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REVIEW

Intersections: photosynthesis, abiotic stress, and the plant microbiome

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Abstract

Climate change impacts environmental conditions that affect photosynthesis. This review examines the effect of combinations of elevated atmospheric CO_2, long photoperiods, and/or unfavorable nitrogen supply. Under moderate stress, perturbed plant source–sink ratio and redox state can be rebalanced but may result in reduced foliar protein content in C_3 plants and a higher carbon-to-nitrogen ratio of plant biomass. More severe environmental conditions can trigger pronounced photosynthetic downregulation and impair growth. We comprehensively evaluate available evidence that microbial partners may be able to support plant productivity under challenging environmental conditions by providing (*1*) nutrients, (*2*) an additional carbohydrate sink, and (*3*) regulators of plant metabolism, especially plant redox state. In evaluating the latter mechanism, we note parallels to metabolic control in photosymbioses and microbial regulation of human redox biology.

Keywords: carbohydrate; electron transport; homeostasis; nitrogen; reactive oxygen species; redox signaling.

Introduction

Photosynthesis by natural and agricultural populations of plants and other photosynthetic organisms is the engine for essential services rendered by these systems, including CO_2 sequestration and the production of food, fuels, and materials. Photosynthesis is linked to plant growth and development, not only *via* the supply of energy but also as a source of information about the state of the plant's environment. The processes of photosynthetic light collection and electron transport provide direct input into essential signaling transduction networks with 'profound influence on almost every aspect of plant biology' (Foyer and Noctor 2016).

Climate change affects many environmental inputs that impact photosynthesis (Dusenge *et al*. 2019, Ainsworth and Long 2021). While both CO_2 and light are necessary inputs into photosynthesis, the proverbial 'too much of a good thing' of either or both profoundly alters the metabolic function and can even disrupt plant metabolism. This metabolic disruption is somewhat reminiscent of the metabolic disruption triggered by an overly energy-dense diet in animals (Gill 1999). Furthermore, today's rising atmospheric CO_2 concentrations impact other environmental factors, including indirect effects on light supply. The hotter and drier summers associated with climate change are driving the relocation of some plant communities and agricultural operations to higher, cooler

Highlights

- Abiotic stress impacts on photosynthesis are comprehensively reviewed
- Abiotic stress combinations disrupt *via* synergistically acting mechanisms
- The plant microbiome can counter multiple disrupting mechanisms

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Abbreviations: AOX – alternative oxidase; ROS – reactive oxygen species.

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latitudes, where plants experience longer photoperiods in the summer (Vitt *et al.* 2010, Hu *et al.* 2019, Carlson-Nilsson *et al.* 2021, Mølmann *et al.* 2021). Moreover, the effect of elevated CO_2 and/or increased light supply varies depending on yet other environmental factors, such as nitrogen supply. This review comprehensively evaluates the effect of combinations of elevated atmospheric CO_2 concentrations, long photoperiods, and/or unfavorable nitrogen supply on photosynthesis, plant growth, and the maintenance of plant redox homeostasis (*see* Fig. 1).

A high supply of CO_2 and/or light can shift the balance between sugar-producing source leaves and sugar-consuming sink tissues (source–sink balance). Carbohydrates backing up in leaves can trigger a sequence of events that alters plant redox balance – a balance between oxidants and antioxidants (Paul and Foyer 2001, Foyer and Noctor 2009, 2020; Demmig-Adams *et al.* 2018). Plant redox state has a central role in adjusting plant growth, reproduction, and defense throughout plant development and in response to shifts in environmental conditions (Wilson *et al.* 2006, Zaffagnini *et al.* 2019). When changes in the environment are moderate, internal signaling networks orchestrate adjustments to maintain growth and rebalance plant source–sink ratio and redox state. However, when environmental conditions are more extreme and exceed the plant's capacity to maintain cellular redox homeostasis, growth rates decline and photosynthesis can be dramatically downregulated (Suzuki *et al.* 2012, Adams *et al.* 2013, 2014, 2018; Demmig-Adams *et al.* 2014). Elevated CO_2 concentrations also strongly interact with plant nitrogen metabolism (Tausz-Posch *et al.* 2020), and both limiting (Agüera and De la Haba 2018) or excessive soil nitrogen supply (Adavi and Sathee 2021a,b) can exacerbate disruption of cellular redox homeostasis.

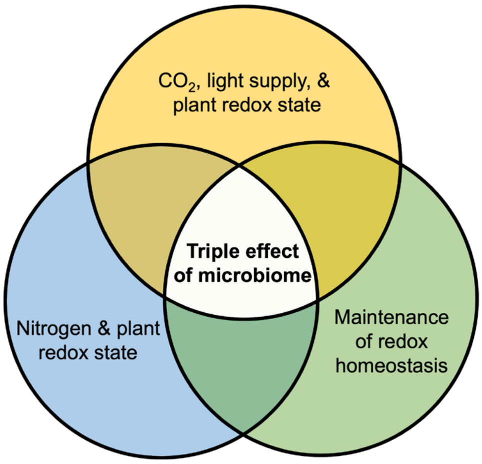

Fig. 1. Schematic depiction of the approach taken in the present review of synthesizing several bodies of literature to identify common themes that provide targets for plant–microbe interaction. The three circles represent the major sections (headers) of this review, and the overlapping area represents the resulting conclusion that the plant microbiome has a triple effect in interacting with each and all of these areas.

Plant–microbe interaction may be able to maintain plant productivity over a wider range of challenging environmental conditions (Fig. 2; Chouhan *et al.* 2021). Our review comprehensively examines the potential of microbial partners to counteract photosynthetic downregulation and metabolic disruption, thereby maintaining plant redox homeostasis both indirectly and directly. The plant microbiome may exert indirect effects on the plant redox state by (*1*) acting as an additional sugar sink that consumes photosynthetically produced sugars as well as (*2*) improving plant nitrogen status. Ainsworth *et al.* (2004) reported photosynthetic downregulation under elevated CO_2 in a soybean line that does not form a symbiotic relationship with bacteria, and prevention of such downregulation in a nodule-forming soybean line forming a symbiosis with *Rhizobium* bacteria that represents a large carbon sink. In addition, microbial manipulation could directly affect plant redox state and the content of reactive oxygen species (ROS). A recent study on the response of mustard (*Brassica juncea*) to drought conditions reported that rhizobacteria-inoculated *vs.* uninoculated plants exhibited enhanced shoot and root biomass, greater water content, higher rates of photosynthesis, and greater expression of antioxidant enzymes. The study concluded that 'rhizobacteria mediated maintenance of ROS homeostasis' (Asha *et al.* 2021). We summarize below available evidence from several

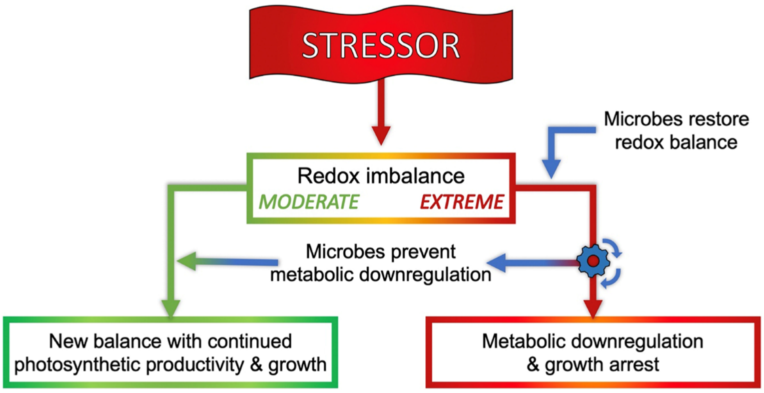

Fig. 2. Schematic depiction of common overarching themes in the effect of environmental stress (stressor) and the plant microbiome. Stressors shift plant redox balance to a degree that is either moderate enough (*green boxes*) to allow continued productivity or extreme enough (*red boxes*) to trigger downregulation of growth and metabolism. Also represented is the conclusion from the literature synthesis in this review that the plant microbiome has the potential to restore redox balance and prevent metabolic downregulation (represented by the blue dial and the arrows pointing from the red to the green zone).

bodies of literature that these microbial effects can support higher plant nitrogen and protein contents under elevated CO_2 and maintain plant growth under combinations of unfavorable abiotic conditions in the plant's environment.

Literature synthesis

Below is a synthesis of evidence from several fields of inquiry, focusing on CO_2, light supply, and plant redox state in the context of plant source–sink balance, nitrogen and plant redox state in the context of imbalances in plant nitrogen metabolism, and mechanisms to maintain redox balance in plants, photosymbioses of algae and their hosts, and other host–microbe systems. Integrative evaluation of these bodies of literature is used to identify the plant microbiome as having multiple effects with the potential to restore the balance of source–sink ratio, nitrogen metabolism, and plant redox state (Fig. 1). Since the focus of the current review is the overlap among these other fields, authoritative reviews in each of these areas are cited that provide a more exhaustive summary in each field than can be provided here. Similarly, the schematic diagrams in the present review highlight connections and common themes rather than aiming to provide specific details.

CO_2, light supply, and plant redox state: This section discusses the effects of elevated CO_2 in the context of plant source–sink balance. Plant photosynthetic capacity (of the sugar-producing source leaves) is controlled by demand from the whole plant (all its sinks) for sugar (Demmig-Adams *et al.* 2017). Key photosynthetic genes subject to this control by the plant's sugar-consuming sinks include the small subunit of the CO_2-fixing enzyme Rubisco, chlorophyll (*a*+*b*)-binding complexes, and ATP synthase (Krapp and Stitt 1995) as well as others (for a report on the photosystem II reaction center protein D1, *see* Kilb *et al.* 1996). Because photosynthesis is controlled by the demand for its products, increased photosynthetic rates under high CO_2 can only be sustained when there is continuously high demand for sugars from sinks, *i.e.*, from sugar-consuming and/or storing plant tissues (Kasai 2008) and/or from the plant's microbial partners (Ainsworth *et al.* 2004; *see* Adams *et al.* 2018). Initial increases in photosynthetic rates in response to elevated CO_2 are followed by adjustments (acclimation) that can include downregulation of photosynthetic activity [*via* repression of the small subunit of Rubisco, chlorophyll (*a*+*b*)-binding complexes, ATP synthase, and others]. Exposure to elevated CO_2 causes plants with modest to low sink strength to successively build up carbohydrates in leaves (Ainsworth *et al.* 2004) or stems (Macabuhay *et al.* 2018), whereas plants with large carbon sinks show no such backup (Tausz-Posch *et al.* 2020). Carbohydrate backup in source leaves, in turn, triggers feedback downregulation of sugar production in photosynthesis (Fig. 3). For example, *Arabidopsis*

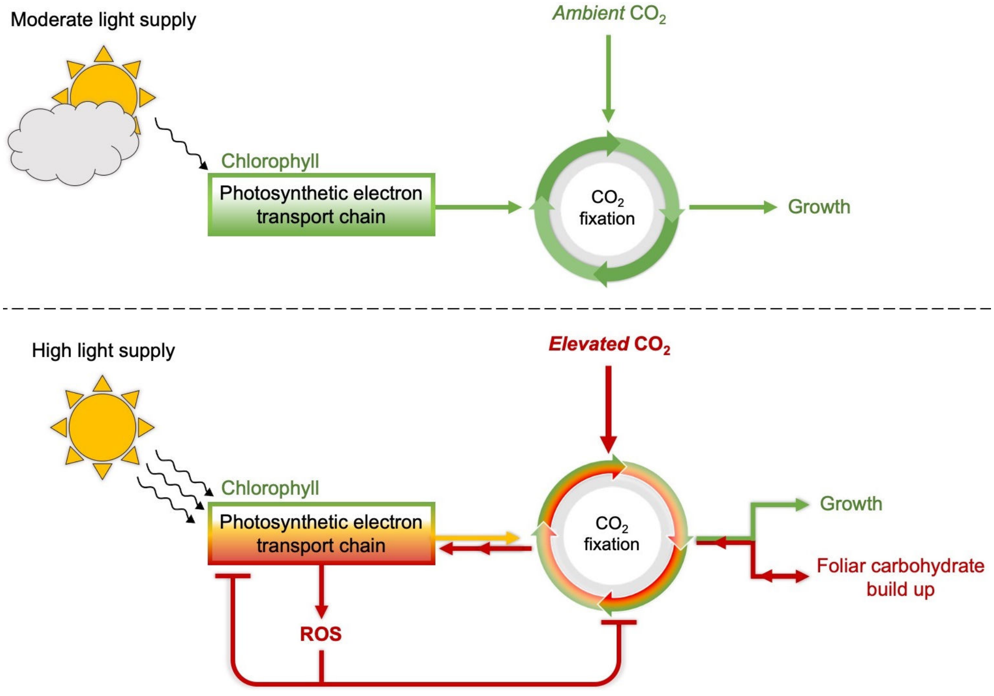

Fig. 3. Schematic depiction of the general principles of how moderate light supply under ambient CO_2 (*top*; *green color*) or a combination of high light supply and elevated CO_2 (*bottom*; *orange to red color*) can act on photosynthetic electron transport and CO_2 fixation. Red arrows running in the reverse direction, back from CO_2 fixation to the photosynthetic electron transport chain, symbolize that elevated CO_2 coupled with high light is likely to trigger foliar carbohydrate build-up and backing up of electrons in the photosynthetic electron transport chain. Additional red arrows symbolize formation of excess reactive oxygen species (ROS) in this situation, and repression of photosynthetic genes involved in the light reactions and CO_2 fixation.

thaliana's response to long-term elevated CO_2 included downregulation of photosynthetic sugar production and was described as 'metabolic perturbation' (Li *et al*. 2008).

In conclusion, high levels of photosynthesis were sustained under high CO_2 concentrations only when other environmental conditions permitted continuous rapid growth (Yilmaz *et al*. 2017) or when plant carbohydrate-storage capacity was extensive (Aranjuelo *et al*. 2011), whereas photosynthesis was downregulated when sink activity was limited (Thomas and Strain 1991, Aranjuelo *et al*. 2005). Significant limitations of plant sink activity, and photosynthetic downregulation, can be imposed by various conditions on their own or in combination (Demmig-Adams *et al*. 2017, Adams *et al*. 2018), such as a low supply of nutrients or water (Porras *et al*. 2017, Wang *et al*. 2017, Tausz-Posch *et al*. 2020), restricted root expansion (Andrade *et al*. 1993, Poorter *et al*. 2012), or genetic constraints to either fast growth (Poorter *et al*. 1990) or efficient nitrogen uptake and utilization (Adavi and Sathee 2021a, Padhan *et al*. 2020). Photosynthetic downregulation is a result of a series of regulatory events, where carbohydrate build-up feeds back into the photosynthetic electron transport chain (Fig. 3). Specifically, when carbohydrates build up in leaves, CO_2 fixation consumes the products of photosynthetic electron transport at a lesser rate, which can lead to a transient backup of electrons and transfer of these electrons to oxygen, resulting in the formation of greater ROS amounts (Fig. 3; Demmig-Adams *et al*. 2014). ROS are regulators of a host of essential genes, and ROS level functions as a means 'to monitor metabolic flux' (Foyer and Noctor 2016), including repression of key photosynthetic genes with roles in the light reactions [*e.g*., chlorophyll (*a*+*b*)-binding complexes and ATP synthase] and CO_2 fixation (*e.g*., the small subunit of Rubisco) when sugar production *vs*. consumption becomes unbalanced (Fig. 3; Foyer and Noctor 2020, Hasanuzzaman *et al*. 2020). In addition, carbohydrate build-up can also repress photosynthetic genes *via* sugar-signaling pathways (Roth *et al*. 2019).

The process of metabolic downregulation can occur with or without accompanying growth penalties. Under moderate stress, such as a combination of elevated CO_2 with long hours of high light in an environment otherwise favorable for growth (*e.g*., favorable nitrogen supply), downregulation of photosynthetic capacity allows C_3 plants to support a similar rate of photosynthesis and growth under high *vs*. lower CO_2 concentrations, but with lesser investment in the components of the photosynthetic machinery that collect light and fix CO_2. This lesser investment lowers foliar protein content (of which the CO_2-fixing enzyme Rubisco is a significant portion, particularly in C_3 plants) and can also lower the protein content of grain (Bahrami *et al*. 2017). Such adjustment of plant metabolism can thus lower crop nutritional quality for the human consumer as well as the nutritional quality of natural vegetation (nitrogen content, protein, and carbon-to-nitrogen ratio) for the nonhuman consumer, thereby reverberating up into higher trophic levels (Sardans *et al*. 2012). The combination of high light and high CO_2 supply can thus have a cost to the consumer in the form of lower protein concentrations in C_3 plants and a higher carbon-to-nitrogen ratio of plant biomass. Combinations of elevated CO_2 with environmental conditions that limit growth can enhance photosynthetic downregulation, exacerbate growth reductions, and trigger early senescence (for details, *see* the following subsections).

It should be noted that engagement of photoprotective measures in their full capacity counteracts metabolic disruption. Such photoprotection includes dissipation of excess excitation energy as heat (Demmig-Adams *et al*. 2012), rerouting of electrons (Kramer *et al*. 2004), and elimination of ROS by antioxidant metabolites and/or enzymes (Havaux and García-Plazaola 2014), all of which counteract the formation or accumulation of ROS. When the capacity of these protective processes is exceeded under severe stress, highly excessive ROS production can shut down photosynthesis in a feedback loop (Adams *et al*. 2006, 2013, 2014; Demmig-Adams *et al*. 2014, Foyer 2018). Prins *et al*. (2009) noted that elevated CO_2 can also trigger accelerated leaf senescence when sugars accumulate to concentrations that inhibit photosynthetic gene expression (*see* Dai *et al*. 1999, Moore *et al*. 1999, Diaz *et al*. 2005).

Nitrogen and plant redox state: Just like excess CO_2 and excess light, unbalanced nitrogen metabolism (either limiting or excess nitrogen) can disrupt plant redox balance (Chaput *et al*. 2020). While nitrogen is required for photosynthesis, the growth of sink tissues is the process that is most sensitive to a shortage of mineral nutrients, especially nitrogen (Burnett *et al*. 2018). Plant sink tissues require carbohydrates and nitrogen in a balanced ratio, and a shortage of nitrogen leads to a backup of carbohydrates. In some scenarios, a plant's capacity to provide reduced forms of nitrogen for amino acid/protein synthesis decreases under elevated CO_2 (Stitt and Krapp 1999, Feng *et al*. 2015, Foyer and Noctor 2020). One suggestion for how the internal availability of nitrogen for amino acid synthesis may decline under elevated CO_2 involves suppression of photorespiration, a process with an important role in the nitrogen metabolism of C_3 plants (Bloom 2015, Busch *et al*. 2018). Another mechanism involves high levels of nitrate supply and the step of nitrate reduction by nitrate reductase. Elevated CO_2 concentrations initially stimulate nitrate reductase activity, which is associated with the enhanced production of redox messengers (nitric oxide and ROS; Bian *et al*. 2020). These messengers can secondarily repress key genes in nitrogen metabolism, including nitrate reductase itself (Wu *et al*. 2020; *see* also Shin and Schachtman 2004, Kim *et al*. 2010), and can trigger plant senescence (Adavi and Sathee 2021a, Padhan *et al*. 2020; *see* also Queval *et al*. 2007, Krasensky-Wrzaczek and Kangasjärvi 2018).

Synergy among environmental factors

Plants sense the availability of CO_2, light, and nitrogen and funnel these environmental inputs into a common master signaling network that orchestrates plant response (Fig. 4). CO_2, light, and nitrogen supply are all inputs into

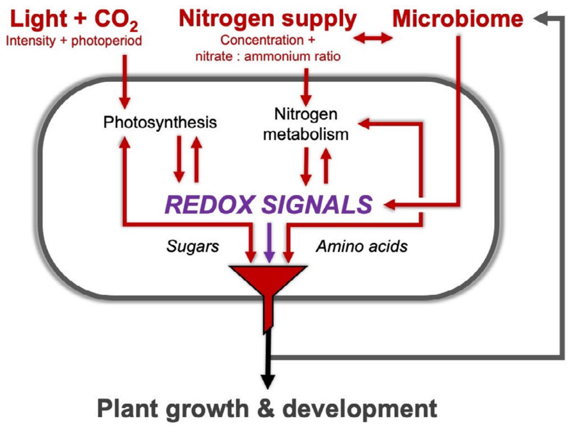

Fig. 4. Schematic depiction of common principles by which signals from environmental inputs of light, CO_2, nutrients (total nitrogen supply and nitrate-to-ammonium ratio), and the plant microbiome are integrated into common redox-signaling networks that orchestrate plant growth and development. The black outer arrow pointing back to the microbiome symbolizes the portion of photosynthetically produced sugars that sustain the plant's microbial partners, with the rest supporting the plant's own growth and development.

plant redox state (Fig. 4; Lake *et al.* 2002, Suzuki *et al.* 2012, Mhamdi and Noctor 2016) that, in turn, regulates photosynthesis, growth, and multiple other essential plant functions. This integration of signals from the environment explains the synergistic effects of environmental inputs, such as the impact of nitrogen supply on plant response to elevated CO_2 (*see* Tausz-Posch *et al.* 2020). For example, elevated CO_2 concentrations induced decreases in the level and activity of nitrate reductase especially when nitrate supply was high (*see* above; Du *et al.* 2008, Bian *et al.* 2020). Conversely, limiting nitrogen supply can exacerbate the effects of elevated CO_2 and high light supply. Limiting nitrogen supply strongly reduces plant sink activity and worsens source–sink imbalance (Paul and Driscoll 1997, Logan *et al.* 1999). Recent reports have, therefore, suggested that some level of nitrogen fertilization in natural plant communities (that are frequently nutrient-limited) may mitigate the negative effects of elevated CO_2 in some scenarios (Wang *et al.* 2020). Furthermore, other environmental factors that lower plant sink activity and exacerbate plant source–sink balance will exacerbate metabolic disruption (Aranjuelo *et al.* 2005).

Maintenance of redox homeostasis in photosynthetic organisms: Plant source–sink imbalance is prevented by a high sink activity. When sink activity is high, sugar transporters (such as glucose 6-phosphate/phosphate translocator GPT2; Knappe *et al.* 2003) that export sugar from the chloroplast and play a role in metabolic adjustment may be upregulated in response to environmental change (Dyson *et al.* 2015). A backing up of electrons in the electron transport chain can be further counteracted by the routing of electron flow to alternative pathways, such as cyclic electron flow in the chloroplast (cyclic flow around PSI and other pathways; Kramer *et al.* 2004, Ivanov *et al.* 2012, Blanco *et al.* 2013, Courteille *et al.* 2013, Strand *et al.* 2016). These alternative routes for electron flow also support dissipative pathways that remove excess absorbed light (excess excitation energy) as harmless heat (Kawashima *et al.* 2017). In addition to the chloroplast, mitochondria, as well as processes associated with the cell membrane, produce more oxidants under elevated CO_2 concentrations, which requires coordinated adjustments across the cell to maintain cellular redox homeostasis (Foyer and Noctor 2020). Plant mitochondrial alternative oxidase (AOX) is a key player in the coordination of alternative electron flow in mitochondria and chloroplasts (Yoshida *et al.* 2007, 2011; Vishwakarma *et al.* 2014, 2015; Shapiguzov *et al.* 2019). AOX serves as a safe outlet for electrons in the mitochondria and maintains cellular redox homeostasis when changes in the environment threaten to disrupt metabolism (Yoshida *et al.* 2007, Voss *et al.* 2013). Moreover, plant AOX levels responded to CO_2 and light supply in the growth environment (Wang *et al.* 2014).

Plant microbiome and plant productivity

The plant microbiome – communities of bacteria, fungi, protozoa, archaea, and viruses (Mueller and Sachs 2015) – is associated with various plant parts (Turner *et al.* 2013), including roots (Pieterse *et al.* 2016) and leaves (Marquez-Santacruz *et al.* 2010). The extent of plant response to the presence of microorganisms depends on environmental conditions (Becklin *et al.* 2016), such as CO_2 concentration (*see*, *e.g.*, Syvertsen and Graham 1999, Gavito *et al.* 2002, Jifon and Wolfe 2002) and nitrogen availability (*see*, *e.g.*, Johnson *et al.* 2010, Weese *et al.* 2015).

In the following section, the available evidence is integrated into support of the potential of symbiotic relationships with microorganisms to enhance plant photosynthetic productivity by multiple mechanisms (Figs. 1, 5, and 6), including:

– **provision of additional sinks for carbohydrates** (Stefan *et al.* 2013, Ishizawa *et al.* 2017, Adams *et al.* 2018, Yamakawa *et al.* 2018);

– **supply of nutrients that support the growth of sink tissues without disrupting nitrogen metabolism**;

– **production of regulators of plant metabolism and growth with an emphasis on restoration of redox homeostasis** *via*, *e.g.*, synthesis of plant hormones (Vacheron *et al.* 2013) and input into central signaling networks that control photosynthetic capacity and growth. Such regulation may specifically include buffering of departures from plant redox homeostasis when environmental conditions shift (*see*, *e.g.*, de Sousa Leite and Monteiro 2019, Ortíz *et al.* 2020).

As stated above, the plant microbiome may be able to contribute to maintaining plant redox homeostasis both indirectly – by consuming photosynthetically produced sugars (acting as sugar sinks) and balancing plant nitrogen status – and directly by manipulation of electron flow routes (Figs. 5, 6). Evidence that symbiotic partners act as sugar sinks is seen in symbioses between photosynthetic and nonphotosynthetic partners (Grant *et al*. 2006, 2013), where starch is mobilized from the chloroplast at higher rates. Fig. 5 depicts the general role of carbohydrates produced in plant photosynthesis in supporting the metabolism and growth of not only the plant, but also its microbial partners, and lists multiple microbial inputs into plant metabolism. An important additional line of support for the ability of symbiotic partners to regulate photosynthesis, other aspects of metabolism, and redox homeostasis of their photosynthetic partners comes from obligate host–algal symbioses. Xiang *et al*. (2020) reported differential expression of genes associated with nitrogen acquisition and assimilation in symbiotic algae growing within *vs*. outside of their nonphotosynthetic host, specifically algal genes for ammonium and nitrate transporters, nitrate reductase, and transporters for organic nitrogen compounds such as urea and purines. These same authors concluded that the symbiotic partners exhibited 'metabolic integration' between them, where nitrogen metabolism was 'decoupled' from photosynthesis in the photosynthetic partner in the sense that photosynthesis proceeded at high rates irrespective of nitrogen status by carbohydrate consumption by the nonphotosynthetic partner and associated relief of back-pressure into photosynthetic electron transport and prevention of excess ROS formation (Xiang *et al*. 2020). Moreover, interaction of the plant rhizosphere microbiome with the plant's AOX was reported by Ortíz *et al*. (2020). Fig. 6 summarizes common themes of how microorganisms provide multiple direct and indirect inputs into networks that regulate plant metabolism.

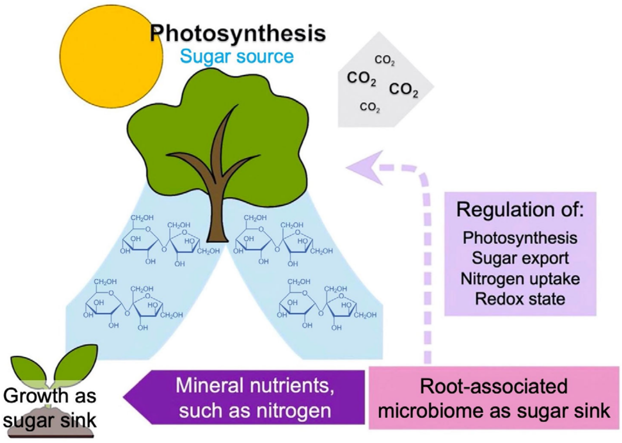

Fig. 5. Schematic depiction of the split flow of carbohydrate produced in photosynthesis (shown here as the transport form sucrose) to either the plant's own sinks (shown here as the growing tissues of the plant) or the root-associated microbiome that provides mineral nutrients to the plant as well as regulatory input into plant metabolism (*purple box*).

Such metabolic integration is reminiscent of the control of vital aspects of human functions by microbial gene regulators that target organellar electron transport chains and modulate the production of ROS (Saint-Georges-Chaumet *et al*. 2015, Ballard and Towarnicki 2020). Plants possess organellar electron transport chains in chloroplasts as well as in mitochondria, and both plant organelles may engage in chemical communication with microorganisms (Han *et al*. 2019, Yang *et al*. 2021). The ability of microorganisms to suppress the formation of ROS – that also participate in host defense against pathogens – presumably played a role in the evolution of host/microbe symbioses. This ability of microorganisms to manipulate the host redox state appears to have a key role in human and plant host health and/or productivity today (Yang *et al*. 2021). Conversely, such modulation of plant metabolism by beneficial microbial partners can also

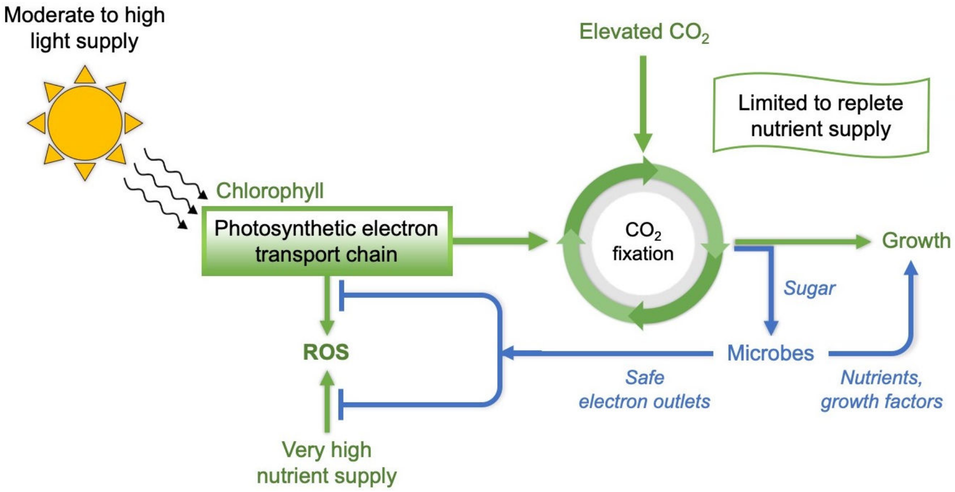

Fig. 6. Schematic depiction that summarizes the multiple ways in which the plant microbiome can support plant growth (*blue arrows*), *i.e*., by provision of nutrients and plant growth factors, acting as an additional or alternative sugar sink, and presumably also by inducing safe outlets for electrons, and preventing excess reactive oxygen (ROS) formation in photosynthetic electron transport as well as nitrogen metabolism under high nitrate supply (presumably by adjusting the ratio of nitrate-to-ammonium supply and utilization).

augment plant defense against pathogens (Vandana *et al.* 2021) as well as participate in redox-mediated quorum sensing in plants and modeling of rhizosphere architecture (Fuller *et al.* 2017). For example, signaling molecules involved in quorum sensing have activity as plant gene regulators (Ohkama-Ohtsu and Wasaki 2010, Phour *et al.* 2020) in a way that is reminiscent of the gene-regulatory activity of gut microbial metabolites in animals, including regulation of host mitochondrial redox homeostasis (Saint-Georges-Chaumet *et al.* 2015). In addition to direct communication between microorganisms and plant organelles, the sugar consumption by microbial partners presumably provides input into the plant's intrinsic source–sink regulatory networks.

Concerning the ability of plant–microbe interaction to elevate the plant's ability to maintain growth under abiotic stress, a recent study on the response of mustard (*Brassica juncea*) to drought conditions reported that inoculated *vs.* uninoculated plants exhibited enhanced shoot and root biomass, greater water content, higher photosynthetic rates, greater expression of antioxidant enzymes, and concluded that 'rhizobacteria mediated maintenance of ROS homeostasis' (*cf.* Figs. 5 and 6; Asha *et al.* 2021). Similar beneficial effects of rhizobacteria are also seen under other environmental stresses (Yang *et al.* 2009, Dhayalan and Karuppasamy 2021).

When plant sink tissues consume large amounts of sugar under conditions that are already favorable for plant growth, additional sugar consumption by microbial partners could hypothetically represent competition for sugar between the plant and its microbial partners. However, if the plant were able to enhance its photosynthetic capacity enough to fully accommodate the combined sugar demands, no competition should result. In other words, upregulation of photosynthetic capacity through the plant's existing regulatory supply-and-demand-based mechanisms should be able to produce enough additional sugar to prevent competition. While experimental manipulation of the plant microbiome is challenging in terrestrial plants growing in soil, some evidence is available for overall enhanced plant productivity in the presence of fungal partners of terrestrial plants (Romero-Munar *et al.* 2017, Yang *et al.* 2020). Inoculation of roots of terrestrial plants with arbuscular mycorrhizal fungi increased plant root volume and activity and triggered photosynthetic upregulation (Chen *et al.* 2017, Romero-Munar *et al.* 2017). Conversely, elimination of the mycorrhizal system of cucumber resulted in a decline in photosynthesis (Gavito *et al.* 2019; *see* also Lamhamedi *et al.* 1994). Transcriptomic analysis of such systems revealed differential gene expression in pathways of photosynthesis, hormone metabolism, carbohydrate metabolism, amino acid metabolism, stress response, signal transduction, and antioxidation (Yang *et al.* 2020), all of which are consistent with, and validate, the general framework summarized in Figs. 2, 5, and 6. There is also some evidence for increased growth of inoculated *vs.* sterile aquatic duckweed plants, which allow facile manipulation of the rhizosphere microbiome (Ishizawa *et al.* 2017, 2020; Toyama *et al.* 2017) that consisted mainly (80–95%) of Proteobacteria (Acosta *et al.* 2020, Huang *et al.* 2020, Ishizawa *et al.* 2020, Rana *et al.* 2020).

However, more work is needed to understand plant interaction with microbial communities in specific environmental contexts. For example, inoculation of a sterile aquatic plant line (genus *Lemna*) with a bacterial strain widely reported to promote plant growth resulted in pronounced growth enhancement under some conditions but in growth penalties under other conditions – where the bacterium competed with the plant for mineral nutrients (Ishizawa *et al.* 2017, Khairina *et al.* 2021). Ishizawa *et al.* (2020) also reported both beneficial and adverse effects of microorganisms on duckweed growth, and future research is warranted to further elucidate the mechanisms of these interactions (for a review on the potential of duckweeds as a model system for research on plant–microbe interaction and other aspects of plant biology, *see* Acosta *et al.* 2021).

Conclusions: In response to combinations of elevated atmospheric CO_2 and excess light, imbalances in plant source–sink ratio and redox state are addressed by the plant *via* downregulation of key photosynthetic genes, which results in reduced foliar protein content in C_3 plants and a higher carbon-to-nitrogen ratio of plant biomass. Any additional stresses that curb growth, however, can trigger more pronounced photosynthetic downregulation, exacerbate growth penalties, and accelerate senescence. Microbial partners may be able to support plant productivity under challenging environmental conditions by providing nutrients, acting as an additional carbohydrate sink, and *via* direct manipulation of plant redox state. While the present review focused on a small set of selected abiotic factors, plant–microbe interaction also plays a critical role under numerous other abiotic conditions. These include conditions (such as heavy metal or saline stress) under which plant–microbe interactions play a critical role in plant tolerance as well for bioremediation (Fester *et al.* 2014, Islam *et al.* 2021). Moreover, future research is needed to integrate microbial services into the framework of plant interaction with not only the abiotic but also the biotic environment (Dodds *et al.* 2020).

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