Viewpoint

Harnessing microbes as sun cream against high light stress

Summary

Plants rely on solar energy for growth through photosynthesis, yet excessive light intensity can induce physiological damage. Despite the considerable harm, inadequate attention has been directed toward understanding how plant-associated microorganisms mitigate this stress, and the impact of high light intensity on plant microbial communities remains underexplored. Through this Viewpoint, we aim to highlight the potential of microbial communities to enhance plant resilience and understand how light stress can shape plant microbiome. A full understanding of these dynamics is essential to design strategies that take advantage of microbial assistance to plants under light stress and to effectively manage the impact of changing light conditions on plant–microbe interactions.

Light stress and plant microbiome

Sunlight fuels plant photosynthesis and serves as a temporal and seasonal indicator. Variations in light intensity and quality, influenced by weather and seasonal changes, are posing challenges to plant adaptation (Roeber *et al.*, 2021). Plants utilize two distinct systems, photoreceptors and chloroplasts to perceive environmental light, both crucial in regulating plant stress responses. Depending on light availability, plants modify grana structure and Chl ratios to optimize photosynthesis and shield the photosynthetic apparatus from high light intensities, ensuring efficient functioning by maximizing photosystem electron transport fluxes and minimizing fluorescence dispersal (Walters, 2004; Waters & Langdale, 2009).

Light is crucial for photosynthesis and varies in intensity and spectral quality, and unsuitable light conditions cause significant stress in plants (Fiorucci & Fankhauser, 2017). Low light limits growth by reducing energy availability, while high light intensity can lead to photodamage (Shi *et al.*, 2022) and photoinhibition, causing a rapid decline in photosynthetic efficiency (Shi *et al.*, 2022).

Given the damaging effects of abiotic stresses on plants, the scientific community increasingly emphasizes the crucial role of the plant microbiome (Sandrini *et al.*, 2022). It comprises a diverse array of microorganisms, which intimately coexist with plants as ecto- or endophytes (Alsanius *et al.*, 2019). Plant-associated microorganisms play crucial roles in supporting plant health and growth through various plant growth-promoting (PGP) mechanisms such as enhancing mineral solubility, modulating phytohormone signaling (such as auxin, cytokinin and gibberellin) and providing nutrients (Bakker *et al.*, 2013; Fadiji *et al.*, 2023). For instance, plant growth-promoting bacteria (PGPB) can enhance plant tolerance to a wide range of environmental stresses, such as salt or water stress (de Souza *et al.*, 2015). These beneficial bacteria, which include genera like *Pseudomonas*, *Bacillus* and *Azospirillum*, colonize the plant's rhizosphere or phyllosphere, establishing intimate interactions that promote plant health and resilience improving nutrient uptake, regulating growth hormones and mitigating stress damage (de Souza *et al.*, 2015; Fukami *et al.*, 2018). In nature, microorganisms commonly form a biofilm matrix mainly composed of extracellular polymeric substances, both at the root and leaf level, with a role of protection to biotic and/or abiotic stressful factors (Flemming *et al.*, 2016). This is particularly true for the upper epidermal layer of the leaf area, an inhospitable environment with high-stress conditions (e.g. UV rays, desiccation), limited shielding effect, lack of a thick cuticle and limited nutrient availability (Haworth & McElwain, 2008; Karabourniotis *et al.*, 2021). Biofilms have been demonstrated to be crucial for the phyllosphere microbiome structure and dynamics contributing to the leaf health and resilience (Chaudhry *et al.*, 2021; Vincent *et al.*, 2022). Biofilm formation, combined with pigment production, serves as an effective defense strategy for microorganisms against light stress (Marín-Sanhueza *et al.*, 2022). Recently, biofilm-forming PGPB, such as *Pseudomonas* spp., *Bacillus* spp. and *Acinetobacter* spp., have garnered increasing interest in agriculture. Their ability to form biofilms has been shown to enhance plant growth and yield in their hosts (Li *et al.*, 2024).

Recent findings have highlighted the pivotal role of plant–microorganism interactions in the evolution of modern plants, during the process of terrestrialization *c.* 450 million years ago. In this context, two key symbiotic interactions played significant roles: arbuscular mycorrhizal (AM) symbiosis and lichenization. Evolutionarily, lichens represent the first example of how microbes can help photosynthetic organisms to cope with light stress. They played a crucial role in the terrestrialization of chlorophytic algae (Puginier *et al.*, 2022). Specifically, in lichens, the algal component resides within the structure of compact fungal hyphae, forming a protective layer known as the lichen upper cortex, that acts as a barrier against harmful UV-B radiation (Puginier *et al.*, 2022). The link between the photosynthetic compartment of plant cells (i.e. chloroplasts) and the plant-associated microbiome is well established. Chloroplasts are involved in the production of several metabolites serving both for defense against biotic stresses or for microbe recruitment (e.g. root exudate compounds such as

flavonoids, malic acid and strigolactones; Sasse *et al.*, 2018). Additionally, a direct link between ROS stress alleviation and specific microbial taxa has been reported (Asha *et al.*, 2021). The evidence suggests that the cooperation between microbes and the photosynthetic compartment of plants has been maintained over the evolution.

On the contrary, AM symbiosis played a vital role in the terrestrialization of embryophytes (Bonfante & Genre, 2008; Humphreys *et al.*, 2010; Puginier *et al.*, 2022). In this symbiotic interaction, the plant's roots form an intimate association with fungal hyphae, forming specialized structures called arbuscules. Currently, research has predominantly emphasized the interactions between plants and microorganisms, including AM symbiosis, under abiotic stresses like salinity or water deficit (Fadiji *et al.*, 2023), while overlooking the potential effects of such interactions under light stress conditions. Understanding how these relationships can significantly enhance plant resilience to light stress through the identification of microbial strains capable of providing support for plants is a relevant point that is to be still addressed.

Exploring the synergy between abiotic stress responses and beneficial microbes: An overview

The environment in which plants dwell is subject to constant changes, impacting their development and fitness. Various abiotic factors such as drought, salinity, extreme temperatures and radiation can dramatically hinder plant growth and development (Yang *et al.*, 2019). For instance, drought stress can affect plants at various stages, influencing water intake and enzymatic changes in cell walls, thus hindering growth (Dos Santos *et al.*, 2022). Similarly, salinity induces osmotic stress and ionic toxicity, hindering nutrient absorption and damaging cell membranes (Sytar *et al.*, 2019; Ahmad *et al.*, 2023). Furthermore, under field conditions abiotic stresses are often combined, affecting various physiological systems, including respiration, photosynthesis and sugar metabolism, thus reducing agricultural productivity (Taylor *et al.*, 2009; Galani *et al.*, 2022; Kopecká *et al.*, 2023).

Plants have evolved biochemical and molecular strategies to mitigate the detrimental effects of abiotic stressors and many of them are influenced by associated microbes. These last can in fact alter the level of phytohormones such as cytokinins, gibberellins and auxins, altering root morphology and enabling plants to withstand harsh climates and stressors like heavy metals, salinity, drought and nutrient deficiencies (Egamberdieva *et al.*, 2017; Kopecká *et al.*, 2023). For instance, several studies have reported that the inoculation of plants with plant growth-promoting rhizobacteria (PGPR) capable of producing the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase might be considered as useful strategy to mitigate the abiotic stress. This enzyme catalyzes the conversion of ACC, a precursor of ethylene, into alpha-ketobutyrate and ammonia, reducing ethylene levels and stress effects (Saleem *et al.*, 2007). PGPR that produces ACC deaminase can increase *Vitis vinifera L.* resistance to water deficiency conditions (Duan *et al.*, 2021). As reported into the study, two PGPR strains, *Pseudomonas corrugata* (DR3) and

Enterobacter soli (DR6), were tested in pots. The results showed that vine plants inoculated with ACC-producing strains exhibited significant improvements in plant height, shoot and root biomass, relative water content, and net photosynthetic rate of leaves, enhancing their ability to withstand drought (Duan *et al.*, 2021). Similar results have been reported also in other crop species such as *Zea mays* L. (Ojuederie & Babalola, 2023), Solanum *lycopersicum* L. (Gowtha*m et al.*, 2020) and *Brassica juncea* (Khan *et al.*, 2023).

Plant-associated microbes play a crucial role in symbiotic interactions throughout the entire plant life cycle, thus making them particularly beneficial in cases of environmental stressors. In this line, looking at the belowground interactions with beneficial microbes, AM symbiosis, is the most studied example of ancient symbiotic relationship for *c.* 80% of land plant species (Lee *et al.*, 2013). Nowadays, the scientific community increasingly recognizes the importance of the synergistic interactions among diverse microorganisms in supporting plant growth. For instance, different bacteria can enhance nitrogen fixation, while fungi can boost phosphorus availability (Harman *et al.*, 2021). When these microorganisms are used together, forming consortia so-called synthetic communities (SynCom), they can synergistically improve plant growth and health by complementing each other's functions and mitigating the weaknesses associated with using a single strain (Harman *et al.*, 2021; Nerva *et al.*, 2022; Poppeliers *et al.*, 2023).

How microorganisms could help plants under high light conditions

Under high light conditions, photosystem II (PSII) is particularly vulnerable to inactivation, a phenomenon known as PSII photoinhibition (Shi *et al.*, 2022). PSII-LHCII supercomplexes are especially prone to damage under high light, with previous research indicating that direct absorption of light quanta leads to the release of manganese ions (Mn^{2+}) and destruction of manganese clusters. This disruption compromises the integrity of the PSII reaction center (Huang *et al.*, 2013). Additionally, both PSII and photosystem I (PSI) produce reactive oxygen species (ROS), causing oxidative damage to chloroplasts and inhibiting PSII repair by suppressing D1 neo synthesis (Fig. 1; Pospíšil, 2009). Moreover, high light intensity is associated with high levels of potentially harmful UV-B radiation. While the ozone layer filters out much of the UV-B component, the remaining UV-B reaching the Earth's surface can damage macromolecules such as DNA and proteins in plants, leading to ROS accumulation (Demarsy *et al.*, 2018). UV-B exposure also disrupts manganese clusters, exacerbating PSII photoinhibition (Takahashi *et al.*, 2010; Takahashi & Badger, 2011; Demarsy *et al.*, 2018).

Under light stress, microorganisms can provide directly or indirectly support to improve plant resilience. Similar to their protective roles during salt or water stress (Fadiji *et al.*, 2023), we hypothesize that, under high light exposure, microorganisms in the rhizosphere and phyllosphere may have the ability to modulate the synthesis of phytohormones, such as abscisic acid (ABA), and other secondary metabolites (e.g. antioxidants), helping plants to face light stress events (Ren *et al.*, 2019). This
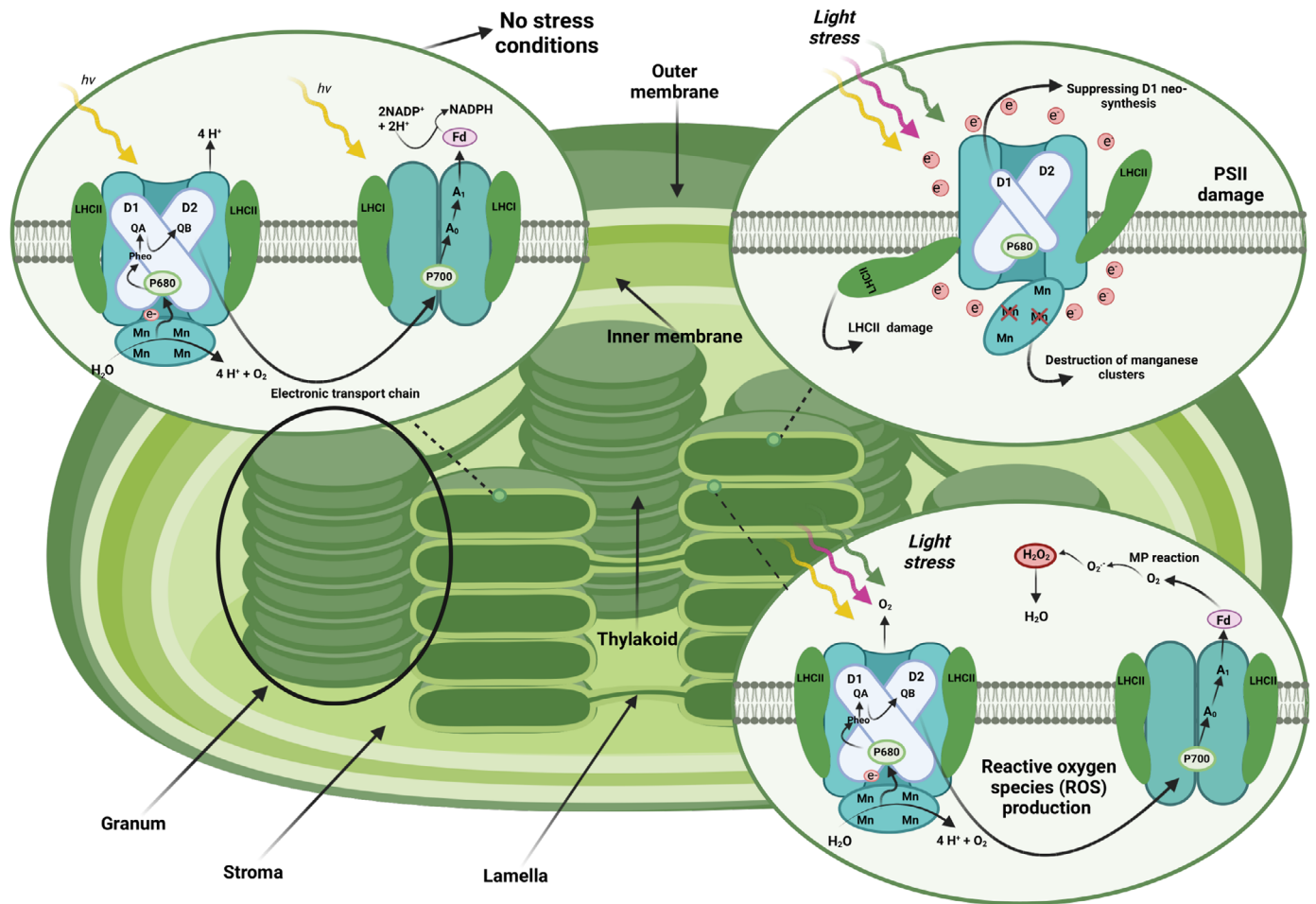
Fig. 1 Overview of the effect of light stress on the photosynthetic activity and photosystems. On the left-hand side, a description of photosynthetic activity under nonstress conditions. On the right side, what happens under light stress. As can be seen on the top right, light stress causes damage to photosystem II, in particular PSII-LHCII supercomplexes are especially prone to damage under high light, with previous research indicating that direct absorption of light quanta leads to the release of manganese ions (Mn^{2+}) and destruction of manganese clusters. This disruption compromises the integrity of the PSII reaction center. At the bottom right, it can be seen how excessive light energy can alter photosynthetic activity leading to reactive oxygen species (ROS) formation. Both PSII and photosystem I (PSI) produce ROS, causing oxidative damage to chloroplasts and inhibiting PSII repair by suppressing D1 neo synthesis.

could be achieved through systemic responses, that activate stress-responsive genes and related pathways in plants (Sandrini *et al.*, 2022). Specifically, in the context of light stress, ABA regulates photosynthesis by influencing the efficiency of the PSII complex and the mobilization of photosynthates. (Gururani *et al.*, 2015). Studies have shown that ABA treatment can enhance Chl and carotenoid accumulation in plants exposed to water stress, leading to improved PSII efficiency. ABA also helps maintain the thermostability of the PSII complex under heat stress, reducing heat-induced damage to the chloroplast structure (Gururani *et al.*, 2015). One of the most significant examples frequently cited in scientific literature revolves around the capacity of AM fungi to bolster plant resilience against abiotic stress. In watermelon, researcher showed that despite the negative impact of water limitation on certain parameters like Fv/Fm (maximum photochemical efficiency of PSII), mycorrhizal watermelon plants exhibited higher values of Fv/Fm and

other parameters related to PSII photochemistry. This suggests that root colonization by AM fungi can mitigate damages and maintain PSII efficiency at higher levels even under drought stress (Balestrini *et al.*, 2020). Moreover, AM fungal colonization in cucumber roots was found to enhance CO_2 assimilation and the expression of genes related to key enzymes in the Calvin cycle (Chen *et al.*, 2017). This protection of major metabolic pathways, including Chl and carotenoid biosynthesis, contributes to preserving photosynthesis under stress conditions (Mathur *et al.*, 2019). It is worth noting that in a transcriptome dataset of tomato leaves from mycorrhizal plants three genes associated with the photosynthesis category (BIN 1) were found as mycorrhizal-responsive. Among them, two of these have roles in the light reactions, while the other gene was related to the Calvin cycle (Cervantes-Gámez *et al.*, 2016).

Considering the evidence available for abiotic stresses, although very limited for high light intensity stress, it would be of paramount
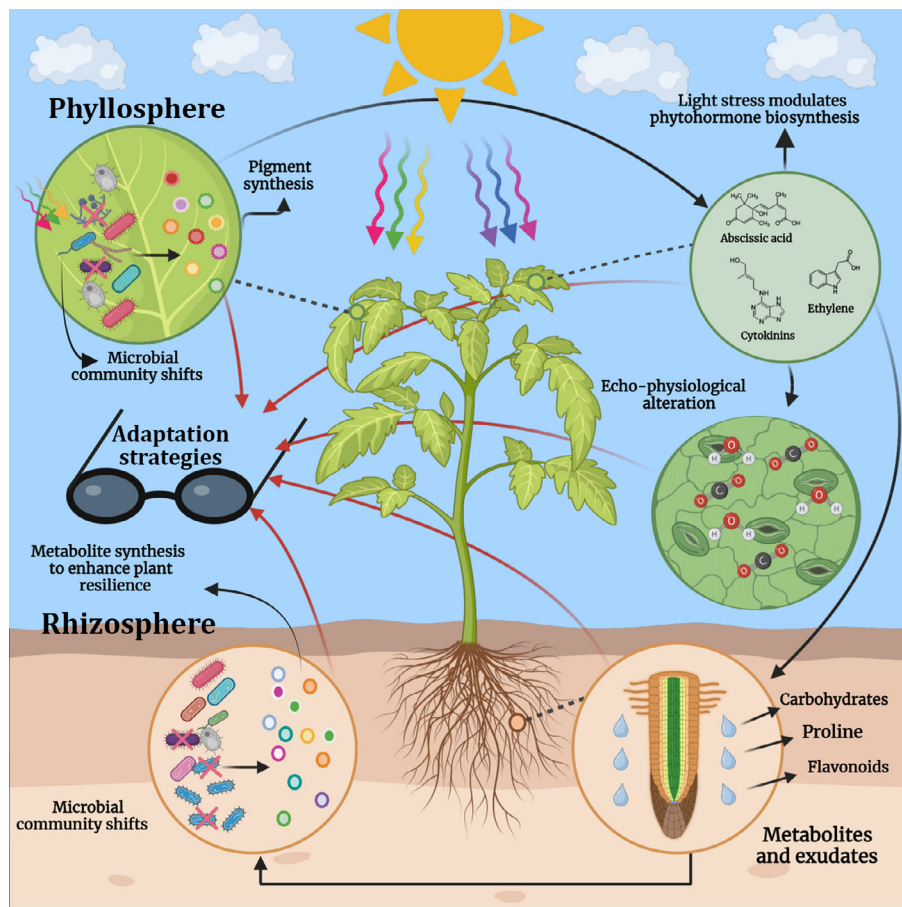
Fig. 2 Overview of the direct and indirect impacts of light stress on microbial communities in the phyllosphere and rhizosphere. When plants experience light stress, it triggers various effects on both the phyllosphere and rhizosphere microbial communities. Direct effects in the phyllosphere include alterations in microbial taxonomy due to high light conditions. This can prompt changes in pigment production, aiding both microorganisms and the plant in shielding themselves from radiation. Additionally, high radiation levels can impact the concentration of phytohormones like ABA, crucial for regulating leaf stomata to counteract radiation and excessive heat. Changes in compound biosynthesis within the phyllosphere can cascade into the rhizosphere. Consequently, variations in phyllosphere induced by light stress can indirectly influence the rhizosphere by altering the production of radical exudates such as carbohydrates, proline and flavonoids. These changes in exudates may, in turn, affect the microbial community in the rhizosphere, attracting microorganisms better equipped to support the plant under light stress. Overall, these direct and indirect factors drive adaptation strategies in response to light stress.

importance to deepen the role of microbes, either directly or indirectly, in protecting plants from light stress under a climate-changing scenario.

Impact of light stress on microbial communities in rhizosphere and phyllosphere

It is widely recognized that environmental conditions can trigger changes in the microbial communities associated with plants, exerting a direct or indirect influence on their composition (Fig. 2; Trivedi *et al.*, 2020). Recent studies have shown that abiotic stresses such as salinity and drought can lead to a shift in the plant microbial community composition (Furze *et al.*, 2017; Fadiji *et al.*, 2023). For salt-sensitive, but not salt-tolerant plants, the diversity of bacterial populations is reduced in response to salt stress, indicating that salt-tolerant plants maintain a diverse bacterial community that may be crucial for the salt tolerance (Fadiji *et al.*, 2023). For example, in the peanut rhizosphere, salt stress led to an increase in *Acidobacteria* with a reduction in the abundance of *Chloroflexi* and *Actinobacteria* (Xu *et al.*, 2020). A comparable scenario may arise in the microbial communities of plants exposed to high light intensity. Indeed, just as with plants under salt stress (Yaish *et al.*, 2016), we hypothesize that those facing high light intensity may also undergo alterations in their microbial communities, probably favoring species that better adapt to intense solar radiation (Jacobs & Sundin, 2001). For instance, we might observe a direct uptick in the

prevalence of species like *Bacillus coagulans* and *Clavibacter michiganensis* in the phyllosphere, known for their remarkable resistance to high UV radiation (Jacobs & Sundin, 2001). Additionally, studies have demonstrated that high doses of UV rays can alter the composition of the microbial community on the plant phyllosphere. This environment favors microorganisms like *Methylobacterium*, which can adapt to intense UV exposure by producing compounds that absorb UVA rays (Yoshida *et al.*, 2017). Exposure to high UV radiation induces significant shifts in the microbial community of the phyllosphere, favoring microorganisms with elevated levels of UV-absorbing pigments such as carotenoids, xanthomonadins and melanin (Jacobs *et al.*, 2005). These pigments play a protective role by reducing the amount of radiation that penetrates plant tissues (Jacobs *et al.*, 2005; Rastogi *et al.*, 2013). Furthermore, many phyllosphere bacteria possess specialized DNA repair mechanisms, enabling them to mitigate DNA damage caused by UV exposure (Jacobs *et al.*, 2005). These adaptations are essential for maintaining microbial populations in the phyllosphere and for supporting plant health under the stress of solar radiation. Equally significant would be the exploration of the indirect impacts of high light stress on the microbial community associated with plant tissues not directly exposed to the light radiation. As previously observed, exposure to intense light radiation triggers alterations in the plant physiological processes, including a reprogramming in the synthesis of specific phytohormones and secondary metabolites (Bayat *et al.*, 2018; Roeber

et al., 2021). These metabolites not only drive adaptations to abiotic stresses, but they can also influence shifts in the plant microbial community (Pang *et al.*, 2021; Wang *et al.*, 2022). Similar to the effects observed under water deficiency (Farooq *et al.*, 2009), constant exposure to solar radiation during light stress can induce alterations in the concentration of metabolites within the plant (Carvalho & Castillo, 2018; Crestani *et al.*, 2024). This, in turn, may prompt changes in the composition of root exudates, consequently favoring the increase in specific microbial taxa such as α-*Proteobacteria* and *Acidobacteria* (Gargallo-Garriga *et al.*, 2018; Vives-Peris *et al.*, 2020). As documented in the literature, exposure to low-light doses induces alterations in both the quality and quantity of root exudates in seagrass (Martin *et al.*, 2018), consequently resulting in a shift in the microbial community composition, with increased beneficial microorganisms like *Sulfurimonas* and *Azospirillum.* Observing the impact of low light on the alteration of beneficial microbial communities, we hypothesize that similar changes may occur under exposure to high light intensities. These microorganisms play a crucial role in alleviating light stress conditions by modulating both physiological processes and hormonal regulation. For instance, *Azospirillum* enhance root development and nutrient uptake, thereby increasing plant resilience (Steenhoudt & Vanderleyden, 2000). Additionally, α-*Proteobacteria* produce ACC deaminase, which lowers ethylene levels, a stress hormone typically elevated under light stress (Glick, 2005; Brenya *et al.*, 2023). Moreover, these microorganisms can regulate the levels of other essential hormones, such as ABA, auxins and cytokinins, aiding plants in adapting to stress by promoting growth and enhancing nutrient availability (Vacheron *et al.*, 2013).

As reported in Lopes *et al.* (2023), different levels of ABA and IAA can trigger alterations, thus affecting the composition of root exudates and consequently resulting in shifts in the plant-associated microbial community. Indeed, *Solanum lycopersicum* plants grown under high R/FR conditions released root exudates containing higher levels of (+)-5-deoxystrigol, an inducer of fungal AM hyphal branching, compared with those from plants grown under low R/FR light (Nagata *et al.*, 2015). Confirming that elevated R/FR light alters the composition of root exudates released into the rhizosphere, thereby enhancing AM symbiosis (Nagata *et al.*, 2015).

As mentioned previously, exposure to light stress can increase the production of secondary metabolites, including flavonoids (Wang *et al.*, 2022; Fang *et al.*, 2024). Recent researches have proved that high flavonoid levels, resulting from the plant adaptation to intense light exposure, can drive alterations in the microbial community (Jacoby *et al.*, 2020). Most flavonoid molecules can act as signals for the recruitment of specific microbial taxa and/or act as substrates for microbial growth, thus linking their production and consumption with the recruitment of specific taxa in the plant rhizosphere (He *et al.*, 2022). Flavonoids secreted by roots as responses to high light stress inhibited the growth of the pathogen *I. destructans*, but also promoted the growth of beneficial bacteria (Fang *et al.*, 2024). This adaptation not only enhances their ability to cope with light stress but also improves their resistance to pathogens. In addition, some flavonoids can also have a negative effect on taxa recruitment, for instance, via antimicrobial activities (Schütz *et al.*, 2021).

Finally, even if experimental data linking the high light stress with the root microbiota are still missing, evidence that root-associated microbes can alleviate the low-light stress has been reported (Hou *et al.*, 2021). Specifically, this work demonstrated a light-dependent microbiota–root–shot circuit able to alleviate plant growth deficiency by modulating the growth–defense trade-off. Indeed, it is important to highlight that shifts in the plant-associated microbial communities can have grater effects also from an ecological point of view. The interconnection of ecosystem (i.e. both among community members and between communities across the ecological niche) has the potential to improve the stability and resilience of the holobiont (Allsup *et al.*, 2023). Moreover, from an ecological point of view, it has already been proved that the consequences of abiotic stresses (e.g. drought) lead to an alteration of the microbial community which is reflected also by the alteration of the microbial gene pool (Xie *et al.*, 2021). Taken together these findings further highlight the crucial role of microorganisms in aiding plants during environmental stresses and pose a new challenge in understanding how light stress, directly and indirectly, alter microbial communities within plants and how such changes can ultimately benefit plant health. In this frame, a validation of the microbiota–root–shoot circuit under high light intensity is still missing leaving this field almost unexplored and requesting the attention of the research community.

Conclusions

Light stress represents a significant challenge for global agriculture. Exposure to excessive light radiation causes metabolic changes in plants, impacting both their health and their interactions with the microbiome. Plant-associated microorganisms play crucial roles in enhancing the growth and overall well-being of plants. Nowadays, it is crucial to understand how microorganisms can support plants under light stress conditions, and, in parallel, how this can reshape plant microbial communities. To elucidate this critical step, further comparative experiments would be ideal to identify and characterize the composition of root exudates in response to light stress and to understand the functional roles mediated by beneficial endophytes in alleviating cellular and photosynthetic damages. Such an approach will enable the identification of more efficient bacterial strains or fungal isolates that could be exploited for the development of microbial breeding strategies (Nerva *et al.*, 2022) to enhance plant resilience against high radiation, a phenomenon predicted to increase in the near future due to ongoing climate change.

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None declared.

Author contributions

FV, RB, LN and WC designed the concept of the viewpoint, discussed ideas and contributed to the writing and editing of the manuscript. [Correction added on 1 November 2024, after first online publication: the initials 'RB' have been added to the following sentence to denote shared senior authorship.] LN, RB and WC share the senior authorship for this work.

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References

Ahmad N, Jiang Z, Zhang L, Hussain I, Yang X. 2023. Insights on phytohormonal crosstalk in plant response to nitrogen stress: a focus on plant root growth and development. *International Journal of Molecular Sciences* **24**: 3631.

Allsup CM, George I, Lankau RA. 2023. Shifting microbial communities can enhance tree tolerance to changing climates. *Science* **380**: 835–840.

Alsanius B, Karlsson M, Rosberg A, Dorais M, Naznin M, Khalil S, Bergstrand K-J. 2019. Light and microbial lifestyle: the impact of light quality on plant–microbe interactions in horticultural production systems—a review. *Horticulturae* **5**: 41.

Asha AD, Nivetha N, Krishna GK, Thakur JK, Rathi MS, Manjunatha BS, Chinnusamy V, Paul S. 2021. Amelioration of short-term drought stress during different growth stages in *Brassica juncea* by rhizobacteria mediated maintenance of ROS homeostasis. *Physiologia Plantarum* **172**: 1880–1893.

Bakker MG, Otto-Hanson L, Lange AJ, Bradeen JM, Kinkel LL. 2013. Plant monocultures produce more antagonistic soil Streptomyces communities than high-diversity plant communities. *Soil Biology and Biochemistry* **65**: 304–312.

Balestrini R, Brunetti C, Chitarra W, Nerva L. 2020. Photosynthetic traits and nitrogen uptake in crops: which is the role of arbuscular mycorrhizal fungi? *Plants* **9**: 1105.

Bayat L, Arab M, Aliniaeifard S, Seif M, Lastochkina O, Li T. 2018. Effects of growth under different light spectra on the subsequent high light tolerance in rose plants. *AoB Plants* **10**: 2186.

Bonfante P, Genre A. 2008. Plants and arbuscular mycorrhizal fungi: an evolutionary-developmental perspective. *Trends in Plant Science* **13**: 492–498.

Brenya E, Dutta E, Herron B, Walden LH, Roberts DM, Binder BM. 2023. Ethylene-mediated metabolic priming increases photosynthesis and metabolism to enhance plant growth and stress tolerance. *PNAS Nexus* **2**: pgad216.

Carvalho SD, Castillo JA. 2018. Influence of light on plant–phyllosphere interaction. *Frontiers in Plant Science* **9**: 2125.

Cervantes-Gámez RG, Bueno-Ibarra MA, Cruz-Mendívil A, Calderón-Vázquez CL, Ramírez-Douriet CM, Maldonado-Mendoza IE, Villalobos-López MÁ, Valdez-Ortíz Á, López-Meyer M. 2016. Arbuscular mycorrhizal symbiosis-induced expression changes in *Solanum lycopersicum* leaves revealed by RNA-seq analysis. *Plant Molecular Biology Reporter* **34**: 89–102.

Chaudhry V, Runge P, Sengupta P, Doehlemann G, Parker JE, Kemen E. 2021. Shaping the leaf microbiota: plant–microbe–microbe interactions. *Journal of Experimental Botany* **72**: 36–56.

Chen S, Zhao H, Zou C, Li Y, Chen Y, Wang Z, Jiang Y, Liu A, Zhao P, Wang M et al. 2017. Combined inoculation with multiple arbuscular mycorrhizal fungi improves growth, nutrient uptake and photosynthesis in cucumber seedlings. *Frontiers in Microbiology* **8**: 2516.

Crestani G, Večeřová K, Cunningham N, Badmus UO, Urban O, Jansen MAK. 2024. Comprehensive modulation of secondary metabolites in terpenoid-accumulating *Mentha spicata* L. via UV radiation. *Plants* **13**: 1746.

Demarsy E, Goldschmidt-Clermont M, Ulm R. 2018. Coping with 'dark sides of the sun' through photoreceptor signaling. *Trends in Plant Science* **23**: 260–271.

Dos Santos TB, Ribas AF, De Souza SGH, Budzinski IGF, Domingues DS. 2022. Physiological responses to drought, salinity, and heat stress in plants: a review. *Stress* **2**: 113–135.

Duan B, Li L, Chen G, Su-Zhou C, Li Y, Merkeryan H, Liu W, Liu X. 2021. 1-Aminocyclopropane-1-carboxylate deaminase-producing plant growth-promoting rhizobacteria improve drought stress tolerance in grapevine (*Vitis vinifera* L.). *Frontiers in Plant Science* **12**: 706990.

Egamberdieva D, Wirth SJ, Alqarawi AA, Abdul Allah EF, Hashem A. 2017. Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. *Frontiers in Microbiology* **8**: 2104.

Fadiji AE, Yadav AN, Santoyo G, Babalola OO. 2023. Understanding the plant–microbe interactions in environments exposed to abiotic stresses: an overview. *Microbiological Research* **271**: 127368.

Fang H, Guo C, Mei X, Hao M, Zhang J, Luo L, Liu H, Liu Y, Huang H, He X et al. 2024. Light stress elicits soilborne disease suppression mediated by root-secreted flavonoids in *Panax notoginseng*. *Horticulture Research* **23**: 26213.

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development* **29**: 185–212.

Fiorucci A-S, Fankhauser C. 2017. Plant strategies for enhancing access to sunlight. *Current Biology* **27**: R931–R940.

Flemming H-C, Wingender J, Szewzyk U, Steinberg P, Rice SA, Kjelleberg S. 2016. Biofilms: an emergent form of bacterial life. *Nature Reviews. Microbiology* **14**: 563–575.

Fukami J, Cerezini P, Hungria M. 2018. Azospirillum: benefits that go far beyond biological nitrogen fixation. *AMB Express* **8**: 73.

Furze JR, Martin AR, Nasielski J, Thevathasan NV, Gordon AM, Isaac ME. 2017. Resistance and resilience of root fungal communities to water limitation in a temperate agroecosystem. *Ecology and Evolution* **7**: 3443–3454.

Galani YJH, Hansen EMØ, Droutsas I, Holmes M, Challinor AJ, Mikkelsen TN, Orfila C. 2022. Effects of combined abiotic stresses on nutrient content of European wheat and implications for nutritional security under climate change. *Scientific Reports* **12**: 5700.

Gargallo-Garriga A, Preece C, Sardans J, Oravec M, Urban O, Peñuelas J. 2018. Root exudate metabolomes change under drought and show limited capacity for recovery. *Scientific Reports* **8**: 12696.

Glick BR. 2005. Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. *FEMS Microbiology Letters* **251**: 1–7.

Gowtham HG, Brijesh Singh S, Murali M, Shilpa N, Prasad M, Aiyaz M, Amruthesh KN, Niranjana SR. 2020. Induction of drought tolerance in tomato upon the application of ACC deaminase producing plant growth promoting

rhizobacterium *Bacillus subtilis* rhizo SF 48. *Microbiological Research* **234**: 126422.

Gururani M, Mohanta T, Bae H. 2015. Current understanding of the interplay between phytohormones and photosynthesis under environmental stress. *International Journal of Molecular Sciences* **16**: 19055–19085.

Harman G, Khadka R, Doni F, Uphoff N. 2021. Benefits to plant health and productivity from enhancing plant microbial symbionts. *Frontiers in Plant Science* **11**: 610065.

Haworth M, McElwain J. 2008. Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **262**: 79–90.

He D, Singh SK, Peng L, Kaushal R, Vílchez JI, Shao C, Wu X, Zheng S, Morcillo RJL, Paré PW *et al.* 2022. Flavonoid-attracted *Aeromonas* sp. from the Arabidopsis root microbiome enhances plant dehydration resistance. *The ISME Journal* **16**: 2622–2632.

Hou S, Thiergart T, Vannier N, Mesny F, Ziegler J, Pickel B, Hacquard S. 2021. A microbiota–root–shoot circuit favours Arabidopsis growth over defence under suboptimal light. *Nature Plants* **7**: 1078–1092.

Huang W, Chen Q, Zhu Y, Hu F, Zhang L, Ma Z, He Z, Huang J. 2013. Arabidopsis thylakoid formation 1 is a critical regulator for dynamics of PSII–LHCII complexes in leaf senescence and excess light. *Molecular Plant* **6**: 1673–1691.

Humphreys CP, Franks PJ, Rees M, Bidartondo MI, Leake JR, Beerling DJ. 2010. Mutualistic mycorrhiza-like symbiosis in the most ancient group of land plants. *Nature Communications* **1**: 103.

Jacobs JL, Carroll TL, Sundin GW. 2005. The role of pigmentation, ultraviolet radiation tolerance, and leaf colonization strategies in the epiphytic survival of phyllosphere bacteria. *Microbial Ecology* **49**: 104–113.

Jacobs JL, Sundin GW. 2001. Effect of solar UV-B radiation on a phyllosphere bacterial community. *Applied and Environmental Microbiology* **67**: 5488–5496.

Jacoby RP, Chen L, Schwier M, Koprivova A, Kopriva S. 2020. Recent advances in the role of plant metabolites in shaping the root microbiome. *F1000Research* **9**: 151.

Karabourniotis G, Liakopoulos G, Bresta P, Nikolopoulos D. 2021. The optical properties of leaf structural elements and their contribution to photosynthetic performance and photoprotection. *Plants* **10**: 1455.

Khan V, Umar S, Iqbal N. 2023. Palliating salt stress in mustard through plant-growth-promoting rhizobacteria: regulation of secondary metabolites, osmolytes, antioxidative enzymes and stress ethylene. *Plants* **12**: 705.

Kopecká R, Kameniarová M, Černý M, Brzobohatý B, Novák J. 2023. Abiotic stress in crop production. *International Journal of Molecular Sciences* **24**: 6603.

Lee E-H, Eo J-K, Ka K-H, Eom A-H. 2013. Diversity of arbuscular mycorrhizal fungi and their roles in ecosystems. *Mycobiology* **41**: 121–125.

Li Y, Narayanan M, Shi X, Chen X, Li Z, Ma Y. 2024. Biofilms formation in plant growth-promoting bacteria for alleviating agro-environmental stress. *The Science of the Total Environment* **907**: 167774.

Lopes LD, Futrell SL, Bergmeyer E, Hao J, Schachtman DP. 2023. Root exudate concentrations of indole-3-acetic acid (IAA) and abscisic acid (ABA) affect maize rhizobacterial communities at specific developmental stages. *FEMS Microbiology Ecology* **99**: fiad019.

Marín-Sanhueza C, Echeverría-Vega A, Gómez A, Cabrera-Barjas G, Romero R, Banerjee A. 2022. Stress dependent biofilm formation and bioactive melanin pigment production by a *Thermophilic bacillus* species from chilean hot spring. *Polymers* **14**: 680.

Martin BC, Gleeson D, Statton J, Siebers AR, Grierson P, Ryan MH, Kendrick GA. 2018. Low light availability alters root exudation and reduces putative beneficial microorganisms in seagrass roots. *Frontiers in Microbiology* **8**: 2667.

Mathur S, Tomar RS, Jajoo A. 2019. Arbuscular mycorrhizal fungi (AMF) protects photosynthetic apparatus of wheat under drought stress. *Photosynthesis Research* **139**: 227–238.

Nagata M, Yamamoto N, Shigeyama T, Terasawa Y, Anai T, Sakai T, Inada S, Arima S, Hashiguchi M, Akashi R *et al.* 2015. Red/far red light controls arbuscular mycorrhizal colonization via jasmonic acid and strigolactone signaling. *Plant and Cell Physiology* **20**: pcv135.

Nerva L, Sandrini M, Moffa L, Velasco R, Balestrini R, Chitarra W. 2022. Breeding toward improved ecological plant–microbiome interactions. *Trends in Plant Science* **2**: 1134–1143.

Ojuederie OB, Babalola OO. 2023. Growth enhancement and extenuation of drought stress in maize inoculated with multifaceted ACC deaminase producing rhizobacteria. *Frontiers in Sustainable Food Systems* **6**: 1076844.

Pang Z, Chen J, Wang T, Gao C, Li Z, Guo L, Xu J, Cheng Y. 2021. Linking plant secondary metabolites and plant microbiomes: a review. *Frontiers in Plant Science* **12**: 621276.

Poppeliers SW, Sánchez-Gil JJ, De Jonge R. 2023. Microbes to support plant health: understanding bioinoculant success in complex conditions. *Current Opinion in Microbiology* **73**: 102286.

Pospíšil P. 2009. Production of reactive oxygen species by photosystem II. *Biochimica et Biophysica Acta (BBA)–Bioenergetics* **1787**: 1151–1160.

Puginier C, Keller J, Delaux P-M. 2022. Plant–microbe interactions that have impacted plant terrestrializations. *Plant Physiology* **190**: 72–84.

Rastogi G, Coaker GL, Leveau JHJ. 2013. New insights into the structure and function of phyllosphere microbiota through high-throughput molecular approaches. *FEMS Microbiology Letters* **348**: 1–10.

Ren A-T, Zhu Y, Chen Y-L, Ren H-X, Li J-Y, Kay Abbott L, Xiong Y-C. 2019. Arbuscular mycorrhizal fungus alters root-sourced signal (abscisic acid) for better drought acclimation in *Zea mays* L. seedlings. *Environmental and Experimental Botany* **167**: 103824.

Roeber VM, Bajaj I, Rohde M, Schmülling T, Cortleven A. 2021. Light acts as a stressor and influences abiotic and biotic stress responses in plants. *Plant, Cell & Environment* **44**: 645–664.

Saleem M, Arshad M, Hussain S, Bhatti AS. 2007. Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. *Journal of Industrial Microbiology & Biotechnology* **34**: 635–648.

Sandrini M, Nerva L, Sillo F, Balestrini R, Chitarra W, Zampieri E. 2022. Abiotic stress and belowground microbiome: the potential of omics approaches. *International Journal of Molecular Sciences* **23**: 1091.

Sasse J, Martinoia E, Northen T. 2018. Feed your friends: do plant exudates shape the root microbiome? *Trends in Plant Science* **23**: 25–41.

Schütz V, Frindte K, Cui J, Zhang P, Hacquard S, Schulze-Lefert P, Knief C, Schulz M, Dörmann P. 2021. Differential impact of plant secondary metabolites on the soil microbiota. *Frontiers in Microbiology* **12**: 666010.

Shi Y, Ke X, Yang X, Liu Y, Hou X. 2022. Plants response to light stress. *Journal of Genetics and Genomics* **49**: 735–747.

de Souza R, Ambrosini A, Passaglia LMP. 2015. Plant growth-promoting bacteria as inoculants in agricultural soils. *Genetics and Molecular Biology* **38**: 401–419.

Steenhoudt O, Vanderleyden J. 2000. Azospirillum, a free-living nitrogen-fixing bacterium closely associated with grasses: genetic, biochemical and ecological aspects. *FEMS Microbiology Reviews* **24**: 487–506.

Sytar O, Kumari P, Yadav S, Brestic M, Rastogi A. 2019. Phytohormone priming: regulator for heavy metal stress in plants. *Journal of Plant Growth Regulation* **38**: 739–752.

Takahashi S, Badger MR. 2011. Photoprotection in plants: a new light on photosystem II damage. *Trends in Plant Science* **16**: 53–60.

Takahashi S, Milward SE, Yamori W, Evans JR, Hillier W, Badger MR. 2010. The solar action spectrum of photosystem II damage. *Plant Physiology* **153**: 988–993.

Taylor NL, Tan Y-F, Jacoby RP, Millar AH. 2009. Abiotic environmental stress induced changes in the *Arabidopsis thaliana* chloroplast, mitochondria and peroxisome proteomes. *Journal of Proteomics* **72**: 367–378.

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK. 2020. Plant–microbiome interactions: from community assembly to plant health. *Nature Reviews Microbiology* **18**: 607–621.

Vacheron J, Desbrosses G, Bouffaud M-L, Touraine B, Moënne-Loccoz Y, Muller D, Legendre L, Wisniewski-Dyé F, Prigent-Combaret C. 2013. Plant growth-promoting rhizobacteria and root system functioning. *Frontiers in Plant Science* **4**: 356.

Vincent SA, Ebertz A, Spanu PD, Devlin PF. 2022. Salicylic acid-mediated disturbance increases bacterial diversity in the phyllosphere but is overcome by a dominant core community. *Frontiers in Microbiology* **13**: 809940.

Vives-Peris V, de Ollas C, Gómez-Cadenas A, Pérez-Clemente RM. 2020. Root exudates: from plant to rhizosphere and beyond. *Plant Cell Reports* **39**: 3–17.

Walters RG. 2004. Towards an understanding of photosynthetic acclimation. *Journal of Experimental Botany* **56**: 435–447.

Wang L, Chen M, Lam P-Y, Dini-Andreote F, Dai L, Wei Z. 2022. Multifaceted roles of flavonoids mediating plant–microbe interactions. *Microbiome* **10**: 233.

Waters MT, Langdale JA. 2009. The making of a chloroplast. *EMBO Journal* **28**: 2861–2873.

Xie J, Dawwam GE, Sehim AE, Li X, Wu J, Chen S, Zhang D. 2021. Drought stress triggers shifts in the root microbial community and alters functional categories in the microbial gene pool. *Frontiers in Microbiology* **12**: 744897.

Xu Y, Zhang G, Ding H, Ci D, Dai L, Zhang Z. 2020. Influence of salt stress on the rhizosphere soil bacterial community structure and growth performance of groundnut (*Arachis hypogaea* L.). *International Microbiology* **23**: 453–465.

Yaish MW, Al-Lawati A, Jana GA, Vishwas Patankar H, Glick BR. 2016. Impact of soil salinity on the structure of the bacterial endophytic community identified from the roots of caliph medic (*Medicago truncatula*). *PLoS ONE* **11**: e0159007.

Yang B, Tang J, Yu Z, Khare T, Srivastav A, Datir S, Kumar V. 2019. Light stress responses and prospects for engineering light stress tolerance in crop plants. *Journal of Plant Growth Regulation* **38**: 1489–1506.

Yoshida S, Hiradate S, Koitabashi M, Kamo T, Tsushima S. 2017. Phyllosphere Methylobacterium bacteria contain UVA-absorbing compounds. *Journal of Photochemistry and Photobiology B: Biology* **167**: 168–175.