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ARTICLE

Do Blue Light and UV-A Interact Synergistically to Affect Growth and Quality of Celery? A Case Study of Individual vs. Combined Effects

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ABSTRACT: Blue light and ultraviolet-A (UV-A) radiation are critical light-quality regulators that coordinately modulate plant growth and quality in protected horticulture. However, their interactive effects on celery (*Apium graveolens* L.) remain inadequately characterized. In the present study, we quantified the individual and combined impacts of supplemental UV-A and blue light on the growth, biomass accumulation, photosynthetic performance, and nutritional quality of celery (cv. Dayehuang) in a plant factory with artificial lighting. Our results demonstrated that sole UV-A or blue light application significantly increased biomass, nutritional quality, and light use efficiency (LUE) of celery. Notably, combined supplementation with UV-A and blue light did not enhance chlorophyll content, biomass accumulation, or nutritional quality in celery relative to supplementation with either light quality alone. The principal component analysis (PCA) score plot exhibited clear separation among the four light treatments, with the UV-A treatment distinctly separated along the positive PC1 axis. Our findings demonstrate that UV-A and blue light regulate plant growth and quality via interactive rather than additive effects. Additionally, sole UV-A irradiation significantly improved celery growth and LUE. These findings provide a theoretical foundation for optimizing the light environment for celery under protected cultivation.

KEYWORDS: Blue light; celery; E-nose; light use efficiency; principal component analysis

1 Introduction

As an economically important leafy vegetable, celery (*Apium graveolens* L.) is abundant in dietary fiber, vitamins, and volatile flavor compounds, with prominent nutritional value and health-promoting functions [1,2]. Due to its nutritional and medicinal properties, celery is extensively grown across East Asia, Europe, and other regions, representing an agriculturally significant crop worldwide [3].

Controlled environment agriculture (CEA), enabled by precise artificial environmental manipulation, serves as a core strategy for modern vegetable production to enhance crop yield and quality [4,5]. As a crucial environmental factor, light quality can be perceived by plant photoreceptors, thereby regulating photosynthetic physiology, plant morphogenesis, and secondary metabolic pathways [6,7]. Specifically, blue light (400–500 nm) plays an essential role in plant growth, stomatal movement, and photosynthetic pigment synthesis, while also improving light use efficiency [8,9]. Furthermore, blue light is involved in

the metabolism of lignin and cell walls, which directly affects the textural and sensory qualities of leafy vegetables [10]. It modulates stem elongation and leaf expansion through its action on cryptochromes (CRY); notably, activated CRY also enhances the accumulation of bioactive compounds, including anthocyanins, ascorbic acid, and phenolics [9,11]. In addition, blue light was found to attenuate the pathogenicity of *Botryosphaeria dothidea* in kiwifruit, delay fruit acidification, and promote ascorbic acid accumulation [12]. Collectively, these findings highlight the diversified regulatory roles of blue light in plant growth, quality formation, and stress resistance, underscoring its substantial potential as a targeted light quality regulation strategy in CEA systems.

UV-A (315–400 nm), as a low-damage near-ultraviolet waveband, does not belong to the photosynthetically active radiation range, but acts as a special environmental signal to regulate physiological metabolism, thereby effectively improving the flavor quality of leafy vegetables [13,14]. However, traditional supplementary lights (red-blue LEDs, white LEDs, white-red LEDs) widely applied in protected cultivation possess spectra without UV-A radiation, thus limiting the accumulation of photosynthetic capacity and quality-related metabolites of horticultural crop [15,16]. The use of supplemental UV lighting in CEA offers a safe and sustainable approach and has shown considerable potential for improving the nutritional quality of plants [17]. For instance, replacing blue light with UV-A against a red-light background can increase the light interception area of tomato plants, leading to enhanced yield [18].

Compared with monochromatic light, combined light spectra exhibit superior effects in enhancing photosynthetic performance and growth status of leafy vegetables [19]. The combinations of red and blue LEDs are widely applied in horticulture production, owing to their spectral composition closely matching the absorption peaks of photosynthetic pigments, which enables efficient light energy conversion for photosynthesis [20,21]. Light quality interactions have also been shown to exert synergistic regulatory effects in horticultural plants. For instance, Yan et al. [22] found that combined supplementary lighting with white, blue, and UV-A light significantly improved the quality of cucumber seedlings, enhancing photosynthetic performance and stress tolerance. Studies on kale have demonstrated that adding moderate-intensity UV-A to red-blue light increases antioxidant enzyme activities and promotes the accumulation of phenolic compounds, showing synergistic impacts between UV-A and visible light on phytochemical biosynthesis [23]. In lettuce, combined UV-A and mixed red, blue, green and far-red light have been shown to significantly enhance leaf secondary metabolite accumulation and improve nutritional quality without inhibiting biomass accumulation, indicating that UV-A radiation combined with visible light can act together to optimize plant quality [24]. At present, there have been numerous studies on the impacts of single blue light or single UV-A on growth and physiology of lettuce [25], tomato [26], celery [21], and cucumber [27]. Nevertheless, systematic research on the synergistic regulation of combined blue light and UV-A supplementary light on photosynthetic characteristics, texture taste, and volatile flavor substances of celery is still insufficient, and the internal mechanism of light signal-mediated metabolic regulation remains unclear.

In this study, three light treatments (single blue light, single UV-A light, and their combination) were established to compare and analyze the regulatory effects of supplementary light on celery growth, photosynthetic capacity, and nutritional quality, clarify the respective roles and interactive (synergistic or antagonistic) effects of UV-A and blue light, explore their regulatory impacts on celery biomass accumulation and flavor formation, and further provide theoretical support and a scientific basis for the optimization of LED supplementary lighting and light environment configuration in high-quality protected celery cultivation.

2 Materials and Methods

2.1 Plant Materials and Experimental Design

Uniform celery (*Apium graveolens* L. cv. Dayehuang) seedlings with five fully expanded true leaves were obtained from Qingdao Macaco Ecological Agriculture Co., Ltd., Shandong Province, China, and transplanted into 1.1 L plastic containers containing peat–vermiculite–perlite (3:1:1, v/v/v) in a plant factory with artificial lighting. Celery plants received the following four light treatments for 35 days after transplantation.

White-red (WR) LED lights (Zhongshan Aier Lighting Technology Co., Ltd., Zhongshan, China) were used for celery cultivation based on our previous study [28]. The photosynthetic photon flux density (PPFD) of 200 μmol m^{-2} s^{-1} with a 12 h d^{-1} photoperiod was adopted, and this light regime was defined as the control treatment. The spectral composition of the WR LEDs was quantified with a spectrometer (PG100N, United Power Research Technology Corporation, Miaoli, China). The relative fractions of blue (400–500 nm), green (500–600 nm), and red (600–700 nm) light within the PPFD spectrum were 31%, 42%, and 27%, respectively. On the basis of the basic WR light environment, three supplemental light treatments were designed: UV-A LEDs (Xiamen Lumigro Technology, Xiamen, China) with a peak wavelength of 380 nm and an intensity of 10 μmol m^{-2} s^{-1} (UV), and blue LEDs (Zhongshan Aier Lighting Technology Co., Ltd., Zhongshan, China) with a peak wavelength of 455 nm and an intensity of 20 μmol m^{-2} s^{-1} (B), and the combinations of UV-A and blue LEDs (UV+B). The light intensities of blue light and ultraviolet radiation were set according to previous studies [28,29]. Day/night temperatures were controlled at 25 ± 1°C and 18 ± 1°C, respectively, with relative humidity kept within the range of 60–70% in the cultivation environment. All celery plants received irrigation with Hoagland's nutrient solution once every 2 days during cultivation. Each treatment included three separate experimental blocks holding 40 seedlings. Three evenly grown individuals were picked randomly per block to perform follow-up physiological determination and data analysis.

2.2 Measurements and Methods

2.2.1 Plant Height, Biomass Accumulation, and Light Use Efficiency of Celery Plants

Plant height of celery was quantified with a ruler. An electronic analytical balance (JY20002, Shanghai Hengping Instrument Co., Ltd., China) was adopted to record the fresh biomass of shoots and roots. All collected plant samples underwent deactivation at 105°C for 3 h in a drying oven, followed by sustained dehydration at 80°C over 72 h to obtain constant dry mass values. Biomass data were further used to calculate light use efficiency (LUE) based on the previous study [30].

2.2.2 Photosynthetic Characteristics of Celery Leaves

Random sampling of fully expanded, evenly grown mature celery leaves was carried out from 9:00 to 10:00 a.m. on harvest day. Leaf chlorophyll and carotenoid levels were quantified with a spectrophotometer (UV1810, Shanghai Yoke Instrument Co., Ltd., Shanghai, China) in line with the analytical procedure reported by Lichtenthaler and Wellburn [31]. Photosynthetic characteristics of celery leaves were obtained by a photosynthesis system (Li-6400XT, LI-COR Corporation, USA). Measurement parameters inside the leaf chamber were configured as follows: light intensity of 200 μmol m^{-2} s^{-1}, leaf temperature of 25°C, air flow rate of 500 μmol s^{-1}, and CO_2 concentration of 400 μmol mol^{-1}.

2.2.3 Texture Properties of Celery Plants

Textural trait detection on celery petioles was conducted via a TMS Touch texture analyzer (Food Technology Corporation, Sterling, USA). This equipment ran Texture Profile Analysis (TPA) mode equipped with a 10 N load sensor. Texture properties of celery petiole were determined following the methods described by Veland and Torrissen [32] and Ahmed and Dennison [33], respectively.

2.2.4 Nutritional Quality of Celery Plants

The anthrone colorimetric method [34] was utilized to quantify soluble sugar content in celery samples. Briefly, fresh celery (0.1–0.3 g) was hot-water extracted (20 mL, 30 min), filtered, made to 50 mL, and a 0.5-mL aliquot was mixed with 1.5 mL H_2O, then treated with 0.5 mL anthrone–ethyl acetate and 5 mL H_2SO_4, heated in a water bath for 1 min, and measured at 630 nm using a spectrophotometer (Shanghai Yoke Instrument Co., Ltd., Shanghai, China). The soluble protein content was quantified according to the protocol proposed by Bradford [35]. Approximately 1.0 g fresh celery tissue were homogenized with 8 mL distilled water and centrifuged at 4000 r/min for 20 min. The supernatant solution was diluted and adjusted to 10 mL. After mixing with Coomassie Brilliant Blue G-250 reagent, absorbance at 595 nm was quantified to determine soluble protein content.

2.2.5 Electronic Nose Analysis for Volatile Compound Characterization

A portable electronic nose (PEN3, Airsense Analytics GmbH, Schwerin, Germany) was utilized to analyze all test samples based on previous study [28]. Briefly, 2 g fresh celery samples were loaded into 100 mL closed headspace vials, equilibrated at 23 ± 3°C for 30 min. Detection conditions were configured as below: 60 s flush time, 5 s pre-sampling, 60 s measurement time, 300 mL min^{-1} chamber and injection flow, with activated carbon-filtered air as carrier gas.

2.3 Statistical Analysis

Shapiro–Wilk and Bartlett's tests were separately adopted to verify the normality of data distribution and homogeneity of variances. One-way ANOVA was performed with SPSS 26.0 (IBM, Armonk, NY, USA). The least significant difference (LSD) method was used to compare differences among all treatments ($p < 0.05$). Principal component analysis (PCA) was applied following the protocol described in a prior study [36], and the matching heatmap was visualized via the online analytical website (https://www.bioinformatics.com.cn).

3 Results

3.1 Impacts of Different Light Qualities on Photosynthetic Characteristics of Celery Leaves

Supplemental UV irradiation significantly promoted the chlorophyll and carotenoid contents in celery leaves (Fig. 1). Compared with control, UV irradiation markedly elevated celery chlorophyll a, chlorophyll b, total chlorophyll and carotenoid contents by 41.1%, 61.2%, 38.7% and 17.6%, respectively.

The net photosynthetic rate (P_n) of celery leaves was markedly elevated under all supplementary light treatments (Table 1). Relative to the control, P_n of celery leaves increased by 25.4%, 9.9% and 7.7% in the UV, blue light, and UV+B treatments, respectively. Stomatal conductance of celery under UV treatment was 52.2% higher than that of the control. Transpiration rate of celery was significantly enhanced by 91.7% and 85.7% under UV and blue light treatments, respectively, compared with the control. In addition, no significant difference in intercellular CO_2 concentration was observed among all treatments.

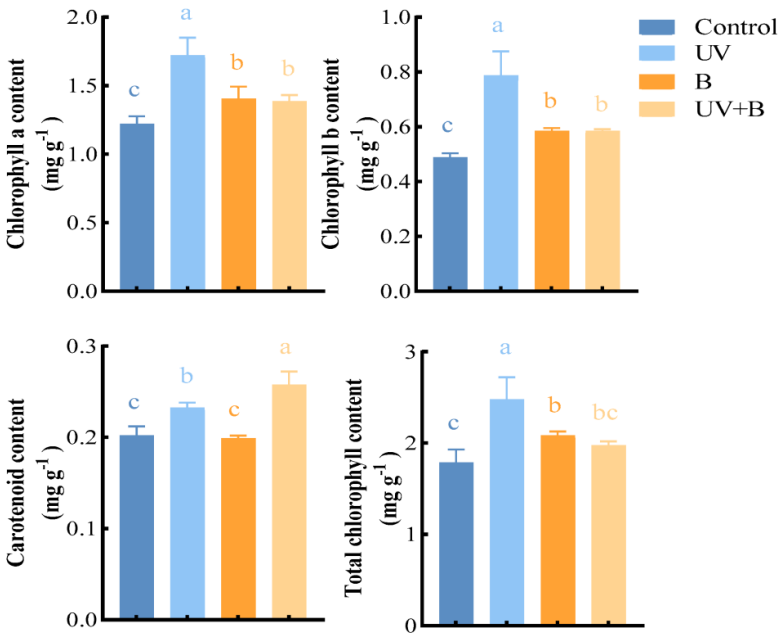

Figure 1: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on the photosynthetic pigment content of celery. Celery without supplementary lighting was used as control. Different lowercase letters mark significant differences ($p < 0.05$) determined via the least significant difference (LSD) test and error bars stand for standard deviation (SD).

Table 1: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on photosynthetic gas exchange parameters of celery.

Treatments	Net Photosynthetic Rate (μmol m^{-2} s^{-1})	Transpiration Rate (mmol m^{-2} s^{-1})	Stomatal Conductance (mol m^{-2} s^{-1})	Intercellular CO_2 Concentration (μmol mol^{-1})
Control	5.47 ± 0.04c	1.33 ± 0.32b	0.23 ± 0.09b	359.66 ± 6.71a
UV	6.86 ± 0.24a	2.55 ± 0.11a	0.35 ± 0.03a	341.79 ± 2.48a
B	6.01 ± 0.23b	2.47 ± 0.24a	0.27 ± 0.03ab	334.71 ± 12.98a
UV+B	5.89 ± 0.20b	1.57 ± 0.17b	0.25 ± 0.04b	344.19 ± 39.14a

Note: Distinct lowercase letters represent significant discrepancies at $p < 0.05$ as determined by the least significant difference (LSD) test. Data were expressed as mean ± standard deviation (SD).

3.2 Influences of Different Light Qualities on Growth, Biomass Accumulation and Light Use Efficiency of Celery

Different supplementary light significantly altered plant height, biomass accumulation and light use efficiency of celery plants (Table 2 and Fig. 2). UV supplementation significantly increased plant height of celery compared with those grown under control. However, no significant difference was found among the supplemental light treatments. Fresh biomass of celery shoots and roots was markedly higher under all supplementary light compared with those grown under the control. Shoot and root dry weights of celery were significantly enhanced by 39.6% and 28.9% under supplemental UV treatment, and by 52.3% and 38.5% under supplemental blue-light treatment, relative to celery grown under the control. In addition, light use efficiency based on dry-weight and fresh-weight was increased by 65.0% and 59.0% in celery under UV exposure, respectively, compared with the control (Fig. 2).

Table 2: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on the biomass of celery.

Treatments	Plant Height (cm)	Shoot Fresh Weight (g per plant)	Root Fresh Weight (g per plant)	Shoot Dry Weight (g per plant)	Root Dry Weight (g per plant)
Control	59.80 ± 2.03b	65.16 ± 2.03b	8.27 ± 0.94b	5.68 ± 1.43b	0.65 ± 0.10b
UV	66.40 ± 4.95a	77.56 ± 8.20a	11.87 ± 1.87a	7.93 ± 0.76a	0.99 ± 0.17a
B	61.33 ± 2.75ab	76.38 ± 2.74a	11.71 ± 1.19a	7.32 ± 0.36a	0.90 ± 0.16a
UV+B	62.30 ± 2.42ab	73.71 ± 3.57ab	10.76 ± 0.90a	7.27 ± 0.49ab	0.89 ± 0.10ab

Note: Distinct lowercase letters represent significant discrepancies at $p < 0.05$ as determined by the least significant difference (LSD) test. Data were expressed as mean ± standard deviation (SD).

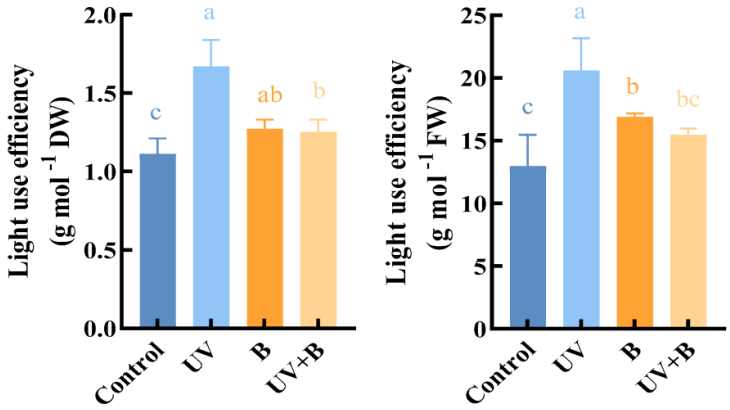

Figure 2: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on light use efficiency based on dry weight (DW) and fresh weight (FW) of celery. Celery without supplementary lighting was used as control. Different lowercase letters mark significant differences ($p < 0.05$) determined via the least significant difference (LSD) test and error bars stand for standard deviation (SD).

3.3 Influences of Different Light Qualities on Texture Properties of Celery

Combined supplementation of blue light and UV radiation significantly increased the firmness, springiness, and chewiness of celery petioles (Fig. 3). Compared with the control, the firmness, springiness, and chewiness of celery petioles in the UV+B treatment increased by 49.9%, 36.5%, and 71.5%, respectively. Moreover, celery petiole chewiness under monochromatic blue light increased by 43.4% relative to the control.

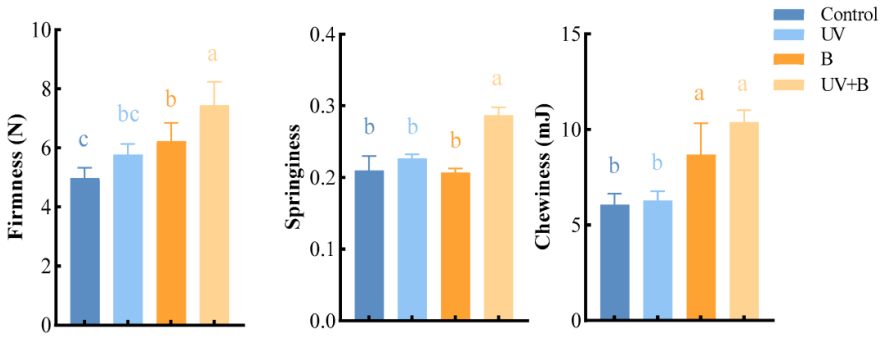

Figure 3: Impacts of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on the texture of celery petiole. Celery without supplementary lighting was used as control. Different lowercase letters mark significant differences ($p < 0.05$) determined via the least significant difference (LSD) test and error bars stand for standard deviation (SD).

3.4 Influences of Different Light Qualities on Nutritional Quality of Celery

All supplementary light treatments significantly elevated the contents of soluble sugar and soluble protein in celery leaves (Fig. 4). In comparison to the control treatment, the soluble sugar contents in celery leaves of UV, B and UV+B treatments increased by 43.4%, 44.1% and 51.9%, respectively; meanwhile, the soluble protein contents in celery leaves increased by 52.3%, 38.9% and 54.2%, respectively.

Soluble sugar content in celery petioles under UV and B treatments were markedly elevated relative to the control, rising by 104.8% and 127.0%, respectively. Similarly, soluble protein contents in celery petioles were markedly enhanced under all supplementary light treatments, which increased by 33.2%, 53.4% and 46.5% in the UV, B, and UV+B treatments relative to the control, respectively.

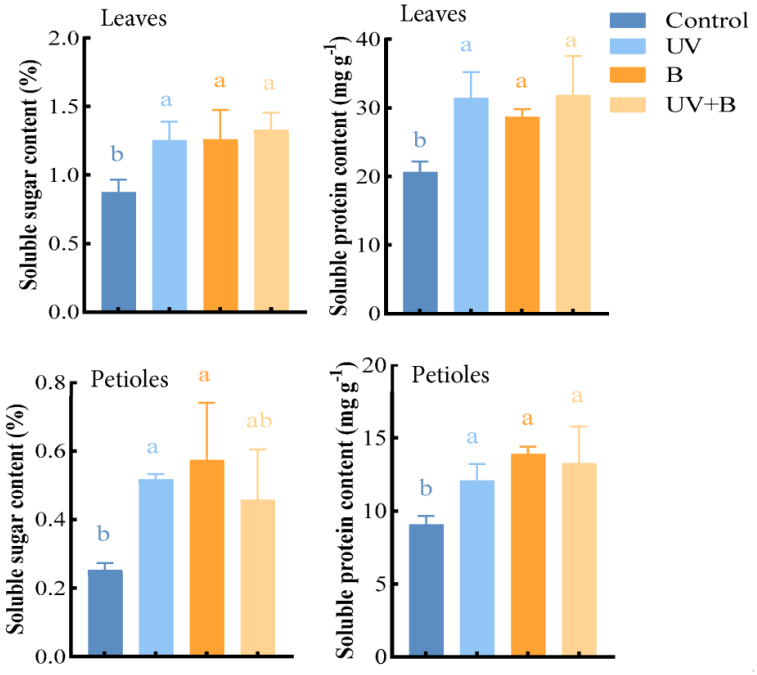

Figure 4: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on the soluble sugar content and soluble protein content in celery leaves (upper layer) and petioles (lower layer). Celery without supplementary lighting was used as control. Different lowercase letters mark significant differences ($p < 0.05$) determined via the least significant difference (LSD) test and error bars stand for standard deviation (SD).

3.5 Volatile Compound Differentiation of Celery under Different Light Qualities

Significant changes were observed in the response values of aromatic compounds (W1C), ammonia and aromatics (W3C), alkenes, aromatics and polar molecules (W5C), alkanes (W1S), alcohols and aromatic compounds (W2S), as well as alkanes and aliphatics (W3S) in celery leaves (Fig. 5). Specifically, the response values of W1C, W3C, W5C, W1S, W2S, and W3S of celery grown under the UV treatment increased by 20.6%, 24.8%, 24.5%, 59.8%, 40.6%, and 65.4%, compared with celery grown under control, respectively.

In celery petioles, significant changes occurred in the response values of ammonia and aromatics (W3C), alkenes, aromatics and polar molecules (W5C), alkanes (W1S), and alcohols and partial aromatic compounds (W2S). Among these, the response values of W3C, W5C, W1S, and W2S of celery grown under the UV treatment were increased by 20.3%, 24.5%, 59.8%, and 32.0%, relative to celery cultivated under control conditions, respectively.

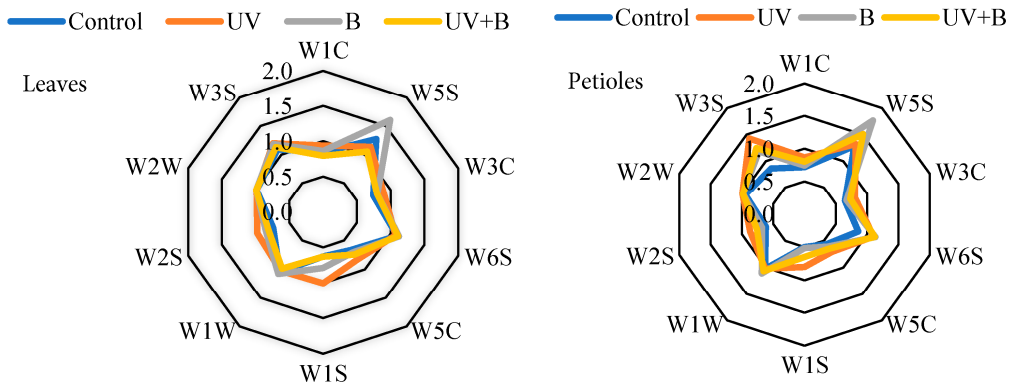

Figure 5: Effects of supplementary UV light, blue light (B), and the combinations of UV and blue light (UV+B) on the response value of the electronic nose sensor of celery leaves (left) and petioles (right). Celery without supplementary lighting was used as control.

3.6 Principal Component Analysis of Celery under Different Spectral Compositions

Principal component analysis (PCA) was adopted to synthesize growth, photosynthesis, biochemical and volatile metabolite indicators of all treatments (Fig. 6). The first two principal components, PC1 and PC2, explained 47.1% and 22.0% of the total variance, respectively, accounting for 69.1% of the cumulative variance. The PCA score plot showed clear separation among the four light treatments. The control group (no supplemental light) was clearly separated from all light-supplemented groups and clustered in the negative PC1 region. The blue light treatment was clustered near the origin of the PCA plot, with intermediate values for most measured parameters. The UV treatment was clearly separated along the positive PC1 axis, while the UV+B treatment was located in the positive PC1 but negative PC2 region.

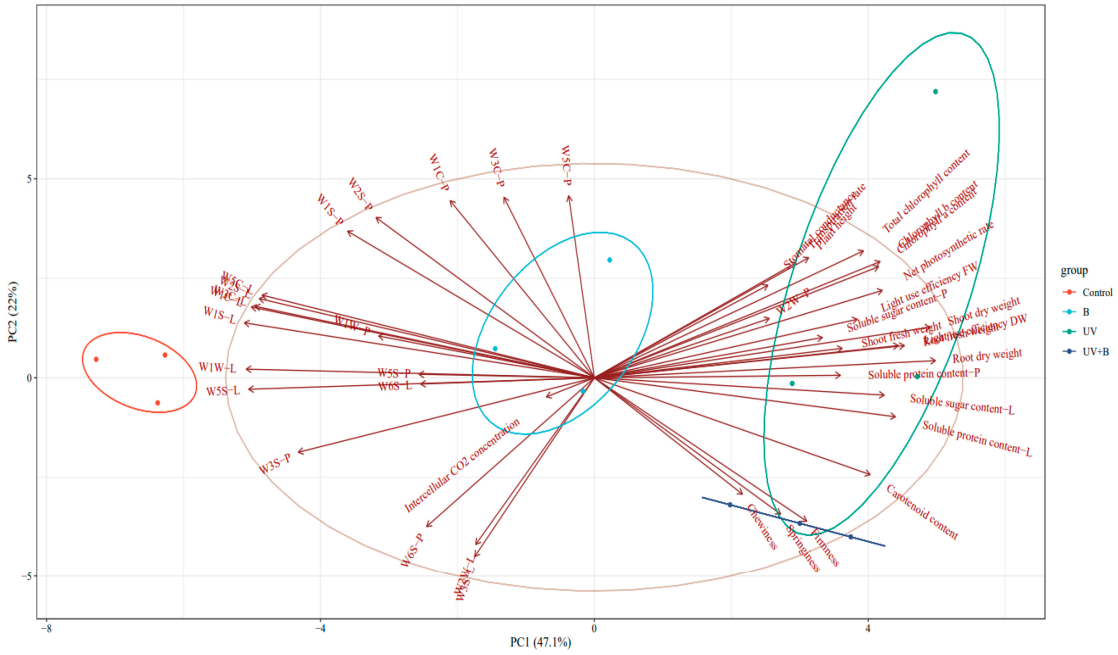

Figure 6: Principal component analysis (PCA) of celery parameters under different light treatments. Celery grown without supplemental light served as the control, and the treatments included supplemental UV light, blue light (B), and combined UV and blue light (UV+B).

4 Discussion

Photosynthetic pigments form the core foundation of photosynthesis, as their contents directly determine the capacity of plants to capture light energy. Our study indicated that single supplementary UV or blue light significantly elevated chlorophyll contents in celery leaves (Fig. 1). This finding is consistent with previous studies. For instance, Sun et al. reported that monochromatic blue light elevated chlorophyll and carotenoid concentrations in gerbera tissue-cultured plantlets, where pigment contents increased in a dose-dependent manner with increasing blue light proportion [37]. Light quality regulates the physiology of horticultural plants primarily through the interactive effects of diverse spectral components, not through the additive effects of individual wavelengths. Previous studies indicated that a decreased red-to-blue (R:B) ratio promotes the accumulation of photosynthetic pigments in spinach leaves [38]. In addition, Van Brenk et al. reported that pre-harvest exposure to low R:B light led to darker leaf pigmentation and higher levels of pigment-associated compounds [39]. Consistent with these previous findings, our study showed that supplemental blue light reduced the R:B ratio from 0.87 (control treatment) to 0.68 (B treatment), which correspondingly increased pigment content of celery leaves. In addition, UV and blue light also regulated stomatal behavior and gas exchange in celery leaves (Table 1). Specifically, supplementary UV significantly increased stomatal conductance of celery, indicating that UV light promotes CO_2 diffusion within leaves, optimizes the supply of photosynthetic substrates, and thus enhances overall photosynthetic efficiency. In addition, Barillot et al. confirmed that blue light increases stomatal density and conductance in *Festuca pratensis* [40], with conductance rising linearly with blue light proportion—an effect mainly attributed to enhanced adaxial stomata development. Previous studies indicated that blue light acts as a key environmental cue governing leaf stomatal dynamics under natural growth conditions, and this response is primarily mediated by blue/UV-A light-absorbing phototropins (PHOTs) and cryptochromes (CRYs) [41]. Specifically, the phototropins PHOT1 and PHOT2 are central regulators of blue light-induced physiological responses, including phototropism, chloroplast movements, and stomatal opening [42]. However, our study also revealed that the combined supplementation of blue light and UV did not trigger a significant synergistic interaction. Instead, the co-application of the two light qualities partially attenuated the promoting effects of single light on celery's photosynthetic characteristics and biomass accumulation (Tables 1 and 2). In contrast, a previous study has demonstrated that individual UV or blue light supplementation increased SPAD values but exerted no significant effects on biomass accumulation of lettuce, whereas their combined application significantly promoted biomass production [43]. The differential functional responses to combined short-wavelength light regimes are likely attributed to multiple factors, such as plant species, developmental stages, physiological properties and ambient environmental conditions.

With the widespread application of LEDs in protected horticulture, there is a growing demand for spectral optimization to enhance light use efficiency, while simultaneously improving crop yield and quality [44]. Our results indicated that improved photosynthetic performance, manifested by increased photosynthetic pigment concentrations and optimized gas-exchange characteristics, ultimately facilitates greater biomass accumulation under desired light conditions (Fig. 1, Tables 1 and 2). Our results showed that individual blue light or UV irradiation significantly improved the LUE of celery. Nevertheless, combined UV and blue light treatment did not exert synergistic effects on LUE; its LUE value was even lower than that under single UV irradiation, indicating a distinct antagonistic interaction between the two light spectra. Consistent findings were also reported in previous research on light quality regulation of cucumber seedlings [22]. Specifically, Yan et al. demonstrated that cucumber seedlings exposed to sole supplemental UV-A radiation possessed higher supplemental light use efficiency than those cultivated under combined white light plus UV-A or white light plus blue light conditions [22].

Textural property is a core sensory indicator that determines the edible palatability of celery, which is highly sensitive to spectral light-quality conditions [45]. Light quality regulates textural performance of vegetable mainly by altering cell wall structure, lignin deposition, and secondary metabolite accumulation, thus changing tissue hardness and chewiness [46]. Numerous studies have confirmed that different light spectra exert remarkable influences on plant morphological development and secondary metabolism. Pedroso et al. found that different light quality treatments could effectively regulate the synthesis of flavonoids and affect seedling growth status [47], proving that light signals can profoundly interfere with plant material metabolism and tissue structural development. In the present study, combined supplemental UV and blue light significantly improved the hardness, springiness, and chewiness of celery petioles, further verifying that short-wavelength light exerts positive regulation on leafy vegetable texture quality. Collectively, supplemental UV combined with blue light effectively optimizes textural quality in celery, offering a feasible strategy for high-quality celery production under protected cultivation systems.

Light quality also influences the volatile compounds in different organs of horticultural plants [29]. Our results demonstrated that the UV increased the response values of sensors detecting aromatic compounds (W3C), alkanes (W5C), methyl compounds (W1S), and alcohols (W2S) in both celery leaves and petioles (Fig. 5). Previous studies on lettuce have shown that UV-A radiation can promote the synthesis of most phenylpropanoids and terpenoids within the shikimate pathway, and the pathways in plastids, namely, the mevalonate (MVA) and methylerythritol phosphate (MEP) pathways [48]. The shikimate and MEP pathways reside in chloroplasts, where their plastidic precursors are produced by the Calvin–Benson cycle, glycolysis and the pentose phosphate pathway [49]. In addition, UV RESISTANCE LOCUS 8 (UVR8) and cryptochromes coordinately regulate gene expression via mutual interactions, which modulates the relative sensitivity of plants to UV-B, UV-A and blue light. The activities of these photoreceptors are subject to negative feedback loops derived from gene expression, signaling crosstalk, and UV photon absorption by phenolic metabolites [50]. Since aromatic compounds and alcohols are largely derived from the shikimate and MEP pathways, it can be inferred that UV-A may also influence volatile metabolites in celery leaves and petioles by modulating these two pathways [51]. In addition, our results discrepancy demonstrates that UV treatment exerts organ-specific regulatory effects on celery. This is consistent with previous findings showing marked differences in the number and types of flavor compounds altered under UV radiation between celery leaves and petioles [29].

Soluble sugar and soluble protein are critical evaluation indices reflecting the nutritional quality of horticultural plants. In our present study, we observed these two metabolites showed distinct tissue-specific responses to supplemental UV and blue light treatments: celery petioles were more sensitive to light-quality regulation in terms of soluble sugar accumulation, whereas celery leaves exhibited greater variation in soluble protein content (Fig. 4). This identical regulatory trend further supports that UV and blue light triggers conserved tissue-specific physiological responses across leafy vegetable species. Liu et al. [52] demonstrated that blue-light remodels primary metabolism of horticultural crops in a product-organ-specific manner, well explaining the divergent soluble protein variations between celery petioles and leaves observed in our study. Meanwhile, in accordance with the findings in tomato reported by Dong et al. [53] blue light induced inconsistent soluble protein changes between different tissues, which further corroborates our leaf-dominant soluble protein variation result. Collectively, our results indicate that UV-blue light drives conserved tissue-specific remodeling of primary osmoregulatory metabolites in leafy horticultural vegetables.

5 Conclusion

Supplemental light application markedly enhanced the photosynthetic capacity, biomass accumulation, and comprehensive quality of celery relative to plants cultivated under the control treatment. Among various supplemental light quality regimes, blue light supplementation exerted a more prominent effect on modulating celery textural traits (e.g., chewiness) relative to UV light supplementation. By contrast, celery cultivated under sole UV light possessed higher chlorophyll concentration and photosynthetic rate than those exposed to sole blue light. Combined UV-blue supplemental light induced no significant variations in the comprehensive quality of celery compared with monochromatic light treatments, and monochromatic and combined light regimes effectively optimized the flavor attributes of celery. Compared with sole UV or sole blue light treatment, combined UV-blue light further improved key textural indices (e.g., firmness and springiness), while it failed to exert significant promotive effects on celery biomass production and nutritional quality. Collectively, UV light and blue light regulate celery growth and quality via interactive rather than additive effects. These findings provide theoretical and technical support for spectral regulation in controlled environment agriculture (e.g., greenhouse and plant factory cultivation) to improve celery productivity and nutritional quality.

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