REVIEW PAPER



Light-altering cover materials and sustainable greenhouse production of vegetables: a review

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Received: 29 April 2021 / Accepted: 26 May 2021 © The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract

Greenhouse horticulture (protected cropping) is essential in meeting increasing global food demand under climate change scenarios by ensuring sustainability, efficiency, and productivity. Recent advances in cover materials and photovoltaic technologies have been widely examined in greenhouses to improve light transmission and solar energy capture with promoting energy-saving. We review the studies on advanced greenhouse cover materials with variable light transmittance, the effects of which on leaf photosynthesis, physiology, and yield. We provide insights into the potential key biological processes of crops responding to these light changes, specifically light receptors, signal transduction, nutrient biosynthesis pathways (e.g., carotenoids, antioxidant compounds) during fruit development and ripening. A better understanding of greenhouse cover materials with a focus towards energy-efficient cover materials equipped in greenhouse is an opportunity for better yield and higher nutrient products production in vegetables in response to global climate challenges. Interdisciplinary research on the application of novel cover materials in greenhouses and biological investigation of light-induced physiology and nutrient formation in vegetables may promote yield and health attributes for protected cultivation of vegetables with energy use efficiency.

Keywords Light-altering cover materials · Greenhouse light environment · Photoreceptors · Photosynthesis · Fruit quality · Sustainable food production · Protected cropping

Communicated by Ben Zhang.

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Introduction

A sustainable supply of crops to meet increased food demand is a global challenge especially in the context of climate change (Dary and Hurrell 2006; FAO 2016). Protected cropping can promote yield with extending harvest period, reducing pests and diseases, and enhancing the stability of production (Abd El-Aal et al. 2018; Ezzaeri et al. 2018; Seven et al. 2019), but the major obstacle is high energy-consumption during production, especially in hightech greenhouses. Innovative energy-saving cover materials have attracted increased attention due to energy saving properties (e.g. reducing cooling and heating needs) (Abdel-Ghany et al. 2012; Samaranayake et al. 2020) and energy self-sufficiency through altering light transmittance (Loik et al. 2017; Gao et al. 2019). However, increased research investigated that variable light altered by covers can have negative effects on greenhouse vegetable production (Ntinas et al. 2019; Chavan et al. 2020; Zhao et al. 2020), which requires future research investigation.

Research towards energy-efficient cover materials on photosynthesis and yield have been tested in key horticultural crops including lettuce (Lactuca sativa L.) (Tani et al. 2014), tomato (Solanum lycopersicum L.) (Ezzaeri et al. 2018), cucumber (*Cucumis sativus* L.) (Alsadon et al. 2016), capsicum (Capsicum annuum L.) (Zhao et al. 2020) and eggplant (Solanum melongena L.) (Chavan et al. 2020). However, the effects of the advanced covers have cultivar difference. As the primary energy source of photosynthesis, light plays an important role in all stages of the vegetable life cycle. Plants display plasticity in terms of their photosynthesis, stomatal behavior, photo assimilates partitioning and distribution adapting to an altered light environment (Llorente et al. 2016; Li et al. 2018a; Gramegna et al. 2019). These changes usually continuedly impact the plant developmental decision, such as balance of vegetative and reproductive organs with flower and fruit shedding, as well as fruit number, individual fresh fruit weight and size that can affect yield (Marcelis et al. 2004; Kalaitzoglou et al. 2019; Zhang et al. 2020). Therefore, understanding the impact of light on crop growth and development will aid in re-engineering the appropriate cover materials and deploying their implementation.

Another potential influence of advanced covers concerns the nutrient accumulation and shelf life, which are less focused. Horticultural crops are excellent sources of carbohydrates, fibers, micronutrients, abundant minerals and offer long-standing nutrition supply (Dary and Hurrell 2006; Ilić and Fallik 2017). Pigments and antioxidant compounds in the epidermis and flesh tissues, such as lycopene, β -carotene, and ascorbic acid can reduce malnutrition, several chronic diseases and cancer (Cazzonelli et al. 2010; Martí et al. 2016; Zhang et al. 2020). The light sensitivity of these nutraceutical compounds provides an opportunity for improving nutrient fortification in the light environment modified by covers (Dary and Hurrell 2006; Mormile et al. 2019; Ntinas et al. 2019). At detection level, increasing research investigated that cover materials can modify the nutrient composition in vegetables (Murakami et al. 2017; Ahmadi et al. 2018; Lemarié et al. 2018; Mormile et al. 2019; Ntinas et al. 2019). Furthermore, the quality of vegetable products subsequently impacts the shelf life (Fukushima et al. 2018; Kalaitzoglou et al. 2019). During storage, agricultural products can respond the light changes promoting nutrition content, such as Ultraviolet (UV-B and UV-C) and blue light treatment improving accumulation of antioxidant compounds (e.g., phenolics) (Getinet et al. 2008; Pataro et al. 2015). Therefore, a better understanding of light-mediated modulation/regulation of gene expression, protein and metabolite abundance is essential for breeding nutrient-fortified crop varieties in combination with the development of energysaving innovative cover materials for sustainable production of nutritious vegetables.

This review mainly focuses on the effects of advanced cover materials on horticultural crops physiology, molecular biology, subsequently impacting the yield and nutrition with regard to the future of advancing the protected cropping industry. In this review, we firstly summarize that the research of advanced cover materials and coating technologies, and then discuss the effects of these covers on major greenhouse crops (e.g., tomato, cucumber, eggplant, melon, and capsicum) growth and development, such as leaf anatomy, photosynthesis, photosynthate allocation, yield, and nutrient formation. We emphasize the potential mechanism of light regulated fruit growth, nutrient accumulation with ripening, and probable influences on shelf life. The readers are directed to other focused reviews either on the advanced cover materials for greenhouse horticulture (Folta 2019; Timmermans et al. 2020) or on the molecular and physiological mechanisms of light response in horticultural crops (Legris et al. 2019; Poorter et al. 2019; Fernie et al. 2020).

Light altering cover materials in protected cropping

Developing innovative cover materials for protected cropping

High transmission diffused glass, light-altering greenhouse covers, and energy generating photovoltaics (PV) technologies all have the potential to advance protected cropping by altering light environments in a variety of ways. For instance, changing the micro- or even nanostructure of the surface of conventional glass (float glass) or melting Ce³⁺/ Mn²⁺/Yb³⁺ ions achieve both light trapping and self-cleaning (Allsop et al. 2005; Wang et al. 2016b). PV technologies installed on the roof of greenhouses or in the open field offer an opportunity for energy-independent and environmentallyfriendly crop cultivation (Zhou et al. 2016). Different forms of PV panels (Cossu et al. 2016), such as semi-transparent modules (Yano et al. 2014) (Fig. 1a and b), and buildingintegrated photovoltaics (Hassanien et al. 2018) (Fig. 1c) have been tested to using in the roof of greenhouse balancing annual energy demand and light transmission for crop production. In addition, wavelength-selective PV systems and sun-tracking dynamic PV system have been developed to allow both light transmittance and energy-production by incorporating luminescent solar cell technology into the conventional silicon-based PV technologies (Loik et al. 2017; Gao et al. 2019).

Glass and PV panels require cleaning and have antireflective problems, which can be addressed using coating technologies. For example, fluorinated ethylene propylene (FEP) coated surface is highly transmissive and superhydrophobic (Roslizar et al. 2019). Some coatings promote diffuse

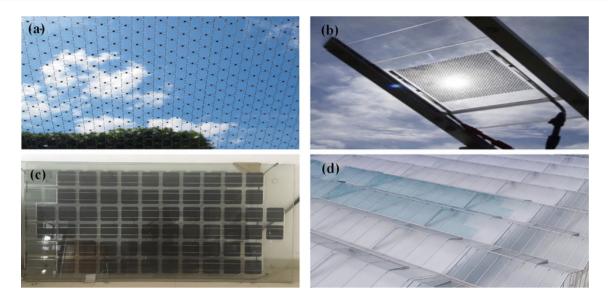


Fig. 1 Advanced materials and PV technologies used in protected facilities. **a** Spherical solar micro-cell (Cossu et al. 2016) (ELSE-VIER License Number: 4999690334689), the cross-section is the spherical solar micro-cell (2 cells cm⁻²), which is promising for greenhouse roof applications with a stable conversion efficiency of 0.2%. The material merely eclipses 9.7% of the sunlight, and the conversion efficiency in the cell can be improved. **b** Semi-transparent photovoltaic modules (Yano et al. 2014) (permits unrestricted use) is also created for greenhouse roof applications without never completely eclipsing the sunlight. The density of micro-cells can be selected, and conversion efficiencies of the 5.1 cells cm⁻² was around 1.6% (test in the Mediterranean, Spain and Sweden) for

light fraction or block some wavelengths of light (e.g. aluminum coating (Mousavi et al. 2017) and Smart Glass film (Chavan et al. 2020). Moreover, Huh et al. (2018) reported a moth-eye structure pattern that can be directly printed on the film, protective glass or solar panels that allows mechanical robustness and anti-reflection. Self-cleaning coatings derived from nature; for example, ultra hydrophobicity as exhibited by the leaf surface of lotus can remove the dust via water droplets (Cheng and Rodak 2005). Sol-gel coating composed of silicon dioxide (SiO₂) nanoparticles and titanium dioxide (TiO₂) has been developed to provide selfcleaning functions by being hydrophobic and scratch-resistant (Mazur 2017; Rosales and Esquivel 2020). The application of these new cover materials and technologies will provide a better microclimate in greenhouse to long lasting benefit to growers towards effective greenhouse production.

Greenhouse light condition modified by advanced cover materials

Cover materials significantly modify light quality and quantity transmitted, such as increase selected light transmission, create diffused light, and generate power. Anti-reflective (AR) coatings can increase the transmittance of glass from

energy consumption (heating, cooling, fan and pumps) in the greenhouse. **c** Building-integrated photovoltaics (BIPV) (Hassanien et al. 2018) (ELSEVIER License Number: 5015380887953) is studied to decrease the light intensity and air temperatures in summer season without impacts on tomato growth setting in both south and north roof with 25° and 20° respectively in Kunming (subtropical area). The generated energy can provide most annual energy demands for the greenhouse environmental control systems. **d** Smart Glass (Chavan et al. 2020) coated (blue area) modifies light transmittance, such as blocking 85% UV, 10% of PAR, 58% far red, and 26% red light reducing the energy-consuming on the cooling system in a high-tech greenhouse

3 to 6% and raise 7.8% electricity (Huh et al. 2017). A new oxyfluoride glass has been created at high temperatures which facilitates broadband light emission that is optimal for absorption by Chlorophyll (ranging from 340-500 nm to 510-700 nm). Air-inflated polyethylene film (DPE) and twin-wall polycarbonate sheet (DPC) are investigated the increase of 70% and 100% diffused light, respectively (Hao et al. 2016). Aluminum coating with scratch-resistance deposits in low iron glass resulted in the transmission of 75-85% visible wavelengths (Mousavi et al. 2017). Recently, Chavan et al. (2020) (Fig. 1d) evaluated Smart Glass (SG), which blocks 85% of ultraviolet (UV) light, 19% of photosynthetically active radiation (PAR), 58% of far-red, and 26% of red light, promotes energy-efficient use in a high-tech greenhouse. Colored semi-transparent PVs allow only the wavebands of light important for plant growth to pass into the greenhouse while the absorbed wavelengths are used to generate energy (Allardyce et al. 2017). Electricity generation and micro-light condition are impacted by the density of PV panels and different installation methods on the roof. For instance, in Europe, 50% PV coverage in the south roof of the greenhouse decreases yearly sunlight availability by 64%, resulting in significant reduction of tomato production (Cossu et al. 2014). However, it is possible to balance annual agricultural yield and energy demand by decreasing to 10% PV coverage (Ezzaeri et al. 2018; Hassanien et al. 2018). The sun-tracking dynamic PV system increases diffused light into the greenhouse by 10% compared to fixed PV technology installed at the same density (Gao et al. 2019).

Light transmittance altered by cover materials generates a series of microclimate changes. The near infrared (NIR) film decreases the temperature and vapor pressure deficit (VPD) (Alsadon et al. 2016), and the reduction of infrared light transmittance reduces the air temperature in SG (Chavan et al. 2020). Similar effects are found in PV and semi-transparent PV-covered greenhouse especially in the summer growing season (Cossu et al. 2014). The increased greenhouse night temperature under PV in winter in Northern Hemisphere may be beneficial for year-round production (Cossu et al. 2014). A temperature rise can affect relative humidity, impacting the inside coating adhesion and quality of light transmission (Moreno-Teruel et al. 2020). In a hightech greenhouse, the energy generated by PV can further improve energy efficiency in protected cropping production (Gao et al. 2019). Therefore, equipped types and method of energy-saving cover materials should consider the geographical light changes climate, and characteristic of crops is another important impact factor achieving high yield.

Influence of light on leaf structure and phenotype of crops

Plant phenotype adapted to the light environment

Plant morphological characteristics are driven by adapting to the light environment to maximize light capture, usage, and availability for photosynthesis, e.g., specific leaf architecture and leaf dry mass content (Wilson et al. 1999; Marcelis et al. 2004). Leaf size, total leaf area and plant height are regulated by photosynthetic metabolic events (Bénard et al. 2015). The decreased light intensity triggers petiole elongation, increased axillary branching or tillering, altered root: shoot ratio and inflorescence development (Jansen 2002; Wargent et al. 2009; Kozuka et al. 2010). While leaves tend to be thicker with an increasing number of palisade and spongy tissue layers, as well as promoting cuticle layer accumulation minimizing photodamage under high radiation (Yano and Terashima 2001; Terashima et al. 2005). High light intensity also induced a high foliar vein density (VD) with increased numbers and cross-sectional areas of both xylem and phloem cells per vein for photosynthetic and water transportation (Stewart et al. 2017).

The light spectrum also plays an important role on morphological characteristics under different cover materials that is normally sunlight dependent. The sunlight is composed of ultraviolet light (UV; 10–400 nm), PAR (or visible light; 400–700 nm), far red (700–780 nm) and infrared

light (>780 nm) (Table 1). UV is high energy light composed of UV-C (< 280 nm), UV-B (280-320 nm) and UV-A (320-400 nm) (Stapleton 1992; Fierro et al. 2015), and can affect antioxidant content such as phenolics, ascorbic acid and flavonoids, that are required to maintain normal plant growth and oxidative stress defense mechanisms (Pataro et al. 2015; Escobar-Bravo et al. 2017; Panjai et al. 2017; Mormile et al. 2019). PAR is regarded as the most important wavelength range for plant growth and development, directly influencing the photosynthesis process (Dou et al. 2017), as well as blue and red light and their ratio are crucial for photosynthesis, stomatal and chloroplast behavior (Kong et al. 2013; Matthews et al. 2020). High PAR intensity reduces stomatal pore areas which may led to lower photosynthesis (O'Carrigan et al. 2014b), which could be compensated by increased blue light promoting stomatal conductance and density (Wang et al. 2016a; Zheng and Van Labeke 2017). Green light increases the photosynthetic efficiency by its higher penetration to chloroplasts adjusting the Rubisco/ chlorophyll ratio than red or blue light, especially in strong white light (Terashima et al. 2009). Red, far-red and red/ far-red light, affects germination, leaf area and leaf net photosynthesis, phytohormone signaling, and reproductive organ development (Castillon et al. 2007; Kalaitzoglou et al. 2019; Kim et al. 2019). Infrared light generates higher leaf temperature, but has less impact on growth of plant (Abdel-Ghany et al. 2012).

Light regulates leaf photosynthesis process

Due to different geographic locations and crop species, variable important physiological traits, specifically photosynthesis, performance under different types of cover materials (Table 2). The photosynthesis of tomato decreased under the dye-sensitized solar cell covered greenhouse (Ntinas et al. 2019). However, the NIR-reducing film improve the photosynthesis in cucumber (Alsadon et al. 2016). We propose that these are consequences of greenhouse vegetables adapting to the light environment altered by cover materials, involving the activation of a sophisticated response between light sensing, absorbing and plant energy transformation.

The light environment altered by cover materials significantly influences photosynthesis. During this process, pigments (chlorophyll and carotenoids) capture the light, specifically PAR, inducing electron transfer to be converted into chemical energy. At the cellular level, chloroplasts may be relocated along with the pigments, and the orientation of the thylakoid membrane changes differently between low light and excess light (Kirchhoff 2019). Photosynthesis involves light sensing and activities of photosystem I (PSI) and photosystem II (PSII). In PSII, pigments absorb light and split water molecules to generate a proton gradient, utilized by ATP synthase for ATP production (Ruban et al.

Plant Growth Regulation	
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Sunlight	Wavelength (nm)	Effective Light (nm)	Light Receptor Protein	Impacts on Plant Growth
UV (5%)	10–400	UV-C (<280)		Absorbed by ozone and not present in sunlight
		UV-B (280–320)	UVR8	Photomorphogenic response, including extension growth, leaf thickness, curling and axillary branching Jansen (2002); Wargent et al. (2009); Fierro et al. (2015); pro- mote antioxidant compounds and pigments biosynthesis Li et al. (2018a); Mormile et al. (2019)
		UV-A (320-400)	PHOTs;	Photosynthetically active radiation, leaf flattening; chlo-
Visible Light (50%)	400–700	Blue (420–470)	CRYs; ZTLs	roplast movement and stomatal behaviour Goh (2009); Wang et al. (2016a); Matthews et al. (2020); seedling development and antioxidant compounds Kim et al. (2013)
		Green (510)		Drives leaf photosynthesis due to higher penetration Terashima et al. (2009)
		Red (610-680)	PHYs	Stomata and chloroplast behavior Wang et al. (2016a);
Far Red and Infrared (45%)	> 700	Far Red (700–780)		Matthews et al. (2020); leaf expansion, stem elongation Zheng and Van Labeke (2017); flower differentiation, photosynthetic allocation, fruit development, dry-mass accumulation and fruit ripening Cozmuta et al. (2016); Murakami et al. (2017); Kalaitzoglou et al. 2019; Zhang et al. (2020)
		Infrared (>780)		Heat generated could be blocked, e.g. Smart Glass Chavan et al. (2020)

 Table 1
 The effect of different light spectra on vegetable growth and light modified for cover materials creation

The picture in the wavelength column represents the wavelength of different light. UV resistant locus 8 (UVR8) is the receptors of UV-B light; Phototropins (PHOTs), Cryptochromes (CRYs), Zeitlupe families (ZTLs); are the UV-A and blue light receptors in vegetables. Phytochromes (PHYs) are the protein responding to red and far-red light

2012). Furthermore, qE triggered by Δ pH electron brings protons into light-harvesting complexes (LHCII), balancing the electron flux and pigments (chlorophyll fluorescence quenching) in light harvesting (Ruban 2016). NADPH provides energy in light independent stage including the Calvin cycle generating carbohydrates catalyzed by Rubisco and chemiosmosis ATP production impacting stomatal activity (Parry et al. 2003; Ruban et al. 2012).

The light altered by cover materials is prominently affected by the seasonal sunlight changes, which leads to a fluctuating greenhouse light environment complicating research within a protected cropping scenario (Table 2). The reduction of PAR by Smart Glass limits photosynthesis and stomatal conductance of eggplant (Chavan et al. 2020), and similar results are observed in a dye-sensitized solar cell without shade effects on photosynthesis in hydroponic tomato (Ntinas et al. 2019). However, there are opposite results in tomato plants under different types of covers, such as NIR ray-reflective film that promoted photosynthesis and transpiration (Alsadon et al. 2016), BIPV and flexible PVs did not impact on photosynthesis (Cossu et al. 2016; Ezzaeri et al. 2018; Hassanien et al. 2018). Research using light-emitting diodes (LED) in model crops has advanced our knowledge of how light can induce phenotypic acclimation. For instance, 300 μ mol m⁻² s⁻¹ photosynthetic photon flux density (PPFD) is suitable for young tomato plants with no less than 8 h of daily illumination for cultivating (Fan et al. 2013), while leafy vegetables prefer some shade with 200 µmol m⁻² s⁻¹ (Wojciechowska et al. 2015). Light spectrums also affect photosynthesis. For instance, increasing the ratio of blue light can improve leaf photosynthetic capacity, photosynthetic rate and quantum yield of PSII under the monochromatic red light (Darko et al. 2014; Wang et al. 2016a). Based on these results from artificial light, the investigation of light receptors on photosynthesis and light acclimation could provide the initial prediction of the yield under different cover materials.

Photoreceptors and light response genes for crop adapting to greenhouse light environment

Plant photoreceptors are the light-sensitive proteins are known to function as molecular switches (Table 1). Plants have distinct photoreceptors in perceiving different light wavelengths. Phototropins (PHOTs), cryptochromes (CRYs) and Zeitlupe families (ZTLs) respond to blue light and UV-A light (Table 1) (Shimazaki et al. 2007; Goh 2009). Phytochromes (PHYs) exist in

Year Country	Covers	Plant species	Plant species Plant growth Yield	Yield	Fruit quality	/ Shelf life	Fruit quality Shelf life Energy consumption/gen- eration	Disease and	References
								insects	
2015 Middle East	Near infrared ray -reflec- tive film	Cucumber	↑a, b	←	NA	NA	NA	NA	Alsadon et al. (2016)
2017 Japan	Near infrared ray -cutting nets	Melon	NA	•	¢A	NA	NA	NA	Murakami et al. (2017)
2018 Morocco	Flexible photovoltaic panels	Tomato	•	NA	₀₽	NA	NA	\rightarrow	Ezzaeri et al. (2018)
2018 China	Semi-transparent photovol- taic (BIPV)	Tomato	•	NA	NA	NA	Generated energy: 637 kWh/year	NA	Hassanien et al. (2018)
2018 France & Spain	Light Cascade®" technol- ogy (LC®)	Melon	NA	12,5	¢A	←	NA	NA	Lemarié et al. (2018)
2018 Canada	Diffused twin-wall polycar- Tomato bonate sheet	Tomato	NA	NA	∎D; ţc	NA	NA	NA	Ahmadi et al. (2018)
2018 Egyptian and British	2018 Egyptian and British UV transmitting cover and UV opaque cover	Cucumber	NA	$\substack{\uparrow 1, 2,\\ 3, 6}$	D	NA	NA	\rightarrow	Abd El-Aal et al. (2018)
2019 Greece	Dye-sensitized solar cell	Tomato	↓a, b	↓5, 6	†B, C	NA	NA	NA	Ntinas et al. (2019)
2019 Spain	Flexible photovoltaic pan- els (9.8% covered)	Tomato	٥Ē	• ; 5	•	NA	Generate energy: 4.96 kW hm ⁻²	NA	Aroca-Delgado et al. (2019)
2019 Italy	UV transmitting films	Rocket salad	NA	•	¢D	NA	NA	NA	Mormile et al. (2019)
2020 Australia	Smart Glass film ULR80, solar Gard®	Eggplant	¢a	↓ 1, 2	. 08	NA	¢8%	NA	Chavan et al. (2020)

6, early fruit maturation. A, sugar; B, antioxidant compounds; C, total carotenoids; D, total phenolic; the NA in the table presents the index did not record in the research

two photo-interconvertible forms: an inactive, red light absorbing "Pr" form and an active, far-red light absorbing "Pfr" form, which are activated by red light and de-activated by far-red light (Devlin 2016). The unique photoreceptor of UV-B light is UV resistance locus8 (UVR8), that mediates photomorphogenic responses (Jenkins 2017). In response to red, blue and UV light radiation photoreceptors tend to trigger similar signaling mechanisms involving specific light-induced protein interactions or several transcription factors, such as CON-STITUTIVELY PHOTOMORPHOGENIC 1 (COP1), a RING motif-containing E3 ligase that acts negatively to regulate photomorphogenesis (Luo et al. 2014), PHY-TOCHROME-INTERACTING FACTORS (PIFs) (Kang et al. 2009) and ELONGATED HYPOCOTYL5 (HY5, the bZIP transcription factor) (Li et al. 2018a). The mutual collaboration of photoreceptors adapts plants to the altered light environment. PHY-A and B2 act antagonistically in far-red light, activating glyoxylate cycle enzyme activity to regulate starch synthesis in germination (Lin 2000; Paik and Huq 2019), and then the interaction of PHY-B and CRY2 control hypocotyl elongation (Más et al. 2000). PHOTs promote plant growth responding to blue light under shading and regulate stomata and chloroplast movement, leaf position and flattening interacting with PHYs (Christie and Briggs 2001; Babla et al. 2020). UVR8 represses hypocotyl growth by interacted COP1, enabling the leaf area and morphology to be adapted to UV-B stress through the upregulation of HY5 (Wargent et al. 2009). The synergy of PHYB and UVR8 along with auxin as the downstream factor, are essential for epinasty of the blade edge (Fierro et al. 2015).

The effects of light quality and quantity on photosynthesis are relatively well studied; however, the mechanisms controlling photosynthesis under typical cover materials remains unclear. PHOTs respond to the fluctuating light, including stomatal opening and chloroplast movement (Briggs and Christie 2002; Wada et al. 2003). PHYs and PIFs are involved in hormone signaling and possibly regulate the leaf expansion and cell size, which might participate in crops responding to cover materials (Kozuka et al. 2010). Recently, Zhao et al. (2020) found that the altered light by Smart Glass reduces stomatal pore size, increase stomatal closing and opening speed without a significant influence on stomatal conductance. Meanwhile, the increase of light receptors (PHOTs, PHYs and UVR8) as well as photosynthesis-related gene (such as Ribulose Bisphosphate Carboxylase Small Chain 1, *RBCS1*) expression participate in the adaption of capsicum to the light environment by Smart Glass (Zhao et al. 2020). How the photoreceptors networks are altered by covering materials requires a deeper understanding to decipher the trade-offs of between manipulating light and consequential effects on physiological traits (e.g., photosynthesis rate, stomatal conductance, and chloroplast behavior).

Potential influence of cover materials on fruit development

In greenhouse horticulture, fruit yield is related to the number of fruits, individual fruit fresh weight and fruit size, which are tightly regulated by the light (O'Carrigan et al. 2014a; Chavan et al. 2020). Cover materials that alter light might could affect fruit development and yield (Table 2). For instance, UV transmission film promotes cucumber yield by increasing the fruit fresh weight and fruit number (Allardyce et al. 2017). In contrast, Smart Glass (window film ULR 80) decreases eggplant yield by increasing flower abortion leading to lower fruit set and total fruit weight per plant (Chavan et al. 2020). It is shown that the light environment in the initial 2 weeks of fruit set can impact the fate of fruit development (Fukushima et al. 2018). Reducing light radiation by dye-sensitized solar cells (Ntinas et al. 2019) and PV (Arabatzis et al. 2018) panels delay fruit ripening and decrease fruit size. On the contrary, the NIR reflective film promotes the total yield of cucumber (Alsadon et al. 2016), and the light cascade technology promotes the yield by increasing fruit number and size (Lemarié et al. 2018). Here, we discuss the light-regulated conversion of photosynthetic assimilation from leaf to fruit, fruit morphology and development, and the regulation of key gene expression potentially impacted by the light-altering cover materials.

Allocation of photosynthetic products controlling reproductive organs abortion

Flower or fruit abortion is a consequence of crop selfregulation to balance source and sink in response to the environmental changes in light intensity and/or quality (Marcelis et al. 2004; Chavan et al. 2020). Photosynthetic products are transported from leaves ('source') to young fruits ('sink') via the vascular systems to provide an energy source for fruit development as well as other physiological processes (Marcelis et al. 2004). Sucrose is the main product of CO₂ assimilates transported from leaves to fruits and sucrose transporters are integral in the communication between 'sink' and 'source' to optimize crop yield (Ainsworth and Bush 2011; Lemoine et al. 2013; Bénard et al. 2015). In a source-limited situation (e.g., low light conditions), competition within the sinks can affect fruit position as a the consequence of interactions between sucrose metabolism and phytohormones signaling (Bertin 1995; Marcelis et al. 2004). Although temporary changes in the intensity of light might affect the production of source photo assimilates, their distribution is dependent upon growth, rather than fluctuations in light intensity (Nishizawa et al. 2009). González-Real et al. (2009) showed that the sink demand of proximal fruit as opposed to light acclimation, controlled by leaf photosynthetic capacity. Thus, how the distribution of assimilates responding to an altered light from cover materials affects fruit set remains a matter of debate.

Fruit morphological and developmental traits in an altered light environment

Horticultural crops management, including pruning, flower, and fruit thinning, as well as harvesting the fruit, modify carbon assimilate allocation and change sink competition to control the number of flowers and fruit set for higher yield. For example, the thinning of female flowers of melon reduces fruit abortion (Bertin 1995; Barzegar et al. 2013). Although shape and size of fruits (e.g., tomato, cucumber, capsicum, and eggplant) are genetically diverse, the initial fruit growth of these vegetables depends on epidermal cell division and expansion (Cheniclet et al. 2005). Cell division occurs typically seven days after anthesis, starting with the outer pericarp (Tanksley 2004; Xiao et al. 2009) and inner pericarp layers with up to a threefold increase in the number of cell layers, contributing significantly to the fruit weight (Cheniclet et al. 2005; Faurobert et al. 2007). Supplemental light, such as PAR, red and far-red light could increase sink strength and accelerate fruit growth and dry mass accumulation 2 weeks after anthesis (Fukushima et al. 2018; Kalaitzoglou et al. 2019). Fruit size of tomato and cucumber is decreased by reduction of light radiation under cover materials (Abd El-Aal et al. 2018; Ntinas et al. 2019), yet an increased in diffuse light reflectance improved fruit grade in a range of vegetables (Hao et al. 2016).

Light-regulated biochemical compounds in the epidermal cells contribute to fruit growth and quality. The elasticity and extensibility of epidermal cuticle are possibly connected to accumulation of flavonoids and composition/ratio of long-chain lipids in epidermal cells, such as trihydroxy-C₁₈ monomers, C₁₆ monomers, and their ratio (Díaz-Pérez et al. 2007; España et al. 2014). Alteration of light by cover materials can potentially result in disordered cuticular layer development, triggering cracking of fruit, loss of external appearance thereby causing increased water loss and pathogen infection that influences the marketability of fruits (Bennett and Wallsgrove 1994; Enfissi et al. 2017). Furthermore, antioxidant compounds participating in the regulation of fruit development can be sensitive to altered light conditions induced from cover materials (Ahmadi et al. 2018; Mormile et al. 2019; Ntinas et al. 2019; Petropoulos et al. 2019). Therefore, photo-oxidative stress may be considered as a component of reduced-oxidation (redox) signaling during fruit organ development (Muñoz and Munné-Bosch 2018).

Regulation of key genes in fruit development and their potential response to cover materials

In recent years, omics technologies have been extensively applied to investigate molecular mechanisms regulating fruit development. However, studies regarding the impact of cover materials on fruit development are constrained due to the temporal and spatial differences in large greenhouse trials and cyclic growth patterns of cultivars. Here, we summarize essential information on key genes in sucrose

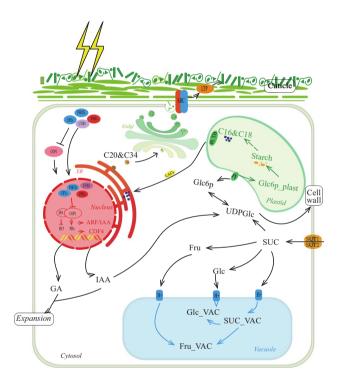


Fig. 2 Schematic diagram of the role of light in sugar and auxin-regulated growth of fruit epidermal cells. Photoreceptors, phytochromes (PHYs, red solid circle), phototropins (PHOTs, blue solid circle), cryptochromes (CRYs, blue solid circle) and UV resistance locus8 (UVR8, purple solid circle) are activated by light. COP1 and SPA protein complex, as well as HY5 and PIFs interacted with light receptors regulate the IAA (ARF) and GA biosynthesis (CYCLING DOF FACTOR, CDF4) in nucleus (red solid lines) promoting fruit growth. Sugar metabolism transported by SUT1/SUT2 (orange solid circle), reused in vacuole (blue arrows) or IAA metabolized to UDPGlc, constructing the skeleton of cell wall (black arrows). In addition, the Glc6p is transported into plastid by Pi for starch biosynthesis or undergoes to lengthen to the C16 and C18, which are hydrolyzed by FATB and converted to CoA thioesters by LACS and then transferred to endoplasmic reticulum (ER) for extending to the long-chain (C20-C34) lipids. The lipids are transported by ABC and by LTPs to the fruit surface for protecting the fruit growth (Xu et al. 2018; Dolgikh et al. 2019; Ma and Li 2019)

metabolism and hormonal pathways regulating fruit growth under altered light environments (Fig. 2).

The carbon source for initial fruit development is supplied via the transport of carbohydrates from leaves to fruits to promote epidermal cell division and expansion. Sucrose/proton co-transporters (SUTs), SUT1/SUT2 transport sucrose to the sink cell, where it becomes metabolized and stored as starch in amyloplasts and later converted to hexoses or imported into the vacuoles (Lemoine et al. 2013). In cucumber, SUCROSE SYNTHASE 4 (SUS4) is predominantly expressed in the reproductive organs, and controls sucrose transport to the fruit and hence regulates fruit size and weight (Fan et al. 2019). Sucrose metabolic process regulate fruit cell division and expansion, which are connected to the cell wall expansion and synthesis through UDP-SUGAR PYROPHOSPHORYLASE AND PHOS-PHOGLUCOMUTASE (Glc6P-Glc1P) (Geserick and Tenhaken 2013; Beauvoit et al. 2014). Invertases (INV) in stem, cytoplasm and vacuolar provides carbohydrates to maintain sink metabolism and exert the hexose production supply for sugar signals to regulate cell cycle and division (Ruan et al. 2010). How INV activity is sustained for fruit set development under abiotic stress and sucrose import system-specific remain to be resolved despite advanced research studies carried out over the years to understand how plants perceive the signals from changing light conditions and transport assimilate from source to sink.

Initial fruit development starts with rapid accumulation of lipids in epidermal cells forming the cuticle layer to provide protection and support the fruits. The Glucose 6-phosphate (Glc6p) is transported into plastid by Pi translocase (Pi) for starch biosynthesis or undergoes to lengthen to the C₁₆ and C₁₈, which are hydrolyzed by acyl-ACP carrier protein thioesterases (FATB) and converted to CoA thioesters by longchain acyl-CoA synthase (LACS and then transferred to endoplasmic reticulum (ER) for extending to the long-chain $(C_{20}-C_{34})$ lipids (Yeats et al. 2014). The free fatty acids are transported by long-chain acyl-CoA synthases (LACS1 and LACS2), and then activated in the form of acyl-CoAs by two long-chain acyl-CoA acyltransferases in ER (Trivedi et al. 2019). The compounds are deposited to epidermal by and lipid transfer protein (LTP) (Maldonado et al. 2002; DeBono et al. 2009), and ATP Binding Cassette (ABC) transporters (Chen et al. 2011; Liu et al. 2020). There is the mevalonate (MAV) pathway of cuticular wax in the cytoplasm, but less is known about it and associated transporters in the lipid deposition (Trivedi et al. 2019). Although a growing number of studies show the positive effects of light on cuticle accumulation in epidermal cells, the role of the light receptors involved in the cuticle biosynthesis pathway is still unclear.

Light is known as one of the core mediators of phytohormone biosynthesis and controls their distribution to promote fruit cell division, expansion, and elongation (McAtee et al. 2013; Babla et al. 2020). Fruit growth and final fruit size are determined by cell division (cell number) and expansion (cell size), which are a function of the interactions between phytohormone signaling and carbon distribution (Azzi et al. 2015). Photoreceptors, PHY, PHOT, CRYs, and UVR8 are activated by light upregulating the IAA and GA biosynthesis via COP1 and SUPPRESSOR OF phyA-105 (SPA) protein complex, HY5 and PIFs. For instance, tomato Auxin Response Factors (ARFs) and a cycling DOF transcription factor (CDF4) enhance fruit size and weight during early fruit development due to an increase in cell size and sucrose-metabolizing enzymes (Liu et al. 2018; Renau-Morata et al. 2020). Auxin promotes cell elongation and expansion by altering the properties of cell wall (e.g., polysaccharide interactions) (Majda and Robert 2018; Ma and Li 2019). Interestingly, the carbon metabolism is accelerated by supplementing red light, which upregulates gene expression controlling the cell wall modification [e.g., Glucose-6-Phosphate (G6P), fructose-6-phosphate (F6P)], lipids location and transport in tomato during fruit set (Fukushima et al. 2018). Thus, an appropriate design for cover materials could improve fruit number and development. Crosstalk between light and hormonal signaling cascades continually regulate fruit ripening and promote nutrient accumulation.

Fruit maturation and shelf life

Light affected maturation and quality formation of fruits

Fruit quality is driven by a series of biochemical processes that require specific light spectral qualities and quantity altered by cover materials. Early maturation of fruit contributes to early yield, and it was found that UV-transmitting and dye-sensitized solar cell for covering materials promote early maturation of fruit impacting overall yield in tomato and cucumber (Abd El-Aal et al. 2018; Ntinas et al. 2019). However, the effects of cover materials on basic quality indexes are diverse results. Some reports showed that the NIR reflective film does not influence the dry mass of melon (Alsadon et al. 2016); however, an increase in sugar accumulation grown under NIR reducing nets and light cascade technology have been observed (Cossu et al. 2016; Murakami et al. 2017). Several metabolic processes of the fruit appear to be linked to the supply of sucrose from photosynthesis during the day, and organic acids (e.g., malate and succinate) tend to accumulate in the pericarp under shade conditions or at night (Bénard et al. 2015). Thus, the harvesting time may significantly affect fruit taste (sugar/organic acid) (Petropoulos et al. 2019).

The fruit visual color, an index determining the economic value, is regulated by the content and ratio of chlorophylls, carotenoids, and anthocyanins influenced by crop genotype, as well as the exposure to specific spectra and intensity of light (Enfissi et al. 2017). photo selected (PE) films are found to have positive effects on fruit color formation and decrease sun scalding-induced fruit injuries (Papaioannou et al. 2012; Petropoulos et al. 2019). The content of pigments varies in different parts of the organism or even in the same fruit due to the positioning of the organs exposed to light or under shade (Li et al. 2018b). In tomato, accumulation of carotenoids, including lycopene and β -carotene, is affected by shade conditions, and promoted by UV-B exposure (Papaioannou et al. 2012; Bénard et al. 2015). Moreover, pigment levels alters during fruit ripening, which requires chromatin and DNA methylation regulatory processes to promote the differentiation of chromoplasts that store these micronutrients (Anwar et al. 2020). Carotenoid biosynthesis in climacteric fruits and non-climacteric fruits correlates with a balance between auxin, ethylene, and abscisic acid (ABA) signaling processes (Su et al. 2015). ABA is a carotenoidderived phytohormone promoting anthocyanins and flavonoids biosynthesis (Mou et al. 2015; Forlani et al. 2019). During fruit maturation, red light increases the accumulation of tocopherol (a critical source of VE biosynthesis) (Gramegna et al. 2019). Both light-dose-dependent and wavelength-dependent reactions trigger the photo response of antioxidant compounds such as lutein, β-carotene, flavonoids, and ascorbic acid content (Jimenez et al. 2002; Ntagkas et al. 2019).

The fruit epidermal cuticle plays an essential role in determining traits of the horticultural crops, including the fruit external appearance, quality and shelf life (Tafolla-Arellano et al. 2018). The hydrophobic cuticle, which is composed of cutin, epicuticular, and extra cuticular waxes, varies across organs and species (Martin and Rose 2014). Cuticular wax is associated with hydrophobic compounds for the scattering of radiation by increasing the transmittance of PAR, and UV light (Trivedi et al. 2019). The increased thickness of the cuticular wax layer of fruits as a response to higher irradiation is shown in many plant species, such as tomato, beans (Phaseolus vulgaris L.), and cucumber (Tafolla-Arellano et al. 2018). The spectral quality of light affects the cuticle biosynthesis and alters the composition of cuticle wax (Qiao et al. 2020). Enhanced UV-B (280-320 nm) levels change the composition and the total content of cuticular wax in cucumber (Zlatev et al. 2012). Moreover, monochromatic far-red light is reported to stimulate cuticular wax biosynthesis, increasing the wax hydrophobicity in both tomato and capsicum fruits during storage (Cozmuta et al. 2016). Red light treatment promotes the cuticular wax content suggesting that PHYs might be involved in the regulation of the cuticular wax biosynthesis (Qiao et al. 2020). Due to the high complexity of the plant secondary metabolism, the mechanisms involved in the light-mediated control of cuticle biosynthesis and the effects of cover materials on cuticle biosynthesis in fruits require more detailed investigation.

Potential impacts of cover materials on fruit shelf life

Fruit quality formation during cultivation and fruit maturation is influenced by the light environment within a greenhouse, which impact the light-controlled biosynthesis of some bioactive compounds that contribute to shelf life extension (Ilić and Fallik 2017). For instance, shortterm monochromatic red, blue, UV light or PAR treatment promote the biosynthesis of ethylene and significantly accelerate the post-ripening process of fruits during storage (Enfissi et al. 2017). However, the effects of light conditions on vegetable shelf life and the biosynthesis of related compounds are cultivar- and crop-specific. It was shown that light treatment on fruit enhances the accumulation of total carotenoids (i.e., lycopene), ascorbic acid, flavonoids, phenolic compounds, antioxidants, and wax in tomato (Castagna et al. 2013; Kim et al. 2013; Pataro et al. 2015; Panjai et al. 2017), which could be responsible for extending the shelf life (Castro et al. 2008; Ahmadi et al. 2018). Far-red and UV light prevent water loss by enhancing wax biosynthesis that changes the surface texture and increases the accumulation of chlorophyll and carotenoids in tomato (Cozmuta et al. 2016; Li et al. 2018a). In contrast, continuous red light combination with 30-min of UV light treatment accelerates the fruit post-ripening with surface softening (Panjai et al. 2017). Furthermore, the reduction of pests and disease in production could contribute to extended shelf life with a decline of microbial loads (Alsadon et al. 2016; Abd El-Aal et al. 2018). Although light cascade technology was reported to extend the shelf life of crops (i.e. melons) (Murakami et al. 2017), the effects and mechanisms of cover materials on fruit shelf life remain to be identified.

Light regulated genes and metabolites during fruit ripening

The fruit ripening process is divided into climacteric and non-climacteric, according to respiration bursts accompanied ethylene generated. Both types of ripening processes share pronounced shifts with distinct patterns related to primary and secondary metabolism, including changes in pigmentation and phytohormone (Dumas et al. 2003; Carrari et al. 2006; Faurobert et al. 2007; Mou et al. 2015;

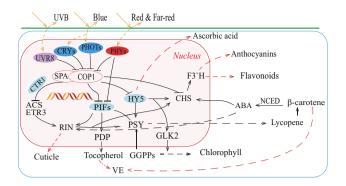


Fig. 3 Potential light receptors induced fruit ripening and quality formation in fruits under different cover materials. The green bold line represents the different cover materials with altered light transmittance. Photoreceptors induced fruit ripening via COP1 and SPA protein complex, as well as PIFs and HY5, regulating the phytohormone (e.g., ACS) and pigments biosynthesis (e.g., carotenoids and anthocyanins) (Enfissi et al. 2017; Li et al. 2018a, b; Gramegna et al. 2019). Dashed arrows indicate multi-step in the pathways; solid arrows demonstrate the one-step regulation; red dashed lines show the unknow pathways such as RIN and ABA regulated fruits ripening, RIN and light-induced nutrition biosynthesis (e.g., ascorbic acid, VE, and cuticle), as well as nutrition composition and metabolism (e.g., VE biosynthesis)

Llorente et al. 2016). The impacts of cover materials on fruit maturation and shelf life are still unclear, but light receptors sensing the light changes which could play a key role in controlling fruit ripening and nutrient metabolism interaction (Fig. 3). Under insufficient light conditions, such as shade effects or altered light quality [e.g. Smart Glass (Chavan et al. 2020), and Dye-sensitized solar cell (Ntinas et al. 2019)], PHOTs could facilitate light sensitivity via the COP1/SPA complex and a negative regulator CTR1 to regulate the ethylene biosynthesis genes expression, including 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID (ACC), ACC SYNTHESIS (ACS), and ACC OXIDASE (ACO) in tomato fruits (Cruz et al. 2018; Dolgikh et al. 2019). Furthermore, the PHYs could play a crucial role on climacteric fruits (e.g. tomato) ripening promoting the ethylene sensitive genes expressions, such as ETHYLENE RESPONSE 3 (ETR3), ETHYKENE INSENSITIVE 2 (EIN2), and ETHYLENE INSENSITIVE 3-LIKE (EIL2) gene expression (Zhang et al. 2020). These genes subsequently regulate RIPENING INHIBITOR (RIN) expression and accelerate color changes.

Fruit maturation promotes pigment abundance changing the fruit color. The precursor of carotenoids is geranylgeranyl diphosphate (GGPP), which is upregulated GOLDEN-LIKE2(GLK2) and acted by UVR8 to promote chlorophyll biosynthesis. Carotenoid accumulation is sensitive to changes in the light environment and different cover materials which can affect their accumulation in synchrony with fruit ripening (Papaioannou et al. 2012; Ahmadi et al. 2018; Cruz et al. 2018; Petropoulos et al. 2019). A synergistic effect between light receptors, hormones, and the regulation by key genes such as RIN and PHYTOENE SYN-THASE (PSY) and ACS have been shown to be impacted by the altered light environment (Carrari et al. 2006; Castillon et al. 2007; Zhang et al. 2020). Furthermore, through COP1 and SPA, the bZIP transcription factors HY5 and PIFs regulate the PSY gene expression in tomato fruit (Llorente et al. 2016). In the carotenoid metabolic pathways, violaxanthin and neoxanthin are catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED) to synthesize ABA (Tan et al. 2003; Perreau et al. 2020) that stimulates the anthocyanin biosynthesis (Mou et al. 2015). ABA plays a predominant role in anthocyanin biosynthesis by promoting FLAVANONE-3-HYDROXYLATE (F3`H) expression without the influence of sugar accumulation (Mou et al. 2015; Chung et al. 2019). Anthocyanin and flavonoid biosynthesis are significantly upregulated by UV light (Fig. 3). The COP1/SPA complex act as a molecular switch of light-induced anthocyanin biosynthesis downstream of the photoreceptors (Li et al. 2018a), and UVR8 regulates the flavonoid biosynthesis by orchestrating responsive genes, HY5 and CHALCONE SYN-THASE (CHS), CHALCONE ISOMERASE (CHI) and F3`H (Brown and Jenkins 2008; Li et al. 2018a, b). Moreover, the flavonoids, lycopene, and β -carotene have antioxidant capacity that are promoted by UVR8 sensing UV-B light and HY5 stimulates COP1 transcription upregulating PSY, CHI expression (Fig. 3), as well as PIFs mediated light controlled tocopherol and ascorbic acid (Bénard et al. 2015; Petropoulos et al. 2019). It indicates that UVR8 and CRYs could participate in the regulation under dye-sensitized solar cells and UV transmitting covers (Ahmadi et al. 2018; Mormile et al. 2019; Ntinas et al. 2019). Due to the blocked UV-B, less UVR8 could be expressed under UV transmitting covers, Smart Glass film with reduction of flavonoids (Abd El-Aal et al. 2018; Mormile et al. 2019; Chavan et al. 2020). However, RIN and ABA regulated fruits ripening, RIN, and light-induced nutrition biosynthesis (e.g., ascorbic acid, VE, and cuticle), as well as nutrition composition and metabolism (e.g., VE biosynthesis) remain unclear. A complex interaction between light and influence of cover materials on its transmittance to the crop canopy, as well as to fruit surface can affect harvesting time, cultivar productivity, fruit ripening and nutrient ion metabolism.

Concluding remarks and future directions

Protected cropping is widely used in horticultural crop production and is significant specifically under global climate change. The altered light condition by cover materials plays an important role in the yield formation and quality accumulation of products. Although the development of innovative cover materials showed great potential to save energy and promote efficient crop production (Ahmadi et al. 2018; Mormile et al. 2019; Ntinas et al. 2019; Chavan et al. 2020), there are unanimous results on the effects of cover materials on yield and fruit quality formation in major greenhouse crops due to the lack of fundamental and systematic research.

From an engineering and energy efficiency perspective, cover materials should be engineered to reduce the high energy wavelength entering the greenhouse during the day (e.g., infrared light transmittance in summer) and to prevent long wavelength heat loss at night, while maintaining essential light levels for crop growth, development, and yield. During the insufficient light condition, the light quality, especially the blue, red light and their ratio, is considered an important role on the photosynthesis (Darko et al. 2014). An appropriate design for cover materials for the roof (balancing blue and red light) and side walls (increasing red and far-red light) could allow sufficient light to promote maximum vegetative and reproductive growth, specifically in vertical cultivation. For the covers relaying on sunlight, there is also a need to choose a balanced between the seasonal light environment during vear-round cultivation for both the short growing season crops (1-2 months, such as lettuce) as well as on the longterm growing season crops (8-12 months, such as tomato, capsicum and eggplant) depending upon the geographical locations.

At the molecular level, the effect of cover materials on the temporal and spatial expression of key genes should be carefully investigated to advance our knowledge in fruit nutrient formation and provide better nutrition values of vegetable in protected cropping. Due to the quality and shelf life of products relay on the fruit's quality accumulation in production process, light altered by cover materials on fruit development and ripening process should be focused on, such as sugar/acid and antioxidant compounds content. The literature reviewed in this paper demonstrates the vital role of light on the complexities in nutrient metabolism of climacteric and non-climacteric fruits. However, the mechanisms of red and far-red light mediated positive regulation of fruit quality and yield are still unclear, especially on the cellular signals and ion homeostasis involved in this process.

Overall, in order to deploy the advanced energy saving cover materials, more research studies on light-regulated network of photosynthesis, yield formation and nutrient accumulation should be conducted to reveal the effectiveness of cover materials on greenhouse vegetable production. An extensive collaboration of researchers in material science, photonics, plant physiology, molecular biology, and greenhouse horticulture will implement suitable cover

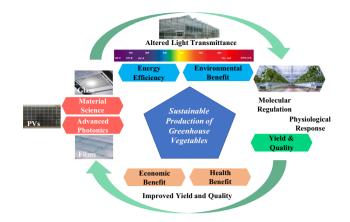


Fig. 4 The feedback loop between cover materials and horticultural sustainable production. Understanding the effects of cover materials on stable yield and nutrition formation of crops contributes to the improvement of innovative cover materials and sustainable production of nutritious vegetables with energy-saving under global climate change

materials for more sustainable protected cropping (Fig. 4). This is likely to improve the yield and quality of greenhouse vegetables for better human health and reduce carbon footprint in horticultural production.

Author contributions ZHC and DT designed research. XH and ZHC prepared the Figures and Tables. XH, ZHC, and DT wrote the manuscript with contributions from all authors.

Funding This work was supported by Horticulture Innovation Australia projects (Grant number VG16070) to D.T., Z.C., O.G. and C.C.), (Grant number VG17003) to D.T., Z.C. and (Grant number LP18000) to Z.C.. C.Z. and Y.A. were supported by the Australian Indian Institute (AII) New Generation Network (NGN) fellowship granted to D.T.. X.H. is doctoral student granted by the Hawkesbury Institute for the Environment Horticulture Innovation Australia Postgraduate Research Scholarship.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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