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Review

Light and Microbial Lifestyle: The Impact of Light Quality on Plant–Microbe Interactions in Horticultural Production Systems—A Review

Beatrix W. Alsanius [1,*], Maria Karlsson [1], Anna Karin Rosberg [1], Martine Dorais [2], Most Tahera Naznin [1], Sammar Khalil [1] and Karl-Johan Bergstrand [3]

1 Department of Biosystems and Technology, Microbial Horticulture Unit, Swedish University of Agricultural Sciences, SLU, P.O. Box 103, SE-230 53 Alnarp, Sweden; maria.e.karlsson@slu.se (M.K.); anna.karin.rosberg@slu.se (A.K.R.); naznin.most.tahera@slu.se (M.T.N.); sammar.khalil@slu.se (S.K.)

2 Département de Phytologie, Centre de Recherche et d'Innovation sur les Végétaux (CRIV), Université Laval, Pavillon Envirotron, Local 1216, Québec City, QC G1V 0A6, Canada; martine.Dorais@fsaa.ulaval.ca

3 Department of Biosystems and Technology, Horticultural Crop Physiology Unit, Swedish University of Agricultural Sciences, SLU, P.O. Box 103, SE-230 53 Alnarp, Sweden; karl-johan.bergstrand@slu.se

* Correspondence: beatrix.alsanius@slu.se; Tel.: +46-40-415336

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Abstract: Horticultural greenhouse production in circumpolar regions (>60° N latitude), but also at lower latitudes, is dependent on artificial assimilation lighting to improve plant performance and the profitability of ornamental crops, and to secure production of greenhouse vegetables and berries all year round. In order to reduce energy consumption and energy costs, alternative technologies for lighting have been introduced, including light-emitting diodes (LED). This technology is also well-established within urban farming, especially plant factories. Different light technologies influence biotic and abiotic conditions in the plant environment. This review focuses on the impact of light quality on plant–microbe interactions, especially non-phototrophic organisms. Bacterial and fungal pathogens, biocontrol agents, and the phyllobiome are considered. Relevant molecular mechanisms regulating light-quality-related processes in bacteria are described and knowledge gaps are discussed with reference to ecological theories.

Keywords: abiotic factors; biocontrol agent (BCA); controlled environment; ecological theory; greenhouse; molecular mechanisms; non-phototrophic bacteria; pathogens; phyllosphere; plant metabolism; plant morphology

1. Introduction

Plants are meta-organisms colonized with microorganisms, including bacteria, fungi, algae, archaea, protozoa, viruses, and, on rare occasions, nematodes. Depending on the environmental and plant-related conditions prevailing in the various habitats surrounding different plant organs (e.g., soil/growing medium, atmosphere), different compartments (so-called spheres) differing in microbial colonization patterns and community structure have been identified. The very well-researched zone affected by the root (*rhizosphere*) consists of an outer layer (*ectorhizosphere*), the root surface (*rhizoplane*), and the interior of the root (*endorhizosphere*). Likewise, aboveground plant parts constitute three spheres, the *phyllosphere*, *caulosphere*, and *carposphere*, which denote zones affected by the leaf, stem, and fruit, respectively. The phyllosphere is divided into the epiphytically colonized leaf *surface* and the leaf *endosphere.*

The phyllosphere and its microbiota have received increasing attention during recent years [1–33], because this can be a powerful tool to improve plant health, growth, development, and human health

metabolites. Studies have been conducted on a wide range of scales, from parts of a leaf to intact leaves, entire canopies of individual plants, and crop stands. Studies on plant stands tend to use the term phyllosphere in a wider sense, including also the caulosphere and carposphere. The phyllosphere can be divided into the epiphytically colonized leaf surface and the leaf endosphere. The leaf surface is a hostile environment for microbes due to exposure to diurnally and seasonally fluctuating environmental and plant physiological conditions and their interactions (e.g., ambient temperature, irradiation, and water and nutrient availability) [30,34,35]. In contrast, the leaf endosphere offers a nutritionally rich and shielded environment [35]. Plant leaves host 10^6–10^7 bacteria/cm^2 leaf surface [30], with microbially available nutrients (organic carbon sources) being the driving force. However, nutrients are not evenly distributed on the leaf surface, so leaves are not covered with an even biofilm, but rather with patches containing assemblages of microorganisms [17,30,35–37]. While the leaf microbiota is affected by external conditions in the habitat, it is also able to respond proactively to suboptimal conditions through the use of light receptor proteins and to modify its habitat to shield itself from harmful environmental effects and to optimize nutrient acquisition and chances of survival [30,35].

Controlled environments, such as greenhouses, polytunnels, and plant factories, reduce the amplitude of fluctuations in the crop environment, which in turn affects plant performance and the structure and function of the associated microbiome. Greenhouse-covering materials and shade netting alter prevailing environmental conditions (e.g., temperature, relative humidity, and carbon dioxide (CO_2) concentration), but also conditions at the crop level and in the crop phyllosphere, as they influence greenhouse light transmission, reflection, absorption, and diffusion within the canopy [38–40]. Figure 1 summarizes the most important growth parameters affecting the phyllosphere of greenhouse crops.

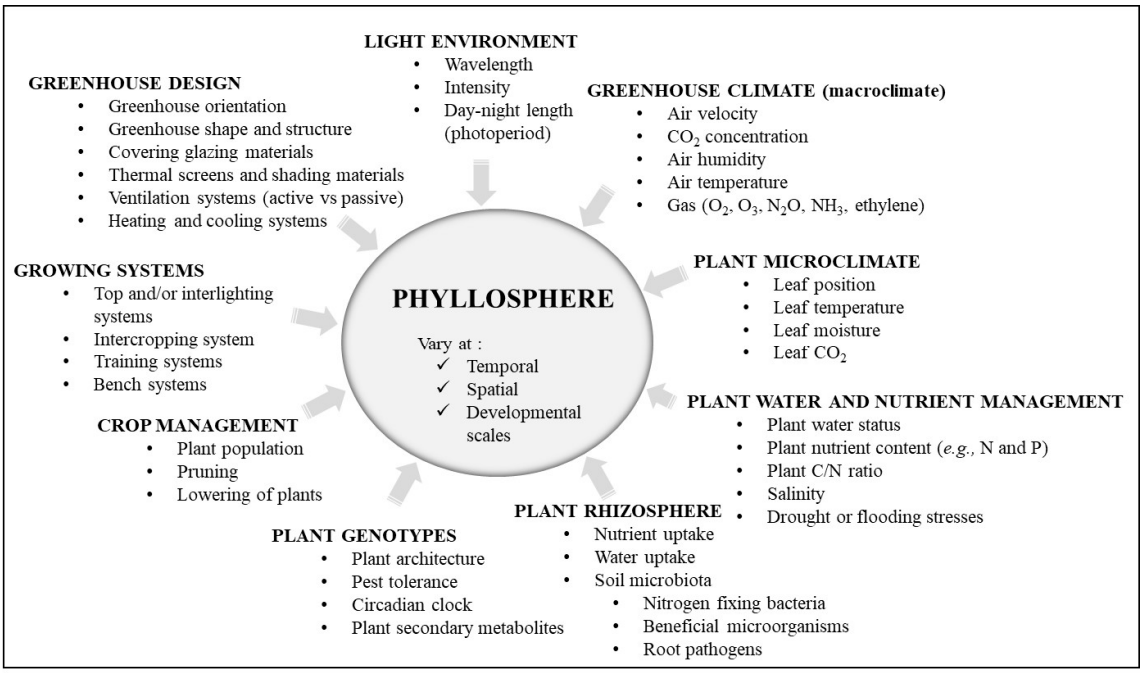

Figure 1. Most important growth parameters affecting the phyllosphere of greenhouse crops. (*Illustration: M. Dorais*).

To compensate for light deprivation under naturally low light conditions and to optimize plant development and quality with respect to crop and market demands, additional artificial assimilation lighting is necessary. Different types of lamps are available (Table 1). Alternative technologies, among these light-emitting diodes (LED), have been introduced during recent years as a measure to reduce energy consumption and costs.

Table 1. Commonly used sources for artificial assimilation lighting (high-pressure sodium, HPS; metal halide; light tube; continuous spectrum polychromatic light-emitting diode (LED). Parameters of importance for plant–microbe interactions are displayed (ultraviolet light, UV; photosynthetically active radiation, PAR). Heat emissions directed towards (↓) or away from (↑) the crop are indicated by arrows.

Lamp Type	Effect (W)	Infra-Red	UV	PAR [1]	Direction of Heat Emissions	References
HPS [2]	400	High	Low	1.6	↓	[41]
Metal halide [3]	400	High	Low	n/a	↓	[42]
Light tube [4]	58	Medium	Low	n/a	↓	
LED 1 [5]	630	None	None	1.85	↑	[43]
LED 2 [6]	550	None	None	2.5	↑	[44]
LED 3 [7]	400	None	None	2.3	↑	[45]

[1] Spectral distribution for different lamp types shown in Figure S1. [2] Philips Master, Philips, Eidhoven, the Netherlands; [3] Philips Master HPI-T plus; Philips, Eindhoven, the Netherlands. [4] Osram G13 T8 58W 840, Osram, Munich, Germany; [5] Heliospectra EOS, Heliospectra AB, Gothenburg, Sweden; [6] Senmatic FL300 Grow, Senmatic A/S, Soendersoe, Denmark; [7] Valoya RX400, Valoya Oy, Helsinki, Finland.

In the horticultural and controlled environment context, light and plant interactions, including light intensity, light quality (*light spectrum*), and day length, have been well-researched (Figure S2), but studies in these disciplines only rarely consider the fact that plants are meta-organisms. In plant microbiology studies, on the other hand, there has been an increasing focus on the phyllosphere in recent years. Prompted by advances in culture-independent techniques, many of these studies focus on the community structure and microbial biodiversity on a descriptive level, but rarely include ecological theories or concepts [19]. Although such studies are often carried out under controlled climate conditions, description and monitoring of environmental factors receive little attention (Figure S3). In fact, the leaf surface and the phyllosphere are often considered a matrix with limited interactions, rather than part of a living and aging system, and very few studies explicitly consider the impact of light quality on the phyllosphere microbiota under greenhouse conditions. With respect to artificial assimilation lighting, the architecture of the plant and crop stand and the position of the light source (top and/or intracanopy lighting) are important. With a rosette-like leaf organization, all leaves are fully exposed to the administered light, whereas only the most outer leaf layer of cushion-forming plants and plants within dense crop stands is exposed, irrespective of top or intercrop irradiation. Leaves inside the canopy are shaded and, thus, dominated by green light (wavelength: 500–565 nm).

The bacterial community structure in the phyllosphere has received more attention than the fungal community structure. Examples of the bacterial community structure of various greenhouse-grown crops are shown in Figure 2. With respect to foliar pathogens, the focus in previous research has been on alternative control of fungi using different wavelengths of light (*light qualities*), rather than on bacteria [46–50]. However, different light technologies influence biotic and abiotic conditions in the plant environment [51]. Modifications in the cropping environment, induced by light intensity and quality and by daylength, influence the structure but also the function of the leaf-associated microbiome [51–53]. Microbes switch lifestyle to adapt to light qualities, as a matter of life and death (i.e., to enable metabolism, function, survival, growth, and nutrient acquisition) [50,52,53].

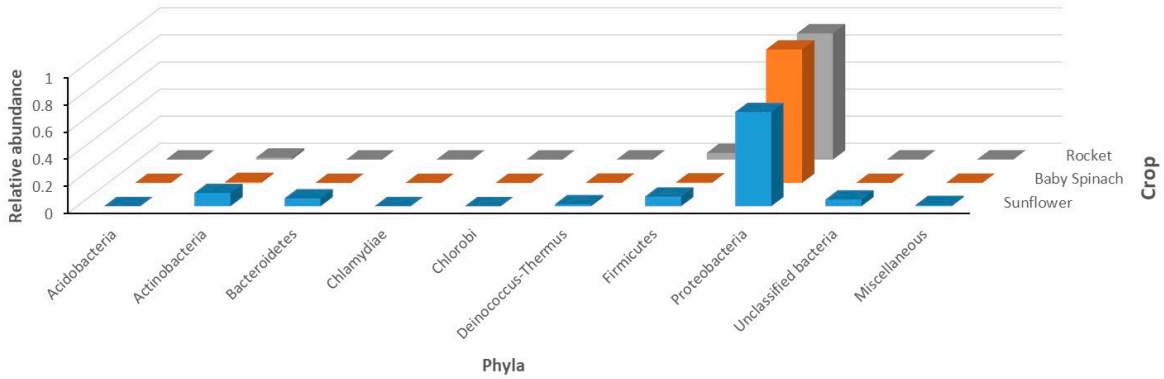

Figure 2. Bacterial phyllosphere community structure of some greenhouse crops artificially illuminated with high-pressure sodium lamps (HPS). Blue: sunflower, *Helianthus annuus* L. [51]. Orange: baby leaf spinach (*Spinacia oleacea)*; grey: rocket (*Diplotaxis tenuifolia)* [Alsanius, unpublished data]. (*Illustration: B. Alsanius*).

In this review, we consider the impact of light quality on plant–microbe interactions in light of current ecological theories and concepts. In particular, we focus on the following research questions:

(i) Which light-dependent plant processes and mechanisms are decisive for phyllosphere colonizers?
(ii) Which morphological plant characteristics are modified by light quality and consequently influence the structure and/or function of the phyllosphere microbiome?
(iii) Which light-quality-dependent microbial processes and mechanisms affect plant traits?
(iv) Which ecological principles and theories apply to microbiome effects in the phyllosphere with regard to artificial illumination?

2. Materials and Methods

In this literature review, we followed recommendations developed for systematic reviews and meta-analyses [54] and covered the literature in a 30-year period (1988–2018). All keywords and keyword combinations are listed in Table S1. Searches were performed in Web of Knowledge (WoK) using all WoK databases (Web of Science Core Collection, Biosis Citation Index, CABI, Current Contents Connect, Data Citation Index, Derwent Innovation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index, Zoological Record).

3. Abiotic Effects of Light on the Leaf Microbiota

3.1. Impact of Lighting Technology on Leaf Temperature, Leaf Moisture, and Humidity

The light environment affects the environment of the leaf surface in several ways. In greenhouse conditions, the most profound effect on the leaf microbiota caused by artificial lighting is due to changes in leaf microclimate [55]. Differences in the amount of infrared (IR) light emitted by different types of light sources is the major cause of these light-source-dependent changes in the leaf microclimate [55]. Conventional high-intensity discharge (HID) lamps, including metal halide (MH) and high-pressure sodium (HPS) lamps, emit most of their waste heat as IR radiation, radiated in the same direction as visible light [55]. In contrast, LED-based light sources mainly produce sensible heat, which has to be cooled away from the fixture using fans, heat sinks, or water cooling [55]. It is well-documented that lighting using HID lamps results in higher leaf temperatures than lighting using LED lamps, e.g., one study [56] reported 0.5–0.7 °C higher air temperature in the canopy in plants illuminated with HPS lights compared with plants illuminated with LED lights [56]. Another study found that air temperatures were around 1 °C higher within the crop stand of potted ornamentals when HPS lighting was applied, compared with LED lighting [57]. Moreover, the relative humidity (RH) in the canopy has been found to be around 5%-units lower when HPS lights are applied compared with LED

lights [57]. Interactions between UV radiation and relative humidity have also been observed [58]. It was observed that attacks of powdery mildew in roses can be reduced to practically zero when applying 24-h lighting, which has been explained by constant moisture conditions on the leaves preventing conidia from germinating [59]. On the other hand, higher relative humidity (lower vapor pressure deficit) is generally known to increase the incidence of infection and sporulation of *Botrytis cinerea* [60]. The ambient air temperature also affects the incidence of Botrytis infection in tomato, with an optimum at 15 °C [60].

A number of studies have also demonstrated lower leaf temperatures when using LEDs instead of HPS lamps [58]. Leaf temperatures exceeding the ambient air temperature create air movement within the canopy, thus removing humidity from the boundary layer of the leaf and supplying CO_2 to the boundary layer. Leaf temperatures higher than the ambient air temperature also eliminate the risk of condensation on the leaf surfaces at dew point temperatures close to the ambient air temperature.

When producing plants in closed environments (i.e., plant factories), high leaf temperatures can be a problem [61]. However, in greenhouse production, leaf temperatures during winter are often sub-optimal due to losses of radiant heat through the greenhouse roof. The need for supplementary lighting typically arises during periods of the year where the greenhouse also needs supplementary heating due to low outdoor temperatures. In addition, increased light intensities should typically be accompanied by higher ambient temperatures [62].

3.2. Effects of Ultraviolet (UV) Light

The amount of ultraviolet (UV) light emitted by light fixtures affects the conditions for microbial growth on leaf surfaces. Greenhouse-covering materials normally filter out a large proportion of the UV light, making the greenhouse a UV-deficient environment. In particular, conventional glass panes filter out most UV light, whereas some plastic films have good transmittance of both UV-A and, in some cases, UV-B light [63–65]. Conventional greenhouse HID fixtures normally emit negligible amounts of UV light, but it is possible to supply UV light by using UV lamps [48].

3.3. Effects of Far Red (FR) Light

At the other end of the light spectrum, far-red (FR) light (710–850 nm) and particularly the red-to-far-red ratio (R:FR photoequilibrium) of light perceived by phytochromes can strongly affect the conditions for the leaf microbiota via physiological processes affecting plant architectural development, flowering, photosynthesis, plant nutrition, and plant tolerance to biotic and abiotic stresses [58,66]. The R:FR ratio varies within the day (e.g., from 0.6 at the beginning and end of the day to 1.0–1.3 at noon) and it is strongly reduced within the canopy (e.g., to 0.03). Greenhouse-covering materials, such as FR-absorbing plastic film, also impact R:FR ratio (e.g., increasing it from 1.0 under natural light up to 5.7) and plant development [67,68].

The spectral distribution of the light also has direct effects on photosynthesis and, thereby, the availability to microbes of carbon sources within the leaf and on the leaf surface. The blue and red parts of the spectrum are generally considered more efficient for photosynthesis than the yellow and green parts [69]. However, more recent research suggests that green light with its better penetration contributes significantly to photosynthesis in the deeper layers of the canopy [70]. Using light sources emitting just red and blue light is, therefore, not recommended [71,72].

4. Plant-Mediated Effects of Light on the Leaf Microbiota

Light is one of the most important environmental factors affecting plant growth, development, and metabolite content. Light within a broad spectrum range (400–700 nm) is essential for plant photosynthesis, plant growth, and crop productivity, while specific light spectra trigger different intracellular processes via diverse photoreceptors that modify gene expression, metabolism, plant morphology, and functions [58,73–75]. Figure 3 summarizes plant processes affected by light that can be targeted to promote beneficial phyllosphere components, contributing to greenhouse crop

productivity and plant resilience to abiotic and biotic stresses. Modifications in plant architecture, plant morphology, and plant physiology processes will then directly or indirectly impact the leaf microclimate, such as leaf moisture and temperature, as well as habitat resource availability (e.g., carbon, nitrogen, and phosphorus compounds) for the phyllosphere microbiota. However, plant–light interactions are often plant-species-dependent.

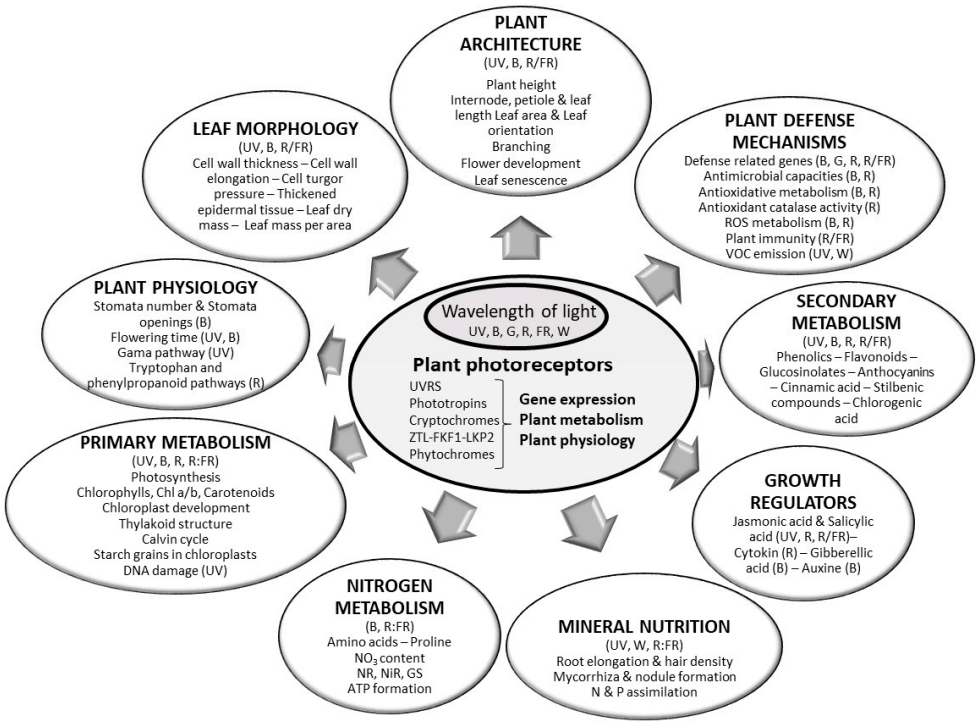

Figure 3. Plant processes affected by light that can be targeted to promote beneficial phyllosphere components, contributing to greenhouse crop productivity. (*Illustration: M. Dorais*).

4.1. Plant–Light Interactions

4.1.1. Plant Architecture and Leaf Morphology

Modulation of light spectra (e.g., R:FR ratio) to control plant architecture and leaf morphology is a well-known technique used by producers of ornamental plants to improve the shape and appearance of their plants, while assimilation lighting (400–700 nm) of vegetables improves crop productivity. However, both these artificial lighting regimens modify the canopy microclimate and plant structure. Blue light controls cell elongation and is an essential signal for the plant to adjust its growth to the surrounding light conditions [75]. Although light responses in horticultural crops differ between genotypes, enhanced amounts of UV light generally increase the thickness of the leaf cuticle [64], which in turn strengthens plant resistance to attacks from fungal pathogens [65,66]. However, for other species and under other exposure conditions, UV radiation can increase plant susceptibility to fungal pathogens [67,68]. A reduction in stem elongation as a result of UV exposure is often observed in greenhouse crops [76], which in turn modifies the plant microclimate. For example, UV-A and blue light increase shoot length and internode length in cucumber, but have the opposite effect on tomato and no effect on rose, while UV-A reduces stem length in rose and internode length in poinsettia [77–81]. Similarly, enrichment of natural and/or HPS light with blue and red light limits stem length in ornamental crops [82]. In combination, UV-B and blue light reduce leaf area in cucumber, leafy vegetables, and rose, while UV-B in combination with red light increases leaf area of pepper compared with monochromatic red light [56,80,83–85]. Blue light also increases leaf mass area, leaf and stem thickness, and shoot dry mass in cucumber [79,86,87], but reduces shoot dry mass in leafy

vegetables [56,84], whereas UV-B increases leaf thickness in lettuce [85]. Plant responses to a light spectrum may be within a small wavelength interval. For example, it has been shown that 430–450 nm gives a greater leaf and stem growth increase in green perilla than 455–470 nm [88]. A combination of blue, red, and far-red light increases dry matter in cucumber and tomato compared with HPS lamps, particularly at a low blue:red ratio [89,90]. Exposure to UV light also alters epicuticular wax, which protects the plant against pathogen invasion [91]. Additionally, it induces morphological changes in trichomes of leaves [92]. Branching is often promoted by UV-B and blue light, while flowering induction, precocity, and duration are species-dependent. Furthermore, elevated parts of far-red light (lowered R:FR ratio) increase elongation of plants due to greater internode elongation [93], while a high R:FR ratio results in plants with a compact growth habit [58], creating a more shaded and moist leaf surface due to slower air movements within the canopy. However, plant ability to respond to R:FR ratio (e.g., via phytochromes PHYA, PHYB) is variety- and species-dependent. Leaf expansion can be promoted or inhibited by FR light [93,94], which may be related to competition for resources between the leaf and stem growth or auxin-induced cytokinin breakdown in leaf primordia. A low R:FR ratio may also decrease leaf mass per area and leaf duration, and cause leaf hyponasty and solar leaf tracking. Reduced branching in many species due to inhibition of bud outgrowth via phytohormones (i.e., auxin, strigolactones, cytokinins, ABA) has been observed under a low R:FR ratio. Flowering of many crops is accelerated under a low R:FR [58], but this varies according to the species [95].

4.1.2. Photosynthesis

Plant growth and metabolite accumulation depend on photosynthesis, which is suboptimal at very weak [96] or excessive light intensity [97]. Light intensity and light quality both have a very strong impact on plant photosynthesis, while daylength may affect the plant circadian clock and primary metabolism via cumulative carbon biomass. Plants modulate their photosynthesis pigments to the prevailing light spectrum and intensity. Although species-dependent, the chlorophyll (chl) content and the chl a/b ratio usually increase with blue light [77,86,98]. For different species, blue and red light increase the plant content of carotenoids, such as lutein and β-carotene, while UV may reduce it [84,89,99–101]. Blue light increases photosynthetic activity when used together with other wavelengths, but reduces it when used alone [77,84,86], whereas UV-B decreases plant photosynthesis efficiency [102]. Studies of several specific wavelengths (from 405 to 700 nm) on photosynthesis of tomato, lettuce, and petunia plants have revealed higher photosynthesis with the blue region (range 417–450 nm) and red region (range 630–680 nm) than the green region (501, 520, 575, 595 nm) [103]. A blue and red light combination allows for higher photosynthetic activity than monochromatic light of either, which can be harmful for plants [104,105]. Opening of the stomata, which are a natural entry point for leaf microorganisms, is driven by blue light, although red light also promotes stomatal opening. Blue light is also involved in chloroplast movement within the cell to increase photosynthetic ability under different light conditions. An increased number of stomata and length of palisade tissue cells have been observed under blue light compared with red or green light [87]. Higher numbers of grana lamellae and more stacked thylakoid membranes have been observed in cucumber grown under low blue light radiation [98]. Blue light also prevents accumulation in the chloroplasts of starch grains, which block the incoming light. In addition to its effect on leaf area, leaf orientation, and leaf branching, thereby modifying crop photosynthesis, a low R:FR ratio may reduce stomatal conductance, stomatal density, chlorophyll content, chloroplast development, thylakoid structure and protein composition, and the activity of some enzymes of the Calvin cycle [58]. As FR light negatively affects root hair density, mycorrhizal colonization, and ATP formation, the R:FR ratio influences plant mineral nutrition. Moreover, a low R:FR ratio promotes nutrient allocation to the shoot at the expense of roots [58].

4.1.3. Primary and Secondary Metabolism

The light spectrum also influences the accumulation of plant primary and secondary metabolites [106]. For example, accumulation of soluble sugars, starch, soluble protein, and polyphenols

is higher when crops are grown under monochromatic red or blue than white light [107–113], which may impact the phyllobiome. Indeed, the phyllosphere microbiota uses leaf surface resources, such as amino acids, carbohydrates, and organic acids, passively leaked by plants [114]. A combination of red, blue, and white light enhances soluble sugar and nitrate concentrations in basil plants [115]. However, a low R:FR ratio downregulates the activity of the key enzymes involved in nitrogen assimilation (nitrate reductase, nitrite reductase, and glutamine synthase), which may impact cell metabolism [58]. Blue light and mixtures of red, blue, and green light increase ascorbic acid accumulation in leafy vegetables [84,116,117], while UV-A may reduce ascorbic acid content [118]. Anthocyanin leaf content is usually promoted by UV-A, UV-B, and blue light [75]. In particular, UV-A, blue, and red light increase the anthocyanin level in leafy vegetables, while green light reverses blue-light-induced anthocyanin accumulation [94,118–120]. Sulfur-containing secondary metabolites, such as glucosinolate, which can protect the plant against predation and pathogens, may also be promoted by blue light or a mixture of red, blue, and green light [121–123]. The R:FR ratio also impacts accumulation of phenolics in different species [115,124]. In addition, light affects the synthesis, profile, and emission of volatile organic compounds (VOCs) by plants, which increases plant attractiveness to plant parasitoids and orientation of predators [124,125]. Release of VOCs from leaves increases when they are exposed to UV, white light, or a low R:FR ratio, although this effect may be species-specific.

4.1.4. Plant Defense Mechanisms

Light, such as UV-B, affects several plant hormones, notably jasmonate (involved in response to attack by necrotrophic pathogens) and salicyclic acid (involved in response to attack by biotrophic microbial pathogens), that coordinate the plant immune response to environmental stresses [66]. Blue light also induces pathogenesis-related gene expression [126], while red light induces salicylic acid content and expression of salicylic-acid-regulating *PR-1* and *WRKY* genes in pathogen-inoculated cucumber plants [127,128]. On the other hand, a low R:FR ratio resulting in high plant population or plant shading may affect plant immunity, which has been linked in some species to reduced transcription of salicylic-acid-responsive genes or to decreased jasmonate sensitivity and reduced biosynthesis of tryptophan-derived secondary metabolites [129,130]. In particular, a low R:FR ratio inhibits salicylic acid and jasmonic-acid-mediated disease resistance in *Arabidopsis* plants [130,131]. Furthermore, a low R:FR ratio may induce high levels of gibberellin and auxin, which are involved in internode elongation, while gibberellin and ethylene are implicated in petiole extension [58,132].

Light spectrum has a strong effect on the antioxidant properties of horticultural plants [109,110,133–136]. For example, UV-B light can cause plant DNA damage, resulting in a cascade of protective events, such as flavonoid synthesis and expression of chalcone synthase genes and photolyase genes [75]. However, UV-B may have no effect or may reduce flavonoid accumulation in some species [100]. Compared with white light, blue and red light increase the activity of various reactive oxygen species (ROS)-scavenging enzymes and reducing substances (reduced glutathione (GSH) and ascorbic acid (ASA)) [137], which play an important role in plant defense mechanisms against plant pathogens in species such as tomato [138]. In tomato, blue light promotes leaf accumulation of proline, polyphenolic compounds, and antioxidants, and ROS scavenger activities, which might be partly related to inhibition of gray mold disease. On the other hand, red- and green-light-treated tomato plants have been shown to exhibit lower proline content [110]. Light of specific wavelengths (UV, blue, red) also promotes synthesis of stilbenic compounds compared with white light [46,139,140]. Stilbenes, which are low-molecular-weight phenolics, play an important role in plant defense responses by overcoming fungal pathogen attacks [110,141]. Similarly, red light induces cinnamic acid synthesis and increases plant resistance via the tryptophan and phenylpropanoid pathways [142]. Moreover, high gamma-aminobutyric acid levels are promoted by plant UV-B exposure, resulting in higher bacterial diversity in the phyllosphere and lower plant resistance to fungal disease [143]. On the other hand, plants exposed to a low R:FR are more sensitive to pathogens due to changes in leaf morphology, chlorophyll content, and downregulation of jasmonate and salicylic acid [58,66].

4.2. Direct Plant–Microbe Interactions Induced by Light

Physiological changes in the plant caused by different light qualities have a major impact on the phyllosphere microbiota. In sunflower plants grown under HPS lamps, white LEDs, or red:blue (80:20 ratio) LEDs, it has been shown that the fungal communities are more affected than the bacterial communities by different light qualities [51]. Although that study did not investigate whether the effects on the microbiota are direct or indirect, other research (presented below) suggests that the effect is often caused by physiological alterations in the plant.

4.2.1. Leaf Leachate

The availability of organic carbon as a prerequisite for microbial colonization in the phyllosphere has been surveyed in several reviews [28,30,36,37]. Microbial phyllosphere communities are limited first by availability of organic carbon sources and only second by availability of organic nitrogen sources [37]. Although the phyllosphere is often characterized as a habitat lacking in nutrients, leaves exude a wide range of carbon compounds, such as carbohydrates, amino acids, organic acids, and sugar alcohols [30]. The availability of these nutrients is highly dependent on photosynthesis, which in turn is highly dependent on light quality and intensity. Leaching of nutrients across the leaf surface occurs in the presence of liquid water, but can also be increased by the phyllosphere microbiota through microbially produced biosurfactants [28]. The most abundant compounds in leachate are photosynthetic compounds, such as glucose, fructose, and sucrose [144,145]. However, the glandular trichomes, which are important sites of leaching, also secrete proteins, oils, secondary metabolites, and mucilage [36,146–148]. Use of red, or red plus blue, LED light has been shown to increase the amount of soluble sugars and proteins in a wide range of plants, as mentioned earlier. This physiological change in the plant, caused by choice of artificial light source, changes the carrying capacity of the leaf and governs which microorganisms are favored by the increase or decrease in compounds specific for their survival. While the microbial community as a whole can utilize a wide range of compounds for colonization and growth, a single microbial species can be quite specific in its metabolism. For example, substrate profiling of *Pseudomonas syringae* has shown that this bacterium uses a restricted number of sugars, organic acids, and amino acids [149]. This implies that, with increased knowledge of the metabolic patterns of specific microorganisms, light could be used as a management tool, not only for plant growth, but also in order to favor microbial species of importance.

4.2.2. Light-Triggered Pathways

While light within the spectral wavelength from 300 to 800 nm can have an effect on plant growth and development, red light seems to have the largest impact relating to defense against microbial pathogens by triggering both plant defense genes and hormonal pathways. The composition of the phyllosphere microbial community is driven by a wide range of factors. However, the plant immune system is thought to play a major role in shaping the community composition. It has been shown that triggering of the salicylic acid pathway leads to reductions in both diversity and population sizes of endophytic bacteria, while epiphytic bacteria are not measurably affected, and that *Arabidopsis thaliana* plants deficient in the jasmonic acid pathway host a greater epiphytic bacterial community diversity [150]. For horticultural species, red and green light have a positive effect on tomato seedlings, with less infection by *Pseudomonas cichorii* JBC1 compared with white light or dark treatment [151]. A similar result was observed for cucumber plants infected with powdery mildew (*Sphaerotheca fuliginea*) and exposed to red light, while no effect was found under green light [128]. This decrease in infection level was related to the upregulation of the defense gene phenylalanine ammonia lyase (*PAL*) and pathogenesis-related protein 1a (PR1a) under red or green light treatments [151]. This leads to the conclusion that light significantly alters the activation of defense-related genes. Differences in results between different studies, however, imply that use of light treatment for control of pathogens has to be customized to the plant–pathogen system.

Downregulation of the salicylic acid and jasmonic acid pathways when plants compete for light against other plants (i.e., a low R:FR ratio) means that the plants become more sensitive to pathogen attack, as shown with *Botrytis cinerea* in *Arabidopsis* [129]. This plant response to a low R:FR ratio has also been reported elsewhere [130]. A low R:FR ratio can be avoided in the greenhouse by spacing out the plants, allowing for more light to enter the lower parts of the canopy. While a high R:FR ratio leads to pathogen susceptibility, use of red light leads to activation of the salicylic acid pathway-mediated systemic acquired resistance (SAR) in *Arabidopsis*, making the plant more resistant to *Pseudomonas syringae* pv. *tomato* [152]. A study on rice has also shown increased resistance to disease, specifically *Bipolaris oryzae*, when rice plants are subjected to red light, with an increasing level of resistance being demonstrated with an increasing dose of red light [142]. However, in rice plants, disease resistance is mediated through the tryptophan and phenylpropanoid pathways, and not by the salicylic acid pathway as suggested in *Arabidopsis*.

4.2.3. Changes in Leaf Physiological Characteristics

Leaf surface properties have a large impact on the establishment and survival of phyllosphere microorganisms [36]. The thickness of the adaxial epidermis layer has been found to be one of the three most important leaf attributes governing the plant–microbe system, where an epidermal layer thicker than 20.77 µm results in lower microbial colonization rates [153].

Changes in epicuticular wax layers and epidermal tissues, in particular, can emerge as consequences of subjecting plants to different light qualities [127]. A difference in effect on leaf morphological characteristics depending on light quality has also been seen between sun-exposed and shaded leaves, with sun-exposed leaves having a thicker cuticle than shaded leaves [154]. It has been suggested that UV-B radiation is the factor responsible for a thicker cuticular wax layer on the leaf surface, with e.g., increased irradiation with UV-B, increasing the wax layer in cucumber, pea, and barley by 25% [155]. A thicker wax layer prevents, or at least delays, pathogen infection, especially for fungal pathogens that use direct penetration as a means of infection. In a detached leaf assay using soybean, it has been shown that disease severity of soybean rust (*Phakopsora pachyrizi*) is negatively correlated with amount of epicuticular wax and that the leaves at the top of the canopy have a higher amount of wax than leaves in middle and lower levels [91].

5. Light-Quality-Mediated Effects on the Leaf Microbiota

Biofilm is a natural way for microorganisms to co-exist on a surface or interface, enclosed in a exopolysaccharide matrix produced by the microbes themselves [156]. Regardless of whether the microorganisms concerned are human or plant pathogens or microbes used as biocontrol agents (BCA), their efficiency depends on how well they establish and survive on a surface. Environmental factors, such as temperature, humidity, and light, are important factors that shape microbial communities. Biofilms protect microbes against antibiotics and harsh environmental factors and maintain nutrient availability [156]. To date, bacteria have been regarded as non-phototrophic organisms and insensitive to light. Only phototrophic bacteria were known to react and respond to light. However, light has been shown to affect bacterial decisions to change from a planktonic single cell motile lifestyle to a surface-attached lifestyle in a multicellular community as biofilm [157]. This is supported by the fact that some of the photo receptor proteins also control mechanisms involved in biofilm formation and these receptors are linked to the GGDEF and EAL protein domains, which are involved in the transition from a planktonic to a sessile life style [158].

5.1. Leaf Pathogens

Irrespective of their growing site (nature, field stand, or controlled environment), plants can be attacked by plant diseases. Amongst the fungal pathogens, grey mold (*Botrytis cinerea*), powdery mildew (*Podosphaera* spp.), and downy mildew (*Peronospora* spp.) are often reported in major greenhouse crops, such as tomatoes, cucumber, strawberries, and ornamental plants (e.g., grey mold in tomato [110];

powdery mildew in strawberries (Fragaria X ananassa), [159,160] and roses (*Rosa* spp.) (*P. pannosa*) [49]; downy mildew (*Pseudoperonospora cubensis*) in cucumber [47]). Different bacterial species, for example *Xanthomonas* spp. and *Pseudomonas* spp., can also cause severe damage to plants [50,161,162]. The idea of using light as a strategy to control leaf pathogens is not new, e.g., 20 years ago, greenhouse experiments with blue-pigmented photoselective sheets showed that these inhibited sporulation and colonization of downy mildew on cucumber [47]. Light regulates biofilm formation, attachment, motility, and virulence of both fungal and bacterial plant pathogens (Table 2), factors which are crucial for establishment on the leaf surface.

Table 2. Summary of different microorganisms, the photoreceptor/s they contain, and the physiological response to different light spectra.

Organism	Light Quality	Wave Length (nm)	Photoreceptor	Photoreceptor Architecture	Effect	Ref.
Acinetobacter baumannii	Blue	415	BLUF, LOV	EAL-GAF-GGDEF-LOV-GGDEF	Biofilm formation, metabolism, virulence	[163]
Bacillus amylolique-faciens	Red Blue	645 458	LOV	LOV-STAS	Swarming motility, biofilm formation, antifungal activity	[164]
Botrytis cinerea	Blue	405	PHY, LOV	PAS-GAF-PHY-HK LOV-PAS, short LOV	Inhibited mycelial growth, virulence	[165]
Pseudomonas aeringiunosa	Blue	405	PHY, LOV	PAS-GAF-PHY-kinase Short LOV	Survival, virulence factors	[166]
P. cichorii	Green	NI	LOV	HATP-HisKA-LOV-RR	Siderophore and phytotoxic lipopeptide production	[167]
P. syringae	Red/Far-red Blue White	680/750 470	PHY, LOV	PAS-GAF-PHY-kinase HATP-HisKA-LOV-RR Short LOV	Decreased swarming motility	[50]
Podosphaera pannosa	Blue	420–520			Reduced germination and conidia formation	[49]
Serratia marcescens	Blue White	470			Antibiotic production	[168]
Sphaerotheca fuliginea	Red	NI [1]			Disease suppression	[127]
Staphylococcus aureus	Blue	405, 470			Growth	[169]
Trichoderma harzianum	Blue	NI			Induced gene expression of *phr1*	[170]
Xanthomonas axonopodis	Light/ dark		PHY, LOV, BLUF	PAS-GAF-PHY-PAS LOV-HK	Motility, adhesion, biofilm formation	[161]
Xanthomonas campestris	Red/ Far-red Blue White	NI	PHY, LOV	PAS-GAF-PHY-PAS HATP-HisKA-LOV-RR	Growth, motility	[162]

[1] NI = not indicated.

Implementation of LED light as an environmentally friendly tool in indoor production has increased in recent years. In this context, it has been shown that light quality has an impact on growth and development of the conidia of *P. pannosa*, which causes powdery mildew disease on roses [49]. Blue light (420–520 nm) was observed to decrease conidial growth in that study, while far-red light (575–675 nm) had the opposite effect, i.e., it increased pathogen growth. However, the same study could not demonstrate a reduction in conidia development when roses were grown with 18 h daylight complemented with 6 h of blue or red light [49]. Exposure to blue light has been demonstrated to increase the antioxidant and polyphenolic content in tomato plants and thereby control the attachment

of *Botrytis cinerea* [110]. Moreover, a study on cucumber plants indicated that light quality affects incidence of powdery mildew and expression of defense-related genes [127]. Bacterial infection in plants can also be suppressed by light of different quality, e.g., green light reduces phytotoxic lipopeptide and siderophore production in *Pseudomonas cichorii*, which might affect survival of this plant pathogen [167]. In *Xanthomonas* spp., light quality has a negative impact on motility, and, thus, host colonization [161,162]. Swarming motility in *Pseudomonas syringae* is suppressed under light conditions (white, blue, red plus far-red) compared with dark treatment, but different light qualities (white, blue, red plus far-red) also have differing effects, with blue light promoting swarming motility [50].

5.2. Microbial Biocontrol Agents

As is the case for deleterious microorganisms, such as pathogens, plant-health-promoting biocontrol agents are also affected by the light regime provided under controlled conditions. A successful BCA should exhibit (i) several antifungal or antibacterial (antagonistic) properties, (ii) ability to spread on the plant surface after application, and (iii) capacity to establish in existing biofilms. However, very little is known about how different light regimes affect BCA when it comes to establishment in the plant canopy. One study demonstrated that, in *Serratia marcescens,* antibiotic pigment prodigiosin concentration in bacterial cells decreases under white and blue light (470 nm) conditions, but growth is not affected [168]. The same study showed that red and far-red light have no effect on the concentration of prodigiosin [168]. Another study [170] isolated the photolyase gene (*phr1*) from *Trichoderma harzianum*, a common soil fungus used as a BCA against phytopathogenic fungi [171] and investigated expression of *phr1* when exposed to blue light. Their results showed that gene expression of photolyase (phr1) is induced very rapidly in both mycelia and conidiphores, and that light induces development of pigmented resistance spores as well as expression of *phr1* [159]. *Bacillus amyloliquefaciens* is another BCA often used in horticulture against soilborne and post-harvest pathogens. In this species, all light quality except blue light affects growth, swarming motility, biofilm formation, and antifungal activity positively [164]. Red light (645 nm) increases biocontrol efficacy and colonization of BCA on fruit surfaces, while blue light (458 nm) has a negative impact on growth, motility, and biofilm formation [164].

5.3. Molecular Interactions

For many years, only phototrophs were considered to respond to light in order to find an optimally illuminated environment for harvesting solar energy [172]. However, the increasing number of papers on bacterial whole genome sequencing has now revealed a large number of putative genes coding for photoreceptor proteins distributed among several taxa. During bacterial evolution, bacteria have evolved photoreceptor proteins that can detect visible light in the environment, in order to protect themselves from damaging UV radiation [172]. Bacteria can also respond to light by switching between the single cell planktonoic lifestyle and the multicellular life style of bacterial communities known as biofilms [173]. Six classes of photoreceptors have been identified in the bacteria photosensory system, based on their structure of their chromophore. These are: cryptochrome, rhodopsin, phytochrome, photoactive yellow protein (PYP), light oxygen voltage receptor protein (LOV), and blue light sensing protein using FAD (BLUF) [172].

Cyclic di-guanosine monophosphate (c-di-GMP), a key role player in the bacterial signal transduction system, regulates bacterial behaviors, such as biofilm formation, virulence, and production of adhesion proteins [174]. It is produced from diguanylate cyclases (DGCs) and is then broken down to 5′-phosphoguanylyl-(3′-5′)-guanosine (pGpG) through hydrolysis by phosphodiesterases (PDEs). Of these, DGCs are associated with the GGDEF photoreceptor domain and PDEs with the EAL domain [175]. Both are involved in light-sensing processes, together with the LOV and BLUF domains [157,158].

Two photoreceptors are involved in blue light sensing in plants and in microbes, namely LOV and BLUF. Both these protein domains have been shown to control attachment, multicellularity, production of adhesion proteins, and virulence (Table 2). Therefore, blue light has been shown to be a promising candidate to combat bacterial and fungal infections in medical science. For example, several studies have reported bactericidal effects on *Pseudomonas aeruginosa* and *Staphylococcus aureus* when exposed to 405 nm light [169]. Furthermore, exposure of methicillin-resistant *Staphylococcus aureus* to 405 and 470 nm light has been shown to bring about a significant reduction in growth [176]. Similar findings have been made in a study on bacteria involved in clinical infections, where both planktonic and bacterial biofilm proved susceptible to blue light, with significant reductions in viability for all tested strains [177]. Blue light exposure in horticulture has been shown to have negative effects on both bacteria and fungi (Table 2). However, blue light conditions have been reported to enhance disease attack caused by the fungus *Sphaerotheca fuliginea* [127]. In *Pseudomonas syringae*, it has been demonstrated that light decreases the swarming motility and that this is regulated by bacteriophytochrome and LOV-HK (Light Oxygen Voltage-Histidine Kinase) [50]. In the plant pathogen *Xanthomonas axonopodis*, LOV is activated by blue light and may be involved in the control of bacterial virulence [161].

All these studies show that light quality has an impact, one way or another, on the behavior of microorganisms. For this to occur, the organism needs to perceive and transmit the signal, which is done by photosensory proteins. As mentioned above, the BLUF and LOV photoreceptor domains are involved in blue light sensing. The LOV domain belongs to the PAS (Per-ARNT-Sim) superfamily connected in a network of conserved domains (GGDEF, EAL, PAS, GAF (c**G**MP-specific phosphodiesterases, **a**denylyl cyclases and **F**hlA), HK, HisKA (histidine protein kinases), and STAS (sulfate transporter and anti-sigma factor antagonist)) [178]. A very extensive bioinformatics study of photoreceptors across kingdoms has been conducted [178]. According to their data for bacteria, different groups of protein architecture dominate across different phyla. Within the Proteobacteria, the combinations EAL-GAF-GGDEF-LOV-PAS and EAL-GGDEF-HAMP-LOV-PAS are the most abundant architectures of photoreceptor proteins, together with HATP-HisKA-LOV. Within the Firmicutes, the combination STAS-LOV is the most common architecture. Across all investigated phyla [169], there are short (150 aa) LOV proteins that can stand alone with a highly conserved motif of five amino acids with a cysteine at position 54 that forms the cysteine–flavin assembly during the LOV photocycle, which is also involved in sensing blue light [179]. The BLUF domain control functions such as photosystem synthesis, biofilm formation, and both swarming and twitching motility [180,181]. It is widespread across the bacterial kingdom, but in anoxygenic and plant-associated species BLUF proteins are not as abundant as LOV proteins. For example, BLUF proteins have not been recovered from Firmicutes, Chloroflexi, or EuArchaea, which instead only carry genes encoding LOV proteins [158]. In many species, BLUF seems to act alone. In *Escherichia coli*, *Klebisella pneumoniae*, and *Magnetococcus* sp., BLUF is combined with EAL [158,173]. The BLUF-EAL protein YcgF in *E. coli* acts as a direct anti repressor in a blue light response, which in turn activates other proteins important for biofilm formation [182].

Photoactive yellow protein (PYP) is a blue light sensor protein first discovered in halophilic purple phototrophic bacteria [183]. With the increasing number of whole genome sequencing studies, there have been reports of PYP proteins in bacteria other than phototrophs, mostly within in Proteobacteria [184]. Photoactive yellow protein is small, only 125 amino acids long, and is often present as part of the PAS domain [185]. Studies have shown that PYP serves as a photosensor for negative phototaxis [186].

6. Discussion

Day length, light intensity, and light quality affect plant architecture and morphology, plant growth, and plant development. Lighting is a crucial tool for greenhouse horticulture and plant production in controlled environments. It plays a central role for the microclimate in the crop stand, e.g., temperature and relative humidity. Light-related effects on the crop can be direct or indirect. The potential of the plant microbiome to influence crop growth and development and the ability to

withstand abiotic and biotic stress has been repeatedly highlighted [28,187,188]. Microbiome-based tools and prediction models have been suggested [187]. Despite the importance of light and illumination in greenhouse horticulture (Figures 2 and 3) and the increasing interest in the phyllosphere microbiome, light-associated factors are only occasionally receiving the attention they deserve in experimental settings or in applied contexts (Figure S3).

At present, knowledge on the influence of light, especially light quality, on phyllosphere–microbe interactions resembles a random mosaic in an otherwise vast field, as previous studies have tended to consider either the behavior of a specific target organism or expression of a light-related gene or receptor, or big metagenomics datasets with limited functional information. To bring phyllosphere studies within the scope of ecological principles and theories, the presence and also the function of microorganisms need to be highlighted. However, it is of utmost importance to discriminate between mechanisms and processes that can be abstracted and those that cannot. In this context, the pathosystem deserves particular attention. In the present literature review, we focused on interactions between selected plant and human pathogens and light quality and considered some of the molecular mechanisms involved. However, in planta studies are rare and often lack sufficient characterization of the growing environment. To understand the interactions between light, especially light quality, plant/crop stand, and microbiome, critical experimental conditions and physiological processes need to be continuously monitored. This requires such disciplines as crop physiology and microbiology/plant pathology to engage with common phenotypic platforms.

The composition and amount of microbially available organic nutrients, a suitable microclimate with respect to temperature and humidity/moisture, and niches providing shelter from deleterious irradiation and unintentional predation are key properties of a suitable microbial phyllosphere environment. Thus, mechanisms affecting these key properties will decide colonization density and composition. Light quality directly or indirectly influences many of these processes (see Figure 2). In this regard, nutrient sources available in the phyllosphere can serve as an example. A few studies have examined the composition and quantity of leaf lysates [144,189,190] and interactions between organic nutrients and microbial proliferation [145]. Two recent studies considering almost 400 different nutrient sources have indicated that the nutritional preferences of some phyllosphere colonizers change in the presence of different light qualities [52,53]. The utilization of compounds themselves, but also their use within carbon, nitrogen, or sulfur metabolism, is moderated in the presence of different light qualities, and, consequently, the secondary metabolites are also moderated. At present, the focus has been on light qualities of major importance for plant photosynthetic activity (blue, red) in such studies. To the best of our knowledge, the impact of other light spectra on microbial utilization of nutrients has not been investigated. Such information, as well as transcriptomics data on the phyllosphere microbial community, needs to be provided, along with plant and environmental monitoring data, in order to reveal the impact of light quality and to assess the potential of light as a tool for habitat management.

The deleterious impact of certain light qualities on plant pathogenic fungi has been investigated since the late 1990s [47], with particular focus on commercially important pathogens (e.g., grey mold and powdery and downy mildew). In contrast to studies on bacteria, these fungi studies primarily concentrate on the disease incidence, while rarely analyzing underlying molecular mechanisms. Such information is needed for non-pathogenic and pathogenic fungi (for endophytic and ectophytic phyllosphere bacteria) in order to implement light quality strategies into greenhouse horticulture and controlled environment production systems. Overall, studies on new, non-chemical control strategies for leaf pathogens are of substantial interest in the development of sustainable horticultural indoor production systems.

It has been suggested that the phyllosphere be used as a platform for the testing of ecological principles [77]. Different literature reviews [187,188] have proposed ecological theories and principles relating to the phytobiome. Given a multidisciplinary and systematic approach, the theories and principles depicted in Table 3 could contribute to a better understanding of light–phyllosphere interactions in greenhouse horticulture and to the development of sustainable growing practices.

Table 3. Ecological theories and principles of interest to use in light-assisted phyllosphere studies.

Theory/Principles	Modes of Action	Potential Research Questions	Light Spectra of Interest
Niche theory			
Priority effects	Pre-emptying of space and resources by the first arriving species	Heterotrophic utilization of leaf lysates/organic compounds and their impact on secondary metabolites	B [1], G [2], Y [3], R [4], R:FR [5]
Competitive dominance	Dominance due to efficient resource use under prevailing stable conditions		
Niche partitioning	Coexistence	Light-quality-associated impact on biofilm community structure Bacterial–fungi symbionts/Suitable microbe combination Plant–microbe and microbe–microbe compatibility	B, G, Y, R, R:FR B, R:FR
Storage effect	Coexistence of microbes within the same ecological community	Storage effects in non-phototrophic non-spore-forming bacterial leaf colonizers	B, G, Y, R, R:FR
Niche modification	Invasion of leaf interior	Light quality as a driver towards an endophytic lifestyle	B, G, Y, R, R:FR
	Biofilm formation	Light quality as a driver for switch from planktonic to biofilm lifestyle	
Complementarity	Diversification of resource requirements leading to less competition between interspecific than conspecific neighbors	Mechanisms of coexistence under various light qualities	B, G, Y, R, R:FR
Resource-based interactions			
Resource competition		Heterotrophic utilization of leaf lysates/organic compounds and their impact on secondary metabolites in microbial aggregate communities	B, G, Y, R, R:FR
Phenotypic plasticity	Formation of different phenotypes under various conditions	Complementary microbe pair for stimulating plant growth and pathogen control	B, R:FR

[1] B = blue, [2] G = green, [3] Y = yellow; [4] R = red; [5] R:FR = red:far red.

Supplementary Materials: The following are available online at http://www.mdpi.com/2311-7524/5/2/41/s1: Figure S1: Relative spectral output from three different light sources: HPS lamps (Philips Master 400 W), fluorescent tubes (Sylvania TLD840 58 W), and LED lights (Valoya B150, spectrum AP673L 144 W). Figure S2: Number of publications considering the topic 'supplementary lighting in greenhouse horticulture'. The literature search considered three keyword combinations, namely artificial lighting*greenhouse*horticulture (102 publications), supplementary lighting*greenhouse*horticulture (201 publications), and artificial illumination*greenhouse* horticulture (21 publications) and was performed in Web of Knowledge (WoK) using all WoK databases (Web of Science Core Collection, Biosis Citation Index, CABI, Current Contents Connect, Data Citation Index, Derwent Innovation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index, Zoological Record). The literature search was restricted to 30 years (1988–2018) (dates of performance: November 19 and 20, 2018). Figure S3: Description of light conditions in study output considering the keyword combination "phyllosphere*greenhouse*horticulture". The search was restricted to 30 years (1988–2018) and entailed 27 publications conducted under greenhouse, climate chamber, or polytunnel. The survey was performed in Web of Knowledge (WoK) using all WoK databases (Web of Science Core Collection, Biosis Citation Index, CABI, Current Contents Connect, Data Citation Index, Derwent Innovation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index, Zoological Record). Values indicate percentage of studies stating or avoiding information on environmental conditions (relative humidity, temperature), light conditions (day length, light intensity) and use of supplementary lighting, as well as control of description of light spectrum in the plant stand. The proportion of publications discussing the impact of light on the results obtained was also determined (3.9% corresponds to one publication) (dates of performance: November 19 and 20, 2018).

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