

Effects of different light emitting diode spectra and intensities on the stomatal functioning of lettuce and basil

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Abstract

Light attributes, including intensity and quality, play crucial roles in regulating gas exchange between a leaf and its surrounding environment by influencing stomatal behavior. Understanding how stomata respond to different lighting conditions remains an intriguing research area. With the advancements in light-emitting diodes (LEDs), it is now possible to study plant responses to specific regions of the light spectrum. Stomatal regulation is essential for maintaining a balance between the plant's need for photosynthesis and the prevention of excessive water vapor loss. While the stomatal responses to red and blue lights have been extensively studied, the effects of green light on stomatal behavior remain largely unexplored. Controlling stomatal function in leafy vegetables during postharvest storage is crucial to prevent excessive water loss and wilting which affects marketability. This research aimed to investigate the stomatal opening response of lettuce (Lactuca sativa) and basil (Ocimum basilicum) to varying light quality (430 nm, 630 nm, 500 nm, 530 nm, 560 nm) and quantity (50 µmol m⁻² s⁻¹, 75 µmol m⁻² s⁻¹, 100 µmol m⁻² s⁻¹, 400 µmol m⁻² s⁻¹ Photosynthetic Photon Flux Density (PPFD)), and to identify wavelengths that induce stomatal closure. Our data reveal that stomatal opening in response to different wavelengths is dependent on light intensity. Under most blue and red light treatments, stomatal opening increased on both the abaxial and adaxial leaf surfaces. However, under green light (530 nm and 560 nm), particularly at lower PPFDs, stomatal opening was reduced. These findings emphasize the efficacy of green light (530 nm and 560 nm) in maintaining stomatal closure compared to other light spectra. Utilizing green light during postharvest storage can effectively help preserve the quality and extend the shelf life of leafy greens. In conclusion, this study sheds light on the influence of light quality and quantity on stomatal behavior in lettuce and basil. It highlights the significance of low intensity green light in regulating stomatal closure and provides valuable insights for maintaining postharvest quality and prolonging the shelf life of leafy vegetables.

Abstract (French)

Les attributs de la lumière, y compris l'intensité et la qualité, jouent un rôle crucial dans la régulation des échanges gazeux entre une feuille et son environnement environnant en influençant le comportement stomatique. Comprendre comment les stomates réagissent à différentes conditions d'éclairage reste un domaine de recherche intrigant. Avec les progrès des diodes électroluminescentes (DEL), il est désormais possible d'étudier les réponses des plantes à des régions spécifiques du spectre lumineux. La régulation stomatique est essentielle pour maintenir un équilibre entre le besoin de photosynthèse de la plante et la prévention d'une perte excessive en eau. Alors que les réponses stomatiques aux lumières rouges et bleues ont été largement étudiées, les effets de la lumière verte sur le comportement stomatique restent largement inexplorés. Le contrôle de la fonction stomatique des légumes-feuilles pendant l'entreposage post-récolte est crucial pour éviter la perte excessive d'eau et le flétrissement qui affectent la commercialisation. Cette recherche visait à étudier la réponse à l'ouverture stomatique de la laitue (Lactuca sativa) et du basilic (Ocimum basilicum) à différentes qualités de lumière (430 nm, 630 nm, 500 nm, 530 nm, 560 nm) et quantité (50 μ mol m⁻² s⁻¹, 75 μ mol m⁻² s⁻¹, 100 μ mol m⁻² s⁻¹, 400 μ mol m⁻² s⁻¹ de densité de flux de photons photosynthétiques (PPFD)), et pour identifier les longueurs d'onde qui induisent la fermeture des stomates. Nos données révèlent que l'ouverture des stomates en réponse à différentes longueurs d'onde dépend de l'intensité lumineuse. Dans la plupart des traitements à la lumière bleue et rouge, l'ouverture des stomates a augmenté à la fois sur les surfaces abaxiale et adaxiale des feuilles. Cependant, sous lumière verte (530 nm et 560 nm), en particulier à des PPFD inférieurs, l'ouverture stomatique était réduite. Ces résultats soulignent l'efficacité de la lumière verte (530 nm et 560 nm) dans le maintien de la fermeture stomatique par rapport aux autres spectres lumineux. L'utilisation de la lumière verte pendant l'entreposage post-récolte peut aider efficacement à préserver la qualité et à prolonger la durée de conservation des légumes-feuilles. En conclusion, cette étude met en lumière l'influence de la qualité et de la quantité de la lumière sur le comportement stomatique de la laitue et du basilic. Il met en évidence l'importance de la lumière verte de faible intensité dans la régulation de la fermeture des stomates et fournit des informations précieuses pour maintenir la qualité post-récolte et prolonger la durée de conservation des légumes à feuilles.

Authorship and Manuscript

This thesis follows a manuscript-based format and the contributions of the individuals involved are as follows:

1) Shafieh Salehi Nia: Lead the design and execution of experiments, along with the collection, compilation, analysis, and interpretation of data communicated in this thesis

2) Dr. Mark Lefsrud: Research supervisor; provided invaluable guidance throughout the experimental design process, oversaw the execution of experiments, and contributed to the comprehensive review of the thesis.

3) Dr. Valerie Orsat: Offered insightful guidance on experimental design, enriching the overall methodology of the research.

4) Dr. Sasan Aliniaeifard: Played a crucial role in the development of the experiment's methodology and provided valuable input during the thesis review process.

5) Dr. Sarah MacPherson: Assisted in the writing process of the thesis, helping to articulate and convey the research findings effectively, ensuring the clarity and coherence of the content.

6) Fardad Didaran: Contributed to the data analysis process, ensuring accurate and meaningful results.

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Abbreviations

- CEA: Controlled environment agriculture FL: Food loss H: Hour(s) LCP: Light compensation point LED: Light emitting diode PAR: Photosynthetically active radiation PGAL: Phosphoglyceraldehyde PPFD: Photosynthetic photon flux density PS: Photosystem RH: Relative humidity Rubisco: Ribulos-1,5-bisphosphate carboxylase/oxygenase VPD: Vapour pressure deficit HID: high-intensity discharge lamps MAP: Modified atmosphere packaging FL: Food loss FL-ctog: Food loss- from cradle to grave FL-gtog: Food loss- from gate to grave **CRYs:** Cryptochromes PHOTs: Phototropines ZTLs: Zeitlupe family PHYs: Phytochromes
- CEA: Controlled environment agriculture

1. General introduction

1.1 Thesis motivation

Food security has become a critical global concern in recent decades, driven by population growth projections and magnified by the oncoming pressures of climate change on agriculture (Rouphael et al., 2018). In the United States, 8.2% of the population (27.3 million people) was food insecure from 2019–2021, while in Canada, 6.5% (2.5 million people) likewise faced food insecurity in the same period (Muth et al., 2019). Fresh food loss and considerable financial losses brought on by poor storage practices are grave issues. Hence, advancing storage technology that may address the aforementioned issues is crucial for ensuring food security (Ma et al., 2017). Vegetable consumption has surged due to their high nutritional value and health benefits, and many essential nutrients humans require may be found in vegetables and fruits (Ilić and Fallik, 2017; More et al., 2020). Vegetables may help improve food security and nutritional quality, particularly when managed in highly intensive cropping systems within controlled environments (Rouphael et al., 2018).

Fresh vegetables are not typically subjected to extensive pre-treatment processes to preserve their original flavour and appearance for an extended period of time and are often consumed fresh. Thus, they are susceptible to spoiling as a result of unfavourable external influences, causing consumer rejection of the produce (Jiang et al., 2018). Light emitting diode (LED) lighting is among the most effective approaches for extending the storage life of vegetable crops (Perera et al., 2022). It has many benefits such as being non-toxic, inexpensive, residue-free, and energy efficient compared to conventional preservation technologies (Zhan et al., 2014; Zhang et al., 2022). LED lighting has proven to be a useful technique for extending shelf life, and maintaining sensory quality parameters and bioactive compounds in harvested vegetables (Jin et al., 2015).

This thesis focused on investigating the impact of different green, red, and blue wavelengths at different intensities on stomata opening in model lettuce and basil plants, as a nonhazardous leafy green preservation technique that might improve vegetable quality and reduce vegetable losses during handling.

1.2 Research problem

Although numerous researchers have examined the effects of LEDs on postharvest storage of vegetables, the majority of prior studies have mostly focused on red (620-680 nm) and blue (430-480 nm) light (Nassarawa et al., 2021), and there is little information addressing the effect of green light on harvested plant responses especially lettuce. Research indicates that different light wavelengths can have distinct physiological effects on plants, including stomata regulation, which plays a vital role in plant water loss and gas exchange (Rufyikiri, 2018). By investigating the impact of green LEDs at various wavelengths (500, 530, and 560 nm) in addition to red (630 nm) and blue (430 nm) LEDs, we aim to fill this knowledge gap and gain a more comprehensive understanding of how different light spectra influence stomata opening in lettuce and basil plants. The project will help establish optimal conditions for vegetable storage applicable to wholesale and retail markets, which have the potential to greatly benefit the Canadian agricultural sector by maintaining the visual and nutritional quality of vegetables. In Canada, food loss and waste, at different points in the Canadian food value chain, are estimated at 35.5 million metric tons, representing 58.1% of food products entering the food system at a cost of \$ 49.5 billion (Von Massow et al., 2019). Development of cost-effective postharvest techniques that lengthen vegetable shelf life could reduce waste and aid farmers, stakeholders, and retailers in decreasing their costs and improve their competitive edge on the international market, helping to position Canada as a global leader in this industry.

1.3 Project objective

This thesis focused on investigating the impact of different wavelengths emitted by green LEDs (500, 530, and 560 nm), as well as red (630 nm) and blue (430 nm) LEDs, at different intensities (50, 75, 100, 400 μ mol m⁻² s⁻¹), on stomata opening in model lettuce and basil plants, as a nonhazardous leafy green preservation technique.

1.4 Hypotheses

• Green wavelengths have greater ability to keep lettuce and basil stomata in a closed state in comparison to other wavelengths.

- Lower light intensity exhibits a greater capacity to maintain lettuce and basil stomata in a closed state.
- An effective shelf-life extension of lettuce and basil can be achieved using green LEDs at a lower intensity compared to dark, delaying senescence and yellowing, preserving colour, texture and nutritional value, and reducing decay or infection in leafy vegetables, particularly lettuce and basil.

Organization of thesis

Chapter 1 serves as the introductory section of the thesis, where the underlying purpose and reasoning behind the project are thoroughly explained. In Chapter 2, a comprehensive literature review is presented, accompanied by a concise discussion of the key topics relevant to the research. Chapter 3 outlines the methodology and findings of the research, specifically addressing the research objective. In Chapter 4, a comprehensive summary of the study is provided, highlighting the significant contributions to knowledge, and offering recommendations for future research endeavors on the topic. The reference section follows, providing a list of cited sources for further exploration.

2. Literature review

2.1 Waste and storage

It is well acknowledged that a substantial contributor to post-harvest losses in underdeveloped nations is the absence of adequate harvesting methods, storage facilities, and access to cutting-edge technology that have the ability to minimise such losses (Wunderlich and Martinez, 2018). Improved storage positively affects food security by reducing negative changes in the diet by allowing for an extended food shelf life (Tesfaye and Tirivayi, 2018). In contrast, the majority of food that is wasted in industrialised nations happens during the final stages of the food supply chain, specifically during distribution and marketing, as well as consumption (Wunderlich and Martinez, 2018).

Food loss (FL) management strategies may be classified into two categories: prevention and approaches for reusing food (Garcia-Herrero et al., 2018). FL prevention generates a society net economic benefit that is three times more than that created by recovery and recycling combined (Wunderlich and Martinez, 2018). Enhancing agricultural infrastructure, gaining technological expertise, and developing procedures for storage, transport, and distribution that are more efficient are all components of prevention initiatives in FL-ctog (food loss- from cradle to grave: from agricultural production to processing). In terms of FL-gtog (food loss- from gate to grave: from distribution to the consumption), the initiatives that must be taken into consideration are the enhancement of food labeling, improved consumer planning, and technical advancements in the packaging of perishable foods (Garcia-Herrero et al., 2018).

Figure 2.1 shows the preventable amounts of food waste in the food supply chain. According to the findings, postharvest handling and storage is the step in which the greatest improvements may be accomplished. This is because this procedure is responsible for 55% of the FL-ctog that might have been avoided. Moreover, there is the potential to save 76% of the economic FL-gtog (Garcia-Herrero et al., 2018). Keeping food in optimal conditions during storage is a difficult task (Tesfaye and Tirivayi, 2018). One effective solution would be to supply and enhance access to modernized storage technologies, as well as the use of novel methods such as postharvest lighting to improve the postharvest shelf life of fresh produce for farmers, markets, and households. This would help reduce not only the amount of food that is wasted, but it would also reduce the amount of people who go hungry. The goal of the European Parliament is to reduce

food waste by 50 percent by the year 2030; this may be accomplished if the focus of efforts is primarily directed on postharvest storage at the wholesale, retail and consumer level (Garcia-Herrero et al., 2018).



Figure 2.1 Preventable amounts of food waste in the food supply chain. Modified from Garcia-Herrero et al. (2018).

2.2 Technologies for extending shelf life of fresh produce

Waste of fresh food is a serious problem worldwide. Every year, incorrect post harvest handling and storage result in the loss of about 40 percent of the world's fresh produce (Dumont et al., 2016; Singh et al., 2014). Thus, it is crucial for food security that we develop better storage technologies that can address these issues (Ma et al., 2017; Tesfaye and Tirivayi, 2018; Zhang et al., 2022). Preharvest factors such as genetic factors, harvesting method and maturity at harvest, as well as postharvest practices from harvesting, handling and marketing through the food supply chain have an impact on fresh produce quality (Dumont et al., 2016). Having desired visual, textural, nutritional and flavour quality, without the presence of food-borne pathogens and microorganisms in crops are important factors for consumers (Singh et al., 2014).

Therefore, one of the main goal of postharvest storage is to delay senescence, maintain quality of fresh vegetables, and decrease the occurrence of microbial spoilage and pathogens (Singh et al., 2014). It is well known that to prolong postharvest quality, some key conditions during storage are low temperature to reduce respiration, high humidity to reduce transpiration,

and modified concentrations of carbon dioxide, oxygen and ethylene (Singh et al., 2014). Precooling, refrigeration, and packaging are essential postharvest techniques when long distances exist between harvesting fresh produce and the market. In order to reduce both the qualitative and quantitative losses after harvest, fruits and vegetables require modern postharvest processing technology (Singh et al., 2014).

Several strategies such as chemical treatments, edible coating, modified atmosphere packaging (MAP), controlled atmosphere, ultrasound, application of ozone, and laser irradiation have been employed to increase the efficiency of storage to mitigate quality deterioration and waste (Alexandre et al., 2012; Ali et al., 2020; An et al., 2007; Chen et al., 2020; Jiang et al., 2019; Kerch, 2015; Shezi et al., 2020; Tian et al., 2014; Zhang et al., 2022). The advantages and disadvantages of some of these methods are summarized in Figure 2.2. Nonetheless, there have been concerns raised over the high pricing and the safety of the food with aforementioned conventional methods (Jiang et al., 2019). Developing an energy efficient method to extend the storage life of harvested vegetables that is inexpensive, and harmless such as LED lighting could help address the aforementioned problems (Jin et al., 2021).



Figure 2.2 Conventional postharvest technologies.

2.3 Lighting systems in horticulture

The most common types of electrical lights conventionally used in horticulture are incandescent lamps, fluorescent lamps and high-intensity discharge lamps (HID) (Piromalis et al., 2018). Conventional lamps, although they are inexpensive, have limitations such as generating significant amounts of heat and thus cannot be installed close to the plant canopy. They have a low conversion efficiency of electrical power into illumination (Paradiso and Proietti, 2022; Piromalis et al., 2018). LEDs are becoming more and more popular for plant-based applications, largely due to their technical features: compact size, longer lifespan, low heat generation, solid-state construction, energy efficiency, and the possibility to control the light spectrum (Massa et al., 2008; Nelson and Bugbee, 2014). Figure 2.3 compares the four different lighting sources commonly found in horticulture.



Figure 2.3 Comparison between four different lighting systems.

LEDs are a revolutionary technique for increasing plant growth rates and improving plant nutrition (Shimizu, 2016). LED lighting, as a revolutionary technique in pre- and post harvest stages, has proven to be a cost-effective method of manipulating crop properties in order to improve not only yield, but also quality and bioactive properties of vegetables associated with human health and wellbeing, delaying senescence and increasing resistance to disease by regulating the spectral composition of light during the growth and postharvest stages (Hasan et al., 2017; Landi et al., 2020).

2.4 Light

Light is a form of energy made of photons 'the smallest unit of visible light' (Zwinkels, 2015). The electromagnetic radiation spectrum has low frequency, low energy, big radio waves on one end, and high-energy high frequency short wavelength gamma waves at another end (Figure 2.4) (Pattison et al., 2018). Visible light makes up only a tiny portion of the spectrum (Zwinkels, 2015).



Figure 2.4 Electromagnetic spectrum. Created by Biorender.com

2.5 Photosynthetic pigments and photosynthesis

The visible portion of the electromagnetic spectrum, known as photosynthetic active radiation (PAR), is absorbed by plant pigments. Plants contain various pigments such as chlorophyll a, b, xanthophyll, carotenoids, and anthocyanins (Kuncham, 2021). The precise location of chlorophyll and other light-capturing pigments is in the granum (stacked thylakoids), causing a sequence of processes known as photosynthesis, in which carbon dioxide and water are utilized to create carbohydrates. The two stages of photosynthesis are summarized with details in Figure 2.5. Chlorophyll b, carotene, and xanthophyll collect light energy during the light reaction and transfer it to chlorophyll a, whose electrons are then elevated to a high energy potential. When chlorophyll is in this excited state, its electrons are redirected into a mechanism that collects and stores energy for use later in the creation of compounds like sugars (Capon, 2010). The pigment's lost electrons are swiftly replaced with new ones produced by the breakdown of water, leaving chlorophyll ready to be excited again and the process is repeated (Capon, 2010). Hydrogen (H₂) and oxygen (O₂) atoms are separated from water molecules through splitting in order to provide free electrons. Through open stomata, oxygen (O_2) escapes into the atmosphere (Capon, 2010). Carbon dioxide from the atmosphere combines with the sugar ribulose diphosphate during the process of carbon dioxide fixing, which is another stage of photosynthesis (dark reaction) (Capon, 2010). The resultant molecules of PGAL (Phosphoglyceraldehyde) are then employed as small building blocks for the development of more intricate molecular structures, using the stored energy from the light reaction (Capon, 2010). The product is split into equal portions and hydrogen from the light reaction is added, and the process is repeated. Ribulose diphosphate, glucose, and fructose are among the sugars that are produced throughout the metabolic building process (Capon, 2010). These sugars can be combined to create sucrose, or ordinary table sugar. The enormous molecules of starch and cellulose are made up of thousands of glucose molecules linked together in lengthy chains (Capon, 2010).



Figure 2.5 Two stages of photosynthesis in plants. Summarized from Capon (2010).

2.6 Action spectrum and absorption spectrum

The action spectrum depicts the rate of photosynthesis at different wavelengths of light (Wu et al., 2019). It shows the effectiveness of different wavelengths of light for photosynthesis (McCree, 1971; Wu et al., 2019). Figure 2.6 shows that maximum photosynthesis occurs in blue and red light. The light absorption spectrum shows the absorption of different wavelengths of light by different pigments during photosynthesis (Schwalb, 2014). It explains the relationship between the quality of light and absorbing capacity of pigments (Moss and Loomis, 1952). Chlorophyll absorbs blue and red light, carotenoids absorb violet and blue-green light. The maximum photosynthetic rate in the blue and red region and maximum absorption of blue and red light by chlorophyll suggest that chlorophyll is the primary pigment driving photosynthesis (Terashima et al., 2009).



Figure 2.6 Absorption and action spectrum. Modified from Janeeshma et al. (2022).

2.7 Photoreceptors

Plants absorb sunlight as autotrophs and use photosynthesis to make their own food and energy; light is essential not just because the energy is needed for photosynthesis, but it also acts as a very important informative signal to control plant development, morphology, and adaptation (Devlin et al., 2007). The photoperiod is very important for determining whether a plant will transit from the vegetative to the reproductive phase, which means it will stop making leaves and it will start making flowers. Light quality and intensity are very important for informing the plant, whether they are under a dense canopy and whether they need to grow higher to capture more light. The capacity of a plant to sense and respond to these factors (light quality, intensity, and duration) is critical to maximizing photosynthetic productivity (Briggs and Olney, 2001). Therefore, light is very important for plants and that is why they have evolved many multiple photoreceptors that are analogous to animal rhodopsin-based visual systems (Higuchi and Hisamatsu, 2016). A plant obtains information from the light that reaches it via special pigments known as photoreceptors.

There are five main classes of plant photoreceptors that enable them to detect changes in light direction, intensity, and quality (Figure 2.7) (Meng and Runkle, 2016). These include UVR8, Zeitlupes, cryptochromes, and phytochromes (Meng and Runkle, 2016). Starting from the shorter wavelength, UV-B (280-320 nm) light is perceived by the UVR8 receptor (Kharshiing et al., 2022). There are three different families of UV-A and blue light (320-500 nm) receptors namely cryptochrome (CRY), phototropines (PHOT), and the zeitlupe family (ZTLs). Red (650-670 nm) and far-red (705-740 nm) light are perceived by phytochromes (PHY) (Huché-Thélier et al., 2016). The green (500-600 nm) light photoreceptor is unknown, depending on the light response of CRYs and phototropins whereas longer wavelengths of green light (570 nm) promote the inactivation of B-light-induced CRYs) and/or phytochromes and can affect developmental processes such as seed germination and photosynthesis (Battle and Jones, 2020; Golovatskaya and Karnachuk, 2015; Thoma et al., 2020).

All of the photoreceptors are found throughout the plant and are responsible for a wide range of specific physiological responses, including plant development and circadian rhythm regulation (Mawphlang and Kharshiing, 2017). These photoreceptors are able to integrate signals to induce hypocotyl elongation, shade avoidance, photoprotection, flowering, clock entrainment depending on the developmental stage and their environmental conditions (Mawphlang and Kharshiing, 2017).



Figure 2.7 Different photoreceptors. Modified from Higuchi and Hisamatsu (2016).

2.8 Stomata structure

Stomata are pores located on the leaf epidermis surrounded by a pair of guard cells (kidneyshaped cells in dicots (and some monocots) or dumbbell-shaped cells in monocots) (Zeiger et al., 1987). Stomata morphological parameters are stomatal density (the number of stomatal pores per unit leaf area), stomatal length, stomatal width and stomatal aperture (Aliniaeifard and Van Meeteren, 2016).

2.9 Function of Stomata

The stomatal aperture (stomatal opening) helps uptake CO₂ for photosynthesis while inhibiting excessive water loss through transpiration (Schroeder et al., 2001 a; Schroeder et al., 2001 b). They play a crucial role in maintaining a balance between water loss and photosynthetic efficiency (Driesen et al., 2020), influencing global water and carbon cycles (Blatt et al., 2017; Schroeder et al., 2001 a) (Figure 2.8). Two stomatal-driven mechanisms—short-term modifications to pore size (stomatal aperture) or long-term developmental regulation of stomatal density, size, and patterning—are principally responsible for achieving this balance. It is crucial to remember that stomatal traits are frequently connected and functionally coordinated (Harrison et al., 2020).



Figure 2.8 Stomatal structure on the leaf surface responsible for regulating gas exchange (CO_2 and water vapour). Modified from Bishnoi et al. (2022) and created by Biorender.com.

2.10 Mechanics of stomata opening and closure

Stomata open as a result of an increase in osmotic pressure (OP) within guard cell vacuoles, which is brought on by an input of K+ and anions like Cl- from the nearby epidermal cells (Srivastava, 2002). The increase in osmotic pressure is further facilitated by organic solutes such as malate and sucrose. These solutes build up in the vacuole, which causes a water influx and subsequent volume change in the guard cells. The thin outer wall of guard cells can inflate out and pull the thicker inner wall (which borders the pore) along with it, opening the pore. K+ and anions (along with other solutes) migrate out of the cell or to intracellular compartments during stomatal closure, which causes water loss and closure (Srivastava, 2002).

2.11 Stomata: linkage of pre-harvest and postharvest quality of horticulture products

Some studies have addressed the importance of pre-harvest environmental conditions on postharvest quality and longevity of the products (Hewett, 2006; Lee and Kader, 2000; Pettersen et al., 2007; Sams, 1999; Yahia, 2019). The question is, how are pre-harvest environmental cues perceived by the plant, how does this influence stomatal activity, and how does this impact the postharvest performance of the product. In many aspects the stomata are the main plant structures in flowers, herbs, vegetables that make the connections between perceiving pre-harvest environmental conditions to post-harvest quality and longevity. It is proposed that the main plant structures that make the connection between growing plants in pre-harvest to their quality performance at the postharvest stage are the stomata (Figure 2.9).



Figure 2.9 Preharvest and postharvest factors linking postharvest quality via stomata.

2.12 Important preharvest factors influencing postharvest quality through stomata

When plants are produced under certain lighting (light quality, intensity, and photoperiod), evaporative demands (low vapor pressure deficit (VPD)), pollutants, and growing or propagation conditions (*in vitro*), changes in metabolite homeostasis and in the signaling pathway of stomatal guard cells take place which can lead improper stomata functioning (Aliniaeifard and van Meeteren, 2013). This stomatal malfunction usually takes a negative role after the harvest of the horticultural products when the water availability for the plant is limited due to separation from the mother plant (Fanourakis et al., 2013 a). Under these conditions, the stomata may stay open even after harvest, leading to extreme water loss from the plant more than its physiological active state, consequently wilting of the leaves and/or flowers (Aliniaeifard and van Meeteren, 2013; Fanourakis et al., 2011; Nejad and Van Meeteren, 2005). In the following sections, the major environmental conditions leading to stomatal malfunctioning are introduced. These include temperature, water availability, pathogens, harvesting time, genetics, human activity, air humidity, and light.

2.12.1 Temperature

Temperature management before and after harvest is one of the most important tools for extending shelf-life and maintaining the quality of fresh fruits and vegetables (Gruda, 2005; Islam et al., 2009). Stomata regulate the gas exchange between the plant and the environment but are additionally involved in controlling plant temperature through transpiration (Schulze et al., 1973). The response of stomata to temperature is not constant across different temperatures and is usually species-dependent (Mai et al., 2010; Rogiers and Clarke, 2013). There are contradictory reports regarding stomatal response to different temperatures, with both stomatal closure and stomatal opening being reported with increased temperature and decreased temperatures (Reynolds-Henne et al., 2010; Wilkinson et al., 2001).

Horticultural products are typically cooled right after harvest. Delays between harvesting and cooling or processing can result not only direct loss of water via the stomata but also indirect losses such as those in flavor and nutritional quality (Gruda, 2005; Islam et al., 2009; Wilkinson et al., 2001). This cooling results in rapid stomatal closure to decrease dehydration of the leaves when the water supply from the roots is limited or stopped (Davies et al., 1982). Rapid stomatal closure is a plant avoidance strategy to cope with chilling stress (Mai et al., 2010). By closing the stomata, products can keep the quality in cold storage after harvest. However, there is little support for the role of stomata in the occurrence of chilling injury in fruits (Purvis, 1984). There are differences in stomatal closure between species after exposure to low temperatures. In response to cold temperatures (7 °C), Asiatic dayflower (Commelina communis) is capable of closing its stomata after one hour when transferred to the cold temperature, while the stomata of tobacco (Nicotiana rustica), do not have closure, leading to uncontrolled water loss and wilting of the leaves after 5 h of cold treatment (Wilkinson et al., 2001). Despite these problems with low-temperature stomata closure for some species, cooling down plant products is a common postharvest practice as the post-harvest shelf life of various fresh fruit and vegetables can be extended by storage at low temperatures (Ning et al., 2022). In a situation where water availability is not limited, stomatal opening takes place after increasing the temperature (Reynolds-Henne et al., 2010). Inducedstomatal opening due to higher temperatures leads to increases in transpiration, which result in scarcity of available water for the product which can result in irreversible situations (e.g. leaf burning) that reduce crop quality and quantity (Gruda, 2005). The effect of temperature on stomata

function as well as on maintaining plant quality is highly species-dependent. For instance, two cooccurring subtropical forest dominating tree species, *Syzygium rehderianum* and *Schima. superba*, respond differently to high temperatures in terms of stomatal morphology (stomatal size or density) and photosynthetic function. Stomatal density decreased while stomatal size was maintained by *S. superba*, which may have prevented excessive water loss but at the expense of lowering carbon gain (i.e., decrease in photosynthetic rate). In contrast, *S. rehderianum* was able to maintain photosynthetic rate in warming circumstances by balancing water loss and carbon absorption by shrinking stomata without affecting stomatal density (Wu et al., 2018). It can be concluded that the temperature can influence the proper function of stomata and as a result, influence product quality.

2.12.2 Water availability

Water availability is one of the production factors that influence postharvest performance, nutrition, and quality of the horticultural products via stomata function of the stomata. Therefore, management of water availability during the production of plants is determinant (Lee and Kader, 2000; Luna et al., 2013).

2.12.3 Pathogens

Many pathogens cannot directly infect plants through the mesophyll. These pathogens can penetrate the plant leaf through natural openings like stomata (Gudesblat et al., 2009). For this reason, plants have evolved the capacity to adjust stomatal apertures not only in response to diverse abiotic environmental factors but also in response to pathogens (Melotto et al., 2006; Noei et al., 2022). Most of the time, pathogens penetrate plants via stomata and after harvest, they penetrate the mesophyll from the inside, which results in decreased horticultural product quality (Kennelly et al., 2005; Noei et al., 2022; Prusky, 1996).

2.12.4 Harvesting time

Harvesting time and age of the plant, can determine the quality of the horticultural products. Choosing the right time for harvest is important to prevent physiological disorders such as in-rolling, off odour, and browning (Becerra-Sanchez and Taylor, 2021; Doi et al., 2013). Freshly-cut lettuce from immature heads produces more CO₂, which is associated with off-flavors, ethanol, and acetaldehyde accumulation (Fanourakis et al., 2013 a). It has been reported

that the stomata play an important role in preventing the occurrence of these physiological disorders (Doi et al., 2013). Management of environmental conditions can prevent the occurrence of calcium deficiency disorders by influencing the transpiration of water vapor through the stomata of the fruit (de Freitas and Mitcham, 2012).

2.12.5 Genetics

Genetics are always considered the main factor influencing product performance and quality during the production and postharvest stages (Tudela et al., 2013). Cultivar selection is a critical earliest decision-making point, for achieving the desired quality of horticultural products. In some horticultural plants, genotypic differences that influence stomatal responses during the production stage have been reported to affect postharvest crop quality (Aliniaeifard and van Meeteren, 2014; Tudela et al., 2013).

2.12.6 Human activities

Human activities in recent decades have led to an increase in the concentration of greenhouse gases such as carbon dioxide (CO₂), ozone (O₃), and sulfur dioxide (SO₂). These greenhouse gases can enter plants mainly via stomata apertures (Hoshika et al., 2012; Mauzerall and Wang, 2001; Overmyer et al., 2008). These gases can lead to both short and long-term positive and/or negative effects on the quality of the plant (Grulke et al., 2007; Mauzerall and Wang, 2001; Mills et al., 2010).

2.12.7 Relative humidity (RH)

Commercial production of vegetables, fruits (such as strawberry), cut flowers, and ornamental plants under controlled environment agriculture (CEA), including indoor vertical and semi-closed (greenhouses) environments, over the recent few decades especially in urban and periurban area (Gómez et al., 2019; Lastochkina et al., 2022; Rabbi et al., 2019). Low VPD and high RH are needed to save energy in those environments (Fanourakis et al., 2013 a).

Plants produced under high RH conditions grow normally but after harvest, harvested plants face some problems (Aliniaeifard and van Meeteren, 2013). In this situation, due to prolonged exposure to high RH, a habituation process occurs in guard cells of the stomata, as a result, stomata stay open after harvest, rendering stomata insensitive to stimuli that would normally

provoke stomata closure (Aliniaeifard et al., 2014). This disturbance in the normal function of the stomata due to previous long-term exposure to high RH has horticultural consequences. High RHgrown plants often have a higher rate of water loss compared to moderate RH-grown plants after harvest (Fanourakis et al., 2013 b; Rezaei Nejad et al., 2006). It has been reported that a higher rate of water loss following harvest under high RH-grown plants is mainly caused by stomata opening rather than the role of cuticle (Fanourakis et al., 2019; Fanourakis et al., 2013 b). Duration of exposure to high RH is critical for the occurrence of stomatal malfunctioning. As a result, despite the short-term exposure to high RH, long-term exposure depending on the species will result in the occurrence of stomatal malfunctioning (Aliniaeifard et al., 2014). The longer exposure to moderate RH at the time of completion of leaf expansion will result in the generation of functional stomata and fewer negative effects (Fanourakis et al., 2011). After full leaf expansion, the function of stomata will not further be influenced by exposure to high RH impacts the function of the stomata but is highly species-dependent (Fanourakis et al., 2011).

Cultivation at high RH conditions not only influences the shelf life and visual appearance of cut flowers, but it can also influence the postharvest life and nutritional quality of leafy vegetables via the stomata. A higher rate of water loss was observed after the harvest of basil (*Ocimum basilicum*) and lemon balm (*Melissa officinalis*) leaves as a result of exposure to 95% RH, compared with plant leaves that were exposed to lower humidity levels (Islam et al., 2009). Postharvest shelf life was negatively correlated to the rate of water loss via stomata after harvest of the plants (Islam et al., 2009). High levels of water loss by the leaf due to malfunctioning of the stomata after production resulted in declined nutritional quality such as decreased vitamin C content in leaves (Ezell and Wilcox, 1959; Lee and Kader, 2000). It has been reported that a decrease in the RH after the production of leafy vegetables will result in the leaves' wilting. Leaves of plants that lose their moisture easier are more vulnerable to losing vitamin C compared with the plants that are resistant to wilting (Ezell and Wilcox, 1959; Lee and Kader, 2000).

The production of flowers and vegetables grown under high RH conditions renders stomata incapable of a suitable response to closing stimuli resulting in a negative water balance of the leaf and flower after harvest. The rate of water uptake in flowers falls below the rate of transpiration, and the ability of leafy vegetables to retain water after harvest is reduced. These changes lead to decreased relative water content and water potential, which causes wilting and lowers the nutritional value and postharvest life of horticultural products.

2.12.8 Light

To maintain plant growth and development, light is a crucial component. Nowadays, CEAgrown crops using artificial illumination is spotlighted in horticulture research, and is an innovative method for increasing productivity and horticultural techniques (Lastochkina et al., 2022). To reduce interaction with the outside climate, CEA has sophisticated control over a variety of environmental parameters (such as temperature, humidity, light, and CO2 concentration) (Lastochkina et al., 2022). Crop production in CEA facilities is gaining popularity and spreading over the world for producing crops due to a variety of benefits, including diversity, absence of dependence on the season and location, exceptionally high resource usage efficiency, and removal of pesticides (Lastochkina et al., 2022; Marcelis et al., 2019). Artificial lighting is not just employed as the only source of light, it is frequently used as a supplement to natural sunlight, particularly in greenhouse production (Aliniaeifard and Van Meeteren, 2017). Greenhouse crop production frequently makes use of supplementary lighting to improve plant productivity in periods of the year when natural radiation is low. This affects several aspects of plant functioning, including photosynthesis, photomorphogenesis, biomass accumulation, water relation as well as plant product appearance and quality (Hewett, 2006; Van Ieperen, 2012).

LEDs are becoming more conventional artificial lighting sources for plant-based applications, largely due to their compact size, robustness, longer lifespan, and low emission temperature (Hewett, 2006). LED lighting's spectral control allows different photoreceptors to be selectively activated, enhancing desirable plant qualities. Such manipulation is impossible with traditional light technology, therefore, LED lighting has the potential to revolutionise horticultural practise by precisely activating different photoreceptors in various crops (Davis and Burns, 2016; Kharshiing et al., 2022; Paradiso and Proietti, 2022). LEDs may be a useful tool for studying stomatal functioning. Young tomato plants grown under supplemental LED (95% red, 5% blue) compared to HPS showed better water status and therefore a higher transpiration capacity because spectral quality of the LED modules positively influenced stomata behaviour and the gas exchange system. The young plants grown under LED tended to have increased photosynthetic capacity. Moreover, the presence of green light in HPS lamps may have led to stomatal closure and/or

reduced stomatal density, in turn reducing transpiration and increasing leaf temperature (Palmitessa et al., 2021).

Although light is the major energy source for photosynthesis, plants respond differently to light intensity, duration, and wavelengths and their growth is affected by these factors. Studying the light environment effects especially light wavelengths on the water loss regulation via stomata, is essential for the horticultural industry because of the increased competition for production of high quality plants and shelf life guarantee in the postharvest stage (Seif et al., 2021).

2.12.8.1 Red light

Due to the greater efficiency of red LEDs, researchers investigated the use of a red LED light (600-700 nm) for growing several plant species in controlled conditions. Increasing the percentage of red photons for greenhouse tomato production with LEDs' controllability can help discern cultivar-specific responses (Kusuma et al., 2022). Some researchers have demonstrated that monochromatic red light has substantial impact on growth and morphological parameters, boosting the generation of fresh mass, the leaf area, and leaf number (Hamdani et al., 2019; Ouzounis et al., 2015; Su et al., 2014). Specific Red: Far Red ratios may also stimulate the development of various photosynthetic structures at different levels, including photosynthesis, stomata function (Kang et al., 2009), leaf thickness (Barreiro et al., 1992), and the development of chloroplasts (Thiele et al., 1999). Some studies have found that monochromatic red lighting has a negative influence on photosynthetic performance, and the term "red light syndrome" refers to this effect (Hernández and Kubota, 2016; Sytar et al., 2021; Trouwborst et al., 2016). The photosynthetic processes were severely hampered in leaves grown under monochromatic red light, including stomatal dysfunction, and low photochemical efficiency was observed in leaves accustomed to darkness or light (Sytar et al., 2021). Lettuce grown with red light results in more stem elongation and reduced biomass (Hoenecke et al., 1992). Red light further decreased stomata size and improved functionality in chrysanthemum, thus enhancing stomatal ability to regulate water loss upon desiccation for a longer period (Seif et al., 2021).

2.12.8.2 Blue light

Long-term exposure of plants to monochromatic blue light may impact growth, and plant morphology in the plant photosynthetic apparatus because in addition to phototropins and cryptochromes, it is highly likely that blue light signalling in the guard cells, which is mediated by zeaxanthin, is involved (Huché-Thélier et al., 2016; Van Ieperen, 2012). Susceptibility of various plant species to a monochromatic blue light environment varies. The stimulating effect of blue light on stomata opening is very important because of blue light effects on photoreceptors (e.g, cryptochromes) (Zeiger et al., 2002). Additionally, under exposure of blue light, stomata density, length, and width were increased in addition to their functionality (Li et al., 2010; Sytar et al., 2021).

The blue spectrum mainly determined stomatal size, whereas a broader spectral range was important for determining stomatal density (Seif et al., 2021). However, monochromatic blue or red light inhibited development of stomata in *Withania somnifera* plantlets (Lee et al., 2007).

2.12.8.3 Green light

Based on the absorption spectra of chlorophyll (Chl) and carotenoids, it was previously believed that green light had limited effectiveness in supporting photosynthesis, photomorphogenesis, and overall plant growth (Sytar et al., 2021). This was further corroborated by the effects of green light, which cause the stem to elongate and the leaf area to expand, but lower biomass output (Folta and Maruhnich, 2007; Sytar et al., 2021). According to research performed to date, adding green light to the growth spectrum does not always improve crop productivity. For example, using 24% green light enhanced lettuce yields; however, using more than 50% green light resulted in decreased yields, likely due to lower total photosynthetic rates (Davis and Burns, 2016; Kim et al., 2004b). Additionally, it has been demonstrated that green light could cause stomatal closure in lettuce, spinach and kale by reducing the activation of cryptochromes (Davis and Burns, 2016; Kim et al., 2004b; Rufyikiri, 2018). Therefore, with the closing ability of certain quality and intensity of light on the stomatal opening and thus reducing the moisture loss, the shelf life of horticultural products can be enhanced (Lester et al., 2010; Noichinda et al., 2007; Rufyikiri, 2018).

2.13 Factors affecting stomatal opening and development

The following factors play a significant role in the regulation of stomatal opening and development:

1. Light: stomatal opening is induced by light, particularly blue and red light. Blue light acts as a signal, while red light acts as an energy source for photosynthesis in chloroplasts (Driesen et al., 2020). Blue light activates PM H⁺-ATPase, leading to hyperpolarization of the plasma membrane and uptake of K+ ions. Red light-induced stomatal opening is associated with a decrease in intercellular CO₂ concentration (Ci) (Driesen et al., 2020).

2. CO_2 concentration: Increasing atmospheric CO_2 levels lead to stomatal closure and downregulation of stomatal development in leaves. Elevated CO_2 concentrations can trigger stomatal closure through both ABA-dependent and ABA-independent pathways (Driesen et al., 2020).

3. Temperature: High ambient temperature inhibits stomatal development, and stomatal opening depends on phototropins and involves the activation of PM H⁺-ATPases (Driesen et al., 2020). A phototropin-independent pathway mediated by ROS production also contributes to stomatal opening (Driesen et al., 2020).

4. Relative Humidity (RH): Stomata close in response to lower RH. The response to low RH involves both passive and active mechanisms. Passive response is due to reduced leaf water content and turgor loss, while active response involves ABA-mediated signaling (Driesen et al., 2020).

In general, to gain a comprehensive understanding of how plants develop, it is essential to investigate the interplay between these environmental factors (summarized in Table 2-1). Exploring the interactions among these factors will provide insights into the complete range of responses exhibited by plants during their growth and development (Driesen et al., 2020).

Table 2.1 Summary of how light, CO₂, temperature, and relative humidity affect stomatal development and opening modified from Driesen et al. (2020).

Environmental factor	Stomatal opening response	Stomatal development response
Light	Light stimulates stomata opening Blue and red light open stomata through separate mechanisms.	Light intensity:stomatal index
	CO2-concentration stimulates stomatal closure	CO2-concentration: downregulation of stomatal development: stomatal index
Temperature	Temperature stimulates stomatal opening	Ambient temperature:stomatal development
Relative humidity	Relative humidity induces stomatal closure	 ↑ RH: ↑ stomatal density ↑ stomatal length

2.14 Senescence

Senescence is a regulated process that leads to cell death in plants and a dramatic decline in fruit quality. Senescence in leafy vegetables is characterized by significant chlorophyll loss and wilting (Pogson and Morris, 2004). Because chloroplast pigments, lipids, and proteins are typically the first compounds to be degraded, chloroplast pigment loss is an indicator of green tissue senescence (Kuai et al., 2018; Noodén et al., 1997; Wu et al., 2012) and loss in photosynthetic capacity will degrade crop quality (Kuai et al., 2018). It involves a number of changes, including tissue wilting, the transfer of residual nutrients from the ageing site to the surviving site, a reduction in cell membrane permeability, the production of reactive oxygen species (ROS), the degradation of protein macromolecules, and a loss of phytochemical content (Buchanan-Wollaston et al., 2005; Zhang et al., 2022). Senescence in crops is further regulated by the phytochrome signalling system (Song et al., 2020). Finally, sugar depletion causes cellular changes that occur during senescence (Penfold and Buchanan-Wollaston, 2014).
Water stress (dehydration), which is one of the most serious consequences after harvesting plants, causes stomatal closure, which accelerates senescence. It can be alleviated by storing vegetables in high humidity and low temperatures (Lipton, 1987; Thimann et al., 1977). However, dark storage hastens the senescence process, resulting in texture loss, a drop in the concentrations of micro and macronutrients, and rapid chlorophyll and protein degradation (Buchanan-Wollaston et al., 2005; Kuai et al., 2018; Saltveit, 2004; Wu et al., 2012). There is a strong relationship between respiration rate and senescence rate in darkness, which has been shown to hasten the ageing process, resulting in lower levels of carbohydrates quickly (Brouwer et al., 2012; Weaver and Amasino, 2001). To prevent senescence during postharvest storage, light has been proposed as a potential solution (Hosoda et al., 2000; Ranwala and Miller, 2000).

2.15 LEDs in postharvest storage

Because of LEDs' low heat emission and high-efficiency luminescence under low temperature conditions, this lighting technology is suitable for postharvest storage particularly in long-distance transportation when combined with refrigeration (D'Souza et al., 2015; Kader, 2004; Nassarawa et al., 2021; Zhang et al., 2022). Leafy vegetables exposed to low light intensity can maintain their initial quality in comparison to the dark (Hasperué et al., 2016; Jin et al., 2015; Woltering and Seifu, 2014). Postharvest lighting at relatively low and modest intensities has been shown to prevent senescence in harvested vegetables (Braidot et al., 2014; Costa et al., 2013; Hasperué et al., 2016; Rufyikiri, 2018; Woltering and Seifu, 2014; Zhou et al., 2020) which are attributed to its effects on stomatal opening and photosystem maintenance (Pogson and Morris, 2004). The loss of photosynthesis in the absence of light, which results in a sharp decrease in carbohydrates, is the primary factor in dark-induced senescence (Buchanan-Wollaston et al., 2005). Numerous studies have demonstrated that postharvest storage in light is linked to an increase in sugars, resulting in a delay of senescence in Chinese kale (Brassica oleracea alboglabra) and cauliflower (Brassica oleracea) (Noichinda et al., 2007; Zhan et al., 2014). Similar results were reported for broccoli (Brassica oleracea), where postharvest light storage delays chlorophyll breakdown and lengthens product shelf life (Kasim and Kasim, 2017; Zhan et al., 2012; Zhan et al., 2014)

Some studies have contrarily demonstrated that continuous or intermittent light exposure has a negative impact on vegetables stored at low temperatures. The exchange of gases between the plant tissue and the atmosphere within the packaging is facilitated by light-stimulated stomata opening as a general response, resulting in significant water loss of vegetables stored in the presence of illumination (Braidot et al., 2014; Pennisi et al., 2021; Xu et al., 2014; Zhou et al., 2020). Furthermore, light stimulated respiratory activity in polypropylene package films with selective gas permeability on cauliflower (*Brassica oleracea var. botrytis*) and broccoli (Olarte et al., 2009).

Effective light treatments in the postharvest stage must be properly selected for light intensity, light quality, and photoperiod, to be able to limit photooxidative stress during storage at low temperatures (Glowacz et al., 2015; Pogson and Morris, 2004). Adequate light duration, intensity and appropriate wavelengths of light could improve quality parameters and phytochemical content in green vegetables (Martínez-Sánchez et al., 2011; Noodén and Schneider, 2004; Rufyikiri, 2018; Zhan et al., 2013; Zhan et al., 2012). Table 2.2 summarizes some of the LED applications tested in postharvest storage of vegetables, which have a promoting effect on their quality parameters and bioactive compounds.

Crop	Light quality	Light	Light duration	Results	Reference
		intensity	and		
			temperature		
Fresh cut	Cool white	50 and 150	-Continuous	-Continuous light (50 and	(Charles et al.,
butterhead	fluorescent	µmol m ⁻² s ⁻¹	For 7 days.	150 μ mol m ⁻² s ⁻¹): inhibited tissue	2018)
lettuces		(LCP: 30	-Intermittent	browning but stimulated dehydration.	
(Lactuca		μ mol m ⁻² s ⁻¹)	For 2 days (2 h	-Intermittent light: minimized browning	
sativa)			on/2 h off), and	and water loss & had positive residual	
			then darkness	physiological change during the following	
			for 5 days	5 d of storage in darkness.	
			6 °C	-All treatments maintained photosyntethic	
				capacity except continuous 150 µmol m ⁻² s	
				⁻¹ Best treatment: intermittent moderate	
				level light (50 μ mol m ⁻² s ⁻¹)	
Pak choi	LEDs:	10, 35, 70	Intermittent	-Red light irradiation (35 μ mol m ⁻² s ⁻¹)	
(Brassica	-R	μ mol m ⁻² s ⁻¹	4, 8, 12, 24 h;	efficiently preserved soluble protein and	(Song et al.,
<i>rapa</i> ssp.	-B		20°C	chlorophyll content, while reducing the	2020)
chinensis)	-FR		For 5 days	expression of senescence-associated and	
				ethylene signaling genes.	
				-Blue light's suppressive impact was far	
				less effective than that of red light.	
				-Exposure to far-red light stimulated leaf	
				senescence, suggesting that senescence in	
				crops is therefore regulated by the	
				phytochrome signaling system.	
Broccoli	LEDs:	24, 21, 27,	Continuous	-White, red, and yellow LEDs had a	
(Brassica	-G (522nm)	66, 40	For 20 days	favourable impact on the redox state of	(Loi et al.,
oleracea.	-B (467 nm)	μ mol m ⁻² s ⁻¹	4 °C	broccoli.	2019)
var. italica)	-Y (567 nm)			-Green LEDs enhanced chlorophyll and	
	-R (625 nm)			ascorbic acid content, and was the only	
				LED light that had a positive effect on	

Table 2.2 The effects of postharvest LED lighting in postharvest storage. B: blue; R: red; G: green; W: white; Y: yellow; FR: far-red LCP: light compensation point; LED: light emitting diode.

	- W (3000 K colour			analyzed quality parameters; suggested to extend broccoli shelf life during cold	
	temperature)			storage.	
Fresh cut	White	7 and 30	Continuous	-Postharvest lighting considerably	
butterhead	Fluorescent	μ mol m ⁻² s ⁻¹	14 days	prolonged shelf life of fresh-cut product	(Woltering and
lettuces			12 °C	compared to storage in darkness; this was	Witkowska,
(Lactuca				reflected in higher overall visual quality	2016)
sativa)				values and delayed cut-edge browning.	
				-An 8x to 10x increase in carbohydrate	
				levels (sugars and starch) whereas	
				carbohydrates decreased when the fresh-	
				cut product was stored in the dark.	
				-Storage in light caused an increase in dark	
				respiration leading to increasingly negative	
				photosynthetic values.	
Fresh-cut red	LEDs:	35	Continuous	-Yellow and blue light in red chard and	
chard (Beta	-G (517 nm)	μ mol m ⁻² s ⁻¹	For 10 days	yellow and green light in rocket decreased	(Pennisi et al.,
vulgaris) and	-B (465 nm)		5°C	microbial numbers.	2021)
rocket	-R (660 nm)		95% RH	-The ability to retain color and chlorophyll	
(Diplotaxis	-FR (730 nm)			content, in rocket, as well as increase	
tenuifolia)	-White (peak at			carotenoids in red chard, was made	
	610 nm)			possible by green and white light.	
				-Both species responded to the application	
				of red or blue light by increasing their total	
				antioxidant capacity and total phenol	
				content.	
				-Biomass loss during storage enhanced by	
				LED light supply when compared to when	
				it was dark, albeit this effect was less	
				pronounced in response to yenow and far	
				red light.	

Pak choi (<i>Brassica</i> <i>campestris</i> ssp. chinensis Makino var. commun is)	White LED (peaks at 448 and 549 nm)	10 μmol m ⁻² s ⁻¹	Continuous For 7 days 20 °C 90 % RH	 Significantly reduced changes in sensory evaluation, respiration rate, and malondialdehyde content while maintaining higher chlorophyll and vitamin C content. LED treatment increased the expression of the chlorophyll synthetase gene BrHEMA1. LED treatment postponed senescence, and preserve pakchoi's quality, possibly by controlling the chlorophyll metabolism and increasing the activity and relative gene expression levels of antioxidant enzymes. 	(Zhou et al., 2020)
Fresh cut butterhead lettuces (<i>Lactuca</i> <i>sativa</i>)	LEDs: -R (660 nm) -B (455nm) -R+B -G (530nm)	5 μmol m ⁻² s ⁻¹	Continuous and intermittent 12 h per day 14 days 12 °C	 -Continuous or 12-h photoperiods extended shelf life over the dark control. -Red+blue and green light treatments had higher total carbohydrates than blue and dark treatments. -Carbohydrate levels and shelf life correlated positively in this experiment. Photosynthetic sugar generation may not be the main process in sugar accumulation because the applied light intensity (5 µmol m⁻² s ⁻¹ PAR) is below the light compensation point. Low-light sugar buildup may entail gluconeogenesis. 	(Woltering and Seifu, 2014)
Lamb lettuce (Valerianella olitoria)	Warm white LED (peaks 460 and 570 nm)	1.4 ± 0.4 $\mu E m^{-2} s^{-1}$	Continuous and intermittent 1 cycle of 8 h or 8 cycles of 1 h, or 16 cycles of 0.5 h per day	-Although continuous light (1 cycle of 8 h per day) was harmful, 8 cycles of 1 h per day and 16 cycles of 0.5 h per day) had a positive effect on chlorophyll, carotenoids, ATP, glucose, and ascorbate.	(Braidot et al., 2014)

			6 °C 6 days		
Fresh cut Amaranth (<i>Amaranthus</i> <i>dubius</i>)	Blue LED (460 nm)	10,20,30 μmol m ⁻² s ⁻¹	Continuous 4°C 90% RH For 12 days	 -Antioxidant enzyme activity can be enhanced and microbial growth efficiently inhibited with irradiating the samples with blue LED 460 nm light; 2-3 d were added to their shelf life. However, biomass loss increased with increasing intensity. -The AsA-GSH cycle was effectively activated with 30 umol. -The principal spoilage bacterium, <i>Pseudomonas aeruginosa</i>, and colony growth on newly cut amaranth were both inhibited by the 460nm LED. 	(Jin et al., 2021)
Fresh cut pakchoi (<i>Brassica</i> <i>rapa</i>)	Red-Violet LED (660 & 405 nm)	15 μmol m ⁻² s ⁻¹	Intermittent 12 h per day For 12 days 4°C 90% RH	-LED treatment postponed senescence and preserved quality by increasing the activity of antioxidant enzymes, regulating chlorophyll and ASA metabolism, and preventing specific spoilage organism growth.	(Zhang and Xie, 2022)
Broccoli (<i>Brassica</i> <i>oleracea</i> ssp. italica)	-White fluorescent -Green LED (520 nm)	13 μmol m ⁻² s ⁻¹	Intermittent 12 h per day For 2 days 25 °C	 Both types of light treatment enhanced antioxidant activity, prolonged shelf life, and prevented the loss of H value and chlorophyll concentration in broccoli florets. The amount of total phenols and glucosinolates were considerably elevated by LED green light. 	(Jin et al., 2015)
Chinese kale	White fluorescent	21.8 µmol m ⁻² s ⁻¹	Continuous For 10 days 1°C	-Fluorescent light induced greater weight loss on the separated leaves of kale while partially preventing vitamin C loss and	(Noichinda et al., 2007)

(Brassica				increasing starch, fructose, and glucose	
oleracea var.				levels.	
alboglabra)					
	LEDs:	W:9.2 V	Continuous	-Chlorophyll content: G>W>R>B>Dark	
	-White	G: 9.7 V	For 18 days	Vitamin C:B>E>G>R>Dark	
Cabbage	-B (436nm)	B: 10.1 V	4 °C	Phenolic: B>W>R>G>Dark	(Lee et al.,
(Brassica	-G (524nm)	R: 7.1 V			2014)
oleracea var.	-R (665nm)	Current:150			
Dongdori)		mA			
Head	Green LED	50	Continuous	-Green light enhanced the Chl	(Amagai et al.,
Cabbage	(525nm)	μ mol m ⁻² s ⁻¹	For 2 days	concentration and colours of the inner	2021)
(Brassica			20°C	leaves of cabbages	
oleracea var					
capitata)					
Broccoli	Red LED	50	Continuous	-Maintained the sensory quality of	(Jiang et al.,
(Brassica.		μ mol m ⁻² s ⁻¹	For 5 days	broccoli and prevented yellowing and	2019)
<i>oleracea</i> var.			20°C	degradation of chlorophyll and weight loss	
italica)					
baby-leaf	White	26.9	Continuous	-Maintaining/enhancing ascorbate, folate,	
spinach	fluorescent	μ mol m ⁻² s ⁻¹	For 9 days	and phylloquinone: storage in light> Dark.	(Lester et al.,
(Spinacia			4 °C	-Carotene and xanthophylls unaffected by	2010)
oleracea var.				dark or light treatment (despite being	
Lazio and				associated with a photosynthetic process).	
'Samish')				-Leaf wilting and decline in turgidity:	
				storage in light > Dark (no decline in	
				turgidity)	

2.16 Using LEDs to preserve plant's post-harvest quality

There is no current and definitive conclusion for how different LED wavelengths can enhance preservation efficiency, despite numerous studies examining the effect of varying wavelengths, irradiation intensity, and irradiation cycle on the quality of produce (Zhang et al., 2022). LEDs may preserve postharvest fruits and vegetables in several ways that are summarized in Figure 2.10.



Figure 2.6 LED possible mechanisms for improving preservation efficiency of fresh produce.

LED irradiation can extend the photosynthesis time of these fruits and vegetables, compensating for the nutritional loss caused by respiration and leading to longer preservation periods. LED irradiation may regulate gene expression and delay the senescence process, possibly through photochrome signaling. LEDs can delay the respiratory and ethylene peaks, leading to a reduction in substrate consumption. Moreover, LED irradiation can change the structure of proteins and affect the activity of enzymes, leading to changes in the content of specific ingredients. In addition, LEDs with a wavelength of 400-460 nm can be used to inactivate food-borne pathogens and bacteria on the surface of fresh food containing photosensitizers or photocatalysts. Ultraviolet (UV)-LEDs may be used to reduce microbial contamination of fresh food, and they are expected to be widely used in the future for the preservation of fresh food (Zhang et al., 2022).

3. Connecting statement to Chapter 3

Chapter 3 is authored by Shafieh Salehinia¹, Fardad Didaran², Sasan Aliniaeifard^{2,3}, Sarah MacPherson¹, Valerie Orsat¹, Mark G. Lefsrud¹.

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Chapter 3 presents a comprehensive analysis of the methodology, results, and discussion regarding the impact of varying light quality and intensity on stomatal opening in lettuce and basil. The objective of the study was to provide valuable insight into the effects of these factors to facilitate storage testing procedures.

Author Contributions:

1) Shafieh Salehi Nia: Lead the design and execution of experiments, along with the collection, compilation, analysis, and interpretation of data communicated in this thesis.

2) Dr. Mark Lefsrud: Research supervisor; provided invaluable guidance throughout the experimental design process, oversaw the execution of experiments, and contributed to the comprehensive review of the thesis.

3) Dr. Valerie Orsat: Offered insightful guidance on experimental design, enriching the overall methodology of the research.

4) Dr. Sasan Aliniaeifard: Played a crucial role in the development of the experiment's methodology and provided valuable input during the thesis review process.

5) Dr. Sarah MacPherson: Assisted in the writing process of the thesis, helping to articulate and convey the research findings effectively, ensuring the clarity and coherence of the content.

6) Fardad Didaran: Contributed to the data analysis process, ensuring accurate and meaningful results.

Chapter 3. Effects of different light spectra and intensities on stomata functioning of lettuce and basil

3.1 Abstract

Light attributes (intensity and quality) have determinant roles in gas exchange between the internal and surrounding environments of the leaf by impacting stomatal operation. Investigating how stomata react to different lighting conditions remains a research area of great interest. With development of light-emitting diodes, it is possible to study plant responses to specified regions of the light spectrum. Stomatal behavior is critical in balancing the plant's need for photosynthesis while preventing excessive water vapor loss. Numerous studies have reported on the stomatal responses to red and blue lights, yet little is known about green light effects on stomatal response. Controlling stomatal functioning in leafy vegetables during postharvest storage is important in order to prevent excessive water loss and wilting during post-harvest storage. This research aimed to examine the stomatal opening response of lettuce (Lactuca sativa) and basil (Ocimum basilicum) to varying light quality (430, 630, 500, 530, 560 nm) and quantity [50, 75, 100, 400 μ mol m⁻² s⁻¹ Photosynthetic Photon Flux Density (PPFD)] and to determine wavelengths that keep the stomata in the closed state. Our data demonstrate that the opening of stomata in response to different wavelengths is intensity dependent. Under most blue and red light treatments, all leaf stomatal opening (abaxial and adaxial) increased. Stomatal opening decreased under green light (530 nm and 560 nm), particularly at lower PPFDs. These findings highlight the effectiveness of green light (530 nm and 560 nm) to keep stomata closed compared to other light spectra. Keeping the postharvest quality of leafy greens and extending the shelf life are most applicable by using green light during postharvest storage.

Keywords: Basil, Green LED, Lettuce, Light quality, Post-harvest storage, Stomata

3.2 Introduction

Stomata are pores in the plant epidermis that are kidney-shaped in dicots and nongraminaceous monocots and dumbbell-shaped in monocots grasses (Driesen et al., 2020). They are essential for photosynthesis because they optimize plant gas exchange, which includes CO₂ uptake for photo assimilation and transpiration (to minimize CO₂ deprivation and excessive 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 temperature regulation (Wei et al., 2020). Stomata regulate water uptake through changes in conductance, opening, and density (Wolf et al., 2016). Plants actively regulate their stomatal aperture by altering the turgor pressure of two guard cells that surround each stomata. As turgor pressure increases, the stomatal aperture expands, and as turgor pressure decreases, it leads to stomatal closure. Therefore gas exchange rates are controlled between the surrounding atmosphere and the leaf interior (Driesen et al., 2020). Many other internal and external environmental elements including light, humidity, CO₂ concentration, plant hormones (abscisic acid and auxins), carbohydrates and biotic and abiotic stressors influence stomatal opening or closing (Driesen et al., 2020; O'Carrigan et al., 2014; Shimazaki et al., 2007; Srivastava, 2002; 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 guard cells' metabolic changes and signaling, photosynthesis, and membrane ion transport (Araújo et al., 2011; O'Carrigan et al., 2014).

Different characteristics of the lighting environment such as intensity, wavelength, and duration, have a significant impact on plant photosynthesis and growth. Light-emitting diodes (LEDs) have become the industry standard for plant growth, largely due to their many benefits including compact size, low energy consumption, less heat emission, and long lifespan (Lastochkina et al., 2022; Massa et al., 2008; Van Ieperen, 2012). To observe the response of plants to a narrow spectrum wavelength, LEDs are able to meet this technical specification (Kusuma et al., 2020).

Stomatal opening is partially regulated by light spectral ranges, groups of photoreceptors, and critical components in their respective signaling pathways (Kochetova et al., 2022). Opening of stomata is initiated when the intercellular CO₂ concentration drops as a result of photosynthetic absorption occurring in the mesophyll (Kochetova et al., 2022). Photosynthesis in the guard cells

provides the soluble sugars and energy for stomatal opening and closing, rising in osmotic pressure in guard cells (Kochetova et al., 2022; Shimazaki et al., 2007). Photoreceptors, through their unique signaling pathways, also trigger stomatal opening (Yang et al., 2020). This is mediated by three different families of blue light receptors namely phototropines (PHOT), cryptochrome (CRY), and the zeitlupe family (ZTLs) (Kochetova et al., 2022). In the case of the first mentioned photoreceptor, PHOT, it acts via phosphorylating downstream signalling kinases. This causes the plasma membrane H+-ATPase AHA2 and 14-3-3 proteins to be activated, as well as the opening of potential-driven inward K+-channels in the plasma membrane and the accumulation of K+, followed by anions and water in the vacuoles of guard cells. Malate and sucrose synthesis and accumulation in vacuoles are provided by starch degradation (Kochetova et al., 2022; Rahmati Ishka, 2022).

Blue wavelengths boost photosynthetic processes in vegetables and fruits by triggering stomatal opening (Assmann and Shimazaki, 1999; Izzo et al., 2021; Talbott et al., 2002) and chloroplast translocation (Paradiso and Proietti, 2022). Cryptochromes, through COP1 signalling, facilitate a less prominent opening in response to blue light. Via ZTL and its entrainment of the circadian clock, blue/UV-A light also exerts its effects, resulting in CO₂ fixation and stomatal opening (Dodd et al., 2004). Red light, which is perceived by phytochromes (PHY), is another wavelength that is most conducive to stomata opening, and a guard cell protoplast reacts to red light (Frechijia et al., 1999; Mansfield and Meidner, 1966; Sharkey and Raschke, 1981). Blue light, but not red light, as identified by Mouravieff (1958) causes starch hydrolysis in the guard cells. Light can have a direct impact on guard-cell starch concentration, and it may help to explain why red and blue light cause different guard-cell opening pattern (Mansfield and Meidner, 1966). Furthermore, it has been demonstrated that the stomatal response to a red light is photosynthesisdependent, in contrast to the stomatal response to blue light, which is both photosynthesisdependent and independent (Sakhonwasee et al., 2017). Although the green (500-600 nm) light photoreceptor is unknown, green light can be absorbed by CRYs. Green light, until 530 nm, is included in the light response of CRYs and PHOT, whereas longer wavelengths of green light (570 nm) promote inactivation of B-light-induced CRYs. This may help explain shade avoidance behaviors in a canopy, affecting developmental processes such as seed germination and photosynthesis (Battle and Jones, 2020; Driesen et al., 2020; Golovatskaya and Karnachuk, 2015;

Thoma et al., 2020). The precise process underlying variations in stomatal opening induced by green light has not yet been discovered.

According to previous reports, some of the light wavelengths can cause a partial stomatal closure (Kochetova et al., 2022). Green light inhibits blue light-mediated stomatal opening responses in a wide range of plant species (Frechilla et al., 2000; Talbott et al., 2002; Wang and Folta, 2013). The green light reversal's action spectrum is quite similar to that of blue light activation, but with a 90-nm shift toward red (Frechilla et al., 2000). The degree of this green light reversal is dose-dependent, with full reversal occurring when the green light flux rate is double that of the blue light (Frechilla et al., 2000). However, the exact mechanism is unknown (Driesen et al., 2020). McCree (1971) noted that the quantum yield response of absorbed light is red > blue > green in the range of photosynthetically active radiation of 400–700 nm considering low intensity (200 μ mol m⁻² s⁻¹). Red and blue lights are mostly absorbed on the adaxial side of the leaf, but green light penetrates the mesophyll and is absorbed in the deeper leaf layers. In this regard, although being less efficient in terms of quantum yield than red and blue light, transmitted green light plays a significant role in photosynthesis in lower and inner leaves due to green light's ability to reach deeper and in greater amounts in the canopy (Terashima et al., 2006).

Although numerous studies have investigated the stomatal response to light quality, the majority of prior studies mostly focused on red and blue light, and there is little information addressing the effect of green light on plant responses. By investigating the impact of green LEDs at various wavelengths (500, 530, and 560 nm) in addition to red (630 nm) and blue (430 nm) LEDs, the present experiment was conducted to fill this knowledge gap and gain a more comprehensive understanding of how different light spectra especially green spectrum and different light intensities can influence stomatal opening of lettuce and basil plants.

Lettuce (*Lactuca sativa*) and basil (*Ocimum basilicum*) are leafy vegetables that are commonly cultivated in controlled environment agriculture (CEA) (Larsen et al., 2020). Basil is known for distinct chemical components and essential oil composition, which have widespread use in cooking, biopesticides, and pharmaceutical applications (Alhasan, 2020; Sabry et al., 2019). Lettuce is one of the most well-known leafy vegetables, consumed daily around the globe (Shi et al., 2022). Lettuce contains between 94 and 95 percent water and has low calorie content; it has reportedly been used to treat diabetes, cancer, and Alzheimer's disease (Shi et al., 2022).

Understanding how stomata opening is regulated in leafy vegetables during postharvest storage is crucial to help extend the shelf life of these plants. Reducing water loss and respiration rate during post harvest storage will allow for higher quality and more nutritious plants for the end users (Aliniaeifard and Van Meeteren, 2016).

3.3 Materials and methods

3.3.1 Plant materials and growth conditions

Romaine lettuce (*Lactuca sativa* var. Breen) (Stokes seed Ltd., Thorold, ON, Ontario, Canada) and basil (*Ocimum basilicum* var. Dolly) were germinated in rockwool cubes (Grodan A/S, Dk-2640, Hedehusene, Denmark) in a growth chamber (Model E15; Conviron, Winnipeg, Manitoba, Canada) under white fluorescent lights (4200 K, F72T8CW, Osram, USA) at 150 μ mol m⁻² s⁻¹ photosynthetic photon flux density (PPFD), determined using a quantum meter (Model MQ500, Apogee Instruments Inc., Logan, UT, US) at ambient CO₂, day/night temperature of 25/20 ± 2 °C, relative air humidity of 70 ± 5 % and a daily photoperiod of 16 h. After 14 days, seedlings were provided full-strength Hoagland's solution (Hoagland and Arnon, 1950). After three weeks seedlings were transplanted to the greenhouse for 40 days.

3.3.2 Application of light treatments

The samples were treated with five different LED wavelengths, namely 430, 500, 530, 560, and 630 nm. Each wavelength was applied at four different intensities, specifically 50, 75, 100, and 400 μ mol m⁻² s⁻¹. Additionally, a control group was maintained in complete darkness. The duration of the light treatment was 40 minutes for all conditions (as shown in Figure 3.1).

3.3.3 Determination of stomatal opening

To observe stomata, the abaxial and adaxial surfaces of the young fully-developed leaves were coated with a thin layer of nail polish. After allowing the polish to dry for 10 minutes, the dried polish was gently peeled off using a transparent tape to obtain the epidermal imprint. The imprints were then mounted on slides and placed under the optical microscope (Leica, ICC50W, Wetzlar, Germany) for analysis using Image J software (U.S. National Institutes of Health, Bethesda, MD, US). The stomatal opening was measured following the method described by Savvides et al (2012) . To ensure accuracy in our observations, the experiment was repeated three times with three replicates. For stomatal measurement data obtained from one leaf were considered independent. Therefore, for each light treatment, we analyzed the stomatal opening of a total of 100 stomata from the abaxial and 100 stomata from the adaxial surfaces of plants.



Figure 3.1 Representative images of basil under 560 nm light treatment (a) and lettuce under 530 nm light treatment (b).

3.3.4 Statistical analysis

Data were analyzed by SAS software (SAS Institute Inc., Cary, North Carolina, USA) using a factorial experiment, at a significance level of P=0.01, and the Duncan multiple comparisons test was used to compare the least square means.

3.4 Results

The stomata openings of lettuce and basil plants were examined by exposure of leaves to a range of light intensities and spectra provided by LEDs. Stomatal opening on the adaxial (upper epidermis facing the source of light) and abaxial (lower epidermis) sides of leaves in both basil and lettuce plants (Figures 3.2 and 3.3; Tables 3.1 and 3.2) was considerably influenced by light quality and intensity.



Figure 3.2 Representative of lettuce plant stomatal opening under different light qualities and quantities on the abaxial surface.





The abaxial (lower epidermis) surface of basil leaves exposed to the lowest light intensity (50 μ mol m⁻²s⁻¹) had the narrowest stomatal aperture under all light treatments (Figure 3.4). The 530- and 630-nm wavelengths displayed the most significant changes, with percentage increases of 57.3 % and 68.3 %, respectively, in comparison to the dark treatment. All intensities exhibited a similar pattern for 500 and 560 nm wavelengths. All wavelengths exhibited a substantial increase in stomata opening with intensity ranging from 50 to 75 μ mol m⁻² s⁻¹, and the 630 nm had a 54.5 % increase compared to stomata in the dark (control). Contrary to other wavelengths, exposure to 500 and 560 nm did not increase the stomatal aperture of the abaxial surface of basil by increasing

the intensity from 75 to 100 μ mol m⁻² s⁻¹, and there was no difference between these two treatments (Figure 3.4). The largest stomatal aperture was under 630 nm light, which increased by 72.7 % compared to dark at 100 μ mol m⁻² s⁻¹ PPFD. Generally, the red light caused a larger stomatal aperture compared to the aperture under other wavelengths.



Figure 3.4 Stomatal opening of basil (abaxial surface) under different light treatments and darkness as control.

All of the experimental wavelengths in the basil's adaxial (upper epidermis) surface exhibited the same pattern, whereby stomatal opening increased with increasing irradiance level (Figure 3.5). The stomatal aperture opening was lowest with 530 nm and 560 nm at the lowest intensity (50 μ mol m⁻² s⁻¹) when compared to other light treatments. The highest intensity (400 μ mol m⁻² s⁻¹) at all wavelengths resulted in the greatest stomatal opening. There was no significant difference in stomatal opening between 100 and 400 μ mol m⁻² s⁻¹ for 630 nm. The maximal aperture was 62.3 % and 64.5 %, at 100 and 400 μ mol m⁻² s⁻¹ for 530 nm, respectively, suggesting the higher

sensitivity of 530 nm to higher intensity 430 nm, 630 nm, and 500 nm light treatment resulted in the same stomatal opening in all intensities with the exception of 630 nm at 100 μ mol m⁻² s⁻¹ which has no significant different with 400 μ mol m⁻² s⁻¹ (Figure 3.5).



Figure 3.5 Stomatal opening of basil (adaxial surface) under different light treatments and darkness as control.

While examining the abaxial surface of lettuce leaves, the stomata aperture was greater under blue light at 50, 75, 100, and 400 μ mol m⁻²s⁻¹, increasing by 43.4 %, 60.0 %, 68.8 %, and 61.5 % relatives to the dark treatment (Figure 3.6). The maximum opening for stomata was obtained under blue light at 100 μ mol m⁻²s⁻¹, with a 68.8 % increase compared to darkness. At the same time, 630 nm and 500 nm induced the same opening under the highest intensity (400 μ mol m⁻²s⁻¹) with 61.5 % and 67.3 % increases compared to the dark control, respectively. Stomata of leaves exposed to the lowest intensities (50 μ mol m⁻²s⁻¹) of 530 nm and 560 nm were the lowest among other light treatments, however, there was no variation in stomata opening when the intensity was increased from 50 to 75 μ mol m⁻² s⁻¹ for 530 nm (Figure 6). In addition, raising the intensity from 50 to 75 μ mol m⁻² s⁻¹ did not result in a significant change in stomata opening for 500 nm. No significant changes occurred between 75, 100, and 400 μ mol m⁻² s⁻¹ for the 560 nm exposure (Figure 3.6).



Figure 3.6 Stomata opening of lettuce (abaxial surface) under different light treatments and darkness as control.

The stomatal opening on the adaxial surface of lettuce exposed to 530 nm light at lower intensities (50 and 75 μ mol m⁻² s⁻¹) was less than the dark control (Figure 3.7). Stomatal aperture under 560 nm at 50 μ mol m⁻² s⁻¹ exhibited a smallest stomata opening similar to 530 nm and with increasing the intensity from 50 to 75 μ mol m⁻² s⁻¹, there was no significant differences between the 560 nm and dark treatment (Figure 3.7). 430 nm light under the lowest intensity (50 μ mol m⁻² s⁻¹) increased the most by 42.0 % which was the same pore aperture as 530 and 500 nm under 400 μ mol m⁻² s⁻¹. After 430 nm, 630 nm and 500 nm had wider stomata opening . However, the

stomata opening was lower for 430 nm , 630 nm, and 500 nm when intensity increased from 50 to 75 μ mol m⁻² s⁻¹, but increased subsequently from 75 to 100 and 400 μ mol m⁻² s⁻¹.



Figure 3.7 Stomata opening of lettuce (adaxial surface) under different light treatments and darkness as control.

Table 3.1 Statistical analysis of stomatal opening for 'Dolly' basil-Abaxial and adaxial leaf surfaces in response to different wavelengths. CV: coefficient of variation; SOV: Source of variation.

SOV	df	Mean Square		
		Stomatal opening	Stomatal opening	
		(abaxial leaf surface)	(adaxial leaf surface)	
Light Intensity	3	0.00004803**	0.000265*	
Error a		0.00000031	0.0000054	
Light Spectrum	4	0.00000736**	0.00006557**	
Error b		0.0000115	0.000625	
Intensity \times Spectrum	12	<0.0001**	<0.0001**	
CV		52.460	62.721	

** Significance at 1% level (p<0.01), *significance at 5% level (p<0.05), ns: non-significant

Table 0.2 Statistical analysis on stomatal opening of 'Breen' lettuce-Abaxial and adaxial leaf surfaces in response to different wavelengths. CV: coefficient of variation; SOV: Source of variation.

SOV	df	Mean Square		
		Stomatal opening	Stomatal opening	
		(Abaxial leaf	(Adaxial leaf	
		surface)	surface)	
Light Intensity	3	0.000054^{**}	0.0000049^{**}	
Error a		0.000001	0.00000021	
Light Spectrum	4	0.0000574^{**}	0.0000067^{**}	
Error b		0.000034	0.0000064	
Intensity \times Spectrum	12	0.0000784^{**}	0.000049**	
CV		49.325	26.627	

** Significance at 1% level (p<0.01), *significance at 5% level (p<0.05), ns: non-significant

3.5 Discussion

Post-harvest applications of light spectra on vegetables and fruits have garnered growing interest in the food and agricultural industries (Dhakal and Baek, 2014; Gong et al., 2015; Hasperué et al., 2016); however, there is little research available on the impact of various light spectra on the response of stomata opening to green light. To further understand stomatal responses, lettuce and basil were exposed to a range of light intensities and spectra provided by LEDs.

Stomata are vital channels for the exchange of water and gases with the surrounding environment. Light quality and intensity are important factors in regulating stomatal movement (Lee et al., 2007). The current investigation revealed that the quality and intensity of light exposed to basil and lettuce leaves significantly regulated stomatal opening on the adaxial and abaxial sides of the leaves (Figures 3.2, 3.3, and Tables 3.1, 3.2). When considering the abaxial surface, the

highest amounts of stomata opening was found at 100 μ mol m⁻² s⁻¹ for 630 nm (72.7 %) in basil (Figure 3.4), and 430 nm light (68.8 %) in lettuce (Figure 3.6). Generally, in our work, red (630 nm) and blue (430 nm) light caused a wider stomatal aperture compared to other wavelengths in almost all intensities in basil and lettuce, respectively, than wavelengths of green light (500 nm, 530 nm, 560 nm). Similar results have been reported previously by Aalifar et al. (2020), Folta and Maruhnich (2007), Mao et al. (2005), Muneer et al. (2014), Savvides et al. (2012), Seif et al. (2021). In agreement with our results, Assmann and Shimazaki (1999), Izzo et al. (2021), Talbott et al. (2002), Paradiso and Proietti (2022) similarly concluded that this is likely because red and blue promote photosynthesis by triggering stomatal opening and chloroplast translocation. Some studies suggest that green light is not used efficiently for photosynthesis (Singh et al., 2015; Sun et al., 2004a; Muneer et al., 2014) and spinach (*Spinacia oleracea*) and kale (*Brassica oleracea*) during postharvest exposure to 500 and 560 nm wavelengths of green LED (Rufyikiri, 2018) due to a decrease in the activation of cryptochromes which can result in reduction of the transpiration rate and stomatal conductance in lettuce.

Stomatal opening is related to light intensity (Hattori et al., 2007; Muneer et al., 2014). Data reported herein showed that lettuce and basil plants exposed to higher light intensities exhibited greater stomata opening for most of the experimental wavelengths (Figures 3.2-3.7). The lowest light intensity (50 µmol m⁻² s⁻¹) had the narrowest stomatal aperture under all light treatments in both basil and lettuce with the exception of 630, 430, and 500 nm on the adaxial surface of lettuce leaves, where 75 μ mol m⁻² s⁻¹ showed narrowest stomata opening (Figures 3.2-3.7). These findings are consistent with Davies and Kozlowski (1975). According to Ghorbanzadeh et al. (2021), this could be because plants compensate for the increased leaf temperature caused by higher intensities in order to prevent any negative effects on the photosynthetic apparatus; therefore, the stomata are wider in higher intensities (Urban et al., 2017). Numerous studies have revealed favorable relationships between light intensity, stomatal conductance, and photosynthetic parameters (Lee et al., 2007; Muneer et al., 2014; Sakhonwasee et al., 2017; Sharkey and Raschke, 1981). Consistent with Sharkey and Raschke (1981), our results showed that in most cases, higher irradiance levels (> 100 μ mol m⁻²s⁻¹) induced larger differences in stomatal aperture opening in both abaxial surface of lettuce and basil when compared to a dark control. Stomatal opening under exposure to 630 nm and 430 nm light had a stronger response at higher intensities (100 and 400 μ mol m⁻² s⁻¹) on the abaxial surface of basil and lettuce, respectively, which was in agreement with Zeiger and Field (1982). However, stomatal opening response to 430 nm in abaxial lettuce was strong at low fluence rate of 50 and 75 μmol m⁻² s⁻¹, which is thought to be mesophyll photosynthesis-independent (Shimazaki et al., 2007; Yang et al., 2020). In adaxial lettuce, 430 nm light under the lowest intensity (50 μmol m⁻² s⁻¹) increased, and most had comparable stomatal aperture to those treated with 530 and 500 nm at 400 μmol m⁻² s⁻¹. After 430 nm, 630 nm and 500 nm exposure, stomatal openings were wider. Our results indicate that to induce stomatal response as seen in the blue (430 nm) and red (630 nm) lights, green light requires higher irradiance levels as shown in a study by Sharkey and Raschke (1981), particularly with 530 nm for abaxial surfaces of lettuce and basil, and 500 nm for abaxial lettuce surfaces (Figures 3.4-3.7). This could additionally be explained that the green light has a lower quantum yield at low intensity than red and blue light because it has less absorptance, while at high intensity, red and blue light exhibit a lower quantum yield than green light (Razzak et al., 2022).

In contrast to other wavelengths, increasing the intensity of 500 nm and 560 nm exposure from 75 to 100 μ mol m⁻² s⁻¹ had no effect on the stomatal aperture of the abaxial surface of basil (Figure 3.4). Furthermore, no distinction was observed between these two light qualities for all intensities evaluated, indicating that these two wavelengths may be more effective at closing stomata than other wavelengths, irrespective of the level of intensity employed in basil (Figure 3.4). We found that the lettuce plant's stomatal opening was narrowest in the dark, with the exception of 530 nm at 50 and 75 μ mol m⁻² s⁻¹ and 560 nm at 50 μ mol m⁻² s⁻¹ on the adaxial leaf surface (Figure 3.7). Green light caused the smallest stomatal opening after dark, and this is consistent with the work of Frechilla et al. (2000) and Talbott et al. (2002). Among the studied green wavelengths, 530 nm and 560 nm light treatments had the narrowest opening under lower intensities, respectively, in basil and lettuce plants on both the abaxial and adaxial leaf surface.

In agreement with previous reports, our results show that the maximum aperture in the abaxial stomata was significantly greater than in the adaxial stomata in both basil and lettuce (Pemadasa, 1979; Savvides et al., 2012). The reason for this difference in behaviour of abaxial and adaxial stomata can be due to differences in starch and potassium concentrations in abaxial and adaxial guard cells. The increased photosensitivity of abaxial stomata is a common phenomenon that occurs regardless of stomatal density differences (Pemadasa, 1979).

Future work could include examining moisture loss, color changes, and texture as quality determinants, as well as examining nutritional values by measuring chlorophyl, carotenoid, anthocyanin, and soluble solid content after application of green light especially at 530 nm and 560 nm in lower intensities.

3.6. Conclusion

Both light spectrum and light quantity generated significant changes in stomatal opening for both abaxial and adaxial leaf surfaces of basil and lettuce plants. Exposure with green light (500 and 560 nm) only caused stomatal closure at lower intensities. Stomatal opening was the narrowest under 530 nm and 560 nm with a lower intensity (50 μ mol m⁻² s⁻¹) on both abaxial and adaxial surfaces of basil and lettuce. Findings suggest that specific LED wavelengths in the green spectrum (530 and 560 nm) at lower intensities can influence stomatal sealing ability, and might reduce mass loss. This information could be manipulated to prolong the shelf life of vegetables by maintaining a positive water balance for a longer amount of time. Further studies should be considered to further elucidate green light's role in postharvest lighting of vegetables during storage and to investigate this potential for extending shelf life and nutritional values.

4. General summary

4.1 General conclusion

LED lighting offers numerous advantages over conventional preservation methods for harvested vegetables and fruits, including its non-toxic nature, cost-effectiveness, absence of residues, and environmentally friendly characteristics (Massa et al., 2008; Nelson and Bugbee, 2014). Extensive research has shown that postharvest LED irradiation is a valuable tool for extending the shelf life of harvested vegetables while preserving their sensory quality attributes and bioactive compounds (D'Souza et al., 2015; Nassarawa et al., 2021; Perera et al., 2022; Zhang et al., 2022). However, there is little information regarding the application of green LEDs on leafy vegetables, particularly for lettuce and basil. The study investigated the impact of light spectrum and intensity on stomatal opening in basil and lettuce plants revealing noteworthy findings. Notably, exposure to green light within the range of 500 and 560 nm resulted in stomatal closure, particularly at lower intensities. Furthermore, the narrowest stomatal openings were observed under 530 nm and 560 nm green light, specifically at a lower intensity of 50 μ mol m⁻² s⁻¹, for both the abaxial and adaxial leaf surfaces of basil and lettuce. Our results were consistent with previous research (Rufyikiri, 2018) showing the effectiveness of green wavelengths in keeping stomata in a closed state in both spinach and kale.

When addressing the limitations of your study, it's essential to be honest and transparent about the potential shortcomings or constraints that might have affected your research. Acknowledging these limitations demonstrates a thorough understanding of your study's scope and helps set realistic expectations for the findings. Here's how you can respond to your examiner's question:

4.2 Limitations

There are certain limitations that should be considered:

1. Generalizability of findings: As with any controlled laboratory study, the results obtained from model lettuce and basil plants may not entirely reflect the responses of all lettuce and basil

varieties in real-world postharvest conditions. Variability among different cultivars and environmental conditions in actual field settings could influence the outcomes differently.

2. Limited plant species: This study focused specifically on lettuce and basil plants, and while these leafy greens are commonly consumed and relevant to the agricultural sector, the findings may not directly apply to other plant species.

3. Simplified environmental factors: The study primarily focused on the effects of light wavelengths and their intensities. However, in real-world scenarios, other environmental factors, such as temperature, humidity, and CO₂ concentration, can interact with light to influence plant responses. These additional factors were not accounted for in the current study, which may limit the direct applicability of the results.

4. Short-term analysis: The investigation of stomata opening was conducted over a short time period. For a comprehensive understanding of long-term postharvest storage effects, it would be beneficial to extend the observation period to assess how the chosen light wavelengths impact the overall shelf life and quality of leafy greens over time.

Despite these limitations, this study provides a foundation for further research and potential applications in the postharvest preservation of leafy greens. Future studies could expand on these findings and consider more complex real-world conditions to enhance the practical applicability of the research.

4.3 Future suggested work

Our findings indicate that specific LED wavelengths in the green spectrum, when applied at lower intensities, have the potential to influence stomatal sealing ability and potentially reduce biomass loss. This information can be used to extend the shelf life of vegetables by maintaining a favorable water balance for an extended duration. Further investigations are warranted to comprehensively understand the role of green light in postharvest lighting during vegetable storage, including:

- Assess the effects of different LED treatments on lettuce and basil's quality attributes, including color, moisture loss, visual quality during cold storage.
- Examine the effects of different LED treatments on lettuce and basil's texture, relative water content (RWC), electrolyte leakage as well as transpiration rate.
- Investigate the impact of different green LED wavelengths on nutritional parameters, including the content of chlorophyll a, chlorophyll b, carotenoids, and total soluble sugars, during the storage period.
- To enhance our understanding of the effects of LEDs on visual and nutritional quality, it is recommended to expand the investigation by exploring a broader range of wavelengths within the green spectrum.
- Conducting tests on a variety of plant species would contribute to a more comprehensive understanding of the impact of LED lighting on produce preservation. By delving into a wider range of wavelengths and plant varieties, we can advance our knowledge and gain deeper insight into the influence of LEDs on visual and nutritional attributes.

By exploring the effects of LED lighting on vegetable quality, this thesis not only contributes to the enhancement of overall vegetable quality but also addresses the pressing issue of reducing food waste by prolonging shelf-life. Ultimately, this research endeavor holds the potential to make a positive impact in reducing food insecurity by improving the shelf life and preservation of vegetables.

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