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Review

Effects of Light Quality on Growth and Phytonutrient Accumulation of Herbs under Controlled Environments

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Abstract: In recent years, consumption of herb products has increased in daily diets, contributing to the prevention of cardiovascular diseases, chronic diseases, and certain types of cancer owing to high concentrations of phytonutrients such as essential oils and phenolic compounds. To meet the increasing demand for high quality herbs, controlled environment agriculture is an alternative and a supplement to field production. Light is one of the most important environmental factors influencing herb quality including phytonutrient content, in addition to effects on growth and development. The recent development and adoption of light-emitting diodes provides opportunities for targeted regulation of growth and phytonutrient accumulation by herbs to optimize productivity and quality under controlled environments. For most herb species, red light supplemented with blue light significantly increased plant yield. However, plant yield decreased when the blue light proportion (BP) reached a threshold, which varied among species. Research has also shown that red, blue, and ultraviolet (UV) light enhanced the concentration of essential oils and phenolic compounds in various herbs and improved antioxidant capacities of herbs compared with white light or sunlight, yet these improvement effects varied among species, compounds, and light treatments. In addition to red and blue light, other light spectra within the photosynthetically active region—such as cyan, green, yellow, orange, and far-red light—are absorbed by photosynthetic pigments and utilized in leaves. However, only a few selected ranges of light spectra have been investigated, and the effects of light quality (spectrum distribution of light sources) on herb production are not fully understood. This paper reviews how light quality affected the growth and phytonutrient accumulation of both culinary and medicinal herbs under controlled environments, and discusses future research opportunities to produce high quantity and quality herbs.

Keywords: light spectrum; photosynthesis; essential oils; phenolic compounds; antioxidant activity

1. Introduction

With rising awareness of health benefits, people are consuming more fresh herbs or taking dietary herbal supplements, among other self-care options, as medicinal alternatives [1]. According to a recent report by Global Industry Analysts, the market for herb products (fresh herbs, herbal materials, herbal preparations, and finished herbal products) is substantial and the global herbal supplement market will reach $107 billion by 2017 [2,3]. For example, over 100 million Europeans are current herb-product users [3], the annual expenditure on herb products in South Korea increased from $4.4 billion in 2004 to $7.4 billion in 2009 [4], and out-of-pocket spending on natural products in the United States was $14.8 billion in 2008 [5].

Diets with fresh or processed herbs are positively related to prevention of cardiovascular diseases, chronic diseases, and certain types of cancer, due to high concentrations of phytonutrients such as essential oils, phenolic compounds, flavonoids, and carotenoids [6–8]. Phytonutrients, or bioactive secondary metabolites, are organic compounds not directly involved in primary metabolic processes of growth, development, or reproduction of plants. Phytonutrients play an important role in plant defense against insects and pathogens, act as attractants to pollinators and seed dispersers in reproductive processes, and some may create a competitive advantage as poisons for rival species [9]. Phytonutrients have been used in various industries such as medicines, flavorings, dyes, fibers, glues, oils, waxes, and perfumes [2,3,9].

The increasing consumption of herb products has been accompanied by quality and consistency issues associated with field production. Varying climatic conditions among seasons or locations and adverse environmental conditions all lead to fluctuating yield and phytonutrient concentrations of herbs [10,11]. Hence, some growers are turning to controlled environment agriculture (CEA) including high tunnels, greenhouses, and indoor vertical farms for herb production. To provide high-quality and stable herb product supply, CEA technologies are an alternative and complementary to field production, especially in areas with limited daylight or arable land, or those with other unfavorable environmental conditions [12–15].

Most CEA technologies or systems use artificial lights to ensure plant growth, and new lighting technologies such as light-emitting diodes (LEDs) have the capacity to meet the light intensity and wavelength requirements of different plant species [16–18]. Until recently, high intensity discharge (HID) lamps and fluorescent lamps (FLs) have been the most popular light sources in CEA systems [12]. HID lamps, such as metal halide and high pressure sodium lamps, are typically used in greenhouses to provide supplemental light due to relatively high luminous efficacy (max. 200 lumens per watt) and photosynthetically active radiation (PAR) efficiency (max. 40%) [19]. However, the high surface temperatures of HID lamps prohibit close placement to plant canopies, and the unsuitable spectra of some HID lamps also limit their use for plant production. FLs are the most widely used supplemental light source in CEA systems, due to the higher PAR output, lower cost, and lower surface temperatures compared with HID lamps [20,21]. It was reported that 60% of indoor vertical farms in Japan used FLs as a light source in 2013, 13% used HID lamps, and 27% used LEDs [12]. There is great and increasing interest regarding the use of LEDs in horticulture. The global market of LEDs grew robustly by 32% while the overall lighting market declined by 15% in 2009 [22]. The increasing use of LEDs is due to their high PAR efficiency (80–100%) [19], decreased cost, ease of control, and availability of specific wavelengths suitable for horticultural uses [20,23–25]. In terms of economics and sustainability, LED technology is predicted to replace FL and HID lamps in horticultural systems and to revolutionize CEA [19].

Both phytonutrient content and yield may be influenced by the light quality used for herb production under controlled environments. Research has indicated that photosynthetic responses of single leaves under artificial light were generally similar, but the morphological responses were largely species- and cultivar-specific, and both photosynthetic and morphological responses contribute to plant yield [26]. The average quantum efficiency of 22 plant species suggested that plants potentially have higher photosynthetic efficiency under red light than blue and green light [26,27]. Red light supplemented with blue light increased leaf net photosynthetic rate and crop yield more than monochromatic red or blue light, but yield decreased when blue light proportion (BP) reached a threshold, which varied among plant species and cultivars [16,18]. On the other hand, long-wavelength red light could enhance phenolic compound accumulation, and short-wavelength blue light could enhance the biosynthesis of flavonoids and lactones [28,29]. In this review, we summarize the effects of red (620–700 nm), blue (400–490 nm), UV (280–380 nm), and photosynthetically less-efficient lights, such as cyan (490–520 nm), green (520–570 nm), yellow (570–590 nm), orange (590–620 nm), and far-red (700–800 nm) light, on growth and phytonutrient accumulation in herbs and discuss the potential for regulating herb productivity and quality through manipulation of light spectra.

2. Photosynthesis and Plant Growth

2.1. Red and/or Blue Light

Photosynthesis is the foundation of food production, and photosynthetic processes are often modified in plants grown under artificial lights, since lamps do not usually provide the same spectrum, light intensity or photoperiod as sunlight. Red light seems to be more effective in improving photosynthesis compared than blue or green light [26,27]. For instance, supplementary red light in a greenhouse increased the leaf area of grape (*Vitis vinifera* cv. 'Jingxiu') as well as the dry mass distribution ratio in leaves compared with sunlight [30]. Goto et al. [31] assessed the gross photosynthetic rate (P_g) of both green and red perilla (*Perilla frutescens*), a popular herb in East Asia used in traditional Chinese medicine, under different combinations of LEDs (405, 465, 530, 595, 660, and 735 nm) at 250 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF) and 16-h photoperiod for 14−21 days in a growth chamber. The highest increment of P_g was obtained with red light (660 nm) for both green and red perilla, and P_g was lowest at 465 and 530 nm for red perilla [31]. Consistent with the above results, red perilla grown under red-enriched light treatments (red light alone, a combination of red and blue light, and a combination of red and green light) had more leaves, bigger leaves, and greater dry weight (DW) than plants grown under blue light alone, a combination of blue and green light, or green light alone [32]. The high efficiency of red light on plant growth is easy to understand because red light wavelengths perfectly fit the absorption peak of chlorophylls and phytochromes and, therefore, red light would be the most efficient light to supplement existing light conditions.

Combining red and blue light is more effective than monochromatic red light for plant growth. Plants grown under monochromatic red light exhibited elongated hypocotyls and cotyledons, a condition known to be phytochrome-dependent [19]. Blue light increased the ratio of chlorophyll a/b (chl a/b), affected plant photomorphogenesis, and promoted stomatal opening in plants [33–35]. The combination of red and blue light provided better excitation of photoreceptors including phytochromes, cryptochromes, and phototropins, and resulted in higher photosynthetic activity than plants under either monochromatic red or blue light [36]. Dong et al. [37] reported that combined red and blue light (1/3 blue light at 450−460 nm + 2/3 red light at 620−630 nm, at 400 lx and 12-h photoperiod for 60 days) increased the DW and bioefficiency of *Cordyceps militaris* mushroom compared with blue light alone, red light alone, and sunlight. For most species, combined light wavelengths with a large proportion of red light supplemented with blue light significantly increased plant yield [16]. However, plant yield reached a plateau or decreased when the BP reached a threshold, which varied among species [38,39]. For instance, fresh and dry mass of coriander (*Coriandrum sativum*), one of the most useful essential oil-bearing herbs as well as medicinal plants, increased when BP increased from 5% to 9% at 120 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 28 days, but decreased when BP was 17%, and was lowest under monochromatic red light [39]. The leaf area of *Anoectochilus roxburghii* was not different when BP was 17% or 25% under combinations of red and blue LEDs with 12-h photoperiod for 40 days, but decreased when BP reached 50% [40]. In contrast, the fresh weight (FW) of sweet basil (*Ocimum basilicum*), one of the most commonly grown herbs in the United States, increased when BP increased from 15% to 59% at 200 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 31 days, and the total lateral shoot FW was highest under monochromatic blue light compared with red, green, blue+green, or white light at 100 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 70 days [16,38].

Within the photosynthetically active radiation (PAR) spectrum from 400 to 700 nm, red and/or blue light affect both photosynthesis and plant morphogenesis. Red and/or blue light affected chlorophyll content, photosynthetic enzyme activity, stomatal opening, and the distribution of carbohydrates in plants [26,27,33,34,41]. Compared with other PAR wavelengths, red light increased the total chlorophyll content in leaves to promote photosynthesis, but inhibited the transport of carbohydrates from leaves to sinks, which suppressed photosynthesis due to the high level of carbohydrates in the leaves [41]. Blue light increased the ratio of chl a/b, improved the activities of ribulose-1,5-bisphosphate carboxylase (Rubisco) and phosphoenolpyruvate carboxylase, and promoted stomatal opening, which improved photosynthesis per unit of leaf area [28]. In terms of plant morphogenesis, red and/or blue light influenced plant yield. Red light promoted cell division and expansion which increased leaf area and root elongation, while blue light inhibited cell division and expansion, thus reducing leaf area [18,30]. The reduced photon capture resulting from reduced leaf area may be the reason for a high level of BP reduced plant growth in spite of increased photosynthesis per unit leaf area.

2.2. Photosynthetically Less-Efficient Lights: Far-Red, Green, and Ultraviolet Light

Little research has been conducted to explore the effects of photosynthetically less-efficient lights on herbs. In addition to red and blue light, photosynthetically less-efficient far-red, green, and ultraviolet (UV) lights are also important environmental signals to plants. For instance, far-red light reversed the effects of phytochrome leading to changes in gene expression, plant architecture, and reproductive response [42]. Far-red-rich light caused increased stem elongation, strengthening of apical dominance, acceleration of flowering, reduced assimilate storage, reduced seed set, reduced branching, shortened fruit development, and reduction in seed quality [43,44]. Li and Kubota [45] demonstrated that supplemental far-red light increased the FW and DW of baby leaf lettuce (*Lactuca sativa* 'Red Cross') at 300 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 12 days, but decreased the concentrations of anthocyanins, carotenoids, and chlorophylls compared with white light alone. The hypocotyl elongation of tomato plants (*Solanum lycopersicum* 'Aloha' and 'Maxifort') grown in the greenhouse was increased by end-of-day far-red light radiation at 3 or 4 μmol m^{-2} s^{-1} PPF for 14 days [46]. Although the effects of far-red light on plant growth have been demonstrated in various vegetables, there has been little research using herbs.

Green light has the lowest quantum yield, but it can penetrate deeper into the plant canopy due to its high transmittance and reflectance than the other wavelengths. Therefore, theoretically, quantum yield of a dense plant canopy should be more equalized under green light. In fact, Paradiso et al. [47] validated that canopy quantum efficiency of green light was not much lower than that of red light in roses (*Rosa* spp. 'Akito'). In addition to intercepting red and blue light, phytochromes and cryptochromes are also green light receptors, which explains why green light affects vegetative growth, organ growth, and plant tropism [42], although the effects of green light may be less significant as light intensity increases [48].

UV light is generally considered a stress factor to plants and leads to smaller plants, reduced photosynthesis, and lower biomass accumulation, but appropriate UV light treatment (suitable light intensity and exposure time) was shown to increase plant yield in some species. Sakalauskaite et al. [49] reported that both 1 h and 2 h supplemental UV-B light per day for seven days increased plant height, leaf area, FW, and DW of sweet basil, and 2 h UV-B treatment had a greater effect than 1 h UV-B treatment. In contrast, a long exposure time at a low intensity or a short exposure time at a high intensity of supplemental UV-B light both decreased net photosynthetic rate of Chinese liquorice (*Glycyrrhiza uralensis*) [50], and reduced the leaf area and leaf DW of sweet basil and perilla [51,52]. Therefore, the effects of light intensity and exposure times of UV light on plant production needs further investigation.

3. Phytonutrient Accumulation

Plants produce a vast and diverse assortment of phytonutrients which are widely used as medicines and flavorings, and are being researched for new drugs, antibiotics, insecticides, and herbicides. The most widely researched phytonutrients in herbs are essential oils and phenolic compounds. Essential oils are naturally occurring volatile aromatic compounds which are found in seeds, barks, stems, roots, flowers, and other parts of plants [9]. In addition to contributing to the distinctive smells of plants, essential oils have long been used in food preparation and health-care practices such as reducing pain, enhancing perspiration, and anti-allergic effects [6]. Phenolic compounds are notably found in herbs, spices, and nuts, which have been studied extensively from the perspective of health protection and pharmacological utility, due to their anticancer, antiviral, antitoxic, and hepatoprotective properties [7–9]. With increasing consumption of herbs, growers are adopting CEA systems for herb production to provide sufficient quantity and quality of natural products. As LEDs are increasingly being used in controlled environment horticulture, the effects of light quality (spectrum distribution of light sources) on phytonutrient accumulation have been increasingly investigated [16,36,49,53], which will be discussed in the following sections.

3.1. Essential Oils

Red, blue, and UV light enhanced the concentration of essential oils in various herbs compared with white light or sunlight, and the level of enhancement varied among species, compounds, and light treatments. For instance, the total essential oil content of *Mentha piperita*, *M. spicata*, and *M. longifolia* were highest under red light at 500 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 60 days, 39% and 86% higher than blue or white light, respectively, and was lowest under sunlight [36]. Similarly, *l*-menthol, the main component of essential oils in *M. arvensis*, was 1.4 times higher under red light than blue or green light, both at 150 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 28 days [6], while the glycyrrhizic acid (an oleanane-type triterpenoid saponin and considered to be 50 times sweeter than sugar) concentration in root tissues of Chinese liquorice was highest under red light, followed by white light, and lowest under blue light at 300 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for three months [50]. However, for sweet basil, the total essential oils under blue light were 1.2–4.4 times higher than plants grown under white light, and was lowest under red light, all at 50 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 70 days [16]. Although supplemental UV light generally inhibits plant growth, it might increase essential oils, resulting in enhanced plant defense and protection against UV light [54]. UV-B or combined UV-A and UV-B light with white light was more effective than white light alone in increasing *l*-menthol and limonene concentrations in *M. arvensis* [55] as well as the content of essential oils in Chinese liquorice, such as glycyrrhizic acid, liquiritin, liquiritigenin, and isoliquiritigenin [56]. Two weeks of supplemental UV-B light for 2.5 h each day enriched the levels of phenylpropanoid and terpenoid concentrations in sweet basil, which were three times higher than the plants under sunlight [52]. Therefore, supplemental red, blue, and UV light treatments could be used as effective processes to enhance plant phytochemical biosynthesis and provide great commercial advantages.

In addition to enhancing the concentrations of essential oils, light quality may also alter the compositions of essential oils in herbs. For example, the second and third major components of essential oils in sweet basil were myrcene and linalool under blue light, and α-pinene and β-pinene under green and red light, and those under white light showed an intermediate response [16]. Mexican mint (*Plectranthus amboinicus*) grown under blue light exhibited greater amounts of sesquiterpene group compounds, while plants under red light showed greater amounts of monoterpene group compounds [57]. Hence, light quality could be manipulated to enhance targeted compound concentrations for various purposes.

3.2. Phenolic Compounds

Phenolic compounds, flavonoids, and anthocyanins in herbs could be enriched by red, blue or UV light, to provide more health-beneficial natural products for human beings. Monochromatic red or blue light treatments significantly increased the concentrations of total phenolic compounds, flavonoids, and anthocyanins in Chinese foxglove (*Rehmannia glutinosa*) and perilla plants compared with white light, and blue light was more efficient than red light [53,58]. However, the amount of rosmarinic acid—the major component of phenolic compounds in sweet basil—under continuous red and white light was double that under blue light, all at 100 μmol m^{-2} s^{-1} PPF for 14 days, whereas chicoric acid content, the second major component, was highest under white light, followed by blue and red light [59,60]. Therefore, it is possible that the application of supplemental red and/or blue light could enhance phenolic compounds accumulation in some herb species, but the enhancement effect might depend on the species and the specific compounds. Similar results were observed with supplemental UV light. Supplemental UV-B light at 2.5 μmol m^{-2} s^{-1} for 1 h each day and 2 h each day for seven days significantly increased the content of total phenolic compounds and anthocyanin concentrations in sweet basil, with the short time UV-B treatment being more efficient for anthocyanin accumulation than the long time UV-B treatment [49]. Levels of caffeic acid and rosmarinic acid of perilla grown under 2 h supplemental UV-A light for seven weeks were eight and seven times higher, respectively, than the plants under sunlight [61]. Accordingly, it could be concluded that supplemental UV light could increase the biosynthesis of phenolic compounds in herbs.

The increase of phenolic compounds, flavonoids, and anthocyanins in herbs may be caused by multiple responses to light quality including increased activities of key metabolic enzymes leading to enhanced synthesis of pigments [62]. As key enzymes in the synthesis of anthocyanins, the expression of phenylalanine ammonia-lyase (PAL), chalcone synthase (CHS), and dihydroflavonol 4-reductase (DFR) increased under blue light, resulting in an enhanced accumulation of anthocyanin in lettuce, *Salvia miltiorrhiza*, and *Gerbera hybrida* [28,62]. Polyphenol oxidase (PPO), which causes enzymatic browning of tissues, is also assumed to play a role in plant defense responses to biotic stresses through the production of reactive oxygen species (ROS) or cross-linking of quinones with proteins or other phenolics, forming physical barriers [63]. The expression of PPO was also increased by supplemental red and blue light in lettuce and *S. miltiorrhiza*, which may be related to the enhancement of phenolic compounds [28]. On the other hand, many plants avoid UV light by accumulating UV-filtering flavonoids and other secondary metabolites. For instance, epidermal flavonoids are enhanced in response to increased UV-B light [12]. The mechanisms of actions of the monochromatic or combined light on phytonutrients have not been clarified yet, but the aforesaid examples suggest that red, blue, UV light and the combinations of different light wavelengths could definitely affect the biosynthesis of phytonutrients.

4. Antioxidant Compounds

The human body produces ROS, such as superoxide anion radicals, hydroxyl radicals, and hydrogen peroxide by many enzymatic systems through incomplete oxygen reduction [64]. Large amounts of ROS may favor human disease such as cancers, cardiovascular diseases, aging, and neurodegenerative diseases [64]. Therefore, the daily intake of exogenous antioxidants is beneficial for protecting the human body against the destructive effects of free radicals [65,66].

Most of the antioxidant compounds in a typical diet are derived from plant sources and belong to various classes of phytochemicals. Since light quality does affect the biosynthesis of phytonutrients, it is possible to improve antioxidant activities of herbs by altering the light spectrum, thus providing more natural antioxidants in our daily food. For instance, monochromatic red and blue LED light both enhanced the antioxidant capacities, total phenolics, and flavonoids in Chinese foxglove compared with white FL, and blue light was more efficient than red light [53]. Similar to the effects of light quality on growth parameters and some secondary metabolites, the enhancement of combined red and blue light was more efficient than monochromatic red or blue light only. The antioxidant activity was 2.0, 1.6, and 1.5 times higher, respectively, for coriander plants under 5:1, 10:1, and 19:1 red:blue ratios at 120 μmol m^{-2} s^{-1} PPF and 16-h photoperiod for 28 days compared with the plants under red light only [39]. Supplemental UV light enhanced the antioxidant activities of the upper leaves of *M. arvensis* [55], as well as sweet basil [49]. In conclusion, red, blue, and UV light treatments could be used to enhance the biosynthesis of antioxidant compounds and improve antioxidant capacities of herbs, which protect human body from various disorders through daily intake of fresh herbs or herb supplements.

5. Light as a Regulator: Controlling Herb Production with LEDs

Herbs grown under broadband sunlight that shifts both in intensity as well as in spectral distribution resulted in varied yield and phytochemical concentrations. Providing sufficient volume of high quality herbs to meet an increasing demand is especially challenging with global climate change and shortage of resources, such as arable land and water. Therefore, application of LEDs in CEA provides an additional method for herb production that has enormous potential for targeted regulation of plant growth and metabolic responses. Based on previous research, future studies of herb cultivation with LEDs should concentrate on the several aspects that follow.

Combinations of red and blue light with different BP—Red and blue light are the most efficient spectra for plant photosynthesis. Previous research only examined the effects of monochromatic red or blue light, and few studies investigated the effects of combined red and blue light, and for those that did so, the BP threshold was not determined. A single LED solution will not solve all problems and may achieve different goals. Therefore, combinations of red and blue light with different BP should be investigated to meet the varied requirements of herbs for specific species, growth stages, and multiple cultivation purposes.

Addition of photosynthetically less-efficient lights—It has been demonstrated that photosynthetically less-efficient lights such as green, far-red, and UV light could improve plant photosynthesis [47], hasten flowering and reverse the effects of phytochromes [42], and enhance the biosynthesis of pigments and phytochemicals in some plants [49,56], respectively. The other light spectra within the photosynthetically active region, such as cyan, yellow, and orange light, are also absorbed by photosynthetic pigments and utilized in leaves [12]. However, the effects of photosynthetically less-efficient lights on the growth and phytonutrient accumulation of herbs are still unknown. To make the best use of photosynthetically active light, the effects of UV, cyan, green, yellow, orange, and far-red light on herb production need to be investigated.

Sideward lighting—When artificial light is given downward to a densely-populated plant community, most light energy, especially red and blue light, is absorbed by the upper leaves while light energy received by lower leaves is nearly equal to or lower than the light compensation point, which significantly decreases photosynthetic productivity [12]. The low surface temperatures of LEDs makes it possible to install them alongside and close to plants or within the plant canopy, reducing the uneven vertical distribution of light energy between upper and lower leaves. Several studies have been conducted with tomato (*S. lycopersicum*), rose, and micropropagated plantlets [12,67], but this has not been investigated for herbs. Such placement may affect herb morphology, physiology, and improve plant yield.

Interactions of light with other environmental factors—Light is one of the most important environmental factors influencing plant growth and secondary metabolism, and use of LEDs would allow growers to induce desired responses in herbs. On the other hand, other factors such as temperature, humidity, carbon dioxide, and fertilization should be adjusted accordingly with light conditions to promote plant growth and development. To achieve high yield with enriched phytonutrient concentrations in herbs, it may be recommended to provide optimal environmental conditions initially to get a fast growth rate and then provide environmental stresses several days before harvest to enhance the production of medicinal components.

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