fluorescence (F'_m), and F'₀ were used to calculate the relative PSII operating efficiency (Φ_{PSII}). Dark-adapted (40 min) F₀ and F_m measurements allowed the calculation of the maximum

quantum efficiency of PSII (F_v/F_m). Non-photochemical quenching (NPQ) was calculated using the following formula:

$$NPQ = F_m/F'_m - 1 \tag{1}$$

The electron transport rate (ETR) was estimated using the equation given by Baker [25]:

$$ETR = 0.5 \times 0.84 \times PPFD \times \Phi_{PSII}$$
⁽²⁾

2.4. Spectral Reflectance Indices

The spectral reflectance was measured using a leaf spectrometer (CID Bio-Science, USA) from 9 to 12 am. Reflection spectra obtained from the leaves were used to calculate the photochemical reflectance index (PRI), which shows changes in the xanthophyll cycle, using the following formula:

$$PRI = (R531 - R570)/(R531 + R570)$$
(3)

The normalized difference vegetation index (NDVI), which shows changes in biomass content, was calculated by:

$$NDVI = (R800 - R680)/(R800 + R680)$$
(4)

The plant senescence reflectance index (PSRI), which shows changes in dry or senescent carbon, was calculated by:

$$PSRI = (R680 - R500)/R750$$
(5)

The carotenoid reflectance index (CRI), which shows changes in the carotenoids to chlorophyll ratio, was calculated by:

$$CRI = (1/R510) - (1/R700)$$
(6)

The anthocyanin reflectance index (ARI), which shows changes in the anthocyanin amount, was calculated by:

$$ARI = (1/R550) - (1/R700)$$
(7)

where R800, R750, R700, R680, R570, R550, R531, R510 and R500 represent the leaf reflectance integrated over a 10 nm wavelength band centered on 800, 750, 700, 680, 570, 550, 531, 510 and 500 nm, respectively.

2.5. Sugars

The fructose, glucose, sucrose, and raffinose content was analyzed in leaves of plants of technical maturity at the end of the experiment, according to the Ma et al. method [26], with some modifications. Half a gram of fresh plant tissue was ground and diluted with deionized H₂O. The extraction was carried out for 4 h at room temperature with mixing. Samples were centrifuged at 14,000 *g* for 15 min. A clean-up step to remove soluble proteins, according to Brons and Olieman's instructions [27], was performed prior to the chromatographic analysis: One (1) mL of the supernatant was mixed with 1 mL of 0.01% (*w*/*v*) ammonium acetate in acetonitrile and incubated for 30 min at + 4 °C. The samples were centrifuged at 14,000 *g* for 15 min and filtered through a 0.22 µm PTPE syringe filter (VWR International, USA). The analyses were performed on a Shimadzu HPLC (Japan) instrument equipped with an evaporative light scattering detector (ELSD). The separation of carbohydrates was performed on a Shodex VG-50 4D HPLC column with deionized water (mobile phase A) and acetonitrile (mobile phase B) gradient. The gradient was maintained at 88% B for 13 minutes, changed linearly to 70% B in 9 minutes, kept at 70% B for one minute, raised back to 88% B in two minutes, and then the column was equilibrated to 88% B for five minutes. The flow rate was 0.8 mL min⁻¹.

2.6. Biometric Measurements

Plant dry weight (DW) was determined by harvesting leaves from five different plants per light treatment. DW was weighed after tissue dehydration at 70 °C for 48 h (Venticell-BMT, Czech Republic). Leaf area (LA) was determined by using a leaf area meter (AT Delta–T Devices, UK).

2.7. Statistical Analysis

The data were processed using XLStat software (Addinsoft, USA, 2019), and analyzed using the Tukey (HSD) test at a confidence level of p = 0.05, or in MS Excel (version 7.0); the standard deviation representing the mean of three replications and multivariate principal component analysis (PCA) were performed. The results are presented in a PCA scatter plot showing the distinct differences in the photosynthetic indices and primary metabolites in lettuce under different lighting spectra, and a correlation circle (based on Pearson's correlation matrix) summarizes the metabolic relationships between the investigated metabolites and minerals under different lighting spectra.

3. Results

3.1. Leaf Pigments, Morphology and Biomass

Both the carotenoid (CRI) and anthocyanin (ARI) reflectance indices of red leaf lettuce increased significantly under RBUV387 treatment during the experiment, compared with RB (control) (Table 2). The CRI and ARI of lettuce under RBUV387 were 1.7 and 1.4 times higher than that of the control plants. A significant increase of dry weight (DW) and leaf area (LA) was observed under RBUV402 treatment, while other UV-A components resulted in a significant decrease of DW and LA. DW and LA were lower by 15.6% and 21.6% under RBUV387, and were 34.4% and 27.8% lower under RBUV367, respectively. Changes of the plant senescence reflectance (PSRI) and normalized difference vegetation (NDVI) indices were not significant between treatments.

Treatments	CRI	ARI	PSRI	NDVI	DW, g	LA cm ²
RB	0.15b 0.03	0.12b 0.02	0.03a 0.01	0.77a 0.05	0.96ab 0.09	798.8ab 98.4
RBUV402	0.08b 0.04	0.05c 0.01	0.06a 0.04	0.65a 0.16	1.17a 0.23	899.5a 81.1
RBUV387	0.26a 0.02	0.17a 0.02	0.03a 0.00	0.85a 0.02	0.81b 0.11	626.0bc 93.4
BRUV367	0.10b 0.02	0.03c 0.01	0.01a 0.00	0.83a 0.00	0.63b 0.02	576.5c 59.3
RB		RBUV402		RBUV387		RBUV367

Table 2. Leaf pigments and growth characteristics of lettuce subjected to different light qualities.

RB—Red 662 and Blue 452 nm (Control); BRUV402—Control with UV-A 402 nm; BRUV387—Control with UV-A 387 nm; BRUV367—Control with UV-A 367 nm. Total PPFD was maintained at 250 μ mol m⁻² s⁻¹, changing the input of red to 662 nm. The data were processed using XLStat software and the Tukey (HSD) test at a confidence level of p = 0.05 (biological replicates, n = 5). CRI—carotenoids/chlorophyll ratio, ARI—anthocyanin amount, PSRI—dry or senescent carbon, NDVI—biomass content, DW—dry weight, LA—leaf area.

3.2. Photosynthetic Response

RBUV367 resulted in a significant increase of the photosynthetic rate (Pr), stomatal conductance (gs), transpiration rate (Tr), and light use efficiency (LUE). The Pr, gs, Tr and LUE of RBUV367 showed values about 1.6 times greater than in control plants. RBUV402 also resulted in a significant increase of Pr, gs and LUE, of up to 1.8 times higher compared to RB treatment. No significant differences between treatments were detected in water use efficiency (WUE) and the ratio between intracellular and ambient CO_2 content (C_i/C_a) (Figure 2). The lowest values of Pr, gs, Tr and LUE were found under BR treatment.



Figure 2. Photosynthetic status of lettuce subjected to different light qualities: RB—Red 662 and Blue 452 nm (Control); BRUV402—Control with UV-A 402 nm; BRUV387—Control with UV-A 387 nm; BRUV367—Control with UV-A 367 nm. Total PPFD was maintained at 250 µmol m⁻² s⁻¹, changing the input of red to 662 nm. The data were processed using XLStat software and the Tukey (HSD) test at a confidence level of p = 0.05 (biological replicates, n = 5). Different letters indicate significant differences at p < 0.05. Pr (a)—photosynthetic rate, gs (b)—stomatal conductance, C_i/C_a (c)—ratio between intracellular and ambient CO₂ content, Tr (d)—transpiration rate, WUE (e)—water use efficiency, LUE (f)—light use efficiency.

The maximum quantum yield of the PSII photochemistry of dark (F_v/F_m) and light (Φ_{PSII}) adapted plants (Figure 3A,B) under RBUV367 was significantly lower (6–7%) compared to the other lighting treatments. The value of the photochemical reflectance index (PRI) under RBUV367 was higher, whereas no significant differences were found between RB or RB402 (Figure 3D). Non-photochemical fluorescence quenching (NPQ) also showed no significant differences between treatments.

3.3. Soluble Sugars

In general, the hexose to sucrose ratio (Hex/Suc) increased with decreasing wavelengths of UV-A radiation (Figure 4). The hex/suc ratio under RBUV367 was 3.2 times higher compared to under RB treatment. Compared to RB treatment, RBUV368 resulted in a significant increase of glucose (1.5 times) and a significant decrease of raffinose (5.9 times). A significant increase of fructose and sucrose was detected under RBUV402, by 1.4 and 1.2 times, respectively, compared to RB. The highest total content of carbohydrates of all lighting treatments was observed under RBUV402.





Figure 3. Quantum efficiency of PSII photochemistry (**a**,**b**), non-photochemical fluorescence quenching (NPQ) (**c**), and the photochemical reflectance index (PRI) photochemistry (**d**) of lettuce subjected to different light qualities: RB—Red 662 and Blue 452 nm (Control); BRUV402—Control with UV-A 402 nm; BRUV387—Control with UV-A 387 nm; BRUV367—Control with UV-A 367 nm. Total PPFD was maintained at 250 µmol m⁻² s⁻¹, changing the input of red to 662 nm. The data were processed using XLStat software and the Tukey (HSD) test at a confidence level of *p* = 0.05 (biological replicates, *n* = 5). Different letters indicate significant differences at *p* < 0.05. Fv/Fm—maximum quantum yield of PSII photochemistry of dark-adapted plants; Φ_{PSII} —actual quantum yield of PSII photochemistry of light-adapted plants.



Figure 4. Alteration of soluble sugars of lettuce subjected to different light qualities: RB—Red 662 and Blue 452 nm (Control); BRUV402—Control with UV-A 402 nm; BRUV387—Control with UV-A 387 nm; BRUV367—Control with UV-A 367 nm. Total PPFD was maintained at 250 µmol m⁻² s⁻¹, changing the input of red to 662 nm. The data were processed using XLStat software and the Tukey (HSD) test at a confidence level of *p* = 0.05 (biological replicates, *n* = 5). Different letters indicate significant differences at *p* < 0.05. Fru—fructose, Glu—glucose, Suc—sucrose, Raf—raffinose, Hex—sum of hexoses.

3.4. PCA Scatterplot and Correlations

The results of the PCA score scatterplot show the average coordinates of the photosynthetic indices (Pr, gs, C_i, C_i/C_a, Tr, WUE, LUE), quantum efficiency for the PSII photochemistry (F_v/F_m , Φ_{PSII}), non-photochemical and photochemical photochemistry (NPQ, PRI), individual sugars (fructose, glucose, sucrose and raffinose), leaf pigments (CRI, ARI), and growth characteristics (PSRI, NDVI, DW, LA) under different supplemental UV-A wavebands. The first two factors (F1 vs. F2) of the PCA, as shown in the scatterplot (Figure 5A) and correlation circle (Figure 5B), explained 64.64% of the total data variance of the red lettuce. F1 explained 35.17%, whereas F2 explained 29.47% of the total variability. To summarize all the effects in the PCA scatter plot, the common reactions of red lettuce to different UV-A treatments were not significantly different from those under RB treatment (Figure 5A). The plant response to RBUV402 and RBUV367 showed a clear distinction in terms of F1 score, while the F2 scores showed a distinction between RB402 and the other lighting treatments. Very strong or strong positive correlations between gs and Pr, gs and Tr, gs and LUE, gs and Fru, gs and Glu, between Pr and Tr, Pr and LUE, Pr and Fru, Pr and Glu, between tr and LUE, Tr and Fru, Tr and Glu, and between DW, LA and Suc were found (Figure 5B and Table S1). Negative correlations between C_i and LUE, and WUE and F_v/F_m , were detected, and the same negative correlation was found for C_i/C_a . Moderate or weak correlations between F_v/F_m or Φ_{PSII} and most of the analyzed indices were detected. Negative moderate correlations between NPQ and C_i , and NPQ and Φ_{PSII} , were found. Very strong or strong negative correlations between Raf and Pr, Raf and tr, Raf and gs, Raf and LUE, Raf and Fru, and Raf and Glu were found. A very strong negative correlation between PSRI and NDVI, a strong positive correlation between PSRI and DV, and moderate positive correlations between PSRI and LA, and PSRI and Suc, were observed. A very strong positive correlation between CRI and ARI, a strong positive correlation between CRI and NDVI, and a negative moderate correlation between CRI and Glu were found. Negative strong correlations between NDVI, DW, LA and Suc were observed.



Figure 5. Principal component analysis (PCA) (**A**) and correlation circle (**B**) demonstrating the photosynthetic, metabolic, and growth responses of lettuce subjected to different light qualities: RB—Red 662 and Blue 452 nm (Control); BRUV402—Control with UV-A 402 nm; BRUV387—Control with UV-A 387 nm; BRUV367—Control with UV-A 367 nm. Total PPFD was maintained at 250 µmol $m^{-2} s^{-1}$, changing the input of red to 662 nm. The data were processed using XLStat software and the Tukey (HSD) test at a confidence level of p = 0.05 (biological replicates, n = 5).

4. Discussion

The findings of the present study indicate that the presence of different UV-A wavelengths can be conducive for proper growth of red lettuce (Table 2). The response in terms of the dry weight (DW) and leaf area (LA), compared with earlier studies carried out with various plant species, including different microgreens [18], baby leaf lettuce [28], basil, leaf lettuce [14], tomatoes [29], and barley [15] was not unique. An increase of the UV-A wavelength and transduction of light energy from the UV-B to UV-A region, and further to longer wavelengths, resulted in a significant increase of DW and LA, and had no significant effect on plant senescence reflectance (PSRI) nor on the normalized difference vegetation (NDVI) index, which represent the chlorophyll to carotenoid ratio and biomass content, respectively (Table 2). The PSRI and NDVI values showed that plants were subject to very good conditions [30]. The negative correlation suggests that UV-A mediated changes in DW and LA cannot be related to biomass accumulation (NDVI) (Table S1). However, the correlation matrix shows that DW and LA positively correlate with the PSII quantum yield (F_v/F_m and Φ_{PSII}), and negatively correlate with the ratio of intracellular to ambient CO_2 content (C_i/C_a). Klem et al. [15] found that the growth of above-ground biomass and photosynthetic performance of barley were enhanced by the combined action of red, blue, far-red, and UV-A (370 nm) light. The formation of LA in basil, beets, and pak choi microgreens was not unique, nor was it UV-A wavelength and/or intensity dependent [18]. One outcome from data analysis is that biomass production decreases with shorter wavelengths of UV-A radiation (Table 2), and this tendency is greater with UV-B radiation [9,20]. The highest values of the carotenoid and anthocyanin reflectance indices (CRI and ARI) and better coloration of red lettuce occurred under RBUV387. Since the phenolic phytochemicals induced by ultraviolet radiation tend to be localized in the leaf epidermal layers, the significantly higher anthocyanin amount under RBUV387 under these treatment conditions may have reduced the photoprotective requirement for chloroplast carotenoids [31]. The changes of the carotenoids to chlorophyll ratio (CRI) was not reflected in the stimulation of carbohydrate production. However, a significant increase of the hexose to sucrose ratio and significant decrease of CRI under RBUV637 (Figure 4, Table 2) were found. The same trend in the photosynthetic rate (Pr) and stomatal conductance (gs) indicated that an increase in the Pr of lettuce under supplemental UV-A radiation was due to the increase of gs, instead of the ratio of intracellular to ambient CO_2 content (C_i/C_a) or stomatal limitation (C_i) (Figure 2, Table S1). The existence of a distinct low-fluence and photosynthesis-independent response to blue light was established by Inoue and Kinoshita [32]. However, it is well known that blue light is one of the dominant signals that controls stomatal movements in the leaves of plants in a natural environment [33]. Van Ieperen et al. [34] also reported that blue light is needed to promote stomatal opening, improving access to CO_2 and driving transpiration, as well as increasing nutrient uptake and water use efficiency (WUE). This blue light response is mediated by blue/UV-A light-absorbing phototropins and cryptochromes [33]. In this study, neither RB nor supplemental UV-A radiation influenced C_i/C_a or WUE (Figure 2). Moreover, Tr increased with decreasing wavelength of UV-A, and the same trend of gs response to lighting treatments was observed (Figure 2). These data suggest that Tr was mediated by incident thermal radiation instead of stomatal opening [11]. A significant decrease in Φ_{PSII} and F_v/F_m (0.76), but no significant change in NPQ (Figure 3A–C) indicates that photo-inhibition occurred under RBUV367, such that an increasing fraction of the absorbed light energy was dissipated as heat (an upregulation of NPQ) [23]. Moreover, the same trend of Φ_{PSII} and ETR (Figure S1) suggests that RBUV367 leads to a reduction of electron receptors in the electron transport pathway. This results in a closure of PSII reaction centers, since the primary PSII electron acceptors are unable to transfer absorbed electrons to the next carrier in the electron transport chain. These reaction centers re-open after light-induced activation of Calvin cycle enzymes [35]. In contrast to RBUV367, high F_v/F_m values (~0.81) under RB, RBUV402, and RBUV387 indicate that there was no damage to PSII. Despite this, phototropins and cryptochromes were both perceived in the blue and UV-A light, and the activation of these photoreceptors can be expected to have similar effects on plant responses [8,9]. However, the photosynthetic, metabolic, and growth responses of red lettuce to different UV-A wavelengths were not the same. The PCA score

scatterplot showed a clear distinction in terms of F1 score between RBUV402 and RBUV367 (Figure 5A). In contrast to 367 nm UV-A radiation, the response to longer UV-A wavelengths was more common than the blue light-mediated response.

5. Conclusions

Treating crops with low dosages of specific narrow-band UV-A radiation at key points in the life cycle could initiate a cascade of responses in the above-ground biomass. We conclude that red leaf lettuces acclimate to longer UV-A wavelengths by increasing biomass production, whereas different UV-A wavelengths had no significant effect either on plant senescence reflectance, or on the normalized difference vegetation index. A significant decrease in the maximum quantum yield of the PSII photochemistry of dark (F_v/F_m) and light (Φ_{PSII}) adapted plants, and non-significant changes in non-photochemical fluorescence quenching, indicate that photo-inhibition occurred under RBUV367, whereas the photosynthetic response under RB, RBUV402, and RBUV387 indicate that there was no damage to PSII. The correlations of the photosynthetic rate (Pr) and stomatal conductance (gs) indicate that the increase in Pr of lettuce under supplemental UV-A radiation was due to the increase of gs, instead of the ratio of intracellular to ambient CO₂ content (C_i/C_a) or stomatal limitation (C_i).

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/10/6/761/s1, Figure S1: Electron transport rate (ETR) of lettuce subjected to different light qualities, Table S1: The correlation matrix (Pearson (n)) between the photosynthetic indices, metabolites, and growth indices in lettuce.

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