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EFFECTS OF DIFFERENT LIGHT SPECTRA AND INTENSITIES ON STOMATAL FUNCTION IN LETTUCE AND BASIL

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ABSTRACT

Light quality and intensity markedly influence stomatal activity, a crucial physiological process regulating gas exchange and water loss in higher plants. Stomata dynamically open and close in response to environmental signals, facilitating carbon dioxide uptake for photosynthesis while modulating transpirational water loss. Although red and blue light are well-established regulators of stomatal function, the effect of green light on this process remains comparatively underexplored. In this study, the effects of multiple light wavelengths (430 nm, 530 nm, 560 nm, and 630 nm) and intensities (50, 75, 100, and 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$) on stomatal responses in lettuce (*Lactuca sativa*) and basil (*Ocimum basilicum*) were systematically evaluated. The results showed that green light (530 nm and 560 nm) effectively maintained stomatal closure at lower intensities, thereby minimizing water loss and preserving tissue freshness during postharvest storage. These findings highlight the potential application of green light to optimize postharvest handling by reducing transpiration and improving shelf life of leafy crops. This evidence provides a foundation for targeted light management strategies aimed at improving the commercial quality and marketability of horticultural produce.

Key words: green LED, *Lactuca sativa*, *Ocimum basilicum*, storage

INTRODUCTION

Stomata are kidney-shaped pores in the epidermis of dicots and nongraminaceous monocots and dumbbell-shaped pores in monocot grasses (Driesen et al. 2020). They are essential for photosynthesis as they optimize plant gaseous exchange, which includes CO_2 uptake for photosynthesis and water vapor loss through transpiration (to minimize CO_2 deprivation and excess water loss) (Kochetova et al. 2022). Transpiration is the outward diffusion of water vapor and is essential for maintaining the balance of water and nutrients in plants, as well as for regulating temperature (Wei et al. 2020). Stomata regulate water uptake through changes in conductivity, opening, and density (Wolf et al. 2016). Plants actively regulate stomatal aperture by altering the turgor pressure of the two guard cells surrounding each stoma. As turgor pressure increases, the stomatal aperture expands, and as turgor pressure decreases, the stomata closes. Therefore, the rate of gas exchange is controlled by the surrounding atmosphere and the interior of the leaf (Driesen et al. 2020). The opening and closing of stomata is influenced by many other internal and external environmental factors, including light, humidity, CO_2 concentration, plant hormones (abscisic acid and auxins), carbohydrates, and biotic and abiotic stressors (Srivastava 2002; Shimazaki et al. 2007; O'Carrigan et al. 2014; Driesen et al. 2020; Yang et al. 2020). Light is one of the most crucial signals that plays a significant role in regulating stomatal movement (Lee et al. 2007; O'Carrigan et al. 2014) through metabolic changes and guard cell signaling, photosynthesis, and membrane ion transport (Araújo et al. 2011; O'Carrigan et al. 2014).

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For example, blue light triggers the activation of phototropins, which facilitates the opening of ion channels and promotes water uptake, thereby increasing guard cell turgor. Green light, on the other hand, is associated with lower cryptochrome activation, which promotes stomatal closure and reduces transpiration rates (Shimazaki et al. 2007).

Various characteristics of the lighting environment, such as intensity, wavelength, and duration, have a significant influence on photosynthesis and plant growth. Light-emitting diodes (LEDs) have become the industry standard for controlled environment agriculture (CEA) plant cultivation due to their numerous advantages, including compact size, low power consumption, reduced heat generation, and long life (Massa et al. 2008; Van Ieperen 2012; Bantis et al. 2018; Lastochkina et al. 2022). To observe the response of plants to narrow spectrum wavelengths, LEDs are able to meet this technical specification (Kusuma et al. 2020).

The stomatal response to red light has been shown to be dependent on photosynthesis, in contrast to the stomatal response to blue light, which is both dependent and independent of photosynthesis (Sakhonwasee et al. 2017). Green light (500–600 nm) is usually less absorbed by chlorophyll pigments (Golovatskaya & Karnachuk 2015; Battle & Jones 2020; Driesen et al. 2020; Thoma et al. 2020). The exact process underlying the changes in stomatal opening induced by green light has not yet been discovered.

Lettuce (*Lactuca sativa*) and basil (*Ocimum basilicum*) are leafy vegetables commonly grown in CEA (Larsen et al. 2020). Basil is known for its distinct chemical components and essential oil composition, which are widely used in cooking, biopesticides, and pharmaceuticals (Sabry et al. 2019; Alhasan 2020). Lettuce is one of the most popular leafy vegetables consumed daily all over the world (Salehinia et al. 2024). Lettuce is 94–95% water and low in calories. It is reportedly used to treat diabetes, cancer, and Alzheimer's disease (Shi et al. 2022). During postharvest storage of leafy vegetables, water uptake is zero. Thus, the water level can only decrease (Lee et al. 2014). Water loss can lead to changes in the physical attributes of the produce, such as wilting, shrinkage, and loss of crispness, all of which can affect its overall appeal and quality (Nunes & Emond 2007; Umeohia & Olapade 2024). Reducing water loss and respiration rates during postharvest storage will result in higher quality plants with greater nutritional value for end users (Aliniaeifard & van Meeteren 2016; Umeohia & Olapade 2024). Understanding how stomatal opening is regulated in leafy vegetables during postharvest storage is crucial to reducing water loss and extending their shelf life. Although numerous studies have investigated the stomatal response to light quality, most have focused primarily on red and blue light. However, there is little information on the effect of green light on plant responses. This experiment was conducted to determine the effect of different wavelengths of light and intensities on the opening of stomata of two species of leafy greens, namely basil and lettuce.

MATERIALS AND METHODS

Plant materials and growth conditions

Romaine lettuce (*Lactuca sativa* 'Breen') (Stokes seed, Canada) and basil (*Ocimum basilicum* 'Dolly') were germinated in rockwool cubes (Grodan, Denmark) in a growth chamber (model E15; Conviron, Canada) under white fluorescent light (4200 K, F72T8/CW, Osram, USA) at a photosynthetic photon flux density (PPFD) of 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, determined with a quantum meter (model MQ500, Apogee Instruments, USA) at ambient CO_2, day/night temperature of 25/20 ± 3 °C, relative air humidity of 70 ± 5%, and a daily photoperiod of 16 h. After 14 days, the seedlings were given full-strength Hoagland solution, a fertilizer solution commonly used in plant research that contains essential mineral elements necessary for plant growth and development (Hoagland & Arnon 1950). After three weeks, the seedlings were transplanted to a greenhouse for 40 days. Lighting conditions prior to specific treatments included natural sunlight and high-pressure sodium (HPS) lighting in a greenhouse (Table 1). These conditions included the spectrum of 300–900 nm with an intensity of 350–500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for growing plants. The environmental conditions for growing plants in the growth chamber and greenhouse are presented in Table 1. The environment was completely isolated and no fungicides or pesticides were used.

Table 1. Environmental conditions for growing basil and lettuce germinated in a growth chamber and grown in a greenhouse

Abiotic factors	Growth chamber conditions (days 0–21)	Greenhouse conditions (days 21–40)
Lighting type	fluorescent bulbs	sunlight and HPS
Light spectrum	400–500 nm	300–900 nm
Photoperiod (day/night) (h)	16/8	16/8
Light intensity (PPFD) ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	150	350–500
Temperature (day/night) (°C)	25/20±3	20/16±3
Relative humidity (%)	70±5	55±5
Water temperature (°C)	22±2	22±2
Hydroponic solution	full strength Hoagland solution 14 days after seeding	full strength Hoagland solution 21 days after seeding
pH	6.0±5	6.0±5
Electrical conductivity ($\mu s \cdot cm^{-1}$)	1000±500	1000±500

Application of light treatments

Forty days after transplanting the plants to the greenhouse, samples of young, fully-expanded leaves were collected. In our experimental design, we considered two primary factors: light spectrum and light intensity level. Whole plants were treated with four different LED wavelengths: 430 nm, 530 nm, 560 nm, and 630 nm. Each wavelength was used at four different intensities: 50, 75, 100, and 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD. The light source was positioned above the plants, illuminating the adaxial surface of the leaves. The control consisted of plants kept in complete darkness. The duration of light treatment was 40 minutes for all conditions (Fig. 1 & 2). In this study, a time frame of 40 minutes was selected due to the time-response characteristics of the stomata. According to the time-response curve of the stomata, it takes approximately 40 minutes to reach a stabilized and steady state. Within the first 5 minutes of light exposure, the stomata reach 90% of their final steady state (Drake et al. 2013; Doi et al. 2015; McAusland et al. 2016).

Determination of stomatal opening

To track stomatal characteristics in response to different light wavelengths and intensities, the abaxial and adaxial (facing the light source) surfaces of young, fully-developed leaves were coated with a thin layer of clear nail polish. After allowing it to dry for 10 minutes, the dried polish was gently peeled off with transparent tape to obtain an epidermal imprint. Then, the imprints were placed on slides and under an optical microscope (Leica ICC50 W, Germany). ImageJ software (National Institutes of Health, USA) was used. Stomatal opening was measured following the method described by Savvides et al. (2012) (Fig. 3), and micrometers (μm) were used as the standard unit.

Statistical analysis

We conducted the experiment using a split-plot design with three experimental runs, each comprising three replicates, to collect data on stomatal opening from both abaxial and adaxial leaf surfaces (100 stomata per surface, 200 total for each light treatment). The three runs were combined using the subreplication method to account for potential inter-run differences; however, no significant differences were detected, justifying pooling of the data for a comprehensive analysis. Statistical analyses were performed using SAS software (SAS Institute, USA) within a split-plot framework. Main effects and interactions were examined at a significance level of $p = 0.01$, and Duncan's multiple range test was used for pairwise comparisons of stomatal characteristics. The letters in Figures 6–9 represent the comparative results of all treatments, including different light spectra and intensities, based on the final interaction results from the split-plot ANOVA. This methodology allowed us to capture the combined effects of light spectra and intensity on stomata behavior, providing a holistic interpretation of the experimental data.



Figure 1. Representative images of basil under 560 nm light treatment at an intensity of 150 µmol·m^{-2}·s^{-1}



Figure 2. Representative images of lettuce under 530 nm light treatment at an intensity of 150 µmol·m^{-2}·s^{-1}

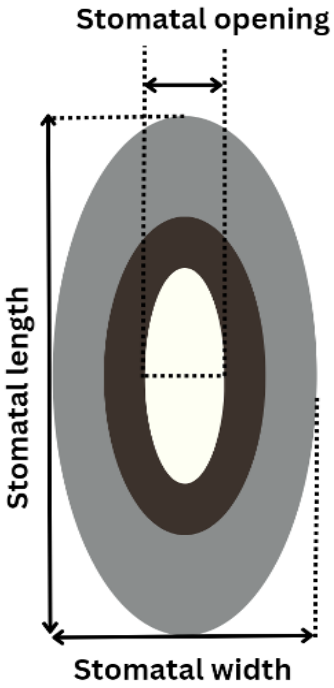


Figure 3. Schematic representation of stomata, illustrating the method of measuring stomatal opening

RESULTS

The opening of stomata on the adaxial and abaxial sides of leaves in basil and lettuce plants (Fig. 4–9; Tables 2 & 3) was considerably influenced by the quality and intensity of light. Stomatal widening increased with light intensity at all wavelengths. Abaxial stomata were more open than adaxial ones in both species.

The abaxial surface of basil leaves exposed to the lowest light intensity (50 µmol·m^{-2}·s^{-1}) had the narrowest stomatal aperture under all light treatments (Fig. 6). The 560 nm wavelength showed the narrowest stomatal aperture on both sides of basil leaves at all light intensities compared to other wavelengths (Fig. 4, 6, & 7). The percentage increased from 40% to 100% at different intensities on the adaxial side and from 17% to 1100% on the abaxial side of the leaves. The increase in stomata opening with intensity was smallest under green light compared to other wavelengths. The largest stomatal aperture was found under red light at 100 and 400 µmol·m^{-2}·s^{-1} PPFD, which increased by 72.7% compared to the stomatal width in the dark. In general, red light caused a larger stomatal aperture compared to the aperture at other wavelengths.

The main patterns of stomatal opening were similar in lettuce, except that the most open were those on leaves grown under blue light. Stomata grown under green light were the least open. On the abaxial side they were only slightly (percentage) more open than those grown in the dark. The differences on the adaxial side compared to those in the dark were even smaller (Fig. 8 & 9).

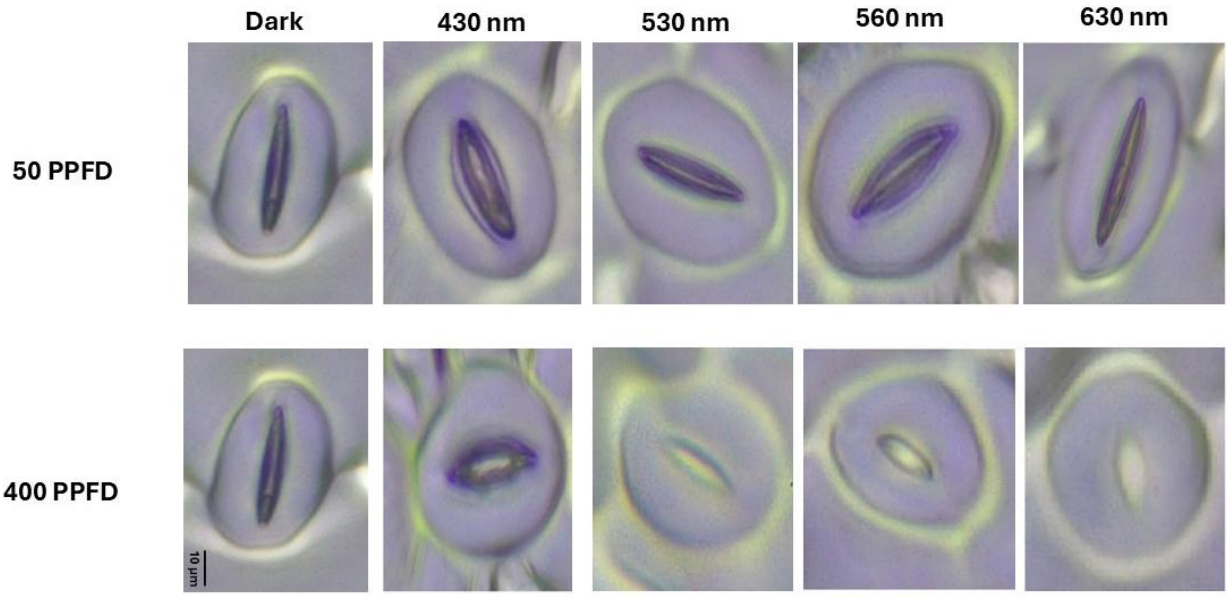


Figure 4. Representative stomatal opening of basil plant under different light qualities – dark, 430 (blue), 530 (green), 560 (green), and 630 nm (red) and quantities (50 and 400 PPFD) on the abaxial surface

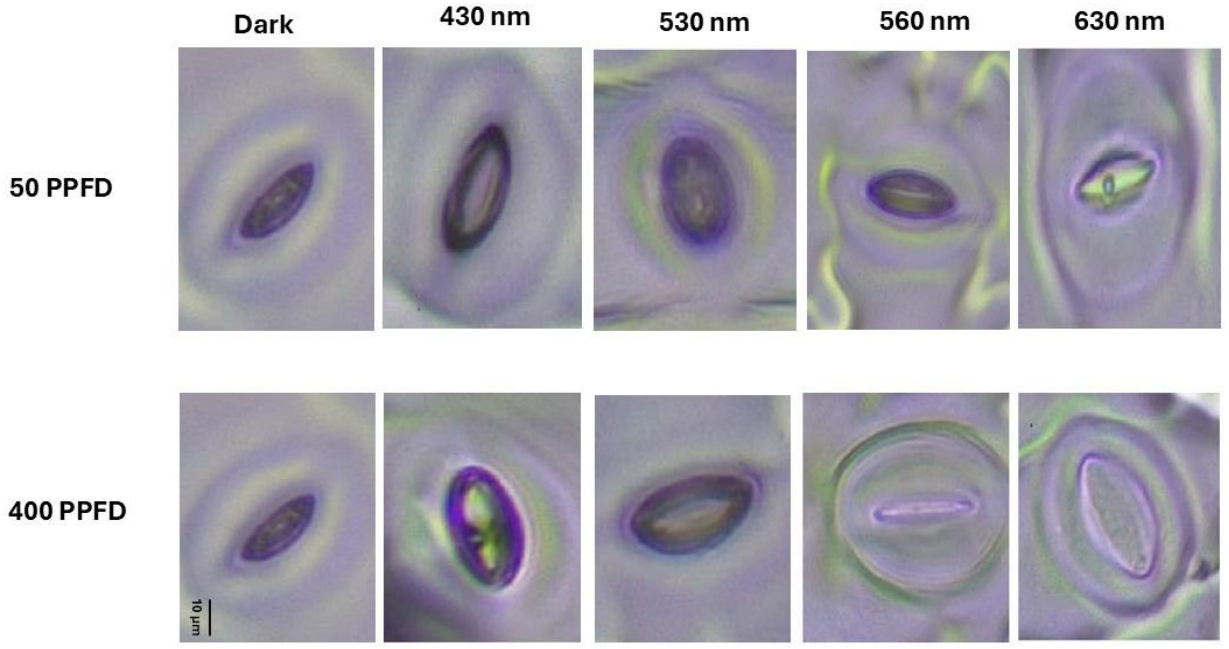


Figure 5. Representative stomatal opening of lettuce plant under different light qualities – dark, 430 (blue), 530 (green), 560 (green), and 630 nm (red) and quantities (50 and 400 PPFD) on the abaxial surface

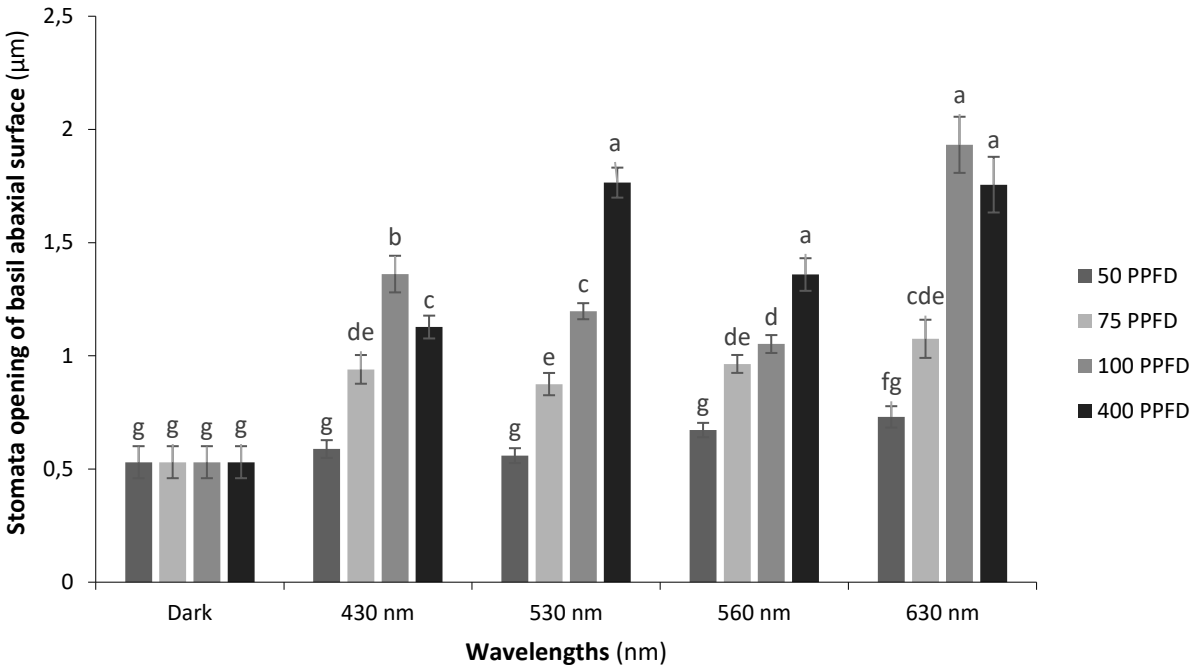


Figure 6. Stomatal opening of basil (abaxial surface) under different light treatments and darkness as control

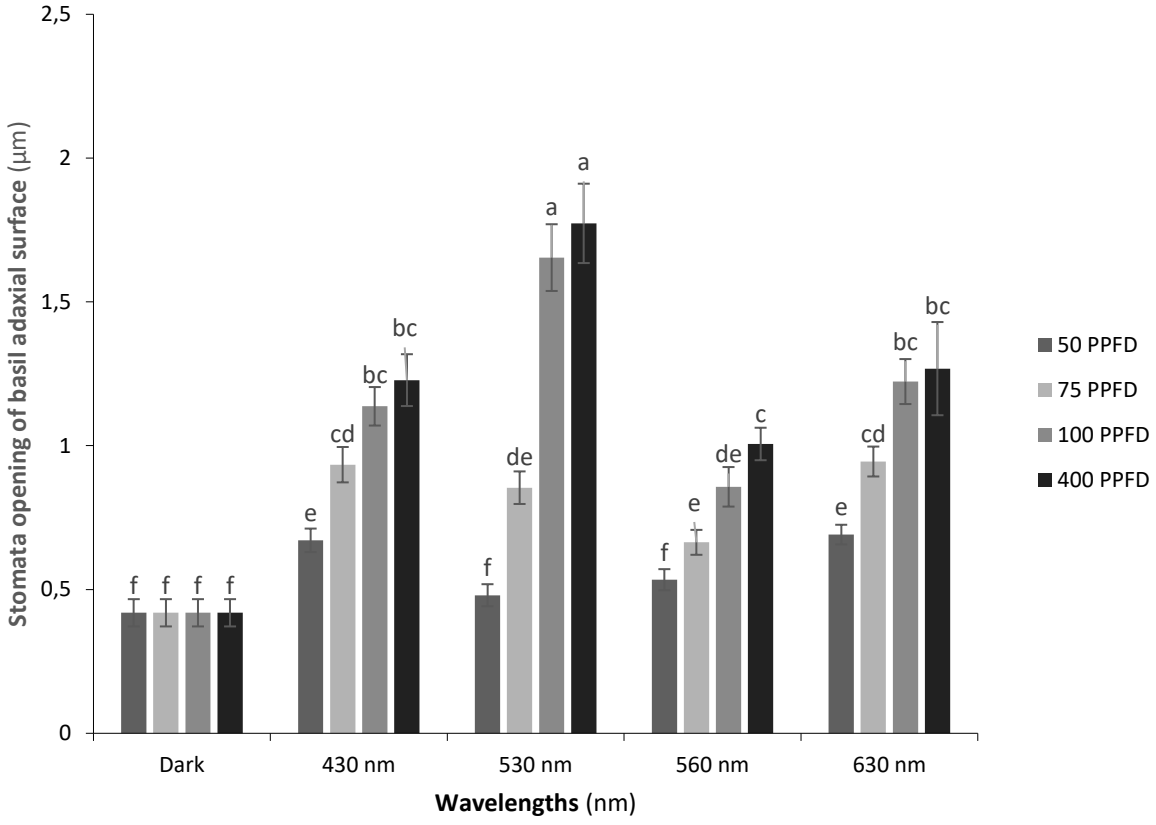


Figure 7. Stomatal opening of basil (adaxial surface) under different light treatments and darkness as control

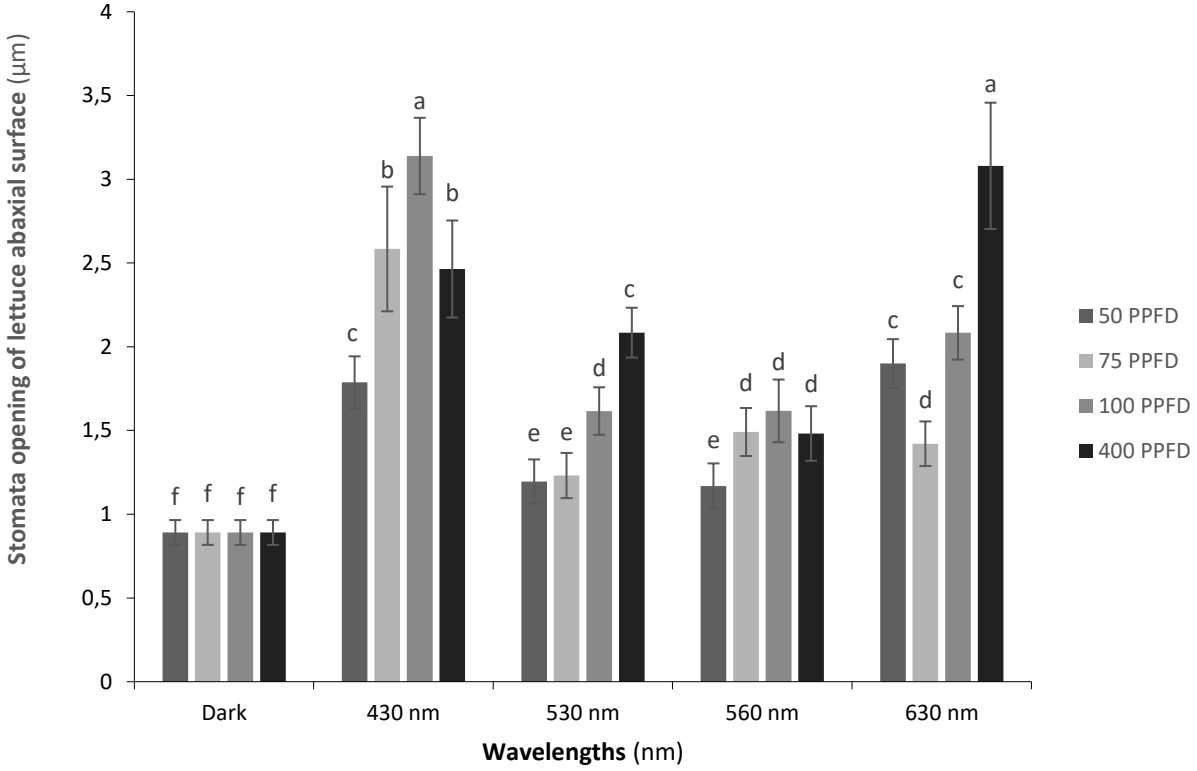


Figure 8. Stomatal opening of lettuce (abaxial surface) under different light treatments and darkness as control

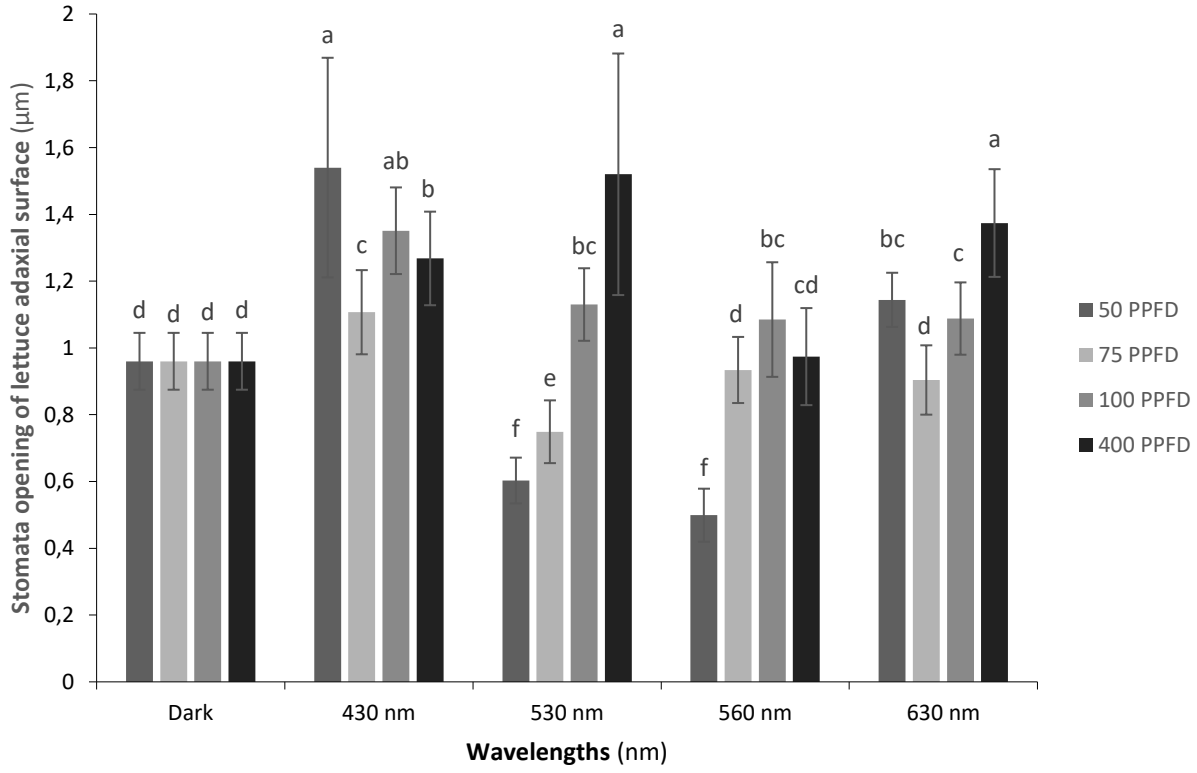


Figure 9. Stomatal opening of lettuce (adaxial surface) under different light treatments and darkness as control

Table 2. Statistical analysis of stomatal opening of 'Dolly' basil – abaxial and adaxial leaf surface in response to different wavelengths

SOV	df	Mean square	
		stomatal opening (abaxial leaf surface)	stomatal opening (adaxial leaf surface)
Light intensity	3	0.04803**	0.265*
Error a		0.00031	0.0054
Light spectrum	4	0.00736**	0.06557**
Error b		0.0115	0.625
Intensity × spectrum	12	0.00293**	0.06547**
CV		52.460	62.721

SOV – source of variation; CV – coefficient of variation; *significance level: $p < 0.05$; ** significance level: $p < 0.01$

Table 3. Statistical analysis on stomatal opening of 'Breen' lettuce – abaxial and adaxial leaf surface in response to different wavelengths

SOV	df	Mean Square	
		stomatal opening (abaxial leaf surface)	stomatal opening (adaxial leaf surface)
Light intensity	3	0.054**	0.0049**
Error a		0.001	0.00021
Light spectrum	4	0.0574**	0.0067**
Error b		0.034	0.0064
Intensity × spectrum	12	0.0784**	0.049**
CV		49.325	26.627

Note: see Table 2

DISCUSSION

Stomata are crucial for gas exchange and water regulation in plants, and their apertures are significantly dependent on light quality and intensity (Lee et al. 2007; Matthews et al. 2020). Our studies have shown that both light quality and intensity significantly affect stomatal opening on the adaxial and abaxial surfaces of basil and lettuce leaves (Fig. 4–9; Tables 2 & 3). Specifically, the largest stomatal opening on the abaxial surface (Fig. 6 & 8) was observed at 630 nm light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for basil (72.7%) and at 430 nm light for lettuce (68.8%). These percentages are notably higher than those observed under green LEDs. Similar findings were reported previously by Mao et al. (2005), Folta and Maruhnich (2007), Savvides et al. (2012), Muneer et al. (2014), Aalifar et al. (2020), Seif et al. (2021). According to Izzo et al. (2021), Paradiso and Proietti (2022), and Talbott et al. (2002), this is likely because red and blue lights promote photosynthesis by triggering stomatal opening and chloroplast translocation.

Conversely, some studies suggest that green light is less efficient for photosynthesis (Sun et al. 1998; Singh et al. 2015) and can lead to stomatal closure in lettuce under 522 nm light during growth (Kim et al. 2004; Muneer et al. 2014), as well as in spinach and kale during postharvest exposure to 500 nm and 560 nm green LED wavelengths (Rufyikiri et al. 2024), due to decreased activation of cryptochromes. This reduction in cryptochrome activation can decrease transpiration rate and stomatal conductance.

Stomatal opening responds directly to light intensity (Hattori et al. 2007; Muneer et al. 2014). Our data showed that lettuce and basil plants exposed to higher light intensities exhibited greater stomatal opening for most experimental wavelengths. The lowest light intensity (50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) resulted in the narrowest stomatal apertures under all light treatments in both basil and lettuce, except for 630 nm and 430 nm on the adaxial surface of lettuce leaves, where 75 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in the narrowest openings. This phenomenon may be attributed to differences in stomatal distribution or leaf orientation between the adaxial and abaxial surfaces, leading to different responses to light intensity (Davies & Kozlowski 1975). Certain wavelengths such as 630 nm and 430 nm can stimulate stomatal opening more effectively, even at lower intensities, due to their effects on ion transport and turgor pressure changes in guard cells. Further molecular and physiological studies are needed to elucidate the mechanisms underlying these observations.

Plants are able to compensate for the increase in leaf temperature caused by higher light intensity by widening their stomata, thus preventing adverse effects on the photosynthetic apparatus (Ghorbanzadeh et al. 2021). Furthermore, Fanourakis et al. (2019) reported that the pore area per leaf surface significantly increases with increasing light intensity. Larger stomata at high light intensities facilitate increased CO_2 uptake and improve leaf cooling through transpirational water loss, which is beneficial when water availability is sufficient.

Numerous studies have shown positive relationships between light intensity, stomatal conductance, and photosynthetic parameters (Sharkey & Raschke 1981; Lee et al. 2007; Muneer et al. 2014; Sakhonwasee et al. 2017; Fanourakis et al. 2019; Yang et al. 2020). Stomatal conductance, which is influenced by stomatal aperture size, density, and environmental conditions such as vapor pressure deficit (VPD), is dependent on light intensity. Although we elucidated the relationship between stomatal opening and intensity increase, we did not measure stomatal conductance or photosynthetic parameters in this study. Future research should investigate these parameters to better understand plant responses to varying light conditions.

In agreement with Sharkey and Raschke (1981), our results showed that higher irradiance levels (>100 $\mu mol \cdot m^{-2} \cdot s^{-1}$) induced greater differences in stomatal aperture on the abaxial surfaces of lettuce and basil compared to dark control. Stomatal opening under 630 nm and 430 nm showed a stronger response at higher intensities (100 and 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$) on the abaxial surfaces of basil and lettuce, respectively, aligning with the findings of Zeiger and Field (1982) and Tabbert (2023). Interestingly, in lettuce, the stomatal response to 430 nm light at the abaxial surface was strong even at low fluence rates (50 and 75 $\mu mol \cdot m^{-2} \cdot s^{-1}$), which is considered to be independent of mesophyll photosynthesis (Shimazaki et al. 2007; Yang et al. 2020). On the adaxial surface of lettuce, 430 nm light at the lowest intensity increased stomatal aperture to levels comparable to those treated with 530 nm at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Exposure to 430 nm and 630 nm light also resulted in wider stomatal openings.

Our results indicate that green light requires higher irradiance levels to induce stomatal responses similar to those observed with blue (430 nm) and red (630 nm) light, particularly at 530 nm for the abaxial surfaces of lettuce and basil (Fig. 6–9). This can be explained by the lower absorbance and quantum yield of green light at low intensities compared to red and blue light, while at high intensities red and blue light exhibit lower quantum yields than green light (Razzak et al. 2022).

Green light (530 nm and 560 nm) caused the smallest stomatal openings under lower intensities in basil and lettuce, respectively, on both leaf surfaces in the dark, consistent with Frechilla et al. (2000) and Talbott et al. (2002).

The ability of specific wavelengths of green light to reduce stomatal opening is likely attributed to the absorption properties of chlorophyll and related physiological responses. Furthermore, this effect is assumed to be due to reduced activation of cryptochromes, which reduces guard cell turgor and lowers transpiration rate (Shimazaki et al. 2007; Rufyikiri et al. 2024). However, to understand why specific green wavelengths are more effective in reducing stomatal aperture, further studies investigating the molecular and physiological mechanisms involved are necessary. Such studies may include examination of gene expression profiles, signaling pathways, and biochemical processes involved in stomatal regulation under green light.

Our findings revealed a significant difference in the maximum aperture between abaxial and adaxial stomata in both basil and lettuce. The maximum aperture in abaxial stomata was significantly larger than in adaxial stomata, which is consistent with previous studies that showed greater light sensitivity in abaxial stomata (Pemadasa 1979; Wang et al. 2008; Savvides et al. 2012; Fanourakis et al. 2019). This difference can be attributed to changes in light absorption and stomatal distribution in the leaf surfaces. While our study did not focus on elucidating the mechanisms underlying this differential sensitivity, further investigation is needed to explore factors influencing these differences.

Vegetables are traditionally stored postharvest in darkness (Chen et al. 2020). However, our study indicates that green light can effectively keep stomata closed. Since water loss is a primary factor contributing to postharvest quality deterioration such as wilt in leafy vegetables, and stomata regulate leaf water loss (Aliniaeifard et al. 2014), we suggest that green light may be beneficial for postharvest storage of leafy greens such as lettuce and basil. Utilizing specific wavelengths of green light can enable precise and energy-efficient regulation of stomatal aperture, potentially preserving chlorophyll and maintaining the nutritional value and visual appeal of leafy vegetables by stimulating minimal photosynthesis (Lee et al. 2014; Loi et al. 2019).

Controlled application of green light could extend shelf life by balancing reduced metabolic activity with the preservation of desirable qualities such as retention of flavor and color (Pennisi et al. 2021). Therefore, the use of green light could be implemented during storage in distribution chains, retail facilities, and display refrigerators.

It is important to note that the effectiveness of green light in postharvest storage may vary depending on light intensity, duration, and specific characteristics of the vegetable. In addition, future research should examine moisture loss, color changes, and texture as quality determinants, and assess nutritional value by measuring chlorophyll, carotenoids, anthocyanins, and soluble solid content after green light application, especially at 530 nm and 560 nm at lower intensities. Extending the exposure time or conducting observations over several days would provide a more comprehensive understanding of the long-term effects in the postharvest phase.

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Conflict of interest
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could potentially constitute a conflict of interest.

Author contributions
Shafieh Salehinia played a role in the design and execution of experiments, collection, analysis and interpretation of data, and writing the manuscript. Fardad Didaran contributed to the data analysis process, ensuring accurate results and writing the manuscript. Sasan Aliniaeifard provided guidance throughout the experiment and was an active editor. Sarah Macpherson was the major editor and helped to effectively formulate the research findings. Valérie Orsat provided guidance throughout the experimental design process and oversaw the execution of the experiments. Mark Lefsrud provided guidance throughout the experimental design, contributed to comprehensive review of the manuscript, and is the corresponding author.

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