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OPINION



Integrating tunable LED-induced plant responses with novel solar cell technologies for energy-efficient agrivoltaic systems

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Societal Impact Statement

The increasing demand for sustainable food production requires innovative solutions that balance productivity, resource efficiency, and environmental impact. Vertical farming systems (VFSs) offer a promising approach; however, their high energy consumption remains challenging. Here, we explore the potential of integrating advanced photovoltaic technologies such as dye-sensitized and perovskite solar cells to power energy-efficient LED illumination systems in agrivoltaics. The optimization of LED spectral "recipes" to enhance plant growth and nutritional quality is introduced. Coordinated research bridging materials science, photobiology, and photophysics, along with targeted urban planning and policy support, can enable VFSs and agrivoltaics to enhance resilience in high-density urban areas.

Summary

Climate change, urbanization, and population growth urgently require the development of innovative agricultural solutions to ensure sustainable food production. Vertical farming systems (VFSs) represent a promising solution to enhance crop productivity irrespective of seasonal variations, weather conditions, or geographical constraints, while simultaneously conserving water and minimizing the use of chemical inputs. By enabling precise control over environmental factors such as radiation spectra, temperature, and CO₂ concentrations, VFS can increase crop yields through local production and improve nutritional quality by enhancing the synthesis of secondary metabolites in plants. One of the primary challenges associated with VFS is the high energy demand required for plant lighting and temperature regulation. Lightemitting diodes (LEDs) play a pivotal role in addressing this issue due to their energy efficiency and the ability to manipulate radiation spectra. The spectral quality of LED radiation can modulate distinct biological responses in plants, which may, in turn, lead

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to increased biomass production and enhanced biosynthesis of bioactive compounds with nutraceutical value. However, achieving energy sustainability in VFSs requires the integration of advanced photon-to-electron conversion technologies. Hybrid perovskite solar cells (PSCs) and dye-sensitized solar cells (DSSCs) are among the most promising technologies for addressing the energy demands of VFS. These advanced solar cells efficiently harvest sunlight to power LEDs, thereby optimizing radiation quality for plant growth while reducing dependence on external energy sources. By coupling these renewable energy technologies with VFS, the overall sustainability and efficiency of food production systems can be significantly improved, contributing to the development of resilient agricultural practices in response to global challenges.

KEYWORDS

agrivoltaics, dye-sensitized solar cells, LED, perovskite solar cells, vertical farming

INTRODUCTION

The agricultural sector is facing a complex interplay of challenges that pose significant risks to global food and nutrition security in the near future. Emerging megatrends are expected to reshape food systems, nutrition, and the sustainability of agroecological frameworks in the coming decades. Current agricultural practices are insufficient to meet the projected food demands, which may result in price volatility and heightened risks of social and political instability. Dietary shifts influenced by urbanization, demographic changes, increasing consumerism, and rising incomes will exert considerable pressure on the entire food value chain, including production, transportation, storage, distribution, and waste management systems. Per capita food demand is expected to rise, with a growing emphasis on fresh produce and plant-based foods, necessitating significant adjustments across food systems (Ruel et al., 2017; Serraj & Pingali, 2018).

The agri-food sector is both a driver and a subject of transformative change. It accounts for approximately 70% of global freshwater use (Ringler et al., 2022) and contributes around 10% of global greenhouse gas (GHG) emissions (Li et al., 2025), making it a critical factor in addressing environmental sustainability and climate change. To address these challenges, transformative agricultural practices are imperative. These practices must optimize resource efficiency by reducing water and chemical inputs, enhancing crop resilience to climatic variability and biotic stressors, and ensuring stable yields. Such adaptations are essential for developing sustainable food systems that can minimize environmental impacts while meeting global food security demands.

The future of food and agriculture is fraught with uncertainties, shaped by diverse and interconnected factors including population growth, dietary transitions, technological advancements, income distribution, resource availability, climate change, and geopolitical stability (FAO, 2018). By 2050, the global population is projected to reach 9.7 billion, reflecting an increase of approximately 18% from current levels, with a significant proportion of this growth concentrated in

developing regions. Urbanization trends indicate that 70% of the global population will reside in urban areas, compared to 55% at present, alongside substantial increases in income levels. Meeting the food needs of a more urbanized and affluent global population will require a 70% increase in food production, excluding resources allocated to biofuel production.

The agri-food system is both a contributor to and a mediator of ecosystem sustainability and climate change. Its extensive use of resources and environmental impact underline the urgency of transitioning toward sustainable practices. The system's significant role in achieving climate and sustainability goals, such as those of the Paris Agreement and net-zero targets, is widely recognized (Rosa & Gabrielli, 2023). Innovations are required to reduce the dependence of the sector on freshwater and chemicals, improve resilience to climate change and biotic threats, and enhance productivity (Decardi-Nelson & You, 2024; Herrero et al., 2020). Furthermore, year-round cultivation of crops is necessary to ensure a consistent supply of fresh products while minimizing the carbon footprint of transport and storage (Hillier et al., 2009). Addressing the challenges facing the agricultural sector necessitates a multi-pronged approach, leveraging technological advancements, sustainable practices, and systemic transformations to ensure food and nutrition security while mitigating environmental impacts. These efforts must prioritize accessibility, affordability, and ecological balance to support current and future generations.

Technological advancements, such as smart vertical farming systems (VFSs) utilizing precision technologies, have emerged as transformative solutions to address the dual challenge of enhancing agricultural productivity and improving the nutritional quality of food close to the consumers in time and space (Benke & Tomkins, 2017; Erekath et al., 2024). In addition to established practices like digital agriculture, it is essential to focus on smart agriculture implemented in urban settings, including rooftops, buildings, or repurposed warehouses in abandoned industrial areas. This approach not only prevents further soil sealing, i.e., the loss of soil resources caused by the

covering of the ground by an impermeable material, but also addresses critical issues such as declining arable land availability, water scarcity, and the increasing risks of drought and desertification exacerbated by climate change, while requalifying dismissed urban areas (e.g., former industrial sites). Indoor vertical farming is a promising method for cultivating high-value crops, including leafy greens, vegetables, and fruits, with rapid growth cycles. By adopting vertical scaffolding systems that grow crops in three dimensions instead of two, these farms enable year-round production independent of external weather conditions (Benke & Tomkins, 2017). Vertical farming significantly enhances the food supply in densely populated cities while minimizing the ecological footprint of traditional agriculture. Localized production also reduces transportation and storage costs, as growing conditions can be precisely managed near consumers (Despommier, 2013).

The resource efficiency of VFSs is particularly noteworthy. These systems utilize up to 95% less water, 90–99% fewer fertilizers, and zero pesticides as compared to conventional farming methods. Additionally, they can achieve productivity increases of up to 10 times per unit of land area, effectively expanding the availability of arable land for horticultural production (Decardi-Nelson & You, 2024; Kozai et al., 2019). Advanced automation and digital technologies, including artificial intelligence, enable real-time control of light intensity, temperature, CO_2 levels, and other environmental variables to optimize crop growth and reduce operational costs (Kaiser et al., 2024).

Furthermore, VFSs address the vulnerabilities of open-field agriculture, such as extreme weather events and pest infestations. These systems dramatically reduce the risks associated with biotic and abiotic stresses, ensuring disease-free cultivation through automated processes and limited human access. Strict cleaning protocols, including chemical and non-chemical disinfection of air, water, seeds, and materials, further enhance plant health and yield reliability (Avgoustaki & Xydis, 2020; Van Delden et al., 2021). Post-harvest contamination risks are also minimized, as controlled environments mitigate the spread of pathogens during processing (Avgoustaki & Xydis, 2020).

In addition to addressing production challenges, vertical farming supports broader sustainability goals. These systems significantly reduce water and chemical usage while contributing to climate change mitigation by lowering greenhouse gas emissions. Their ability to integrate excess heat from urban infrastructure, such as data centers, further enhances their resource efficiency (Paradiso & Proietti, 2022; Sowmya et al., 2024). Moreover, vertical farming aligns with global climate initiatives, helping to adapt agriculture to a warming planet while slowing climate change.

Recognized as one of the top urban innovations, vertical farming is already making a positive impact on urban quality of life and economic development. By facilitating sustainable, efficient food production in urban environments, VFSs represent a critical advancement in addressing the food security challenges posed by global population growth and environmental change (Harada & Whitlow, 2020; Kaiser et al., 2024; Oh & Lu, 2023; Payen et al., 2022).

In plant production factories equipped with artificial lighting and heat pump systems for environmental control, such as VFSs, electricity

constitutes a significant energy expenditure, accounting for over 28% of total operational costs (Engler & Krarti, 2021; Stanghellini & Katzin, 2024). To address this challenge, integrating solar cells made of advanced materials, such as hybrid perovskite solar cells (PSCs) or dyesensitized solar cells (DSSCs), into VFSs has gained significant attention (Lu et al., 2024). These solar cells have the dual capability of generating electricity and optimizing light quality. By harnessing sunlight, they can power heat pumps and artificial LED systems while directing specific wavelengths of light toward plants. This integration reduces dependence on external energy sources, enhances production sustainability, and offers economic benefits (Lu et al., 2024).

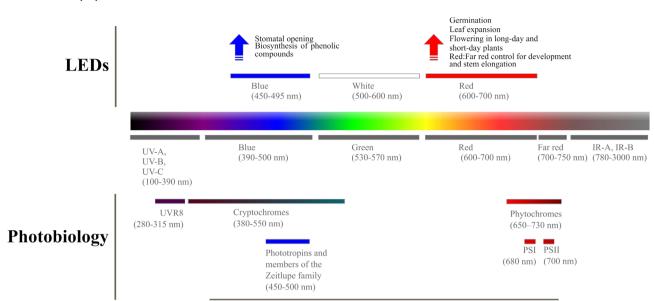
Research efforts in this domain lie at the intersection of biology, physics, chemistry, and engineering, as all these disciplines collectively influence the design, functionality, and application of solar conversion devices in agrivoltaics. Agrivoltaics, which combines photovoltaic systems with agricultural practices, enables the dual use of land for energy generation and crop cultivation (de Falco et al., 2025). Studies suggest that this emerging technology holds significant promise, particularly in regions with abundant solar exposure, and could provide strategic advantages for sustainable agriculture (Dhonde et al., 2022). In a modeling study across three different climate zones (the Netherlands, Sweden, and the UAE), plant factories were reported to deliver the best overall energy efficiency. They require 1,411 MJ kg⁻¹ of dry crop (lettuce) weight, compared to 1,699 MJ kg⁻¹ for the most optimized Swedish greenhouse. Plant factories also outperformed greenhouses in terms of CO2 emissions and land productivity (Graamans et al., 2018). Even in the challenging climate of the UAE, the net energy benefit of using natural sunlight in greenhouses outweighed the additional costs of climate control, suggesting that the abundant solar resource in the Middle East could be used to power energy-intensive indoor agriculture (Graamans et al., 2018). Advances in high-transparency perovskite materials have already demonstrated the potential for designing glass with desirable properties for agrivoltaic applications (Fu et al., 2016). Additionally, the development of radiation "recipes", in combination with LED strip arrays, can support the growth of plants with specific nutritional and morphological traits. PSCs and DSSCs can be engineered to selectively filter and transmit specific wavelengths of radiation, tailoring the radiation spectrum to meet the requirements of various plant species. This capability promotes optimal growth conditions, further enhancing the efficiency of vertical farming systems (Figure 1).

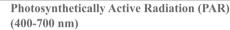
Given the energy-intensive nature of artificial lighting in VFSs, integrating advanced solar technologies offers a promising approach to significantly reducing reliance on external energy sources. By simultaneously generating electricity and optimizing the spectral quality of radiation, these systems enhance the sustainability and resource efficiency of agricultural practices (Lu et al., 2024; Figure 2). Following an overview of plant photobiology and the critical role of LEDs in optimizing plant growth and improving product quality, this discussion highlights the development and application of innovative photovoltaic technologies, such as DSSCs and PSCs, within agrivoltaic systems. These innovations demonstrate substantial potential to improve energy efficiency and promote sustainable practices in vertical farming.

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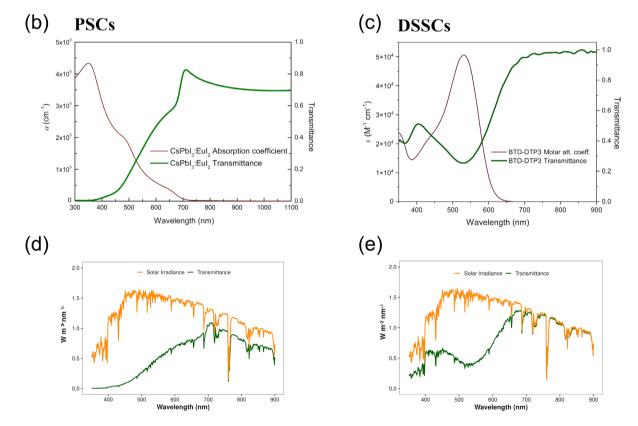


FIGURE 1 Legend on next page.

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FIGURE 1 Spectral properties and photobiological effects of different natural and LED radiation sources (a). Interactions between specific wavebands and main plant photoreceptors are reported. Arrows indicate the biological processes positively affected by blue and red wavelengths emitted by LEDs. In (b) and (c), the transmittance and absorption coefficient of solid CsPbl₃:Eul₂ perovskite photoactive layer in hybrid perovskite solar cells (PSCs) and a BT-DTP3 dye-sensitized TiO₂-based photoanode in dye-sensitized solar cell (DSSCs), respectively. In (c), the UV-vis absorption spectrum of the BTD-DTP3 dye in solution and the transmittance spectrum of the same dye adsorbed on a TiO₂ electrode in DSSCs is reported. In (d) and (e), transmitted solar spectra by PSCs and DSSCs, respectively. Solar spectra were computed using the ASTM standard G-173-03 (international standard ISO 9845-1:2022) and the reference solar spectral irradiances at air mass 1.5 (AM1.5 global) derived by SMARTS 2.9.2 (Gueymard, 2001). IR: infrared; UVR8: UV resistance locus 8; PSI: photosystem I; PSII: photosystem II; ε: molar attenuation coefficient.

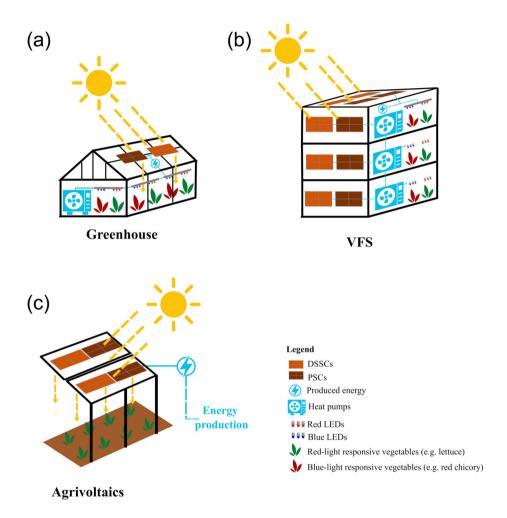


FIGURE 2 Different application examples of hybrid perovskite solar cells (PSCs) and dye-sensitized solar cells (DSSCs). In (a), greenhouses, where solar cells can be used both as cover rooftops to allow sunlight to reach the plants and as a source of energy for warming/cooling purposes; in (b), vertical farming systems (VFSs), in which solar cells can be applied on roofs and/or on the sides of the building to produce energy for the systems; in (c), agrivoltaics, in which solar cells can be used as a cover, optimizing land use by simultaneously generating renewable energy and supporting plant growth.

2 | USE OF DIFFERENT IRRADIATION SPECTRA FOR OPTIMIZING PLANT GROWTH AND METABOLISM: HOW TUNABLE LEDS MEET PLANT NEEDS

In controlled-environment agricultural systems, such as VFSs (which receive 0% natural radiation) and greenhouses (receiving 20–60% natural radiation), crop performance is governed by the interaction between three distinct attributes of radiation: frequency, quantity,

and duration. At the energy level, the light reactions of photosynthesis are driven by photons absorbed by chlorophyll a/b in photosystems II and I. Net CO₂ assimilation increases with rising photosynthetic photon flux density (PPFD) until saturation is reached (Farquhar et al., 1980). Plants use a diverse array of photoreceptors. These include photosynthetic pigment-protein complexes that harvest light energy, as well as specialized non-photosynthetic receptors that detect and respond to variations in the frequency and quantity of radiation (Mawphlang & Kharshiing, 2017; see Figure 1).

Phytochromes preferentially absorb light in the red and far-red spectral regions and are activated upon absorption of photons by the bilin chromophore (Hughes & Winkler, 2024). Beyond their roles in seed germination, shade avoidance, and regulation of flowering, phytochromes also reorganize development as the seedling emerges from the soil into ambient light conditions (Hughes & Winkler, 2024). Cryptochromes and phototropins are most sensitive to blue light, triggering hypocotyl elongation, setting the circadian phase, and regulating phototropism and stomatal opening (Christie, 2007; see Figure 1). In parallel, the UV-B photoreceptor UVR8 is activated by ultraviolet-B radiation, initiating signaling cascades that include the induction of flavonoid biosynthesis and DNA repair mechanisms, which often enhance stress tolerance (Jenkins, 2014; see Figure 1). Consequently, the spectral composition of irradiance significantly influences plant morphology, physiology, and leaf biochemistry. This contributes to the regulation of photosynthetic efficiency as well as the biosynthesis of secondary metabolites (SMs) (Darko et al., 2014). These SMs play a crucial role in protecting plants against abiotic and biotic stresses, stress signaling, growth, and development. Moreover, they significantly impact the organoleptic properties of crops and, because they have antioxidant, anti-inflammatory and neuroprotective properties, are beneficial to human health (Balestrini et al., 2021: Minutolo et al., 2023; Pagare et al., 2015). While the production of these metabolites is genetically regulated, the spectral composition of incident radiation is a key factor influencing their synthesis and accumulation in plant tissues (Menicucci et al., 2025). Furthermore, by modulating both the biochemical profile and concentration of flavonoids—which play a role in modulating auxin transport—spectral quality exerts a direct influence on the plant phenotype by inducing morphogenic responses (Loi et al., 2020; Potters et al., 2009).

Adjusting the red-to-blue irradiance ratio is considered among the most effective strategies for enhancing the concentrations of plant metabolites such as anthocyanins and carotenoids (Lobiuc et al., 2017). Red waveband (600-700 nm) promotes germination and leaf expansion and can trigger flowering in both long-day and shortday plants (Demotes-Mainard et al., 2016; Paradiso & Proietti, 2022). The integration of red light with blue light mainly enhances photosynthetic performance through a higher quantum yield of CO2 assimilation, thus facilitating growth and biomass increase (Liu & Van lersel, 2021; Paradiso & Proietti, 2022; Pettai et al., 2005). Conversely, blue radiation (400-500 nm), known to induce stomatal opening and increase CO2 transport from the leaf intercellular spaces to the chloroplasts (Loreto et al., 2009), plays a crucial role in the biosynthesis of isoprenoids (Pallozzi et al., 2013) and phenolic compounds. This process may involve longer wavelengths absorbed by cytochrome P450 in response to reactive oxygen species (ROS) accumulation (Lobiuc et al., 2017; Paradiso & Proietti, 2022). For example, carotenoid synthesis is maximized with combined red and blue radiation supplemented by far-red radiation. Best spectral combinations include blue (\sim 476 nm), red (\sim 658 nm), and far-red (\sim 734 nm) as reported by Li and Kubota (2009), as well as blue (~447 nm), red (~638-665 nm), and far-red (~731 nm) as observed by Samuolienė et al. (2016). Species-specific responses to particular irradiation

combinations have been extensively documented, emphasizing the importance of tailoring radiation spectra to achieve optimal outcomes for different plant species (Appolloni et al., 2022).

Plants are regulated not only by the spectral composition of the radiation but also by the number of photons they receive and the duration of exposure. Incident radiation is expressed as PPFD (μmol m⁻² s⁻¹), which reflects the instantaneous photon flux, and as Daily Light Integral (DLI, mol m⁻² day⁻¹), which represents the cumulative incident radiation over a 24-hour period (Korczynski et al., 2002). For leafy crops, maximum light-use efficiency is typically achieved at PPFD values ranging from 200 to 300 μ mol m⁻² s⁻¹, which corresponds to a DLI of approximately 10 to 17 mol m⁻² day⁻¹. For example, in iceberg lettuce, peak growth and resource-use efficiency were recorded at a DLI of approximately 11.5 mol m⁻² dav⁻¹, achieved through a constant PPFD of 200 μmol m⁻² s⁻¹ (Gavhane et al., 2023). By contrast, fruiting crops require significantly higher light intensity, particularly during fruit ripening. Commercial tomato production typically targets a DLI of approximately 25 mol m⁻² day⁻¹, which corresponds to a PPFD of 400 to 600 μ mol m⁻² s⁻¹ (Palmitessa et al., 2021). However, exceeding the light requirements of a given crop may result in photoinhibition, as evidenced by declines in the quantum efficiency of PSII $(\Phi PSII)$, reduced photon yield, and oxidative stress once the DLI or PPFD surpasses the optimal window. For instance, lettuce exposed to DLIs exceeding 17 mol m⁻² day⁻¹ (corresponding to approximately 800 µmol m⁻² s⁻¹ PPFD) showed diminished photochemical efficiency and reduced fresh weight (Yang et al., 2024). Thus, accurate calibration of both PPFD and DLI is essential for maximizing biomass accumulation while minimizing energy waste and avoiding photodamage. Light duration, or photoperiod, defined as the length of the light period within a 24-hour cycle, also plays a vital role in regulating plant growth and development. Photoperiod affects key physiological processes, including flowering (Song et al., 2015), tuber initiation (Sarkar, 2010), and dormancy cycles (Singh et al., 2017). Proper management of photoperiod, in conjunction with optimized radiation intensity and spectral quality, is therefore fundamental in controlledenvironment agriculture.

Light-emitting diode (LED) illumination systems offer precise control over both the radiation intensity and the spectral composition of radiation, making them invaluable for optimizing plant productivity and yield in VFSs (Folta & Carvalho, 2015; Pattison et al., 2018; Singh et al., 2015). Their ability to dynamically modulate radiation composition over time and space offers significant advantages for cultivating food crops (Lazzarin et al., 2021). From an operational perspective, a key challenge in implementing LED illumination systems is designing arrays that ensure uniform irradiance, given the different emission properties of various LED types (Wu et al., 2024). Well-designed LED illumination systems can be tailored to the specific requirements of different plant phenological stages, providing targeted stimuli to promote growth, biomass accumulation, or the synthesis of SMs (Arena et al., 2016), particularly when combined with optimal plant nutrition and environmental conditions (Trivellini et al., 2023). In terms of temporal light management, both intensity and photoperiod can be

precisely controlled using programmable LED systems. Recent advancements enable real-time dimming through high-frequency duty-cycle algorithms that maintain the PPFD at the canopy level within \pm 0.2 μ mol m⁻² s⁻¹ of the target value every second. Moreover, these advanced lighting systems can reduce energy consumption by 20 to 92% compared to fixed-output systems (Stamford et al., 2023). Furthermore, photoperiod duration is another controllable parameter. It has been suggested that the efficacy of a "long/low" strategy (i.e., extending the photoperiod to \geq 16 hours while lowering PPFD) can improve biomass accumulation and chlorophyll content by operating photosynthesis closer to its more efficient quantum yield. The low thermal output of LEDs enables photoperiod manipulation without inducing thermal stress. This allows photoperiod blocks to be scheduled during off-peak electricity hours or split into sub-daily cycles (Stamford et al., 2023).

Interestingly, empirical evidence has confirmed that dynamic LED tunability can meet crop radiation requirements while significantly reducing the energy costs of supplemental illumination in greenhouse production (van Iersel & Gianino, 2017). In terms of spectral modulation, red and blue wavelengths are widely used in indoor horticulture. These are often applied in specific ratios to elicit the targeted physiological and metabolic responses (Appolloni et al., 2022). Tailoring LED spectral "recipes" to specific requirements of different plants can maximize productivity and nutritional quality in urban vertical farming, particularly for high-value crops with higher amounts of healthpromoting compounds such as carotenoids, flavonols, and anthocyanins. Meta-analyses' findings have shown that red LED irradiation (620-700 nm) can significantly affect catalase (CAT) activity and ascorbate peroxidase (APX) activity, increasing and decreasing their activity in perennial and annual plants, respectively. However, it can also reduce shoot length by 63% and carotenoid content by 37% compared to white fluorescent light (400-700 nm) (Ma et al., 2021). Conversely, blue LED irradiation (450–495 nm) increased anthocyanin content by 68%, but negatively affected leaf area (by 73%), shoot dry weight (by 37%), and length (64%) (Ma et al., 2021). Notably, a 1:1 red-to-blue ratio was particularly effective, increasing dry weight by 161% (Ma et al., 2021). Furthermore, manipulating the light spectrum provides a strategy to enhance plant

immunity by improving tolerance to pathogens and insects. Low doses of UV-B radiation (290-315 nm) may activate pathways related to salicylic and jasmonic acids, and prime defense against plant pathogens, in a species- and genotype-dependent manner (Demkura & Ballare, 2012; Meyer et al., 2021). However, it should be noted that in most VF systems based on LEDs, UV-B wavelengths are typically absent from the light environment to save energy and avoid surface damage risks. At high doses, UV-B becomes detrimental, causing photo-oxidative stress, growth retardation, and morphological changes (Meyer et al., 2021). By contrast, low levels of UV-B normally drive phenylpropanoid and flavonoid biosynthesis (e.g., flavonols, anthocyanins; Jenkins, 2014). In the complete absence of UV-B, plants may be affected by a shade-like syndrome, developing longer hypocotyls/internodes, reduced branching, lower leaf thickness, and altered root: shoot ratios (Liang et al., 2019; Robson et al., 2015). In line with this, it has been suggested that including low doses of UV-B into tailored radiation "recipes" for plant development can help to both maintain compact phenotypes as well as improve the contents of antioxidant compounds (Weiland et al., 2023; Zhu et al., 2025).

Similarly to low doses of UV-B, a high red/far-red ratio activates plant defense signaling pathways, including those mediated by jasmonic acid and salicylic acid (dos Nascimento et al., 2020; Lazzarin et al., 2021; Lee et al., 2016; Stratmann, 2003). In summary, there is extensive evidence that blue radiation primarily regulates plant morphology and the biosynthesis of antioxidant flavonoids, while red radiation drives photosynthetic carbon gain. Moderate supplementation with far-red radiation (15–25%) can increase canopy photon capture and biomass synergistically. However, when the threshold for triggering shade-avoidance responses is exceeded, biomass productivity declines (Table 1).

3 | ENERGY DEMAND AND MITIGATION MEASURES IN LED-EQUIPPED VFSS AND GREENHOUSES

In VFSs, electricity accounts for approximately 30% of total operational costs (Arcasi et al., 2024). Within a typical VFS energy budget,

TABLE 1 Summary of the main physiological and developmental responses of crops to blue (400–500 nm), red (600–700 nm), and far-red (700–750 nm) wavebands.

Spectral waveband	Main targets	Typical plant responses
Blue (400- 500 nm)	Cryptochromes and phototropins	High B:R: Stomatal opening; deetiolation and photoperiodic flowering control; increase in content of flavonoids, anthocyanins, isoprenoids; reduction in biomass, leaf area, shoot length when blue fraction > 30%; seed germination inhibited in cereals via CRY1-mediated ABA accumulation
Red (600-700 nm)	Phytochrome B and photosystems	High R:FR: Increase in biomass and dry matter, especially at 80–95% R; promotion of stem/root growth; delays of shade-avoidance; increase in carotenoid content; delays flowering; enhanced nitrogen assimilation
Far-red (700- 750 nm)	Phytochrome A and shade- avoidance related pathways	Low R:FR: Increase in internode length; leaf expansion; acceleration of flowering in long-day species; high FR beyond threshold triggers shade-avoidance (elongation, reduced leaf thickness) and can weaken JA/SA-mediated defense

Data are from Fantini and Facella (2020) for wavelengths in the blue spectral region (cryptochrome-mediated effects) and from Demotes-Mainard et al. (2016) for red and far-red (phytochrome-mediated effects). CRY1: cryptochrome circadian regulator 1; JA: Jasmonic acid; SA: salicylic acid.

electric lighting is the main power consumer, accounting for about 65-85% of total usage (Arcasi et al., 2024; Engler & Krarti, 2021). In this context, LEDs have demonstrated advantages over traditional white fluorescent lamps, allowing enhancement of plant performance and reducing energy consumption. Compared to high-pressure sodium (HPS) lamps and fluorescent systems, LEDs can reduce lighting-related energy costs by over 50% (Nelson & Bugbee, 2014). For instance, replacing HPS lamps with blue, red/blue, or red LED arrays has been shown to reduce annual electricity costs. Red/blue LEDs, for example, can lower costs from approximately \$210 m⁻² to \$144 m⁻² (Stamford et al., 2023). Further efficiency gains can be achieved by incorporating additional spectral channels. Including far-red, blue, and, to a lesser extent, green wavelengths can enhance yields with only a modest increase in costs while reducing electricity use by 0.6% to 4% across trials (Stamford et al., 2024), effects attributed to energy use (Stamford et al., 2023). It has recently been proposed that specific farred or blue supplementation could increase yield per kilowatt-hour by up to 40% under UK electricity prices in 2022 (Stamford et al., 2023). These findings emphasize the vital role of optimizing the LED spectrum and enabling real-time tunability in advancing both the sustainability and economic viability of modern controlled-environment agriculture.

Experimental trials in *Eruca sativa* further demonstrate the potential of light scheduling for energy optimization. Using a sinusoidal radiation intensity profile (peaking at PPFD = 250 μ mol m⁻² s⁻¹) to deliver the same DLI rather than a conventional square-wave pattern increased edible biomass by ~20%, improved photochemical efficiency, and reduced non-photochemical quenching during the latter part of the day (Stamford et al., 2024). This supports the use of dimmable LED illumination systems, which allow for the real-time optimization of the spectrum, intensity, and diel patterns. This ultimately enhances physiological efficiency while reducing operational costs in fully enclosed vertical farming systems.

However, lighting accounts for only a portion of the overall energy demand in VFSs and greenhouses. Due to the minimal radiant heat produced by LEDs, additional energy must be allocated for active heating and dehumidification, particularly during the colder seasons. In VFSs, heating, ventilation, and air-conditioning (HVAC) systems account for an additional 10-20% of total energy use, while aircirculation fans contribute less than 1% (Arcasi et al., 2024). Furthermore, although HVAC represents the second-largest energy load in plant factories such as VFSs, modeling studies have demonstrated that it can become the primary energy consumer in greenhouses (Harbick & Albright, 2016). The climate zone plays a critical role in determining the energy demand related to HVAC systems. In warmer regions, HVAC systems may account for up to 50% of the total operational costs, whereas in extreme or northern climates, this can rise to 70-85% (Iddio et al., 2020). To mitigate these thermal energy demands, the integration of solar-assisted heat pumps has been proposed. Such systems have demonstrated the potential to reduce electricity consumption for climate control by 18-30% (Engler & Krarti, 2021), offering a practical strategy to enhance the energy efficiency of indoor crop production facilities.

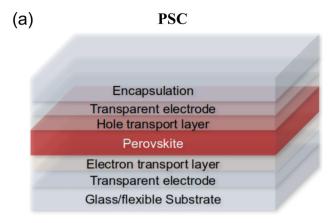
ENHANCING HIGH-VALUE CROP 4 | PRODUCTION THROUGH THE INTEGRATION OF LEDS AND ADVANCED PHOTON-TO-ELECTRON CONVERSION **TECHNOLOGIES**

One of the most promising strategies for meeting the high energy demands of VFSs and greenhouse facilities is to integrate solarassisted photovoltaic systems. The integration of high-efficiency LEDs with advanced photon-to-electron conversion technologies represents a promising approach for the optimization of plant growth and SM production while reducing energy-related operational costs. Third-generation solar cells emerged as promising solutions for innovative photon-to-electron conversion systems with potentially high solar-to-light power conversion efficiency (Murakami & Koumura, 2019; Yun et al., 2018). Unlike conventional silicon-based and thin-film solar cells, third-generation technologies such as DSSCs and hybrid PSCs offer the advantage of lower processing costs in advancing the PV sector (Yun et al., 2018). These solar cells are comprised of similar structures with two charge-extracting materials sandwiching a photoactive region. They work on the principle of photosynthesis since dye molecules and perovskite film replace the light-yielding element (chlorophyll), with electrons promoted into excited states after photon absorption. Photoexcited electrons and holes are separated and transferred to an electron-transporting layer (photoanode) and a hole-transporting layer (counter electrode), respectively, generating the required potential difference to produce an electric current. The light-harvesting photoactive material can be a metal-free or an organometallic dye in DSSCs, while in PSCs, inorganic or hybrid metal halides are used (Shah et al., 2023; Figure 3).

DSSCs and PSCs are particularly well-suited for agricultural applications due to their complementary properties. DSSCs allow for customizable radiation absorption using specific sensitizers, enabling spectral properties to be tailored to the needs of different plant species (Lu et al., 2024). Their semi-transparent design and efficient performance under different radiation conditions make them versatile options for integration into greenhouse covers or vertical panels (Fu et al., 2016). Although DSSCs are less efficient in terms of photovoltaic performance compared to other technologies, their scalability, stability, and adaptability confer significant benefits for large-scale agricultural deployment (Dhonde et al., 2022). Conversely, PSCs have achieved record-breaking photovoltaic efficiencies, surpassing traditional silicon-based solar cells (Machín & Márquez, 2024). In addition, the use of DSSCs and PSCs for green electricity generation to power LEDs offers a competitive advantage over commercial solar cells, since colored, lightweight, and semi-transparent devices that operate in a wide range of irradiation conditions do not suffer from the angular dependence of incident radiation and can be produced on rigid glass or flexible plastic substrates (Xue et al., 2018). By integrating DSSCs and PSCs for renewable electricity generation, horticultural systems gain a competitive edge over traditional solar energy technologies. The ability to customize light quality, enhance sustainability, and reduce energy costs underscores the transformative potential of

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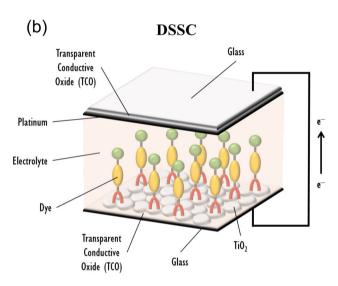


FIGURE 3 Schematic representations of a hybrid perovskite solar cell (PSC) (a) and a dye-sensitized solar cell (DSSC) (b).

these advanced photovoltaic solutions in promoting the growth of high-value crops enriched with bioactive compounds in greenhouse conditions, VFSs, and agrivoltaics (Figure 2).

The successful integration of these technologies into agricultural systems requires weighing their pros and cons. Since their first appearance in the literature in 1991 (O'Regan & Grätzel, 1991), DSSCs have been distinguished by their unique aesthetic properties, such as color, which can be modulated according to the photosensitizer used, and semitransparency. These characteristics make DSSCs an attractive option for building-integrated photovoltaics (BIPVs) (Barichello et al., 2024; Muñoz-García et al., 2021). The essential role of the dye in DSSCs is to harvest solar radiation and initiate the electron transfer process that generates a clean electric current. By selectively modifying the dye structure, it is possible to fine-tune both the absorbed and transmitted radiation, making DSSCs particularly wellsuited for systems requiring specific spectral compositions, such as agrivoltaics (La Notte et al., 2020; Lu et al., 2024). Most of the existing literature published on DSSCs in agriculture has studied the quality of different vegetable species using commercial dyes not specifically

designed for agricultural purposes. Studies have investigated the effects of DSSC-shielded solar radiation panels, containing commercial organometallic dyes such as Z907, on crops grown in greenhouses, including tomato (Ntinas et al., 2019), Orthosiphon stamineus (Roslan et al., 2021), coleus (Solenostemon scutellarioides) (Park et al., 2024), and petunia (Kim & Oh, 2024). These studies assessed various plant characteristics, including morphological features, as well as physiological and physicochemical parameters, and antioxidant capacity. In many cases, DSSCs proved beneficial effects by shading plants, reducing greenhouse temperature, and increasing the production of phytochemical compounds. When the light filtered through DSSCs was insufficient for proper growth and morphology, the deficiency was mitigated by supplementing with specific LED wavelengths tailored to the plant requirements (Park et al., 2024; Kim & Oh, 2024). Similarly, moderate shading under field conditions, such as that provided by elevated solar panel arrays, has been shown to enhance crop performance in hot, dry, high-irradiance environments. This improvement has been attributed to multiple physiological benefits, including: (i) reducing leaf and soil temperatures, thus reducing stomatal closure and photoinhibition; (ii) decreasing evaporative water loss, contributing to improved soil moisture; and (iii) extending the growing season by mitigating thermal extremes (Barron-Gafford et al., 2019).

Despite these advancements, further progress requires modifications to DSSC designs and materials. Some researchers have adapted the DSSC architecture of the cell (Barichello et al., 2021) by altering parameters such as TiO₂ layer thickness or the sealing method. Others have explored alternative chemical structures of the photosensitizers to replace commercial Ru-based dyes (Kim et al., 2014) and organic, metal-free molecules, such as di-carbazole-based dves (Chalkias, Charalampopoulos, Aivali, et al., 2021), triphenylamine-based dyes (Chalkias, Charalampopoulos, Andreopoulou, et al., 2021), and hydrazonothiazole-based dyes (Badawy et al., 2023). One of the major challenges is to achieve compatibility between DSSCs and PPFD in agrivoltaic systems. Despite significant advances in DSSC technology, there is still a lack of comprehensive studies investigating plant development, SM production, and plant molecular responses under light filtered by these devices. The selection of dyes such as thiazolo[5,4-d] thiazole- (Dessì et al., 2020) and dithienopyrrole-based (Dessì et al., 2021) photosensitizers that balance transparency with the absorption spectra of key plant photoreceptors while maintaining high photovoltaic performance is critical to overcoming this limitation.

The introduction of metal halide PSCs has marked a significant turning point in the development of third-generation photovoltaic technologies (Giuri et al., 2024). The exceptionally high photovoltaic performances, with laboratory efficiencies exceeding 27% (Park et al., 2023; https://www.nrel.gov/pv/cell-efficiency.html), coupled with the low-temperature processing, easy bandgap modulation across the entire visible spectrum, and the capability to manufacture highly efficient semi-transparent devices, have unlocked a wide range of applications, from building-integrated photovoltaics to agrivoltaics (Bati et al., 2023; Kim et al., 2025). The general crystal structure of 3D perovskite is ABX3, where the different constituents

(e.g., A = Cs, $NH_2CH_2NH_3$ (FA) or CH_3NH_3 (MA), B = Sn, Pb, and X = I, Br, or CI) can be modified by simply varying the composition of the material. Changing the halide from I to Br and then to Cl widens the optical band gap and induces a blue shift in the absorption properties of the material. This shift results from increased ionization potential (Li et al., 2016), allowing the bandgap and therefore the color of the material to be changed across the entire visible spectrum from 420 to 800 nm. Importantly, mixed halide compositions can be designed to achieve fine control of the absorption properties (Correa-Baena et al., 2017). Higher band gap perovskites do not absorb the red and IR part of the solar spectrum, whereas low band gap perovskites can shield solar radiation up to the NIR region. It is noteworthy that perovskite materials can easily achieve high transmittance and light-harvesting efficiency. This tunability allows the material to be adapted to the specific requirements of different crop species or climatic conditions. In this respect, the ability to modify both the transmitted frequency and the transmitted light while maintaining high photovoltaic performance is advantageous for agrivoltaics applications in general and vertical farming in particular. The feasibility of fabricating PSC layers at temperatures below 120°C allows their implementation on plastic and flexible substrates. PSCs can be integrated into VFSs through complementary technology schemes. They can act as sunlight energy converters to power LEDs tailored for plant illumination and/or directly generate energy while filtering sunlight. A recent study by Spampinato et al. (2025) demonstrated, on a small scale, the potential of integrating semi-transparent CsPbl₃:Eul₂ PSCs into greenhouse roofs to enhance seedling growth while simultaneously generating clean energy for energy self-sufficiency, paving the way for scalable, cost-effective agrivoltaic solutions. To support this applicative field, the durability of the photovoltaic rooftop must be ensured through perovskite stabilization (Alberti et al., 2021), and the concern about possible Pb release into the soil needs to be mitigated with focused actions (Valastro et al., 2022).

Last but not least, quantifying the investment required for integrating PSCs or DSSCs remains challenging, as it is closely tied to the production costs of the chosen technology. These costs depend on several factors, including the kind of substrate, the solar cell architecture, the materials employed, and the fabrication methods used for each layer, such as solution processing or physical vapor deposition (Smecca et al., 2021). Recent studies estimate the manufacturing cost of perovskite solar modules at approximately \$0.57 W⁻¹ (Liu et al., 2025), based on a production capacity of 100 MW year⁻¹. For dye-sensitized solar modules, too, the price-per-watt could vary a lot (PCE: 7%; process output yield 90%) (Fakharuddin et al., 2014) to \$0.18 W⁻¹ (Syed & Wei, 2022). These average prices are higher than those of conventional silicon PV modules, which currently range between \$0.10 and \$0.20 W⁻¹. It is important to note that the production costs of PSCs and DSSC modules can vary, and potentially increase, depending on the geographical location, due to differences in infrastructure, labor, materials, and equipment costs. In some cases, higher production costs may also reflect enhanced product quality and long-term reliability. In the context of greenhouse applications,

for example, the elevated cost of perovskite and dye-sensitized modules compared to traditional silicon technology may be justified by their unique semitransparency and color, which in theory, allows for dual land use by enabling crop cultivation beneath the solar panels without the typical limitation on the roof coverage for Si-based panels (Dupraz, 2024). Spampinato et al. (2025) estimate that semitransparent perovskite solar cells installed on greenhouse rooftops can achieve a production capacity of 243 kWh m⁻², sufficient to meet the energy demands of both high-energy-intensity greenhouses (83-222 kWh m⁻²) and low-energy-intensity greenhouses (1-5 kWh m⁻²). As a general comment, it is important to note that the costs of perovskite solar modules will decrease by increasing the production capacity toward the GW scale. Similar considerations can be made for DSSCs, with production costs that can be reduced by moving to larger scales and optimizing the materials used (conductive glass, sealing, etc.). For vertical farming applications, Arcasi et al. (2024) conducted a comparative analysis of energy requirements for lettuce cultivation in vertical farms under varying climatic conditions. Their findings indicate that energy consumption in Riyadh reaches 10.1 GWh per year, approximately 86% higher than in Stockholm and 38% higher than in Naples. In this context, PSCs and DSSCs offer a solution to partially offset energy demands, as they can be integrated into multiple surfaces of vertical farming structures, including rooftops and facades, due to their compatibility with both glass and flexible substrates.

However, in this scenario, and especially under open-field or greenhouse cultivation, one of the key benefits of new-generation agrivoltaic systems is the ability to integrate semitransparent photovoltaic technologies (PSC/DSSC) directly above or within the crop area without requiring additional land use. The land dual-use model is a crucial advantage over technologies such as wind turbines or biomass plants, which typically demand separate land allocation and often present greater visual, environmental, or logistical impacts (Porté-Agel et al., 2020). For instance, wind infrastructure may be infeasible in certain agricultural settings due to turbulence, noise, and shadow flicker, while biomass systems require continuous feedstock supply and significant space for processing and storage, potentially conflicting with farming operations.

As for VFSs, which typically occur in indoor, controlled environments, PSCs present significant advantages over other renewable sources. Unlike wind or biomass, which cannot be directly implemented within an enclosed VF facility, PSCs can be integrated into building facades, rooftops, or even as part of the glazing systems due to their lightweight, flexible, and semitransparent properties (Rahmany & Etgar, 2020). On the other hand, greenhouse-based agrivoltaic systems using PSCs face several challenges, inherent to the PSC technology itself and related to its integration with plant cultivation. Key issues include the limited long-term stability of PSCs (Zhu et al., 2023), the presence of toxic Pb in their composition (Li et al., 2020), and issues related to cost sustainability. Additionally, the impact of PSC-filtered light on crop growth and agronomic performance requires further investigation through dedicated and targeted experiments. It is essential to optimize the spectral characteristics of perovskite materials, such as their light absorption and

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transmission properties, through composition engineering to suit the specific needs of different crop types. Since various plants respond differently to specific wavelengths of light, tailoring the perovskite composition and optical profile to match the photosynthetic and developmental requirements of the cultivated crops is crucial for maximizing both agricultural productivity and energy generation in agrivoltaic systems.

A comparable argument can be made regarding DSSCs: this technology can be well-suited to agrivoltaic applications in greenhouses thanks to its remarkable aesthetic properties, which can be easily modulated by changing the dye structure inside and the electrolyte nature. DSSCs do not contain toxic or environmentally harmful elements and can be easily integrated into both the roof and facades of the greenhouse and cover it completely, unlike traditional silicon technology or other renewable sources, such as wind and biomass, which require dedicated spaces. Unfortunately, at the current state of research, production costs are still an issue for large-scale applications, as well as the long-term stability of the sealing and the cell components (ranging from months to a few years). Moreover, like PSCs, there are no materials that have light absorption properties that are universally suitable for every crop: theoretically, it would be necessary to customize the dye and electrolyte for each specific plant species, as well as optimize the transmittance level of conductive glasses and semiconductors. In other words, DSSCs and PSCs can play a pivotal role in semi-transparent building-integrated photovoltaics, especially in VFSs and agrivoltaics, as an alternative to silicon-based technology, but extensive optimization work on the light-absorbing properties of the materials employed is still necessary to tailor them to specific applications.

5 | CONCLUSIONS

The integration of VFS with advanced photovoltaic technologies, such as DSSCs and PSCs, represents a significant step toward sustainable food production. However, several challenges must be addressed to fully realize the potential of these systems. One of the most critical factors for successful VFS implementation is energy efficiency. While LEDs are essential for tailoring radiation spectral quality to optimize plant metabolic and physiological responses, artificial lighting systems account for a significant proportion of VFS energy consumption. Advanced LED technologies capable of realtime spectral tunability enable the dynamic modulation of radiation spectra, allowing for the delivery of customized radiation "recipes" tailored to the specific requirements of plant species and growth stages. This innovation has the potential to significantly improve the balance between energy consumption and plant productivity in VFS, contributing to more sustainable and resource-efficient cultivation practices. In addition, integrating renewable energy technologies, particularly DSSCs and PSCs, offers a promising solution to meet the energy demands of VFS. DSSCs, while highly adaptable, show lower efficiencies compared to PSCs and conventional solar technologies. To maximize their potential, careful optimization of dye structure

and light transmission properties is essential, ensuring compatibility with the spectral requirements of plants. These advancements can enable DSSCs to contribute more effectively to energy-efficient and sustainable VFS operations. PSCs offer high performance for energy generation, with potential energetic self-sustainability for greenhouses and vertical farming, but challenges related to their longevity and environmental safety remain significant. A primary concern is the presence of lead, which poses environmental and health risks. To mitigate this issue, efforts are underway to develop advanced encapsulation materials or lead-adsorbing materials (Valastro et al., 2023) that prevent lead leakage. Additionally, the exploration of lead-free alternatives is required to reduce these problems. Beyond safety, improvements in the long-term durability and performance of PSCs under different environmental conditions are necessary to support their broader application. Advances in perovskite materials will play a critical role in overcoming these limitations. Enhancements in material stability, the development of recyclable components, and innovations to extend device lifespan are key areas of focus. Concurrently, the dynamic nature of plant responses to radiation must be integrated into broader crop management decisions. Factors such as radiation intensity, duration, and interaction with other environmental parameters, such as rising temperatures and elevated CO2 concentration, profoundly influence the effectiveness of the spectral adjustments. The integration of far-red and UV radiation will also be important to both improving plant resilience against environmental stresses and modulating secondary metabolism, increasing the production of antioxidant compounds. Bridging gaps in materials science, environmental safety, plant physiology, and device scalability will require coordinated research efforts. In summary, with continued technological advancements and strong policy and research support, agrivoltaics solutions hold high potential to address critical global challenges. They can significantly contribute to food security, environmental sustainability, and climate resilience in a changing world.

AUTHOR CONTRIBUTIONS

A.D., C.S., F.S., S.V., A.G., J.-P. S., A.A., and R.B., planned and designed the manuscript. A.D., C.S., F.S., and S.V. wrote the first version of the manuscript. A.D., C.S., F.S., S.V., M.C., C.B., A.G., J.-P. S., G.R., A.R., A.A., and R.B. contributed to the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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