REVIEW ARTICLE

Morpho‑physio‑biochemical, molecular, and phytoremedial responses of plants to red, blue, and green light: a review

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Abstract

Light is a basic requirement to drive carbon metabolism in plants and supports life on earth. Spectral quality greatly afects plant morphology, physiology, and metabolism of various biochemical pathways. Among visible light spectrum, red, blue, and green light wavelengths afect several mechanisms to contribute in plant growth and productivity. In addition, supplementation of red, blue, or green light with other wavelengths showed vivid efects on the plant biology. However, response of plants difers in diferent species and growing conditions. This review article provides a detailed view and interpretation of existing knowledge and clarifes underlying mechanisms that how red, blue, and green light spectra afect plant morphophysiological, biochemical, and molecular parameters to make a signifcant contribution towards improved crop production, fruit quality, disease control, phytoremediation potential, and resource use efficiency.

Keywords Eco-friendly lighting · Morpho-physiological responses · Phytoremediation · Disease control · Fruit quality

Introduction

Plants play a signifcant role in human lives. The plants are dependent on light for photosynthesis to get their energy. Plants can perceive ultraviolet, blue, green, red, and farred light wavelengths through the photoreceptor families

(Huché-Thélier et al. [2016\)](#page-14-0). With the advancement in agriculture, the demand for artifcial or supplementary lighting is rising continuously. Unlike natural sunlight, which provides a complete range of light spectrum, artifcial lights include limited range of spectrum and for that reason, the composition of the spectrum can be added and/or adjusted to achieve required efficiency. Therefore, under controlled environment, the selective spectrum of artifcial lights can

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be applied to optimize the growth of plants (Rehman et al. [2017\)](#page-17-0). Artifcial supplementary light can favor photosynthetic efficiency by optical regulation of plant photoreceptors to improve plant production efficiency and accumulation of metabolites for getting the products with better nutritional quality (Appolloni et al. [2021;](#page-12-0) Jiang et al. [2017](#page-15-0); Rehman et al. [2017;](#page-17-0) Ouzounis et al. [2015](#page-17-1)). Supplemental light is necessary to boost greenhouse production during winter especially in areas with low sunlight to meet the rising demand for fresh produce (Lanoue et al. [2022\)](#page-15-1). For instance, the use of a specifc light spectrum can improve the nutritional properties of vegetables and their yields in the commercial production system (Kuan-Hung et al. [2012\)](#page-15-2). When it comes to artifcial lighting, these spectrum and colors can have signifcant efects on the plant growth and development (Rehman et al. [2020](#page-17-2)). Such as red light caused larger and longer stems and helps to fower in plants. However, under the exposure of blue light, plants likely be more compact with smaller, thicker, and darker green leaves (Izzo et al. [2020](#page-14-1)). Among diferent colors of light, red and blue lights are more efective for leaf photosynthesis (Zhang et al. [2020\)](#page-19-0). Over decades, the monochromatic or binary red and blue light (in various ratios) has been successfully used in plant morphogenesis both in vitro and in vivo (Naznin et al. [2016](#page-17-3); Gupta and Jatothu [2013](#page-14-2); Vitale et al. [2023](#page-18-0)). In case of green light in the visible spectrum, previous research showed that green light wavelengths are less efficient for photosynthesis but it is still useful in photosynthetic process and to regulate the plant architecture. New research revealed that green light under stronger illumination can drive more efficient photosynthesis than the red light (Arsenault et al. [2020\)](#page-12-1). Similarly, recent studies have been proved the efectiveness of green light for plants (Razzak et al. [2022;](#page-17-4) Schenkels et al. [2020](#page-18-1); Vitale et al. [2020](#page-19-1)).

The use of artifcial lighting to enhance crop productivity was made successful by the invention of long-lasting and robust electrical lamps in the start of twentieth century. Traditionally, high pressure sodium lamps were used as a source of artifcial light. While, currently, electric lighting could be applicable as a most reliable and steady radiation source to control the plant growth environment (Gupta [2017\)](#page-14-3). Among various available lighting, the light emitting diodes (LEDs) are advertised as most energy efficient and environment friendly lighting because they do not contain mercury (Lim et al. [2011](#page-16-0)). According to Ramesh et al. [\(2023\)](#page-17-5), LEDs are more energy-efficient, eco-friendly and have a lesser impact on environment. LEDs have been verifed to present remarkable features for their application in plant lighting designs in greenhouses and other closed growth chambers for in vitro cultures (Rehman et al. [2017;](#page-17-0) Agarwal and Gupta [2016](#page-12-2)). LEDs consume low energy or give higher lighting efficiency over compact fuorescent or incandescent lamps (Nardelli et al. [2017](#page-17-6); Zeb et al. [2016](#page-19-2)). Therefore, LEDs are receiving

great interest in greenhouse production due to their high photon efficacy and possibility to finely modulate light intensity and spectrum (Lanoue et al. [2022](#page-15-1); Paradiso and Proietti [2022](#page-17-7)).

In present review, we aim to shed light on the multidimensional benefts of artifcial light spectra on plant growth while underscoring the need for their judicious application in modern agriculture under controlled conditions. Therefore, this review summarizes the growth responses of plants under artifcial light conditions especially the roles of red, blue, and green light wavelengths on plant morpho-physiological, biochemical, and molecular aspects both in confned and/or in vitro environment (Fig. [1](#page-2-0)).

Light as a source of energy for plants and an environmental signal

Light is an important environmental factor which is essential for photosynthesis and afects the growth and development of plants starting from seed germination to flowering or fruit production. Earth's climate system is driven by the terrestrial sunlight, which consists of ultraviolet (UV) radiation (100–400 nm), visible light (400–700 nm), and infrared radiation (700–1000 nm) (Taylor et al. [2022](#page-18-2); Wong et al. [2020](#page-19-3); Rehman et al. [2017](#page-17-0); McCree [1971](#page-16-1)). Each range of light wavelengths can persuade certain responses in plants (Bayat et al. 2018). Light affects the plants in different ways for instance, by light duration, light intensity, and light quality (Wong et al. [2020\)](#page-19-3). However, plant pigments (Fig. [2](#page-2-1)) can only absorb photosynthetically active radiation which is visible light spectrum required for photosynthesis (McCree [1971\)](#page-16-1). Plants sense light by photoreceptors, which are made up of a protein linked to a pigment called a chromophore. Absorption of light in chromophore causing a change in protein shape modifes its activity and initiated a signaling pathway to elicit a change in growth habit or development. Research advances in this feld are necessary to know how plant photoreceptors act under narrow band light? Which looks to be diferent from normal light environment (Kochetova et al. [2023\)](#page-15-3).

Morpho‑physio‑biochemical responses of plants to diferent colors of light

Monochromatic red light

Red light is useful for plants to produce chlorophyll and an energy source for photosynthesis to promote the growth (Table [1\)](#page-3-0). A plethora of research reported essential role of red light in chlorophyll production and photosynthesis. For instance, red light (660 nm) showed higher quantum

Fig. 1 A diagram showing possibly main effects of monochromatic red, blue, and green light wavelengths and their combination on plant growth and development (Guo et al. [2023](#page-14-4); Heo et al. [2002;](#page-14-5) Razzak

et al. [2022;](#page-17-4) Rehman et al. [2020](#page-17-2); Rehman et al. [2017;](#page-17-0) Golovatskaya and Karnachuk [2015](#page-14-6)). Chl, chlorophyll

Fig. 2 A presentation of main photoreceptors and pigments in the plants

Table 1 Morphological, physiological, and biochemical changes in plants under monochromatic red, blue, or green light

**ROS*, reactive oxygen species; *SA*, salicylic acid; *IAA*, indole-3-acetic acid (auxin); *Pn*, net photosynthesis; *Tr*, transpiration rate; *Gs*, stomatal conductance; Ci , intercellular $CO₂$

efficiency in terms of photosynthetic rate in *Fragaria ananassa* L. leaves (Yanagi et al. [1996](#page-19-4)). Red light enhanced the chlorophyll content, net rate of photosynthesis, and the Fv/ Fm ratio in senescing grape leaves (Wang et al. [2016\)](#page-19-5). Red light increased chlorophyll a/b ratio in *Asplenium* (Leong et al. [1985](#page-16-2)). However, a comprehensive infuence of red light on photosynthesis is observed as it increases photosynthesis by improving total chlorophyll in leaves while suppressing photosynthesis by inhibiting carbohydrate transport from source (leaves) to sink (Dou et al. [2017;](#page-14-7) Bondada and Syvertsen [2003](#page-13-1)). In contrast to far-red light, red light activated the phytochromes (Cosgrove [1981\)](#page-13-2). Wavelengths of red light also promote seed germination, growth of stems, fowering, and fruiting (Fan et al. [2013;](#page-14-8) Rehman et al. [2020](#page-17-2)). Generally, plants under red light treatment have longer roots and larger leaf areas as it stimulates cell division and expansion (Dou et al. [2017\)](#page-14-7). The maximum dry-mass in broccoli (*Brassica oleracea* L.) seedlings was produced under red light (Pardo et al. [2014\)](#page-17-8). Compared with control, red light signifcantly improved plant growth, biomass, chlorophyll content, and photosynthesis in ramie (*Boehmeria nivea* L.) (Rehman et al. [2020\)](#page-17-2) and rapeseed (*Brassica napus* L.) (Saleem et al. [2020](#page-18-3)) grown under greenhouse conditions. Red light can support growth of stem in Norway spruce (*Picea abies L.*) seedlings by regulating GAs biosynthesis (Ouyang et al. [2015](#page-17-9)). Red light stimulates division of cells and expansion. In addition, red light favors stem and root elongation in tomato (*Solanum lycopersicum*) seedlings (Wu et al. [2014](#page-19-6)).

Monochromatic blue light

How much blue light is necessary for diferent plant species is an important aspect for research on crop plants. Ouzounis et al. ([2014](#page-17-10)) reported that blue light wavelength has a comparatively little infuence on single leaf photosynthetic process; however, it was stated that increasing proportion of blue light can increase the photosynthetic capacity of leaves (Graham et al. [2019](#page-14-9); Hernández and Kubota [2016](#page-14-10); Terfa et al. [2013](#page-18-4)). Available literature showed more efectiveness of blue light than red light to suppress shoot or leaf elongation in diferent plant species (Kong et al. [2012](#page-15-4); Cosgrove [1994](#page-13-3)). Thus, elongation could be promoted as shade avoidance response using pure blue light; however, these efects may vary among different plant species (Johnson et al. [2020\)](#page-15-5). Blue light encourages root growth and photosynthetic activity to support vegetative growth (Table [1](#page-3-0)). Usually, blue light is used to promote seedling growth, where fowering is not required. In a previous study on tomato, the stem elongation was found to be dependent on blue light quantity (Naya et al. [2012](#page-17-11)). Similarly, in a study, an increase

of 5 to 20% in blue light resulted in increased leaf thickness and photosynthesis (Terfa et al. [2013\)](#page-18-4). Furthermore, in cucumber, blue light proportion up to 50% at higher light intensity increased its photosynthetic potential (Hogewoning et al. [2010](#page-14-14)). In another study, blue light proportion up to 10% increased leaf area and dry weight (Hernández and Kubota [2016\)](#page-14-10). Similarly, some characteristics for radish and soybean are superiorly predicted using blue light (Cope and Bugbee [2013\)](#page-13-5). Blue light enhanced chlorophyll a/b ratio and improved photosynthetic rate/unit of leaf area (Li and Kubota [2009](#page-16-6)). Blue light signifcantly improved gaseous exchange in industrial hemp plants and increased the shoot fresh weight, dry weight, leaf number, stem diameter, root length, and chlorophyll content by 15%, 27%, 14%, 10%, 7%, and 7%, respectively (Cheng et al. [2022\)](#page-13-6).

Blue light plays a key role in several plant processes during growth and development, including chlorophyll synthesis (Naznin et al. [2019b\)](#page-17-12), photomorphogenesis and phototropism response (Christie [2007](#page-13-7); Saebo et al. [1995](#page-18-8); Senger [1982](#page-18-9)), stomatal opening or stomatal conductance and photosynthesis (Matthews et al. [2020;](#page-16-7) Inoue and Kinoshita [2017;](#page-14-15) Hernández and Kubota 2016), water relations and $CO₂$ exchange (Bula and Zhou [2000](#page-13-8)), and stem or leaf elongation (Matsubara et al. [2005](#page-16-8)). Blue light gives feasible strategy for artifcially regulating indican synthesis and fowering in *Polygonum tinctorium* L. (Nakai et al. [2020](#page-17-13)). In contrast, few studies reported inhibitory or suppressive roles of blue light in different plant species for example, Dou et al. ([2017\)](#page-14-7) reported that blue light restrain cell division and extension growth which results in plants with smaller leaf area. Nis-sim-Levi et al. ([2019\)](#page-17-14) investigated the growth and flowering in *Chrysanthemum morifolium* under diferent light quality and duration of day length illumination and their results revealed that overnight blue light illumination inhibited fowering in Chrysanthemums.

Monochromatic green light

Green light can play a key role in plant development but its signifcance in photo-biology was neglected previously. However, research of present era realized that green light also deserves attention (Zhang et al. [2022](#page-19-10)). Green light wavelength penetrates deeper into canopy and excites the chlorophyll deeper into leaf tissue (Liu and van Iersel [2021](#page-16-9); Smith et al. [2017;](#page-18-10) Snowden et al. [2016](#page-18-11); Wang and Folta [2013;](#page-19-11) Sun et al. [1998](#page-18-12)). It has been observed that some of the green light is important in photosynthesis processes as well as plant growth and development (Kusuma et al. [2021](#page-15-7); Kaiser et al. [2019](#page-15-8); Snowden et al. [2016;](#page-18-11) Terashima et al. [2009](#page-18-13); Folta and Maruhnich [2007](#page-14-16)). Blue light and red light drive carbon dioxide $(CO₂)$ fixation for most of the parts in upper palisade mesophyll, whereas green light drives $CO₂$ fixation in the lower palisade (Sun et al. [1998](#page-18-12)). Therefore,

after the saturation of upper parts of canopy and leaves by red and blue lights, the additional green light could be of use to enhance plant photosynthesis (Nishio [2000](#page-17-15)). Low light response to green light suggests that it may possibly involve in growth adaptation under foliage or within the close proximity of other plants. However, Wang and Folta ([2013\)](#page-19-11) reported an opposed response of plants under green light to those of blue and red wavebands.

Green light is useful to drive photosynthesis in plants (Kusuma et al. [2021](#page-15-7); Terashima et al. [2009](#page-18-13)), and it afects processes in plants via cryptochrome dependent as well as cryptochrome independent ways (Folta and Maruhnich 2007). Plants can utilize green light to fine tune the efficacy of whole canopy and to optimize stomatal aperture (Smith et al. [2017](#page-18-10)). Green light can regulate morphology of cells, tissues and organs, growth, respiration, photosynthesis, and the duration of plant ontogenesis stages (Golovatskaya and Karnachuk [2015\)](#page-14-6). Green light increases plant defense to biotic or abiotic stresses by triggering specifc gene expression (Nagendran and Lee [2015](#page-17-16)). Green light signifcantly improved leaf photosynthesis and shoot dry biomass in *Lactuca sativa* L. (Johkan et al. [2012](#page-15-9)). Presence of green light resulted shade symptoms in *Arabidopsis thaliana*. Furthermore, an unknown sensor for light and cryptochrome receptors contributed in acclimation to green environment (Zhang et al. [2011\)](#page-19-12). Due to deep penetration of green light, it increases sweet pepper fruit weight and dry matter content (Lanoue et al. [2022\)](#page-15-1). Addition of green light or partial replacement of other spectra with green light caused an increase in biomass production in basil, tomato, and lettuce (Schenkels et al. [2020](#page-18-1); Kaiser et al. [2019;](#page-15-8) Kim et al. [2004a](#page-15-10)). Green light can afect the chlorophyll phytyl chain saturation level (Materová et al. [2017](#page-16-10)). Introducing green light can increase mesophyll conductance and maintain high photosynthetic potential under drought stress (Bian et al. [2021,](#page-13-9) [2019](#page-13-10)). Supplementing green light enhanced photosynthetic capability by increasing net photosynthesis rate, maximum photo-chemical efficiency, electron transport for C fixation, and content of chlorophyll, but decreased hydrogen per oxide (H_2O_2) and malondialdehyde (MDA) accumulation by enhancing SOD and APX activities (Bian et al. [2018\)](#page-13-11). Liu and Iersel [\(2021](#page-16-9)) investigated photosynthetic physiology of red, blue, and green lights. Their results showed that at low PPFD, green light showed lowest photosynthetic efficacy due to its low absorptance. Contrarily, at high PPFD, QY_{inc} [gross CO_2 assimilation (A_g) /incident *PPFD*] was among the maximum, possibly resulting from uniformly distributing green light in the leaves. Compared to monochromatic blue light or monochromatic red light treatments, green light showed higher leaf area and lower specifc leaf weight (mg cm−2) in shoots of pepper plant (Claypool and Lieth [2020](#page-13-12)). A previous study of metabolic reprogramming in leaf lettuce under varying light intensity and quality showed that energy transmitted by green light could be useful to create a balance between the production of plant biomass and defenserelated secondary metabolites. (Kitazaki et al. [2018](#page-15-11)). Green light enhanced the chlorophyll and soluble sugar, protein, and starch content in tomato (Ma et al. [2015](#page-16-11)). However, in another study, the tomato plants grown at 40% G along with 35% R and 25% B light exhibited a reduced net *P*n, and consequently, a decreased dry biomass accumulation (Trojak et al. [2022\)](#page-18-14).

Dichromatic red and blue light

Light is necessary for photosynthesis, and each pigment can absorb a specifc wavelength from visible light (Fig. [2](#page-2-1)). Light modulation in terms of quality deeply influences plant morphogenesis, photosynthesis, and growth (Vitale et al. [2021\)](#page-18-15). Several review works available in the literature consider the efect of combined spectra in eliciting morphophysiological and biochemical responses of plants (Table [2](#page-6-0)). In general, specifc spectra are more encouraging for normal growth and development of plants (Alrifai et al. [2019\)](#page-12-4), such as red and blue lights (Li et al. [2021b;](#page-16-12) Lee et al. [2014](#page-16-4)). The absorption percentage of red or blue light in the plant leaves is about 90% (Terashima et al. [2009\)](#page-18-13). Therefore, plant development and physiology are strongly infuenced by the light spectrum of the growth environment (Whitelam and Halliday [2007](#page-19-13)). Red and blue lights signifcantly improved plant growth, photosynthetic pigments, total conductance to $H₂O$ vapor and $CO₂$, maximum quantum yield of photosystem (PS)II, apparent electron transfer chain, and net photosynthesis in grape (*Vitis vinifera* L.) seedlings (Dong et al. [2023](#page-14-17)). Composite red and blue light improved *Paris polyphylla* growth (Li et al. [2023\)](#page-16-13). Similarly, previous research revealed that red blue lights in combination afected plant growth, pigment contents, antioxidative defense system, and accumulation of volatile compounds in *Aeollanthus suaveolens* (Araújo et al. [2021\)](#page-12-5), micropropagated *Urtica dioica* L. plantlets (Coelho et al. [2021](#page-13-13)), and *Lippia rotundifolia* Cham (De Hsie et al. [2019\)](#page-13-14) under in vitro environments. Phytochromes and cryptochromes are the two photoreceptor systems that mediate elongation growth in the plants. Phytochromes are activated by red light, while cryptochromes are the blue light receptors (Cosgrove [1981\)](#page-13-2). Monochromatic red light, monochromatic blue light, or their combination can promote photosynthesis and fnal production. Red and blue lights in combination can excite photoreceptors in an efficient way, thus increase the plant growth and photosynthesis as compared to monochromatic red light or monochromatic blue light (Spalholz et al. [2020\)](#page-18-16). Blue and red lights in equal quantities are more useful for higher fresh and dry biomass production in upland cotton (Li et al. [2010](#page-16-14)). Similar fndings with blue and red lights (1:1) were also recorded under in vitro plant cultures of banana (Nhut et al. [2003a\)](#page-17-17), strawberry (Nhut et al. [2003b\)](#page-17-18), and chrysanthemum (Kim et al. [2004b\)](#page-15-12). Similarly, combined exposure of red and blue lights was favorable for the growth and development of eggplant (*Solanum melongena* L.) seedlings (Di et al. [2021\)](#page-14-18) and frigo strawberries (Samuolienė et al. [2010\)](#page-18-17). Similarly, Hung et al. ([2015\)](#page-14-19) reported that 70% red with 30% blue light is effective in strawberry culture systems. Mixed blue, red, and white lights of peak outputs in blue and red regions with supplemental broad spectral energy (500–600 nm) caused improvements in lettuce plant growth, development, and nutritional quality (Lin et al. [2013](#page-16-15)).

Quality of light plays an important role in the processes of photosynthesis, and its energy inevitably modulates the photosynthetic processes. Furthermore, light quality alters the structure and function of chloroplasts in leaves (Albertsson [2001](#page-12-6)). Shaver et al. ([2008\)](#page-18-18) analyzed the infuence of light on the amount of chloroplast DNA in *Medicago truncatula* during development and found that cpDNA declined under white and blue light whereas remained constant under red light. Red and blue lights afect the primary barley leaf physiology in terms of ATP and ADP contents (Bukhov et al. [1995](#page-13-15)). Zhang et al. ([2010\)](#page-19-14) reported that red and blue light supports normal development of chloroplasts in tomato leaves. Maximum photosynthetic rate, high pigment content, and superior growth characteristics in tomato plantlets were recorded at red to blue (10:01) light ratio (Naznin et al. [2019a\)](#page-17-19). Combined red and blue light increased the growth and phenolic acid contents of *Salvia miltiorrhiza* Bunge (Zhang et al. [2020](#page-19-0)). Red blue binary light with intensity of 1000 μmol m⁻² s⁻¹ resulted in the highest energy sustainable anthocyanin production in *Eruca sativa* (Mill) Thell plants (Veremeichik et al. [2023](#page-18-19)). Furthermore, combined red blue light showed highest aliphatics in cabbage (Demir et al. [2023\)](#page-14-11). Ratio of red to blue light afects cannabinoid metabolism in medical cannabis (*Cannabis sativa* L.) and blue-rich light stimulated CBGA accumulation (Danziger and Bernstein [2021\)](#page-13-16). Meanwhile, Lalge et al ([2017\)](#page-15-13) reported that full spectrum of light infuences *C. sativa* growth and development better than combined blue red lights.

Combined red‑blue‑green light

Red and blue lights pose great infuences on the growth of plants because of their high quantum yield of $CO₂$ assimilation per mole of photons during photosynthesis (Liu and Iersel [2021\)](#page-16-9), and the action spectra have action maxima in blue and red wavelength ranges (Kasajima et al. [2008](#page-15-14)). However, photosynthetically active radiation including and red (600–699 nm), blue (400–499 nm), and green (500–599 nm) wavelengths designates spectral range offering light energy for photosynthesis, consequently affecting the plant biomass production (Kozai et al. [2015\)](#page-15-15). Green light wavelengths also induce variable responses in photosynthesis and

Light quality	Plant species	Morpho-physio-biochemical changes	Reference
70% red 30% blue	Cucumber seedlings	Increased stem diameter, Dixon Quality Index (DQI), and rate of net photosynthesis	Jin et al. (2023)
50% red 50% blue	Anoectochilus roxburghii	Promote accumulation of biomass. Enhanced area of stomata pores. Increased total phenolica, total flavo- noids, and soluble proteins and sugars	Wu et al. (2022)
50% red 50% blue	Ginkgo biloba	Elongated petiole. Increased leaf flavonol content. Slen- der leaves with reduced leaf area, and Gs	Wang et al. $(2022b)$
83% red 17% blue Impatiens		Increased cuttings number per Impatiens plant in winter. Kobori et al. (2022) Reduced plugs height Impatiens White	
70% red 30% blue	Basil plant	Higher yield and absorption of N and K under low applied nutrient quantity	Ren et al. (2022)
75% red 25% blue Tomato seedlings		Increased biomass accumulation and $CO2$ assimilation. Thicker leaves. Enhanced Pn, Gs, pigment content, and photosynthetic electron transport capacity. Upregulation of Calvin cycle-related activity and level of enzyme expression. Inhibition in GA concentration Increment of IAA in stem and root	Li et al. $(2021a)$
	75% red 25% blue Solanum melongena L	Maximum growth of plants, development of leaves, pig- Di et al. (2021) ments, and C and N metabolism	
75% red 25% blue <i>Tomato</i> fruit		Enhanced melatonin content in tomato fruit. Accelerated Li et al. (2021b) fruit softening. Upregulated ethylene and lycopene biosynthesis, rate of respiration, activity of antioxi- dants, and the accumulation of carbohydrates	
		90% red 10% blue Mesembryanthemum crystallinum L Promote plant growth with high biomass production	Kim et al. (2021)
	70% red 30% blue Salvia miltiorrhiza	Promote growth. Enhanced phenolic acids accumulation by upregulated SmPAL1 and Sm4CL1 transcription	Zhang et al. (2020)
50% red 50% blue Tomato		Higher leaf Gs and Pn	Yang et al. (2019)
	60% red 40% blue Lepidium sativum L	Increased fresh biomass. Increased length, total area, stem diameter, and number of leaves. Enhanced chlo- rophyll content	Ajdanian et al. (2019)
	90% red 10% blue Lachenalia 'Rupert'	Stimulated inflorescence development Increased length, stem diameter, and florets number of inflorescences	Wojciechowska et al. (2019)
75% red 25% blue	Lettuce	Increase the yield, leaf chlorophyll, and flavonoid con- centrations. Increase the uptake of N, P, K, and Mn	Pennisi et al. (2019)
	80% red 20% blue Digitalis purpurea L	Higher number of leaves. Longer root Larger width of leaf stomata and leaf area Higher leaf or root fresh weight and dry weights	Verma et al. (2018)
Red blue	Lippia alba	Higher fresh and dry weights, and levels of photosyn- thetic pigments	Batista et al. (2016)
80% red 20% blue	Broccoli	Increased conc. of shoot tissue chlorophyll, a-carotene, lutein, total carotenoids, Ca, Mg, P, S, B, Cu, Fe, Mn, Mo, Zn, glucoiberin, glucoraphanin, 4-methoxygluco- brassicin, and neoglucobrassicin	Kopsell et al. (2014)
25% red 75% blue Rapeseed		Higher rate of differentiation, high fresh and dry bio- mass, chlorophyll a conc., soluble sugar conc., stem diameter, length of abaxial surface of leaf stomata, adaxial surface stomata frequency, and transplantation survival rate in the plantlets	Li et al. (2013)
50% red 50% blue	Cotton	Higher fresh and dry weights. Maximum stem length and length of second internode	Li et al. (2010)

Table 2 Morpho-physio-biochemical changes in plants under dichromatic red and blue light

**GA*, gibberellin; *IAA*, indole-3-acetic acid (auxin); *Gs*, stomatal conductance; *Pn*, net photosynthesis/photosynthetic rate; *conc.*, concentration; *C*, carbon; *N*, nitrogen; *P*, phosphorous; *K*, potassium; *Ca*, calcium; *Mg*, magnesium; *S*, sulfur; *B*, boran; *Cu*, copper; *Fe*, iron; *Mo*, molybdenum; *Zn*, zinc; *Mn*, manganese

plant morphogenesis (Johkan et al. [2012](#page-15-9)). For instance; *O. basilicum* grown in red, green, and blue (4:1:1) light treatment showed high photosynthesis, high quantum yield, and photosynthetic electron transport (Lin et al. [2021](#page-16-18)). Then, 30 µmol m^{-2} s⁻¹ of red and blue light supplemented with green light improved the growth and yield of lettuce (Razzak et al. [2022](#page-17-4)). However, supplementary green light at 76 µmol m⁻² s⁻¹ and 129 µmol m⁻² s⁻¹ reduced fresh biomass in lettuce (Kim et al. [2004a\)](#page-15-10). According to Claypool and Lieth ([2020\)](#page-13-12), red, blue, and green light wavelengths caused higher shoot dry weight accumulation and plant compactness in pepper seedlings. A red-to-blue spectrum partially replaced by green light can improve plant biomass up to 6.5% (Kaiser et al. [2019](#page-15-8)). Meng et al. [\(2019\)](#page-16-19) reported that substituting green light or far-red light for blue light triggers shade avoidance and accelerates plant growth while reducing pigment concentration. According to Bian et al. [\(2016](#page-13-18)), 24 h continuous red blue LED light with green light exposure could be applied to reduce nitrate content and to improve lettuce quality. Green light exposure results in high number of leaves, stem diameter, and higher sodium content in okra (Degni et al. [2021\)](#page-13-19). Quantum yield response of absorbed light is as red>blue>green under 400–700 nm radiation ranges. Inclusion of 24% green light (500 to 600 nm) to red and blue LEDs improved the plant growth (Kim et al. [2004c\)](#page-15-20). Supplementation with green light signifcantly enhanced nitrite reductase (NiR), nitrate reductase (NR), glutamate synthase (GOGAT), and glutamine synthetase (GS) activities, compared with red and blue LEDs. Furthermore, supplementary green light efficiently promote nutritional quality of plants by maintaining higher net photosynthesis and photochemical efficiency (Bian et al. [2018](#page-13-11)). However, in a previous study, inclusion of green light decreased shoot biomass in basil and brassica species compared with the plants, grown under combined red and blue light (Table [3\)](#page-7-0) (Dou et al. [2020\)](#page-14-20).

Molecular responses of plants to red, blue, and green light

Plant growth is modulated by diferent photoreceptors, including phytochromes and cryptochromes (Zhu and Lin [2016\)](#page-19-19). Several insights are being discovered with respect to molecular regulation of plant processes in relation to spectrum, intensity, photoperiod, and light timing. For instance, in a recent study, Zhou et al. ([2023](#page-19-20)) observed expression levels of photosynthesis-related genes in Cassava seedlings under diferent light quality and found that *MeLHCA1*, *MeLHCA3*, *MePSB27-2*, *MePSBY*, *MePETE1*, and *MePNSL2* in leaves were at their lowest under red light treatment, while *MePSB27-2*, *MePSBY*, *MePETE1*, and *MePNSL2* were at their highest after blue light. Red light promoted starch accumulation in *Spirodela polyrhiza* L., but the high content of protein under blue light was linked with the upregulation of most differentially expressed

Table 3 Morpho-physiological and biochemical changes in plants under combined red, blue, and green light

Light quality	Plant species	Morpho-physiological changes	References
72% red 18% blue 10% green	Lettuce	Improved growth and yield	Razzak et al. (2022)
35% red 15% blue 50% green	Nasturtium officinale L	Enhanced secondary metabolites production and antioxidant potential of micro shoot cultures	Klimek-Szczykutowicz et al. (2022)
47% red 34% blue 19% green	Microgreen species	Promote dry biomass production and bioactive phytochemical accumulation in the majority of the microgreen species	Orlando et al. (2022)
Red:blue:green (4:1:1) O. basilicum		Larger plants. High photosynthetic capacity, quantum yield, and photosynthetic electron transport	Lin et al. (2021)
33.3% red 33.3% blue 33.3% green	N. officinale	Positive role in increasing the functional compo- nent. Negative effect on the growth	Choi et al. (2020)
44% red 12% blue 44% green	Green basil Green mustard	Stimulated stem elongation	Dou et al. (2020)
80% red 10% blue 10% green	<i>L. sativa</i> (red leaf 'Sunmang') Higher fresh weight of shoot		Son and Oh (2015)
$Red + blue + green$ (a broad spectrum)	Pepper seedlings	Maximum shoot dry weight and plant compact- ness	Claypool and Lieth (2020)

genes (DEGs) enriched for specifc GO terms and KEGG pathways (Zhong et al. [2022\)](#page-19-21). Sucrose at 100 mM in the presence of red light wavelengths or blue light wavelengths could promote detached ripening of strawberry through positive regulation of abscisic acid (ABA) signaling and negative regulation of auxin signaling (Jiang et al. [2023\)](#page-15-22). In another study on tomato plant, Bian et al. ([2021\)](#page-13-9) revealed that bZIP transcription factor-HY5 played a very important role in drought response under green light and other transcription factors, and WRKY46 and WRKY81 could be involved for the stomatal aperture regulation and ABA accumulation. Liu et al. (2020) (2020) (2020) evaluated the effectiveness of supplementary green, white, and yellow light added to red-blue and sole white light on the growth and photosynthesis of rapeseed seedlings. Compared with red-blue light, in total, 449, 367, 813, and 751 DEGs were identifed under supplementary green, yellow, and white and sole white light, respectively. The transcriptomic analysis showed more distinctive efects of supplementary green light to enhance photosynthesis and plant growth. In another study, partial replacement of red light and blue light with green light increased drought tolerance in cucumber seedlings via upregulated CsGAD2 expression and improved GABA synthesis which further downregulated CsALMT9 expression, induced stomatal closure, enhanced H_2O use, and conse-quently lessen the effects of drought (Ma et al. [2022\)](#page-16-21). Blue light played a constructive role in lignin biosynthesis by the activation of transcription of lignin biosynthesis-related genes in ornamental bromeliad Neoregelia 'Fireball' plants (Shi et al. [2023\)](#page-18-22). Dong et al. ([2023](#page-14-17)) investigated grapevine morphology under red, blue, green, and white (control) light using multivariate sequencing analysis. The results of analysis showed 1065 metabolites (in total), 318 were negative, and 747 were positive. Kyoto Encyclopedia of Genes, Gene ontology, and Genome analyses showed that various DEGs were related to secondary metabolites biosynthesis of such as favonols, favones, and alkaloids, and metabolic and phenylpropanoid pathways. In addition, *WRKY* (*29 DEGs*), *NAC* (*31 DEGs*), *bHLH* (*32 DEGs*), and *MYB* (*37 DEGs*) transcription factors were reported. Furthermore, the genes such as*PsaD*, *PsaO*, *PsbB*, *PetC*, *PetE*, *PetF*, *PetH*, *PetJ*, and *Lhca* played essential roles in photosynthesis. Weighed gene correlation network analysis found 4 metabolites, 7 module relationships, 14 structural genes, and 36 transcription factor-related genes. In a recent study on the photosynthetic capacity and fruit quality of 'Yanli' strawberry grown in a solar greenhouse, Wang et al. ([2023\)](#page-19-22) found diferentially expressed genes between red/blue light $(R/B = 4:1)$ before sunrise and after sunset supplementation and control by RNA-seq, including sucrose metabolismrelated genes (*SWEET9/BAM1*) and light-responsive genes (*PRR95/LHY/CDF3/CO16/bHLH63/BBX21/PAR1/SIGE*).

Insect, pest, and disease control using red and blue light

Being a source of electromagnetic radiation energy from sun, light plays an important role to regulate plant growth, development, and other cellular processes. Biotic stress due to insects or pests plays a critical role in loss of crop production worldwide (Manosathiyadevan et al. [2017](#page-16-22)). Thus, plant protection measures are inevitable. Besides direct killing methods for pathogens in crops, environmental light could also play a signifcant role to regulate plant resistance to defend against pathogen invasion (Wang et al. [2022c](#page-19-23)). Research revealed the benefts of using diferent specifc light bands to promote plant defense against pathogens, infections, or herbivore infestation (Balamurugan and Kandasamy [2021](#page-13-21)). Normally, red light infuences plant defense mechanisms and enhances plant resistance to diferent pests and diseases (Gallé et al. [2021](#page-14-12)) and root-knot nematodes (Yang et al. [2018](#page-19-24)); however, the molecular mechanisms still need to study in depth. In a previous study, Gallé et al. [\(2021\)](#page-14-12) investigated the infuence of red light on biotic stress responses in plants to fungi, bacteria, viruses, and nematodes. Their results evidenced the changes in levels of salicylic acid which could beneft plants to survive infections. Chen et al. ([2015](#page-13-22)) assayed the infuence of diferent light quality on interaction of *Nicotiana tabacum* and cucumber mosaic virus (CMV). The Western blotting and quantitative real-time polymerase chain reaction (QRT-PCR) based analysis revealed that red light and blue light can delay the symptom expression and CMV replication on *N. tabacum*. Yang et al. [\(2015](#page-19-25)) investigated diurnal variations in tomato resistance to *Pseudomonas syringae* pv. tomato DC3000. Analysis of RNA sequencing data showed red light induced set of circadian rhythm-related genes contributed in the phytochrome and salicylic acid (SA) regulated response to resistance. Thus, salicylic acid-mediated signaling pathways contribute red light induced resistance to pathogens. Red and blue light treatment of detached leaves caused stilbenic compound accumulation and the diferential expression of the genes which are involved in response to defense and inhibited lesion development of Grey mold (Ahn et al. [2015](#page-12-8)). Being an environmental catalyzer red light encourages mutualism of whitefly begomovirus by stabilizing β C1, which interacts with PIFs transcription factors. PIFs positively control the plants defense to whitefy (Zhao et al. [2021](#page-19-26)). Light wavelength signifcantly afected the induction of tree-top disease in *Helicoverpa armigera* 3rd instar larvae infected with HearNPV (Bhattarai et al. [2018](#page-13-23)). Blue light application could be a pest control approach by adjusting the wavelength to target specifc developmental stages. *Conopomorpha sinensis* Bradley larvae can bore into fruit, damage fowers, tender shoots, and leaves. However, blue and green

light treatment at 460 and 520 nm can reduce its activity, fecundity, and damage rate (Fang et al. [2023\)](#page-14-21). Specifc light spectrum can afect the plant feeding arthropod behavior and their carnivorous enemies directly or through variations in plant morpho-physiology (Lazzarin et al. [2021\)](#page-16-23). Fruits under supplemental red light could have higher tolerance to *Botrytis cinerea* thus reducing agrochemical inputs (Lauria et al. [2023a,](#page-15-23) [2023b\)](#page-15-24). Exposure of green light during night on litchi production can reduce the activities of *C. sinensis* and pesticide usage (Fang et al. [2023\)](#page-14-21).

Light traps may also be used to control insect related problems in crops. Balamurugan and Kandasamy ([2021\)](#page-13-21) investigated the efectiveness of a portable solar-powered LED light trap (red-630 nm, blue-470 nm, green-525 nm, and ultraviolet-405 nm) for monitoring insect pests in groundnut crop during autumn for 15 days. The results showed that the ultraviolet (405 nm) trap captured maximum number of insects and the red (630 nm) trap captured minimum number of insects but the attraction of *Amsacta albistriga* to red (630 nm) trap was higher as compared to blue (470 nm) and green (525 nm) traps. Furthermore, some hemipteran species exhibit a mechanism of blue green opponency in which high blue light causes repellence (Stukenberg and Poehling [2019](#page-18-23)). In another study, use of red light reduces the attraction of melon thrips *Thrips palmi* (Thysanoptera: Thripidae) towards plants (Murata et al. [2018\)](#page-17-23). It was observed that the adult lepidopteran insects were attracted towards blue light or light of shorter wavelengths (Castrejon and Rojas [2011](#page-13-24)). Furthermore, Bantis et al. ([2020](#page-13-25)) disclosed that bichromatic red and blue LED light can increase grafted watermelon seedling vegetative growth during healing. Utilization of diferent colored cladding materials that optically repel or arrest pests can also boost crop protection and reduce the insecticide uses especially for tomato and pepper crops (Ilić and Fallik. [2017\)](#page-14-22). For example, blue color net is known to attract thrips (Ben-Yakir et al. [2012\)](#page-13-26). Above reports showed that the application or supplementation of red and blue light in greenhouses could be efective in reducing insects, pests, and diseases, while at the same time benefting crop production.

Vegetable production and fruit quality using red, blue, and green light

Rising food demands under global population pressure are a serious threat to food security (Carthy et al. [2018\)](#page-13-27). Present conditions pointed out that food demand might be doubled up to 2050 (de Fraiture et al. [2007\)](#page-13-28). Consequently, adaptation of scientifc or technical developments in agriculture is very important for food security to feed the growing population (Odegard and van der Voet [2014\)](#page-17-24). Díaz-Galián et al. ([2021\)](#page-14-23) tested the efects of red and blue light combinations on strawberry production and concluded that increasing red and blue lights improved strawberry production and fruit quality. Blue light could be a signifcant factor that modulate growth and development and biochemical properties of tomato hp mutants, thereby afecting nutritional characteristics, shelf life, and product quality (Vereshchagin et al. [2023](#page-18-24)). Wei et al. ([2023\)](#page-19-27) studied the efects of red, blue, yellow, and white light wavelengths on anthocyanin biosynthesis gene expression and fruit quality in blueberry (*Vaccinium corymbosum*). Their results showed that maximum fruit weight, fruit height, and fruit width were recorded under blue and white light treatments. Red light (150–200 µmol m⁻² s⁻¹) increases the height of lettuce (Chen et al. [2021a](#page-13-29)), Chinese cabbage (*Brassica campestris* L.) (Fan et al. [2013\)](#page-14-8), and soybean seedlings (Fang et al. [2021\)](#page-14-24). Combination of red light (30%) and blue light (70%) at 100 µmol m^{-2} s⁻¹ improved plant height, diameter of stem, number of leaves, internode distance, fresh and dry, and shoot and root biomass in passion fruit (*Passifora edulis*) seedlings (Liang et al. [2021](#page-16-24)). According to Tang et al. ([2020\)](#page-18-25), red blue green spectrum signifcantly increased the growth, gas exchange, and antioxidant activities of tomato, radish, and lettuce. Blue light addition in red LEDs increased the growth attributes, photosynthetic pigments, and antioxidant capacity in sweet pepper, basil, kale, spinach, and lettuce (Naznin et al. [2019b](#page-17-12)). Moreover, different light spectra also affect the nutritional quality of the diferent species. Orlando et al. ([2022\)](#page-17-22) tested the effects of different spectrum of light wavelengths and irradiance levels on the growth, yield, and nutrition quality of four vegetables (China rose radish, chicory, alfalfa, and green mizuna) and two fowers (celosia and French marigold) of microgreens species. Their results revealed that addition of green light at 340 µmol m^{-2} s⁻¹ in the red-blue light increases growth in terms of dry biomass production and bioactive phytochemical accumulation in microgreen species. Supplemental red light enhanced plant productivity and "photomodulates" quality of strawberry fruits (Lauria et al. [2023a\)](#page-15-23).

Bedsides LED lights, Dissanayake and Wekumbura ([2021\)](#page-14-25) proposed that green and red shading on tomato plant is more favorable for the healthy lycopene rich fruit production. In addition, the vegetables produced under red nets retained high content of phytochemicals (Ilić and Fallik [2017](#page-14-22)). Signifcantly higher vitamin C content was recorded in greenhouse pepper integrated with red shade net (Milenković et al. [2012\)](#page-16-25). Previous studies reported that red and pearl photo selective nets make favorable growing conditions for plants and produce fruits with thicker pericarp in sweet pepper (Ilić et al. [2017\)](#page-14-26) and in tomato (Ilić et al. [2015\)](#page-14-27). The photo selective red screen promoted plant growth and increase (about 4%) in the commercial fruit yield of sweet pepper, when grown in Midwest climatic conditions of Brazil (Santana et al. [2012](#page-18-26)).

The vibrant light spectra can offer benefits of improved growth and production in high value production systems (Dieleman et al. [2019](#page-14-28)). Furthermore, diferent LED wavelengths can induce the synthesis of bioactive compounds, which in turn can improve the nutritional quality of crops (Hasan et al. [2017\)](#page-14-29). For instance, LED lighting during carrot sprouting improved the synthesis of health-promoting compounds (Martínez-Zamora et al. [2021](#page-16-26)). Exposure of red and blue mix light (70 µmol m⁻² s⁻¹) induced the synthesis of carotenoids, starch, sucrose, glucose, and fructose in *Doritaenopsis* hort (Shin et al. [2008](#page-18-27)). Exposure of red light or blue light at 50 µmol m⁻² s⁻¹ induced sugar and starch synthesis in vitis root-stock (Heo et al. [2006;](#page-14-30) Poudel et al. [2008](#page-17-25)). New techniques to adjust light quality should be conveyed to the vegetables and fruits producing farmers also. Moreover, post-harvest LED treatment has increased the accumulation of vitamins, chlorophyll, carotenoids, phenolic compounds, glucosinolates, and total soluble solids (Nassarawa et al. [2021\)](#page-17-26). Thus, future studies on the light manipulation are essential to get more sustainable and demand oriented vegetables or fruits (Table [4](#page-11-0)).

Heavy metal phytoremediation using red, blue, and green light

With the development of industry and modern agriculture, more toxic chemicals are released into the environment (Shen et al. [2022\)](#page-18-28). Heavy metals can alter soil chemical properties, physical structure, and biological system, as a result, reduce the soil fertility and enzyme activities (Cameselle et al. [2013](#page-13-30)). Plant-based soil remediation methods are environment friendly, applicable, and may be considered as a sustainable approach for heavy metal removal from contaminated soils (Raj and Singh [2015;](#page-17-27) Rehman et al. [2023](#page-17-28)). Light is increasingly used as a physical trigger in agriculture and studies reported changes in heavy metal contents in different plant tissues under diferent light spectra (Xie et al. [2023](#page-19-28); Marques et al. [2018\)](#page-16-27). For instance, red and blue light combined in diferent ratios improved phytoremediation potential of *Noccaea caerulescens* and *Eucalyptus globulus* L. for Pb, Cd, and Cu and alleviated the leaching risk (Luo et al. [2020,](#page-16-28) [2019a](#page-16-29), [2019b](#page-16-30)). Red light signifcantly increased Zn and Cu extraction ability of *Chlorella vulgaris* L. (Kwon et al. [2017\)](#page-15-25). Xie et al. ([2023](#page-19-28)) suggested that 20% red, 70% blue, and 10% green trichromatic light signifcantly increase Cd extraction, hence improving the phytoremediation of Cd by *Bidens pilosa* L. Zafar et al. [\(2020](#page-19-29)) studied metallic nanoparticles (ZnO NPs) for their optimistic and pessimistic infuence on *Brassica nigra* (Linn.) Koch plant growth and physiological indices under varied light regimes. According to their results, diferent spectral lights afect ZnO NP toxicity. The HPLC analysis showed that chlorogenic acid (CGA) upregulated under NP efects in red and white light, whereas quercetin increased under NP stress in the blue light. Chen et al. $(2021b)$ reported that the phytoremediation efficiency of *A. thaliana* could beneft from combinations of blue and red light. Red and blue lights enhance Cd stress tolerance in rice seedlings (Sebastian and Prasad [2014\)](#page-18-29). Yellow light with combined spectra of blue and red light improved Cd decontamination effect of *A. thaliana*, consequently increasing the Cd phytoextraction ability of *A. thaliana*. In another previous study, Kwon et al. [\(2015](#page-15-26)) reported that phytoremediation using red LED (650 nm) and benthic microalgae showed potential as a new and environment-friendly method for the remediation of eutrophic coastal sediments. Thus, phytoremediation, using plants and the accompanying light wavelengths to clean up contaminants in the soil, could be a suitable solution for heavy metals polluted soil.

Challenges to eco‑friendly lighting

Sunlight serves as a major resource of energy for crops, and light intercepted by plants in natural environment fuctuates and is much complicated. Artifcial or supplementary lighting is a competent stratagem to get full beneft of spectral compositions during crop production (Liu et al. [2022\)](#page-16-31). Thus, artifcial or supplementary lights have gained vast popularity for indoor farming as an innovative experimental platform to fnd out the regulatory mechanisms of light on morpho-physiological, biochemical, and molecular responses of plants. These lights, for example, LEDs are environment friendly and offer several advantages including energy savings, target spectrum, and fast harvest cycle (Bula et al. [1991\)](#page-13-32). Despite numerous benefts of artifcial lighting, there are few challenges such as (i) one of the main challenges is that artifcial lights can increase temperature in experimental environment. Although LEDs produce less heat as compared to other grow lights, but they do produce heat that can push the greenhouse above the ideal temperature for growing plants. Thus, it will increase the air conditioning cost associated with keeping experimental conditions at the ideal temperature. (ii) Higher upfront cost is another drawback associated with LED grow lights and can be prohibitive especially for small-scale farmers in developing countries. Solutions could lie in scaling up production, government subsidies, or developing cost-efective LEDs that do not compromise the quality. (iii) Limited light penetration into the densely grown crops canopies. However, artifcial grow light manufacturers tried to come up with solutions to increase the penetration of artifcial light for example, by changing the designs of grow lights and by adjusting the spectrum. All of the above issues can be solved by the introduction of advanced technologies in lighting in the controlled production systems. In essence, the future of artifcial lighting in agriculture hinges on the

Table 4 Efects of red, blue, and green light wavelengths on pre- or post-harvest fruit quality

Table 4 (continued)

synergy between innovation and responsibility. While the potential benefts are vast, they must be pursued with an unwavering commitment to safety, sustainability, and inclusivity. As the nexus between artifcial LED lighting and agriculture strengthens, it promises to revolutionize farming and food production in the coming decades.

Summary and future prospects

Evidences presented in this study proved the efectiveness of red, blue, and green light wavelengths for plant growth and development. Although monochromatic red, blue, or green light wavelengths or their combinations have been applied to diferent plants in the greenhouses. However, studies on these spectra still are not informative enough for crop production and application of these spectra are yet to design for largescale crop production. Future studies should focus on how red, blue, and green light spectral composition infuences crop growth, secondary metabolism, fruit quality and storage, plant defense, behavior of insect/pest, and disease control.

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