

<https://helda.helsinki.fi>

The benefits of informed management of sunlight in production greenhouses and polytunnels

Robson, T. Matthew

2022-07

Robson , T M , Pieriste , M , Durand , M , Kotilainen , T K & Aphalo , P J 2022 , ' The benefits of informed management of sunlight in production greenhouses and polytunnels ' , Plants, people, planet , vol. 4 , no. 4 , pp. 314-325 . <https://doi.org/10.1002/ppp3.10258>

<http://hdl.handle.net/10138/345979>

<https://doi.org/10.1002/ppp3.10258>

cc_by_nc_nd

publishedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

OPINION

The benefits of informed management of sunlight in production greenhouses and polytunnels

T. Matthew Robson¹  | Marta Pieristè¹  | Maxime Durand¹  |
Titta K. Kotilainen^{1,2}  | Pedro J. Aphalo¹ 

¹Research Programme in Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of Biological and Environmental Science, University of Helsinki, Helsinki, Finland

²Natural Resources Institute Finland, Turku, Finland

Correspondence

T. Matthew Robson, Research Programme in Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of Biological and Environmental Science, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland.

Email: matthew.robson@helsinki.fi

Societal Impact Statement

The effective management of light is beneficial for growers of plants in greenhouses, polytunnels and under cloches. The materials and structures used to construct these environments often create light-limited conditions for crops and change the spectral composition of sunlight they receive. Combining practical measures, drawn from knowledge of plant photobiology, allows growers to monitor, forecast and optimise conditions in their growing environment according to its geographical location and the crop grown. Improved management of light through these measures could be expected to improve food quality and yield, and potentially reduce use of energy, water and pesticides.

Summary

Horticultural production in greenhouses and in polytunnels expands the viable geographic range of many crop species and extends their productive growing season. These semi-controlled growing environments buffer natural fluctuations in heat, cold and light and hold potential to improve food security with a low environmental footprint. Over the last decade, technological advances in cladding materials, smart filters, photo-electric cells for energy production and LED lighting have created opportunities to improve the light environment within these structures. In parallel, there have been large advances in plant photobiology, underpinned by progress in identifying the mechanisms of photomorphogenesis and photoprotection, mediated by plant photoreceptors and their interactions, across regions of the spectrum. However, there remains unexploited potential to synthesise and transfer knowledge from these fields to horticulture, particularly with respect to tailoring the use of sunlight to specific locations and production systems. Here, we systematically explain (1) the value of modelling and monitoring patterns of sunlight to allow for informed design of the growth environment; (2) the means of optimising light conditions through selection of materials and structures; (3) the requirements of different crop plants in terms of the amount and spectral composition of light that will benefit yield and food quality; (4) the potential to combine this knowledge for effective management of the

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *Plants, People, Planet* published by John Wiley & Sons Ltd on behalf of New Phytologist Foundation.

sunlight; and, finally, (5) the additional benefits these actions may bring to growers and society at large, beyond the crops themselves, in terms of water use and energy efficiency.

KEYWORDS

controlled plant production, energy efficiency, food security, horticulture, photobiology, solar radiation, ultraviolet radiation

1 | INTRODUCTION

A great challenge of the 21st century is how efficiency of food production can continue to be improved, in terms of efficient resource and energy use, while maintaining yields along with better quality food with high nutritional value (FAO, 2014; IPCC, 2019; Ort et al., 2015). A suite of approaches will be needed to meet this challenge, including improvements in the crop varieties available to farmers and growers, integrated pest management and plant nutrition through soil science. In addition to biological aspects, there is great scope to manipulate the environment under semi-controlled conditions to approach the optimum growing conditions for specific crops (Bergstrand, 2017; Poel & Runkle, 2017). Greenhouses, polytunnels (typically walk-in structures used with a wide range of crops, potentially over large areas; sometimes called 'high tunnels') and cloches (plastic coverings of less than a metre high that are employed commercially, e.g., over strawberries or salads, or in small-scale production; sometimes called 'low tunnels') are used to provide seasonal or year-round protection from undesired fluctuations in temperature, moisture, wind, irradiance and extreme weather events. The application of new technologies in supplemental lighting, to produce a spectrum of radiation which better matches that used by plants in photosynthesis and provokes desirable changes in plant form, is already reaping benefits through more energy-efficient crop production (Nelson & Bugbee, 2014). Further, in greenhouses and polytunnels, by tuning the amount and spectral composition of sunlight reaching plants, the benefits of supplemental lighting can be maximised (Zheng et al., 2019). The purpose of manipulating the spectral irradiance reaching plants growing in greenhouses, polytunnels and under cloches depends on whether they receive predominately insufficient or excessive radiation. In protected cropping systems, the ambient solar radiation is filtered through cladding materials (by which we refer to greenhouse window-panes, panels and climate screens, plus plastic coverings over polytunnels to reduce heat transfer or light transmitted). Well-informed selection from the variety of structural and cladding materials available, which selectively filter regions of the solar spectrum, should allow growers to make the best use of sunlight according to a crop's requirements (Folta & Carvalho, 2015; Kotilainen et al., 2018).

Even modest alterations in the configuration of structures used in production environments can affect shading and change the spectral quality (i.e., the composition of spectral irradiance received by plants). These changes will have consequences for plant growth rate,

morphology, physiology, phenology (the timing of plant development) and biochemistry; thus, nutrition, yield and desirability of the crop (Alvarado et al., 2020; Folta & Carvalho, 2015). The application of this knowledge gives scope for greater efficiency in light and energy use by tailoring a production environment to meet the particular requirements of a crop at a given location (Impron et al., 2007). Typically, mapping spectral irradiance in the production environment has not been prioritised by growers, because relatively little attention has focussed on the opportunities to improve productivity by manipulating the light environment compared with other environmental factors. This lack of awareness could be overcome by better dissemination of materials and information from researchers and manufacturers to groups representing farmers and growers. To date, most manufacturers and greenhouse consultants concentrate on thermal characteristics for regulating temperature when designing plastics or shading materials for production environments, giving little attention to their spectral attenuation in those regions utilised by photosynthesis and in perception of light, that is, photosynthetically active radiation (PAR) 400–700 nm (similar to that region of the spectrum visible to people) and ultraviolet radiation (UV-B 290–315 nm and UV-A 315–400 nm). Beyond the lack of awareness of how spectral quality affects crops, this deficiency largely occurs because the instruments required to measure spectral irradiance accurately have until recently been relatively expensive. Furthermore, we lack reliable estimates of the economic benefits gleaned from improving the light environment as these are highly crop and location specific. All these issues mean that the transfer of knowledge from biosciences to plant production has been slow. Growers remain to be convinced about the cost-benefit trade-off of purchasing devices and require training to interpret measurements spectral irradiance, or the investment required to tailor the lighting of their production environments to specific purposes.

Here, focussing on optimising the use of sunlight, we suggest several steps towards addressing this shortfall in knowledge transfer among researchers, growers and manufacturers: (1) better characterisation of the light environment within production environments (greenhouses and polytunnels); (2) illustration of how substituting one material for another in a given environment can improve the quality of produce; (3) application of existing knowledge of plants' photobiology to guide decisions about spectral composition; (4) combining the preceding steps involving characterisation of environments, substitution of materials and crop responses to spectral quality, to create simple models that forecast how growers might be able to adjust the

environment to suit their needs; and, finally, (5) we consider which production environments and end-users might most benefit from these approaches and the potential consequences for food security and energy use.

2 | GET TO KNOW THE LIGHT ENVIRONMENT

Greenhouses, shade-houses and polytunnels are typically employed either to protect from excessive sunlight and its detrimental effects on plants when combined with high temperatures; cold temperatures; excessive moisture from rainfall; extreme weather events such as intense hail or dust storms; to increase control over fluctuating conditions in the growing environment; or a combination of these factors depending on the season and geographical location. At the most basic level, simulation models can be used to map the light environment within a growing environment, enabling growers to pre-emptively identify hot-spots of light and excessively shaded areas. Where conditions allow, modern commercial greenhouses are designed to create homogeneous illuminated areas for growing plants and reduce the effects of structural shading, which can otherwise cause large reductions in received irradiance (Figure S1). The optimal height and shape of greenhouses, as well as their orientation, differs according to latitude and accounting for these factors can increase crop yield up to 17% (Impron et al., 2007; Sahdev et al., 2019; Xu et al., 2020). Thus, accounting for these effects at the planning stage should ensure that the selected structure is appropriate for a given location and crop, or later will allow a grower to correctly select and position supplemental lighting (Figure 1). The north-south versus east-west orientation of greenhouses and polytunnels will determine the daily pattern of sunlight received (Sethi, 2009; Ting & Giacomelli, 1987). North-south ridges maximise annual ingress of sunlight whereas east-west orientation allows most light to enter in winter (14% more at 50°N), which is critical at high latitudes. Additionally, mapping radiation can highlight the effect of dirt and algae hence the need for more frequent cleaning of greenhouse windows, as well as the effect of surrounding buildings, topography and aging materials on the spectral quality as well as the total irradiance (Casilla, 2013; von Zabeltitz, 2011). Beyond these effects, the influence of surrounding vegetation is not usually considered when planning the position of greenhouses, but radiation reflected from vegetation as far as 50 m away can affect the red to far-red ratio of incident radiation (660 nm/730 nm), particularly during periods of low solar elevation (Kotilainen et al., 2020). The location of structures within the growth facility (e.g., benches, vents and irrigation), the display angle and thickness of glass or plastic cladding, can also be optimised according to geographic location—which determines sun angle and day length—balance of radiation and heat, and spectral regions requiring targeted enhancement or attenuation (Figure 1).

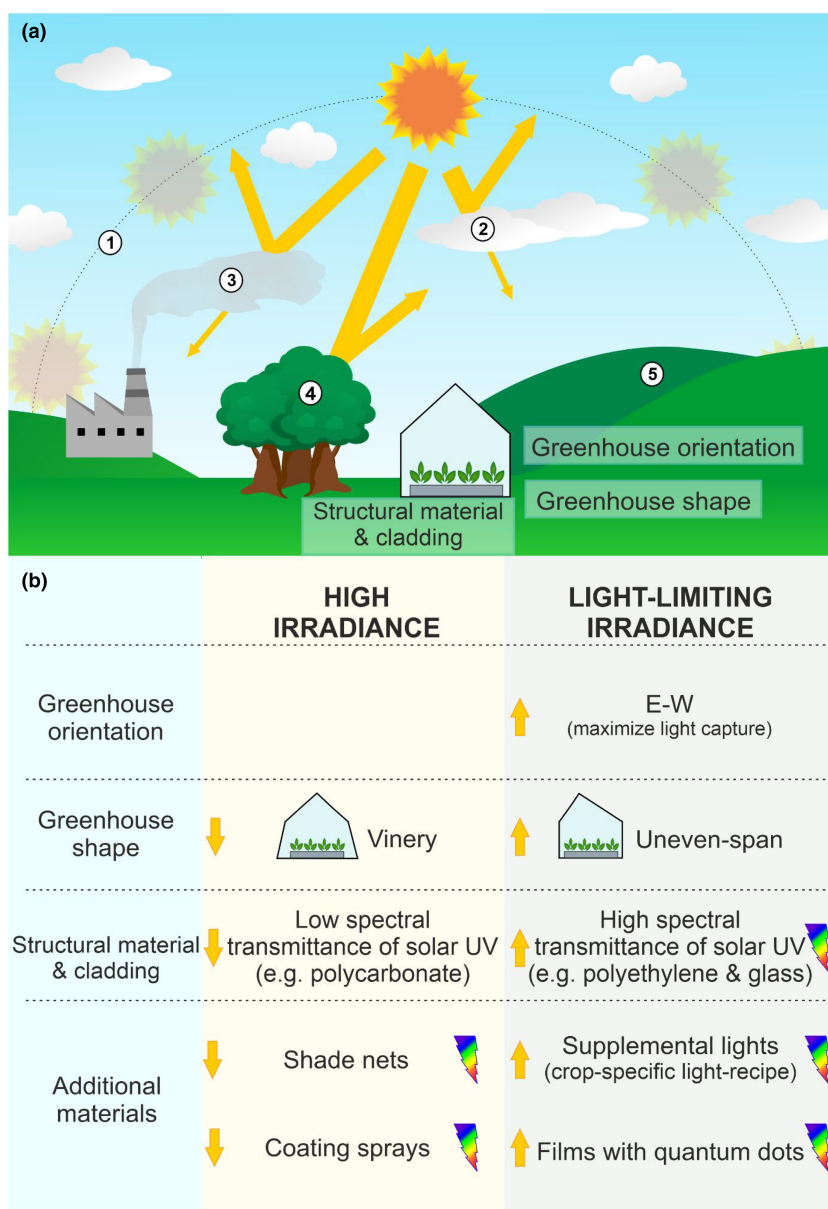
Sensors for PAR can provide growers with instantaneous readings in units of energy or photons (Watts or $\mu\text{mol m}^{-2}$), a daily light integral (DLI) or total over the day. Unfortunately, less interpretable

information on light is often still gathered using sensors that measure units of foot-candles or lux that do not directly scale with plant responses. Measuring spectral irradiance is useful to identify variation across production environments in those specific regions of the spectrum involved in photomorphogenesis, photoprotection and shade avoidance responses. This will facilitate the assessment of whether supplemental lighting is required, or a change in the structure itself, cladding used or crop grown, to make better use of a particular growth space. Local sensors or remote monitoring using meteorological services should feed into greenhouse climate control systems. This allows the amount of supplemental light needed over the whole day to be calculated, which enables more efficient use of energy than instantaneous feedback or repeated daily patterns of illumination. In Denmark, such an approach has achieved savings of up to 5% by reducing the reliance on supplemental lighting so lowering the costs of electricity (Kjaer et al., 2011, 2012). While a variety of such systems are becoming available to growers, the high initial financial outlay and expertise required for individual growers to map their production environments and install smart monitoring systems provides a barrier to their uptake. The provision of general guidelines on the effects of latitude and materials for given combinations of location and structure would help users make informed management decisions. To be of practical value, estimates are also needed of the increased market value of crops facilitated by improving the light environment for plants in growth facilities.

3 | THE MATERIALS USED IN PRODUCTION ENVIRONMENTS MAKE A DIFFERENCE TO SPECTRAL QUALITY

Two contrasting approaches towards the efficient use of sunlight are required depending on whether plants are light limited or receive excess solar radiation. At high-latitude locations, where for much of the year growth is limited by low irradiances, it can be advantageous to maximise the transparency and spectral range transmitted by greenhouse materials to allow more UV radiation and blue (400–500 nm) light to reach the plant (Quintero-Arias et al., 2021; Snowden et al., 2016; Ting & Giacomelli, 1987; Wargent, 2017) (Figure 1). The optical properties of the glass or plastic material are important, as are their thickness and durability, and whether double or single layers/panels are used. These considerations represent a compromise between transparency and heat retention (Ting & Giacomelli, 1987). At locations where plants often receive excessive sunlight, as well as reducing the total irradiance, growers can use filters or spray-on coatings that increase the diffuse fraction of sunlight (Riga & Benedicto, 2017) or absorb and reflect in the infra-red region (El-Bashir et al., 2019; Timmermans et al., 2020). These type of ‘spectral filters’ also allow for improvements in the management of temperature in greenhouses and polytunnels, releasing heat at low temperature and absorbing heat between 30°C and 40°C to reduce excessive warming (Timmermans et al., 2020). An alternative approach is to incorporate photovoltaic cells on the roof of

FIGURE 1 (a) Site-specific environmental and structural factors that determine the spectral radiation entering a greenhouse or polytunnel. The yellow arrows represent solar radiation passing through atmosphere, and their changes in thickness suggest its partial attenuation by various features. (1) Geographical location, latitude and elevation, the time of the year and of the day determine the sun angle above the horizon (dotted arc). (2) Clouds and (3) pollutants and gases in the atmosphere attenuate and scatter radiation and can affect spectral quality: for example, by increasing B:R and R:FR ratios. (5) The surrounding vegetation and (4) the topography of the area both provide shade and alter the R:FR ratio, especially when the sun is close to the horizon. Greenhouse features (orientation, shape, height, structure and cladding materials) affect the transmittance of sunlight inside. (b) These factors can be modelled prior to selection of a structure or mapped in existing structures to optimise the light conditions of high or low irradiances according to crop selection. Greenhouse shape (Sethi, 2009; Xu et al., 2020) and orientation (Sethi, 2009) can be adjusted to maximise (yellow arrows up) or reduce (yellow arrows down) light capture. Materials with high spectral transmittance in particular regions (multi-coloured zigzag symbols) can be selected for the greenhouse construction and cladding where required for to enhance specific aspects of crop quality (Sahdev et al., 2019)



greenhouses that absorb blue and green light (500–600 nm) to generate electricity (Cossu et al., 2020; Loik et al., 2017). At locations where the light is limiting to photosynthesis or unevenly obscured by the greenhouse structure, in principle, enhancement of photosynthesis could be achieved via technological approaches that shift the spectral composition to enrich those wavelengths of PAR that give the greatest photochemical yield of photosynthesis (Figure 1) (Loik et al., 2017). This approach has been explored using films containing dyes or quantum dots that selectively absorb short wavelength regions but reemit some of this energy as red light (600–700 nm) (Parrish et al., 2021; Ravishankar et al., 2021). In practice, the effectiveness of this trade-off between spectral regions in maintaining or improving yield remains to be established across a variety of crops and environments, particularly as this approach also assumes that the reductions in blue light and UV radiation have a minor effect on plant photobiology. This is not necessarily the case in light demanding crops, such as aubergine (*Solanum melongena*) and red lettuce (*Lactuca*

sativa), where a loss of yield (23% lower yield and 20% lower DW with less anthocyanin content, respectively) is reported under energy-saving films designed to lower the heat load in warm environments, but which also substantially reduce the PAR and UV radiation transmitted inside production environments (Chavan et al., 2020; Ravishankar et al., 2021). While these emerging technologies hold potential to allow greater flexibility in manipulating the solar radiation reaching plants in light-limiting and excessive light/heat conditions, the optimal spectral quality will depend on the amount of natural light and the crop and variety grown. In addition, this approach requires an appreciation of the roles of different spectral regions affecting yield and produce quality, as well as plant pests/pathogens and their management.

Beyond intentional manipulation of the spectral composition, the optical properties of shading material used to reduce the heat load and reduce excessive solar radiation will also greatly affect the spectral composition of radiation beneath them (Ilić & Fallik, 2017). This is

particularly important when considering the shade avoidance syndrome (SAS) mediated largely by the red to far-red ratio but also interacting with blue light and UV responses (Ballaré & Pierik, 2017). In most high-light scenarios, growers will look to reduce the irradiance without triggering shade avoidance in the crops beneath shade nets or screens (Alokam et al., 2002). Maintaining a high red to far-red ratio, and avoiding depletion of blue and UV radiation, overcomes the need to use chemical growth regulators to keep plants compact by inhibiting the shade avoidance responses (Latimer & Whipker, 2012; Palonen et al., 2011; Paul et al., 2005).

In addition to structural and cladding materials, the latitude, day length and time of year of crop growth will all affect the input of radiation to greenhouses and polytunnels. They need to be included as interacting factors when considering how to optimise the light environment for a particular purpose. Likewise, the height of the structure and of the plants grown within production environments will create vertical gradients in total irradiance and spectral quality (Ting & Giacomelli, 1987). In fruit crops, like tomatoes (*Solanum lycopersicum*), foliage in the canopy causes a large reduction in UV radiation and PAR reaching close to the ground, potentially detrimental to plant health and ripening of fruits (Shin et al., 2021). Mapping or modelling vertical gradients in spectral irradiance provides the information required to plan countermeasures that can be implemented to diminish their effect (Cossu et al., 2018). Such measures would include making the sunlight transmitted into the production environment more diffuse and the judicious positioning of supplemental inter-row lighting (Figure 1).













Diffusive glass, plastic and spray-on coatings scatter the sunlight incident on cladding materials. Under a clear cloudless sky, where irradiance is high and the proportion of diffuse radiation low, they enable a more even vertical and horizontal distribution of radiation through the day in the crop canopy (at least 10% more light in the lower canopy; Shin et al., 2021), while retaining a similar overall absorption of radiation by leaves in the canopy (Li et al., 2014; Timmermans et al., 2020). A more uniform light distribution across leaves is typically beneficial to those crop canopies with high leaf area index, which implies more self-shading (Li & Yang, 2015), and helps curtail photoinhibition and responses to high temperatures associated with strong direct radiation (Burgess et al., 2015). This results in better canopy light use efficiency by enhancing whole-canopy photosynthesis without altering the amount of absorbed radiation (Li et al., 2014; Shao et al., 2019; Shin et al., 2021), which may benefit overall productivity, evident as increased fresh weight of harvested fruits (up to 10% for tomato and cucumber) and through enhanced produce quality due to more even ripening (Hemming et al., 2014; Li et al., 2014; Li & Yang, 2015). Improvements in light and heat distribution can also be made by considering the optical properties of the ground surface or mulches over the growing medium. As well as affecting energy balance, a red reflective mulch may accelerate fruit ripening increasing anthocyanin content in peach and tomato, compared with a mulch that absorbs light, and can increase total yield: for example, of tomatoes by 16% (Decoteau et al., 1989; Lee et al., 2021).





4 | PHOTOBIOLOGICAL RESPONSES OF PLANTS CAN BE UTILISED TO PRODUCE BETTER CROPS

Traditional greenhouse and polytunnel production environments typically shift the solar spectrum away from the shorter wavelengths. However, photobiology research has found UV-B and UV-A radiation and blue light can benefit crops grown under glass or plastic, and in controlled conditions (Figure 2): for example, by improving the form and colour of many herbs and salad crops (Stutte & Edney, 2009). High-value short-rotation crops such as these often provide a good return on the investment required to create a favourable growing environment, for example, by replacing traditional glass and plastic with alternatives that transmit more short-wavelength UV radiation and blue light. These spectral regions serve plants as cues to stimulate the production of secondary metabolites, improving defence against herbivores and pathogens, and increasing colouration of the crop (Robson et al., 2015). Flavonoids, anthocyanins and tannins are favoured, for example, in berry production, as they give flavour and colour, and are perceived to be healthy (Tomás-Barberán & Espin, 2001). It is desirable to increase tannins in tea bushes grown under shade cloth (to reduce the heat load) and flavonoids in soft fruits, which are often grown in polytunnels in northern Europe (Xu et al., 2014), and likewise tomatoes among those crops grown under cloches in southern Europe (Casilla, 2013) (Figure 2).

Manipulating spectral quality affects a suite of photoreceptor-mediated responses that can be tailored to fit tomato growers' requirements, for example, reduced whole plant water use through changes in branching and stomatal closure or increased biomass/flower production, without the use of plant hormones (Kotiranta et al., 2015; Williams et al., 2022). Transmittance of UV radiation is responsible for improving fruit quality (c +12% weight, yield c +41%) and shelf life (firmness, slower desiccation and decay) of tomatoes (Ibrahim et al., 2018). Additionally, UV-A radiation can lead tomato plants to produce larger leaves and increased leaf area (+17%–21%), improving canopy light interception in production environments (Zhang et al., 2020). Analysis of the canopy architecture of tomatoes under a variety of different spectra found that the most-open canopy, allowing greater penetration of light to deeper canopy layers, was achieved using a spectrum enriched in green light but that canopy photosynthesis was most efficient when this canopy received a spectrum enriched in red light (c 10%–17% increase in gross photosynthesis at the crop level compared with green and blue light; Dieleman et al., 2019). Recent studies in cucumbers (*Cucumis sativus*) have found that UV-A radiation helps maintain a compact morphology without reducing yield (Jeong et al., 2020; Qian et al., 2020). Both UV-A and UV-B radiation lead to the upregulation of desirable flavonoids (c 20% and 40% more respectively in leaves after 5 days; Qian et al., 2019), although the beneficial effects of UV-B radiation are strongly conditioned by the composition of the PAR received (Palma et al., 2020). Perhaps the most visually apparent effects of spectral composition are found in red lettuce, which even at high elevations in the Andes displays increased colouration and anthocyanins content

FIGURE 2 The consequences of controlling spectral quality in horticultural environments. UV radiation and blue light increase phenolic compounds, known to enhance colour, taste, nutritional value and shelf life of various crops (Qian et al., 2019; Quintero-Arias et al., 2021; Robson et al., 2015; Tomás-Barberán & Espín, 2001). UV radiation, blue and green light may also increase fruit-set as a consequence of an increased pollination (Chittka & Wells, 2004; Dag, 2008; Toni et al., 2021). Blue and green light regulate water use efficiency (WUE) through stomatal opening (Kotiranta et al., 2015). Pathogens can be inhibited or promoted by UV radiation and blue light (Egan et al., 2020; Fountain et al., 2020; Merfield et al., 2019; Paul et al., 2005). Crop canopy architecture can be altered to maximise light capture through UV radiation, blue, green, red and far-red light and their ratios (Ballaré & Pierik, 2017; Dieleman et al., 2019; Jeong et al., 2020; Latimer & Whipker, 2012; Palonen et al., 2011; Paul et al., 2005; Qian et al., 2020). Plant flowering time and the number of flowers are affected by red light and the red-to-far-red (R:FR) ratio (Gautam et al., 2015; Lopez et al., 2020; Meng & Runkle, 2020). Regulating UV radiation and blue light (Mao et al., 2021) and the R:FR ratio (Zou et al., 2019) can affect biomass accumulation, for example, in leafy greens. UV radiation promotes hardening of seedlings prior to transplanting (Hernandez Velasco & Mattsson, 2020). The symbols in each box indicate the direction of the effect of each spectral region: that is, '+' (increase, enhance or accelerate) or '-' (decrease, impair or delay), where both symbols are present the direction of the effect differs according to the environment, crop plant or specific pathogen

	Crops	UV	BLUE	GREEN	RED	FAR RED
Colour		+	+			
Taste		+	+			
Nutritional value		+	+			
Shelf life		+				
Fruit set and pollination		+	+	+		
WUE		+	-	+	+	
Protection against pathogens		+/-	+/-			
Plant/canopy architecture		+	+	+	+	-
Number of flowers					+	
Flowering time			+		+/-	+/-
Plant biomass		+/-	+		+	+
Hardening		+	+			

 = Tomatoes & fruit
  = Leafy greens
  = Flowers
  = Tree seedlings

(2.9 times more) in UV transparent greenhouses without a significant loss of productivity (Quintero-Arias et al., 2021).

At high latitudes, it is often necessary to precondition young tree seedlings to reduce transplant shock from production environments to planting outdoors. The use of 380 nm UV-A LEDs can be effective in hardening Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) seedlings, but the trade-off between the energy consumed and reduced mortality means that UV irradiation is not always cost effective (Hernandez Velasco & Mattsson, 2020). The use of plastic or glass cladding that is UV transparent might be expected to aid the hardening of tree seedlings under most circumstances (outside high latitudes in winter) by allowing more of the UV region of sunlight to reach the plants prior to their transfer outdoors. This should also allow them to be propagated at higher density without loss of fitness. Manipulation of the spectral quality in this way enhances photoprotection by reducing photoinhibition on transfer outdoors (Hernandez Velasco & Mattsson, 2020; Klem et al., 2015). More of this type of research into plant responses to changes in spectral quality and shading is required

to better understand how to fine-tune photomorphogenic responses by shifting spectral composition either with filters or supplemental lighting or both. To date, research has not addressed how these 'light recipes' are moderated by the changes in day length and natural signals that are specific to location, time of year and the sort of material used in greenhouses (Figure 2).

Pollinating insects are used in greenhouses to increase the proportion of fruit set in several crops, tomato being the most prominent (Toni et al., 2021). Bumblebees use UV, blue and green wavelengths to navigate (Chittka & Wells, 2004), so the attenuation of UV radiation by most polycarbonate hinders their navigation. This impaired flower visibility for pollinators decreases their effectiveness, and low solar irradiances during winter exacerbate this issue. The consequences can include reduced bumblebee colony sizes and smaller clusters of tomatoes or misshapen raspberries, although sometimes bees have been found to adjust to the lack of UV radiation avoiding a decline in pollination (reviewed by Dag, 2008, and Kendall et al., 2021). Greenhouse climate computers can wirelessly link the

release of pollinators from colonies to the intensity of incoming sunlight, so extending their life span by reducing the unproductive flying time of bees (van Velden, 2013). Further refinements of this system allowing response to dynamic changes in spectral quality at the relevant wavelength may also improve the efficiency of pollination. However, the improved visibility produced by UV transparency of greenhouse panels and most standard cladding materials represents a compromise between promoting the activity (orientation and take-off stimulus) of beneficial insects versus that of pests and pathogens. Standard cladding materials cut at 360 nm, while spectral filters and nets employed for specific horticultural purposes may cut out more of the UV-A to 380 or 400 nm, or alternately may transmit all of the solar UV radiation down to 290 nm (Fennell et al., 2019). Spectrally selective UV-attenuating filters over soft fruit crops have successfully been used to restrict populations of *Drosophila* (*D. suzukii*), which use wavelengths below 405 nm to navigate, to less than 50% of those under UV-transmitting filters (Fountain et al., 2020). Likewise, meshes that attenuate UV radiation are more effective than those that are UV transparent in reducing potato blight outdoors, presumably due to reduced sporulation of *Alternaria solani* and *Phytophthora infestans* (Merfield et al., 2019) (Figure 2).

Although the benefits of using materials that block UV radiation have often been thought to outweigh the benefits of UV transmittance when considering pest and pathogen control, in reality, responses are highly pest and crop-species specific (Fennell et al., 2019; Paul et al., 2005). These responses have been insufficiently studied to draw general conclusions as to the cost-benefit balance of employing panels and cladding materials transmitting solar UV radiation in greenhouses and polytunnels as part of an integrated pest and pollinator management system (Egan et al., 2020; Paul et al., 2005). The balance of evidence suggests that the benefits of transmitting UV radiation to production environments in terms of producing desirable, tasty and robust plants, and fruits with longer shelf-life, usually outweigh negative effects such as fungal sporulation and the aforementioned herbivore vision and take-off response triggered by UV-A radiation. Drawbacks of UV radiation entering the production environment must also be accounted for, including the accelerated photodegradation of equipment and material, and the need for workers to take precautions against sunburn and protect their eyes. Eventually, the provision of a spectrum of solar radiation that could be altered through the stages of plant development and according to pollinator requirements and integrated pest/pathogen management would be desirable (Figure 2).

5 | COMBINING KNOWLEDGE OF MATERIALS, LOCAL ENVIRONMENT, AND PHOTORECEPTOR RESPONSES TO INFORM THE DECISIONS TAKEN BY GROWERS

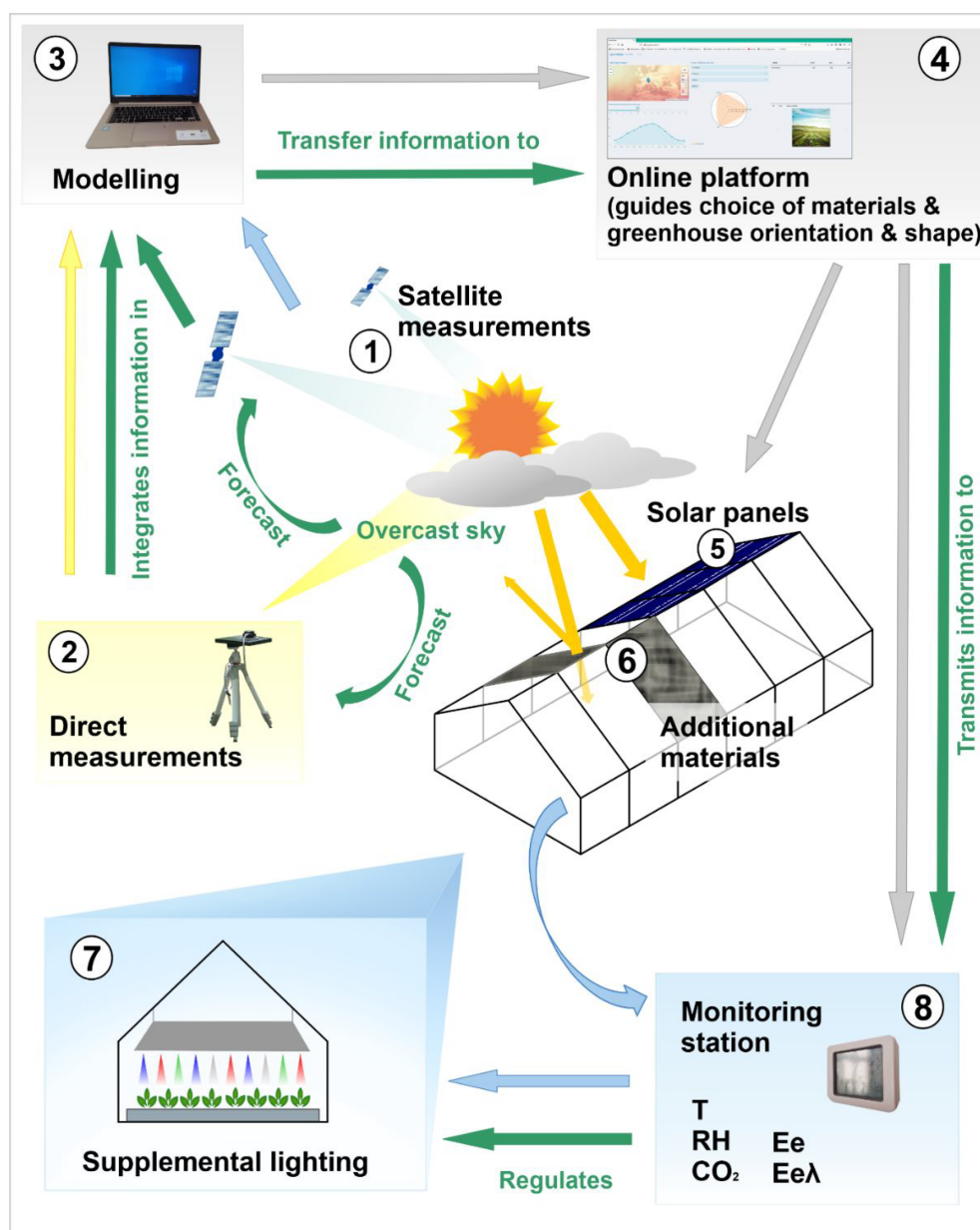
In agriculture, information about the site-specific solar irradiance has been used to improve yield forecasts (Mitchell & Sheehy, 2018; Trmka et al., 2007), for example, to model the protein content of wheat (*Triticum aestivum*) by combining real-time monitoring of the weather

with assessment of nutrient status (Shu et al., 2021). This approach has potential to be applied in greenhouse horticulture, if models that give the spectral radiation at the bottom of the atmosphere, incident on the greenhouse structure, can be extended to include the filtering effect of cladding, so allowing the irradiance received by the plants within to be calculated (e.g., Shin et al., 2021). Radiative transfer models are generally used to explore how solar radiation interacts with the constituents of the atmosphere (Lindfors et al., 2009; Liou, 2002). Modelling radiative transfer within canopies is an active but challenging area of research, because plants provide a complex, heterogeneous and non-randomly distributed array of absorptive surfaces, unlike most atmospheric particles (Durand et al., 2021). Nevertheless, radiative transfer models could be expanded to also simulate the spectral irradiance at the bottom of the atmosphere and then through greenhouses and polytunnels using a transfer function. The library of radiative transfer models, libRadtran (Emde et al., 2016), which accounts for the patterns of absorption and scattering of H₂O, O₃, O₂, CO₂, NO₂ and aerosols depending on their optical properties the sun angle, and so forth, is well suited for this purpose (Mayer, 2009; Mayer & Kylling, 2005). Validating such models against spectrometer measurements within the production environment would let them be extended to simulate how changing location and filter material affects the spectral quality and total radiation received within a production environment. Hence, a modelling approach could be developed, which circumvents the need to make exhaustive measurements of spectral irradiance. Such a model could be coupled by site-specific data on solar spectral irradiance and a database of greenhouse and polytunnel cladding materials (Robson & Kotilainen, 2018 [dataset]) and put into an accessible interface such as <https://agronomous.shinyapps.io/spectramap/> to provide real-time information to growers.

6 | OPPORTUNITIES FOR OPTIMISATION OF THE LIGHT ENVIRONMENT FOR PLANT PRODUCTION

Improvements in the efficiency of crop production are possible by optimising the light environment, which may reduce energy consumption, and through the manipulation of spectral quality, which may also allow reduced application of chemicals. These benefits could be particularly large in regions where temperature versus natural-light trade-offs are important, or where supplemental lighting is required in plant production. The greatest potential impact can be achieved if these advances are placed within a knowledge framework allowing disparate aspects of horticultural research and technology to be combined. For example, by using remote monitoring systems to track local and regional weather patterns, and modelling how external conditions feed back on temperature and light conditions within the production environments, better environmental regulation could be achieved using supplemental lights and dynamic filters to anticipate growing requirements. By utilising the internet of things, sensor data can be transmitted to a centralised database, implementing a smart horticultural system that can be controlled remotely by the grower (Figure 3). While an integrated system of this sort may initially be too expensive

FIGURE 3 An integrated system using technological solutions to optimise light conditions in the production environment. Monitoring of solar radiation through satellite data (1) and direct measurements (2) can improve radiation modelling (3). This information can be integrated in an interface for growers (e.g., <https://agronomous.shinyapps.io/spectramap/>) providing real-time information to a mobile device (4). This knowledge of the light environment assists in crop and even greenhouse choice. This may entail solar panels (5), filters/smart-screens (6) and supplemental lighting (7), all adjustable in real time to the accommodate changes in the light environment. Feedback from a monitoring station (8): temperature (T), relative humidity (RH), CO₂, total irradiance (E_e) and spectral composition (E_{eλ}). Green (regulation); yellow (direct detection); blue (remote monitoring); and grey (modelling) arrows show how the system works to regulate the growing conditions inside the greenhouse when conditions change



to implement outside of industrial-scale greenhouse production, automation and continued technological innovation should drive down these costs of over time, and the development of apps for use with mobile phones should allow for trickle down of this knowledge to individual growers.

Large fluctuations in sunlight available for plant growth in greenhouse environments and polytunnels create conditions requiring dynamic solutions to optimising the growing environment. Currently, diffusive spray-on coatings, which can be spectrally selective, are employed seasonally to avoid acute high irradiances, but these lack the short-term flexibility to adjust to daily weather conditions. Whereas, climate screens can be automatically deployed when conditions change, but must be coupled with expensive well-calibrated monitoring systems and be well maintained to function effectively (Berruto et al., 2008; Hernandez Velasco & Mattsson, 2020; Kotilainen et al., 2018). A more-elegant solution may be to use

cladding materials to manipulate the spectral composition in coordination with plant growth stages (e.g., transmitting UV during pollination, enhancing green light to create an open canopy or blue light for compact plants). Technical progress and reduced costs may eventually allow the employment of smart materials that actively adjust their transmittance properties to the light environment, becoming more absorptive during periods of high solar radiation and more transparent when light levels are low (Baeza et al., 2020; Timmermans et al., 2020). Such materials would allow spectrally differential attenuation to create favourable growth environments, so reducing the need for temperature control or supplemental greenhouse lighting.

We have highlighted the largely under-exploited potential to optimise the light environment in greenhouses and other production environments, which modify incoming sunlight to maximise plant growth and productivity, and the means to achieve this through effective monitoring, design and feedback systems. Combining knowledge

from photobiology, atmospheric sciences and plant ecophysiology gives scope to improve crop yield models and the business model of growers by matching the managed light environment at a given location to the crop grown. Selecting those materials that filter sunlight to produce the best spectral composition for a given location and time of year will allow for most efficient light use, where necessary complemented with strategic deployment of supplemental lighting and photovoltaic technology. Maximising yield and produce quality in this way will also increase energy efficiency and would reduce the environmental footprint from greenhouse crop production.

ACKNOWLEDGEMENT

This work was funded by the Academy of Finland grants to T.M.R., #304653 and #324555.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

The paper was conceived by T.M.R. and T.K.K. and written by T.M.R.; figures were created by M.D., M.P. and P.J.A. All authors edited the text and approved the final version.

DATA AVAILABILITY STATEMENT

Data sharing was not applicable—no new data were generated.

ORCID

T. Matthew Robson  <https://orcid.org/0000-0002-8631-796X>

Marta Pieristè  <https://orcid.org/0000-0001-6515-0833>

Maxime Durand  <https://orcid.org/0000-0002-8991-3601>

Titta K. Kotilainen  <https://orcid.org/0000-0002-2822-9734>

Pedro J. Aphalo  <https://orcid.org/0000-0003-3385-972X>

REFERENCES

- Alokam, S., Chinnappa, C. C., & Reid, D. M. (2002). Red/far-red mediated stem elongation and anthocyanin accumulation in *Stellaria longipes*: Differential response of alpine and prairie ecotypes. *Canadian Journal of Botany*, 80, 72–81. <https://doi.org/10.1139/b01-137>
- Alvarado, K. A., Mill, A., Pearce, J. M., Vokaet, A., & Denkenberger, D. (2020). Scaling crop production in low sunlight scenarios. *Science of the Total Environment*, 707, 136012. <https://doi.org/10.1016/j.scitotenv.2019.136012>
- Baeza, E., Hemming, S., & Stanghellini, C. (2020). Materials with switchable radiometric properties: Could they become the perfect greenhouse cover? *Biosystems Engineering*, 193, 157–173. <https://doi.org/10.1016/j.biosystemseng.2020.02.012>
- Ballaré, C. L., & Pierik, R. (2017). The shade-avoidance syndrome: Multiple signals and ecological consequences. *Plant, Cell and Environment*, 40, 2530–2543. <https://doi.org/10.1111/pce.12914>
- Bergstrand, K. J. I. (2017). Methods for growth regulation of greenhouse produced ornamental pot- and bedding plants – a current review. *Folia Horticulturae*, 29(1), 63–74. <https://doi.org/10.1515/fhort-2017-0007>
- Berruto, R., Busato, P., & Debenedetti, A. (2008). Retractable roof greenhouse systems for sloped areas: Comparison of two systems. *Acta Horticulturae*, 801, 441–448. <https://doi.org/10.17660/ActaHortic.2008.801.47>
- Burgess, A. J., Retkute, R., Pound, M. P., Foulkes, J., Preston, S. P., Jensen, O. E., Pridmore, T. P., & Murchie, E. H. (2015). High-resolution three-dimensional structural data quantify the impact of photo-inhibition on long-term carbon gain in wheat canopies in the field. *Plant Physiology*, 169(2), 1192–1204. <https://doi.org/10.1104/pp.15.00722>
- Casilla, N. (2013). *Greenhouse technology and management* (2nd ed., p. 335). CABI International. ISBN 978-1-78064-103-4. <https://doi.org/10.1079/9781780641034.0000>
- Chavan, S. G., Maier, C., Alagoz, Y., Filipe, J. C., Warren, C. R., Lin, H., Jia, B., Loik, M. E., Cazzonelli, C. I., Chen, Z. H., Ghannoum, O., & Tissue, D. T. (2020). Light-limited photosynthesis under energy-saving film decreases eggplant yield. *Food & Energy Security* 2020, 9, e245. <https://doi.org/10.1002/fes3.245>
- Chittka, L., & Wells, H. (2004). Color vision in bees: Mechanisms, ecology and evolution. In F. R. Prete (Ed.), *Complex worlds from simpler nervous systems* (pp. 165–191). The MIT Press. <https://doi.org/10.7551/mitpress/1994.001.0001>
- Cossu, M., Cossu, A., Deligios, P. A., Ledda, L., Li, Z., Fatnassi, H., Poncet, C., & Yano, A. (2018). Assessment and comparison of the solar radiation distribution inside the main commercial photovoltaic greenhouse types in Europe. *Renewable and Sustainable Energy Reviews*, 94, 822–834. <https://doi.org/10.1016/j.rser.2018.06.001>
- Cossu, M., Yano, A., Solinas, S., Deligios, P. A., Tiloca, M. T., Cossu, A., & Ledda, L. (2020). Agricultural sustainability estimation of the European photovoltaic greenhouses. *European Journal of Agronomy*, 118, 126074. <https://doi.org/10.1016/j.eja.2020.126074>
- Dag, A. (2008). Bee pollination of crop plants under environmental conditions unique to enclosures. *Journal of Apicultural Research*, 47(2), 162–165. <https://doi.org/10.1080/00218839.2008.11101444>
- Decoteau, D. R., Kasperbauer, M. J., & Hunt, P. G. (1989). Mulch surface color affects yield of fresh-market tomatoes. *Journal of the American Society for Horticultural Science*, 114(2), 216–219.
- Dieleman, J. A., De Visser, P. H. B., Meinen, E., Grit, J. G., & Dueck, T. A. (2019). Integrating morphological and physiological responses of tomato plants to light quality to the crop level by 3D modeling. *Frontiers in Plant Science*, 10, 839. <https://doi.org/10.3389/fpls.2019.00839>
- Durand, M., Matule, B., Burgess, A., & Robson, T. M. (2021). A method to identify and measure sunfleck properties from irradiance time series of fluctuating light in agricultural crop canopies. *Agricultural and Forest Meteorology*, 308-309, 108554. <https://doi.org/10.1016/j.agrformet.2021.108554>
- Egan, P. A., Dicks, L. V., Hokkanen, H. M. T., & Stenberg, J. A. (2020). Delivering integrated pest and pollinator management (IPPM). *Trends in Plant Science*, 25, 577–589. <https://doi.org/10.1016/j.tplants.2020.01.006>
- El-Bashir, S. M., Al Salhi, M. S., Al-Faifi, F., & Alenazi, W. K. (2019). Spectral properties of PMMA films doped by perylene dyestuffs for photo-selective greenhouse cladding applications. *Polymers*, 11(3), 494. <https://doi.org/10.3390/polym11030494>
- Emde, C., Buras-Schnell, R., Kylling, A., Mayer, B., Gasteiger, J., Hamann, U., Kylling, J., Richter, B., Pause, C., Dowling, T., & Bugliaro, L. (2016). The libRadtran software package for radiative transfer calculations (version 2.0.1). *Geoscientific Model Development*, 9(5), 1647–1672. <https://doi.org/10.5194/gmd-9-1647-2016>
- FAO. (2014). European Parliament resolution of 11 March 2014 on the future of Europe's horticulture sector—Strategies for growth (2013/2100(INI)). European Environment Agency Report. *Official Journal of the European Union* P7_TA(2014)0205 ISSN 1977-8449
- Fennell, J. T., Fountain, M. T., & Paul, N. D. (2019). Direct effects of protective cladding material on insect pests in crops. *Crop Protection*, 121, 147–156. <https://doi.org/10.1016/j.cropro.2019.04.003>

- Folta, K. M., & Carvalho, S. D. (2015). Photoreceptors and control of horticultural plant traits. *HortScience*, 50(9), 1274–1280. <https://doi.org/10.21273/HORTSCI.50.9.1274>
- Fountain, M. T., Badiie, A., Hemer, S., Delgado, A., Mangan, M., Dowling, C., Davis, F., & Pearson, S. (2020). The use of light spectrum blocking films to reduce populations of *Drosophila suzukii* Matsumura in fruit crops. *Scientific Reports*, 10, 15358. <https://doi.org/10.1038/s41598-020-72074-8>
- Gautam, P., Terfa, M. T., Olsen, J. E., & Torre, S. (2015). Red and blue light effects on morphology and flowering of *Petunia* × *hybrida*. *Scientia Horticulturae*, 184, 171–178. <https://doi.org/10.1016/j.scienta.2015.01.004>
- Hemming, S., Mohammadkhani, V., & van Ruijven, J. (2014). Material technology of diffuse greenhouse covering materials—Influence on light transmission, light scattering and light spectrum. *Acta Horticulturae*, 1037, 883–896. <https://doi.org/10.17660/ActaHortic.2014.1037.118>
- Hernandez Velasco, M., & Mattsson, A. (2020). Light shock stress after outdoor sunlight exposure in seedlings of *Picea abies* (L.) Karst. and *Pinus sylvestris* L. pre-cultivated under LEDs—Possible mitigation treatments and their energy consumption. *Forests*, 11, 354. <https://doi.org/10.3390/f11030354>
- Ibrahim, H. A., Abdullah, M. A. A., Hassan, N. M. K., & El-Batran, H. S. (2018). Effect of different levels of solar ultraviolet radiation on the vegetative growth, yield and quality of cherry tomatoes. *Bioscience Research*, 15(3), 2408–2415. Print ISSN: 1811-9506 Online ISSN: 2218-3973
- Ilić, Z. S., & Fallik, E. (2017). Light quality manipulation improves vegetable quality at harvest and postharvest: A review. *Environmental and Experimental Botany*, 139, 79–90. <https://doi.org/10.1016/j.envexpbot.2017.04.006>
- Impron, I., Hemming, S., & Bot, G. P. A. (2007). Simple greenhouse climate model as a design tool for greenhouses in tropical lowland. *Biosystems Engineering*, 98(1), 79–89. <https://doi.org/10.1016/j.biosystemseng.2007.03.028>
- IPCC. (2019). In P. R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, et al. (Eds.), *Climate change and land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. Intergovernmental Panel on Climate Change (IPCC). <https://doi.org/10.25561/76618>
- Jeong, H. W., Lee, H. R., Kim, H. M., Kim, H. M., Hwang, H. S., & Hwang, S. J. (2020). Using light quality for growth control of cucumber seedlings in closed-type plant production system. *Plants*, 9(5), 639. <https://doi.org/10.3390/plants9050639>
- Kendall, L. K., Evans, L. J., Gee, M., Smith, T. J., Gagic, V., Lobaton, J. D., Hall, M. A., Jones, J., Kirkland, L., Saunders, M. E., Sonter, C., Cutting, B. T., Parks, S., Hogendoorn, K., Spurr, C., Gracie, A., Simpson, M., & Rader, R. (2021). The effect of protective covers on pollinator health and pollination service delivery. *Agriculture, Ecosystems & Environment*, 319, 107556. <https://doi.org/10.1016/j.agee.2021.107556>
- Kjaer, K.-H., Ottosen, C.-O., & Jørgensen, B. N. (2011). Cost-efficient light control for production of two campanula species. Author links open overlay panel. *Scientia Horticulturae*, 129(4), 825–831.
- Kjaer, K.-H., Ottosen, C.-O., & Jørgensen, B. N. (2012). Timing growth and development of *Campanula* by daily light integral and supplemental light level in a cost-efficient light control system. *Scientia Horticulturae*, 143, 189–196. <https://doi.org/10.1016/j.scienta.2012.06.026>
- Klem, K., Holub, P., Štroch, M., Nezval, J., Špunda, V., Tříška, J., Jansen, M. A. K., Robson, T. M., & Urban, O. (2015). Ultraviolet and photosynthetically active radiation can both induce photoprotective capacity allowing barley to overcome high radiation stress. *Plant Physiology and Biochemistry*, 93, 74–83. <https://doi.org/10.1016/j.plaphy.2015.01.001>
- Kotilainen, T., Robson, T. M., & Hernández, R. (2018). Light quality characterization under climate screens and shade nets for controlled-environment agriculture. *PLoS ONE*, 13(6), e0199628. <https://doi.org/10.1371/journal.pone.0199628>
- Kotilainen, T. K., Aphalo, P. J., Brelsford, C. C., Böök, H., Heikkilä, A., Hernandez, R., Kylling, A., Lindfors, A. V., & Robson, T. M. (2020). Geophysical factors affecting spectral photon ratios relevant for plant photobiology. *Agricultural and Forest Meteorology*, 291, 108041. <https://doi.org/10.1016/j.agrformet.2020.108041>
- Kotiranta, S., Siipola, S., Robson, T. M., Aphalo, P. J., & Kotilainen, T. (2015). LED lights can be used to improve the water deficit tolerance of tomato seedlings grown in greenhouses. *Acta Horticulturae*, 1107, 107–112. <https://doi.org/10.17660/ActaHortic.2015.1107.14>
- Latimer, J., & Whipker, B. (2012). Selecting and using plant growth regulators on floricultural crops. Produced by Communications and Marketing, College of Agriculture and Life Sciences, Virginia Polytechnic Institute and State University, publication 430-102. VT/0612/web/HORT-43P
- Lee, D. B., Lee, G. J., You, Y. J., Ahn, S. Y., & Yun, H. K. (2021). Reflective film mulching before harvest promotes coloration and expression of ripening-related genes in peach fruits. *Horticultural Science and Technology*, 39(3), 324–331. <https://doi.org/10.7235/HORT.20210029>
- Li, T., Heuvelink, E., Dueck, T. A., Janse, J., Gort, G., & Marcelis, L. F. (2014). Enhancement of crop photosynthesis by diffuse light: Quantifying the contributing factors. *Annals of Botany*, 114(1), 145–156. <https://doi.org/10.1093/aob/mcu071>
- Li, T., & Yang, Q. (2015). Mini review: Advantages of diffuse light for horticultural production and perspectives for further research. *Frontiers in Plant Science*, 6, 704. <https://doi.org/10.3389/fpls.2015.00704>
- Lindfors, A., Heikkilä, A., Kaurola, J., Koskela, T., & Lakkala, K. (2009). Reconstruction of solar spectral surface UV irradiances using radiative transfer simulations. *Photochemistry and Photobiology*, 85(5), 1233–1239. <https://doi.org/10.1111/j.1751-1097.2009.00578.x>
- Liou, K. N. (2002). *An introduction to atmospheric radiation* (2nd ed.). Academic Press. Hardcover ISBN: 9780124514515 eBook ISBN: 9780080491677
- Loik, M. E., Carter, S. A., Alers, G., Wade, C. E., Shugar, D., Corrado, C., Jokerst, D., & Kitayama, C. (2017). Wavelength-selective solar photovoltaic systems: Powering greenhouses for plant growth at the food-energy-water Nexus. *Earth's Future*, 5(10), 1044–1053. <https://doi.org/10.1002/2016EF000531>
- Lopez, R. G., Meng, Q., & Runkle, E. S. (2020). Blue radiation signals and saturates photoperiodic flowering of several long-day plants at crop-specific photon flux densities. *Scientia Horticulturae*, 271, 109470. <https://doi.org/10.1016/j.scienta.2020.109470>
- Mao, P., Duan, F., Zheng, Y., & Yang, Q. (2021). Blue and UV-A light wavelengths positively affected accumulation profiles of healthy compounds in pak-choi. *Journal of the Science of Food and Agriculture*, 101(4), 1676–1684. <https://doi.org/10.1002/jsfa.10788>
- Mayer, B. (2009). Radiative transfer in the cloudy atmosphere. *The European Physical Journal Conferences*, 1, 75–99. <https://doi.org/10.1140/epjconf/e2009-00912-1>
- Mayer, B., & Kylling, A. (2005). Technical note: The libRadtran software package for radiative transfer calculations—Description and examples of use. *Atmospheric Chemistry and Physics*, 5(7), 1855–1877. <https://doi.org/10.5194/acp-5-1855-2005>
- Meng, Q., & Runkle, E. S. (2020). Growth responses of red-leaf lettuce to temporal spectral changes. *Frontiers in Plant Science*, 11. <https://doi.org/10.3389/fpls.2020.571788>
- Merfield, C. N., Winder, L., Stilwell, S. A., Hofmann, R. W., Bennett, J. R., Wargent, J. J., & Hodge, S. (2019). Mesh crop covers improve potato yield and inhibit tomato potato psyllid and blight: The roles of

- mesh pore size and ultraviolet radiation. *Annals of Applied Biology*, 174, 223–237. <https://doi.org/10.1111/aab.12489>
- Mitchell, P. L., & Sheehy, J. E. (2018). Potential yield of wheat in the United Kingdom: How to reach 20 t ha⁻¹. *Field Crops Research*, 224, 115–125. <https://doi.org/10.1016/j.fcr.2018.05.008>
- Nelson, J. A., & Bugbee, B. (2014). Economic analysis of greenhouse lighting: Light emitting diodes vs. high intensity discharge fixtures. *PLoS ONE*, 9(6), e99010. <https://doi.org/10.1371/journal.pone.0099010>
- Ort, D. R., Merchant, S. S., Alric, J., Barkan, A., Blankenship, R. E., Bock, R., Croce, R., Hanson, M. R., Hibberd, J. M., Long, S. P., Moore, T. A., Moroney, J., Niyogi, K. K., Parry, M. A. J., Peralta-Yahya, P. P., Prince, R. C., Redding, K. E., Spalding, M. H., van Wijk, K. J., ... Zhu, X. G. (2015). Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proceedings of the National Academy of Science of the USA*, 112(28), 8529–8536. <https://doi.org/10.1073/pnas.1424031112>
- Palma, C. F. F., Castro-Alves, V., Morales, L. O., Rosenqvist, E., Ottosen, C. O., & Strid, Å. (2020). Spectral composition of light affects sensitivity to UV-B and photoinhibition in cucumber. *Frontiers in Plant Science*, 11, 610011. <https://doi.org/10.3389/fpls.2020.610011>
- Palonen, P., Karhu, S., Savelainen, H., Rantanen, R., & Junttila, O. (2011). Growth and cropping of primocane and biennial raspberry cultivars grown under a film absorbing far-red light. *The Journal of Horticultural Science and Biotechnology*, 86(2), 113–119. <https://doi.org/10.1080/14620316.2011.11512735>
- Parrish, C. H., Hebert, D., Jackson, A., Ramasamy, K., McDaniel, H., Giacomelli, G. A., & Bergren, M. R. (2021). Optimizing spectral quality with quantum dots to enhance crop yield in controlled environments. *Communications Biology*, 4(1). <https://doi.org/10.1038/s42003-020-01646-1>
- Paul, N. D., Jacobson, R. J., Taylor, A., Wargent, J. J., & Moore, J. P. (2005). The use of wavelength-selective plastic cladding materials in horticulture: Understanding of crop and fungal responses through the assessment of biological spectral weighting functions. *Photochemistry and Photobiology*, 81(5), 1052–1060. <https://doi.org/10.1562/2004-12-06-RA-392>
- Poel, B. R., & Runkle, E. S. (2017). Spectral effects of supplemental greenhouse radiation on growth and flowering of annual bedding plants and vegetable transplants. *HortScience*, 52(9), 1221–1228. <https://doi.org/10.21273/hortsci12135-17>
- Qian, M., Kalbina, I., Rosenqvist, E., Jansen, M. A. K., Teng, Y., & Strid, Å. (2019). UV regulates expression of phenylpropanoid biosynthesis genes in cucumber (*Cucumis sativus* L.) in an organ and spectrum dependent manner. *Photochemical and Photobiological Sciences*, 18, 424–433. <https://doi.org/10.1039/C8PP00480C>
- Qian, M., Rosenqvist, E., Flygare, A.-M., Kalbina, I., Teng, Y., Jansen, M. A. K., & Strid, Å. (2020). UV-A light induces a robust and dwarfed phenotype in cucumber plants (*Cucumis sativus* L.) without affecting fruit yield. *Scientia Horticulturae*, 263, 109110. <https://doi.org/10.1016/j.scienta.2019.109110>
- Quintero-Arias, D. G., Acuña-Caita, J. F., Asensio, C., & Valenzuela, J. L. (2021). Ultraviolet transparency of plastic films determines the quality of lettuce (*Lactuca sativa* L.) grown in a greenhouse. *Agronomy*, 11, 358. <https://doi.org/10.3390/agronomy11020358>
- Ravishanker, E., Charles, M., Xiong, Y., Henry, R., Swift, J., Rech, J., Calero, J., Cho, S., Booth, R. E., Kim, T., Balzer, A. H., Qin, Y., Hoi Yi Ho, C., So, F., Stingelin, N., Amassian, A., Saravitz, C., You, W., Ade, H., ... O'Connor, B. T. (2021). Balancing crop production and energy harvesting in organic solar-powered greenhouses. *Cell Reports Physical Science*, 2(3), 100381. <https://doi.org/10.1016/j.xcrp.2021.100381>
- Riga, P., & Benedicto, L. (2017). Effects of light-diffusing plastic film on lettuce production and quality attributes. *Spanish Journal of Agricultural Research*, 15, e0801. <https://doi.org/10.5424/sjar/2017151-10315>
- Robson, T. M., Klem, K., Urban, O., & Jansen, M. A. (2015). Re-interpreting plant morphological responses to UV-B radiation. *Plant, Cell & Environment*, 38(5), 856–866. <https://doi.org/10.1111/pce.12374>
- Robson, T. M., & Kotilainen, T. K. (2018). Transmittance of spectral irradiance by climate screens and nets used in horticulture and agriculture (Version 1.1.1) [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.1561317>
- Sahdev, R. K., Kumar, M., & Dhingra, A. K. (2019). A comprehensive review of greenhouse shapes and its applications. *Frontiers in Energy*, 13, 427–438. <https://doi.org/10.1007/s11708-017-0464-8>
- Sethi, V. P. (2009). On the selection of shape and orientation of a greenhouse: Thermal modeling and experimental validation. *Solar Energy*, 83(1), 21–38. <https://doi.org/10.1016/j.solener.2008.05.018>
- Shao, L., Li, G., Zhao, Q., Li, Y., Sun, Y., Wang, W., Cai, C., Chen, W., Liu, R., Luo, W., Yin, X., & Lee, X. (2019). The fertilization effect of global dimming on crop yields is not attributed to an improved light interception. *Global Change Biology*, 26(3), 1697–1713. <https://doi.org/10.1111/gcb.14822>
- Shin, J., Hwang, I., Kim, D., Moon, T., Kim, J., Kang, W. H., & Son, J. E. (2021). Evaluation of the light profile and carbon assimilation of tomato plants in greenhouses with respect to film diffuseness and regional solar radiation using ray-tracing simulation. *Agricultural and Forest Meteorology*, 296, 108219. <https://doi.org/10.1016/j.agrformet.2020.108219>
- Shu, M., Gu, X., Zhou, L., Xu, B., & Yang, G. (2021). Establishing NDRE dynamic models of winter wheat under multi-nitrogen rates based on a field spectral sensor. *Applied Optics*, 60, 993–1002. <https://doi.org/10.1364/AO.410470>
- Snowden, M. C., Cope, K. R., & Bugbee, B. (2016). Sensitivity of seven diverse species to blue and green light: Interactions with photon flux. *PLoS ONE*, 11(10), e0163121. <https://doi.org/10.1371/journal.pone.0163121>
- Stutte, G. W., & Edney, S. (2009). Photoregulation of bioprotectant content of red leaf lettuce with light-emitting diodes. *HortScience*, 44(1), 79–82. <https://doi.org/10.21273/HORTSCI.44.1.79>
- Timmermans, G. H., Hemming, S., Baeza, E., van, E. A. J., Schenning, A. P. H. J., & Debije, M. G. (2020). Advanced optical materials for sunlight control in greenhouses. *Advanced Optical Materials*, 8(18), 2000738. <https://doi.org/10.1002/adom.202000738>
- Ting, K. C., & Giacomelli, G. A. (1987). Solar photosynthetically active radiation transmission through greenhouse glazings. *Energy in Agriculture*, 6(2), 121–132. [https://doi.org/10.1016/0167-5826\(87\)90010-6](https://doi.org/10.1016/0167-5826(87)90010-6)
- Tomás-Barberán, F. A., & Espín, J. C. (2001). Phenolic compounds and related enzymes as determinants of quality in fruits and vegetables. *Journal of the Science of Food and Agriculture*, 81(9), 853–876. <https://doi.org/10.1002/jsfa.885>
- Toni, H. C., Djossa, B. A., Ayenan, M. A. T., & Teka, O. (2021). Tomato (*Solanum lycopersicum*) pollinators and their effect on fruit set and quality. *The Journal of Horticultural Science and Biotechnology*, 96(1), 1–13. <https://doi.org/10.1080/14620316.2020.1773937>
- Trnka, M., Eitzinger, J., Kapler, P., Dubrovský, M., Semerádová, D., Žalud, Z., & Formayer, H. (2007). Effect of estimated daily global solar radiation data on results of crop growth models. *Sensors*, 7(10), 2330–2362. <https://doi.org/10.3390/s7102330>
- van Velden, P. (2013). Koppeling instraling en schermregeling met hommelmasten—Innovatief programma helpt hommels bij bestuiving in belichte teelt. *Onder Glas*, 10, 58–59. Translation of the article “Controlling bumblebee nest boxes based on incoming sunlight and screening—Innovative software helps improve bumblebee pollination in artificially-lit greenhouses” accessed on 18.04.2016: <https://digimagazine.onderglas.nl/2013/10/magazine.php>

- von Zabeltitz, C. (2011). Cladding Material. In *Integrated greenhouse systems for mild climates*. Springer. https://doi.org/10.1007/978-3-642-14582-7_7
- Wargent, J. J. (2017). Turning UV photobiology into an agricultural reality. In B. R. Jordan (Ed.), *UV-B radiation and plant life: Molecular biology to ecology* (pp. 162–176). CAB International, Chapter 11. <https://doi.org/10.1079/9781780648590.0000>
- Williams, T. B., Dodd, I. C., Sobeih, W. Y., & Paul, P. D. (2022). Ultraviolet radiation causes leaf warming due to partial stomatal closure. *Horticulture Research*, uhab066. <https://doi.org/10.1093/hr/uhab066>
- Xu, D., Li, Y., Zhang, Y., Xu, H., Li, T., & Liu, X. (2020). Effects of orientation and structure on solar radiation interception in Chinese solar greenhouse. *PLoS ONE*, 15(11), e0242002. <https://doi.org/10.1371/journal.pone.0242002>
- Xu, Q., Gosselin, A., Desjardins, Y., Medina, Y., & Gauthier, L. (2014). Red raspberries production under high tunnel, umbrella-like structure and open field under northern Canadian climate. *Acta Horticulturae*, 1037, 771–776. <https://doi.org/10.17660/ActaHortic.2014.1037.101>
- Zhang, Y., Kaiser, E., Zhang, Y., Zou, J., Bian, Z., Yang, Q., & Li, T. (2020). UVA radiation promotes tomato growth through morphological adaptation leading to increased light interception. *Environmental and Experimental Botany*, 176, 104073. <https://doi.org/10.1016/j.envexpbot.2020.104073>
- Zheng, L., He, H., & Song, W. (2019). Application of light-emitting diodes and the effect of light quality on horticultural crops: A review. *HortScience*, 54, 1656–1661. <https://doi.org/10.21273/HORTSCI14109-19>
- Zou, J., Zhang, Y., Zhang, Y., Bian, Z., Fanourakis, D., Yang, Q., & Li, T. (2019). Morphological and physiological properties of indoor cultivated lettuce in response to additional far-red light. *Scientia Horticulturae*, 257, 108725. <https://doi.org/10.1016/j.scienta.2019.108725>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Robson, T. M., Pieristè, M., Durand, M., Kotilainen, T. K., & Aphalo, P. J. (2022). The benefits of informed management of sunlight in production greenhouses and polytunnels. *Plants, People, Planet*, 4(4), 314–325. <https://doi.org/10.1002/ppp3.10258>