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The essential nutrient elements in photosynthesis

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Essential plant nutrient elements are "eaten" along with light in the process of photosynthesis, primarily in the leaves. Two pigment-protein systems embedded in the thylakoid membrane, Photosystem I and Photosystem II, mediate light absorption, excitation energy transfer, primary photochemistry, electron transfer, oxidation of water, and reduction of $NADP^+$ to NADPH. In addition to electron transfer, several membrane complexes release protons (H^+) into the thylakoid lumen, generating an H^+ gradient which is utilized by ATP synthase to produce ATP. Here, we describe how essential nutrient elements play vital roles in the metabolic pathways of photosynthesis and how their absences limit productivity because they are integral to the trafficking and turnover of metabolites. We provide an overview of key processes of photosynthesis, activation by metalloproteins, and the sites of their interactive roles in plants. An original open-source figure of the Z-Scheme of photosynthesis and the location of elements therein is provided for education and lectures. Signaling between nutrients, as well as crosstalk with plant growth regulators are important for directing metabolic pathways of photosynthates, such as sugars, highlighting the significance for management of minerals in the modulation of photosynthesis in the field.

KEYWORDS
electron transport chain, essential mineral elements, photosynthetic protein complexes, plant physiology, metalloproteins, oxygenic photosynthesis, redox regulation

1 Introduction

Essentiality signifies that the absence of even one essential plant nutrient element renders growth or reproduction impossible (Arnon and Stout, 1939). Here, we discuss the roles of elements that are essential to photosynthesis, acknowledging that this process is just one of many in which minerals may be involved (Naithani et al., 2021). In limited cases, the field of ionomics is investigating transcriptomes that encode gene expression in the metabolome to better understand crosstalk among mineral nutrient elements (see, for example, Fan et al., 2021). Analyses of the relationship between organelle function in the plant cell and these nutritive elements suggest that they can be factors in directing crosstalk among plant signaling networks (see, for example, Fakhimi and Grossman, 2024). Our goal is to clarify the relationship between the involvement of the mineral elements and the major processes of photosynthesis without providing a comprehensive review of fertilizers.

2 Essential elements in photosynthesis

When treating a crop to improve photosynthetic efficiency, supplementation with *essential* nutrient elements is a notable consideration, particularly for consistency of crop yields, as demonstrated in pivotal studies with growers (Nonomura et al., 2018;

TABLE 1 The functional roles elements in photosynthesis and related processes, and their primary sites of action. Photosynthesis is facilitated by essential elements that collectively sustain the light and carbon reactions, as well as their integration of the process with metabolism in the entire plant. Key functions are coordinated through their principal sites and associated components, including the Photosystem II (PSII) and Photosystem I (PSI).

Elements	Key functions in photosynthesis	Main sites/Associated component(s)
Carbon (C)	Backbone of organic molecules (proteins, lipids, pigments, etc.). HCO_3^- regulates PSII electron (e^-) transport	Chloroplast, CBB cycle, rubisco, PETC
Hydrogen (H)	Constituent of water and organic molecules. Proton gradient for ATP synthesis	PSII, thylakoid lumen, Q-cycle, ATP synthase
Oxygen (O)	Constituent of water, organic molecules, and the Mn_4CaO_5 cluster of PSII. Released as O_2 during water oxidation	PETC
Nitrogen (N)	Constituent of amino acids, proteins, chlorophyll, nucleic acids, NADPH, and ATP. Building block of CBB cycle enzymes	Chloroplast, PETC proteins and pigments
Phosphorus (P)	Energy transfer and storage (P*i*, ADP, ATP, NADP, and NADPH), membrane phospholipids, ATP synthase activity, and CO_2 fixation	ATP synthase, ferredoxin (Fd), FNR, rubisco
Potassium (K)	Enzyme activation, ion transport, thylakoid ion homeostasis, lumen acidification, e^- transport, CO_2 diffusion	Chloroplast, thylakoid K^+ channels and K^+/H^+ antiporters
Calcium (Ca)	Structural element of the Mn_4CaO_5 cluster required for water oxidation and O_2 evolution. Implicated in regulation of e^- transfer and carbon reactions proteins. Ca is involved in the reversible binding of carbohydrates to lectin	PSII, lectins, signaling-related proteins
Magnesium (Mg)	Central atom to chlorophyll. Required for key CBB cycle enzymes, as well as rubisco activation	Light-harvesting complexes chlorophylls and reaction-center chlorophylls of PSI and PSII, ATP-dependent enzymes, rubisco activase
Sulfur (S)	Essential for e^- transfer. Forms FeS clusters. Component of key amino acids of proteins	Cyt b_6f, PSI, Fd, proteins
Iron (Fe)	Essential for photosynthetic e^- transfer reactions as a component of FeS clusters. Involved in PSII regulation, chloroplast metabolism, and photorespiration	PSII, Cyt b_6f, PSI, Fd, chloroplast enzymes
Zinc (Zn)	Cofactor of Cu/Zn-superoxide dismutase and carbonic anhydrase. Contributes to C-metabolism	Cu/ZnSOD; carbonic anhydrase, chloroplast and cellular enzymes
Manganese (Mn)	Core constituent of the Mn_4CaO_5 cluster responsible for water oxidation. Serves as cofactor in other catalytic reactions and may participate in photorespiration. Involved in the reversible binding of carbohydrates to lectin	PSII and other plant enzymes
Copper (Cu)	Redox cofactor of plastocyanin (PC), mediating e^- transfer from Cyt b_6f to PSI. Functions in Cu/ZnSOD and other Cu-dependent enzymes	PETC, PC, Cu/ZnSOD, other metalloenzymes
Boron (B)	Involved in carbohydrate metabolism	Developing plant tissues
Molybdenum (Mo)	Cofactor in redox enzymes, particularly those involved in N-assimilation. May indirectly support photosynthesis through effects on chloroplast development	N-assimilation enzymes and other Mo-containing enzymes
Chlorine (Cl)	Required as Cl^- for PSII activity. Involved in proton-transfer regulation via Cl^-channels	PSII; Cl^- channels/transporters
Nickel (Ni)	Associated with chloroplast Fe^{2+} transport	NiCo-PIC1, chloroplast inner membrane transport/homeostasis systems
Cobalt (Co)	Associated with chloroplast Fe^{2+} transport	NiCo-PIC1

Nonomura et al., 2020). Indeed, the availability of these elements to the chloroplasts and other plant organelles is crucial for enhancing photosynthesis and supporting sustainable crop productivity, particularly in cases where deficiencies have been diagnosed. Therefore, growers supplement crops with fertilizers containing elements that are required for fundamental processes, including those that keep the engines of photosynthesis running. By convention (see, for example, farmers' field guides, such as Pier, 2023; Pier and Barlow, 2019), the essentials for plant nutrition include the following elements: Carbon (C), Hydrogen (H), Oxygen (O), Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca), Magnesium (Mg), Sulfur (S), Iron (Fe), Zinc (Zn), Manganese (Mn), Copper (Cu), Boron (B), Chlorine (Cl), Molybdenum (Mo), Nickel (Ni), and to the extent that it is

accepted as an essential mineral element Cobalt (Co) (Rochaix, 2011; Shevela et al., 2019; Schmidt et al., 2020; Hu et al., 2021; Osman et al., 2021). On a dry-weight basis, air- and water-derived C, H, and O elements account for ~94–96% of plant biomass, whereas primary macronutrients (~2–3.5%), secondary macronutrients (~0.5–1.5%), and micronutrients (<0.1%) together comprise only a small fraction of dry mass, despite their roles in photosynthesis.

As summarized in Table 1, the elements associated with photosynthesis operate in a highly coordinated manner across the light reactions, carbon fixation, and related metabolic pathways. Thus, C, H, and O derived from air and water, provide the molecular framework for the substrates and products of photosynthesis, including water, carbohydrates, and evolved oxygen. The primary macronutrients N, P, and K, support the synthesis of chlorophylls, nucleic acids, proteins, and energy-transfer molecules, while also contributing to membrane transport, ATP and NADPH formation, carbon assimilation, and translocation of photosynthates. The secondary macronutrients, Ca, Mg, and S are integral to core structures and activities of photosynthesis including the water-oxidizing complex of Photosystem II (PSII), chlorophyll molecules, ATP-dependent enzymes, the Calvin-Benson-Bassham (CBB) cycle, the plant lectin cycle, and iron-sulfur (FeS) proteins of Photosystem I (PSI) and the Cytochrome (Cyt) b_6f complex. The micronutrients Fe, Mn, Cu, Zn, Cl, Mo, B, Ni, and Co function mainly as structural or catalytic cofactors, and as regulators of electron (e^-) transport, photoprotection, carbon metabolism, nitrogen assimilation, and chloroplast metal homeostasis. Collectively, these elements sustain light harvesting, water oxidation, e^- transport, ATP and NADPH production, the carbon reactions, and the integration of photosynthesis with whole-plant metabolism.

2.1 Air- and water-derived elements

Carbon (C) is the backbone of all organic molecules, most notably those of the carbohydrates in the carbon reactions of photosynthesis (see discussion of the C-reactions in: Govindjee et al., 2020; Nonomura et al., 2017). In plants, C is primarily acquired from atmospheric carbon dioxide (CO_2), which diffuses into leaves through stomata and serves as the inorganic C-source for the synthesis of organic compounds via the CBB cycle (Benson et al., 2009; Sharkey, 2024). Thus, CO_2 in the air is crucial for plant growth and biomass formation. Further, the bicarbonate ion (HCO_3^-) is a critical cofactor of PSII, regulating the photosynthetic e^- transport chain (PETC) (Brinkert et al., 2016; Shevela et al., 2012; Shevela et al., 2020; Sharkey, 2021; Vinyard and Govindjee, 2024).

Hydrogen (H) and Oxygen (O) make up water (H_2O) that is split during water oxidation after the transformation of light to chemical energy. This process is the core of oxygenic photosynthesis since molecular O_2 is generated. We note that H and O are components of all proteins, pigments, lipids, carbohydrates, and many other biomolecules. Furthermore, H^+ ions released during water oxidation, as well as during other steps, play essential roles in the generation of pH gradients (ΔpH) across the thylakoid membrane, leading to the production of ATP (see discussion in Junge and Nelson, 2015; Wydrzynski, 2008).

2.2 Primary macronutrients

Nitrogen (N) is the key component of all amino acids that make up the proteins in plants; and it is an essential constituent of chloroplast membranes, chlorophylls, nucleic acids, NADPH, and ATP molecules. Further, the activities of many of these abundant nitrogenous compounds across the paths of photosynthesis involve signaling networks (Li et al., 2021) and crosstalk (Fan et al., 2021). Unlike most mineral nutrients whose influence on photosynthesis saturates once a threshold concentration is reached, leaf N content shows an approximately proportional relationship with photosynthetic capacity across a wide physiological range. This relationship arises because a large fraction of N is invested directly in the photosynthetic apparatus within the leaf, particularly in rubisco and thylakoid proteins involved in the PETC. Thus, the capacity for e^- transport in the chloroplast is directly proportional to cytochrome *f* (Cyt *f*) content (Evans and Clark, 2019) while N-assimilation is integral to C-assimilation (Nunes-Nesi et al., 2010). Nitrogen use and allocation differ substantially between C_3 and C_4 plants. See Sections 3.4, 3.5 for details on N.

Phosphorus (P) is a constituent of inorganic phosphate (P_i) and of the key energy-transfer molecules NADP, NADPH, ADP, and ATP. Also, it is an essential component of proteins and lipids, for example, phospholipids are embedded in the thylakoid membrane. In photosynthesis, P_i plays a central role in both the light reactions and the C-reactions. Carstensen et al. (2018) showed that under deficiency of P, the PETC is disrupted, restricts ATP synthase activity, and reduces CO_2 fixation, and thus, P is linked to both the light reactions and C-reactions of photosynthesis. For example, the fixation of 3 CO_2 molecules to produce one molecule of glyceraldehyde-3-phosphate (G3P) requires the consumption of 9 ATP and 6 NADPH molecules. Therefore, the fixation of 6 CO_2 molecules via the CBB cycle, corresponding to the synthesis of one glucose equivalent, requires 18 ATP and 12 NADPH (Sharkey, 2021; Shevela et al., 2019). During the light reactions, oxidation of two H_2O molecules at PSII releases one O_2 molecule and supplies four electrons that drive the formation of 2 NADPH molecules. The associated e^- transfer reactions result in the translocation of protons into the thylakoid lumen, generating a proton-motive force sufficient to synthesize up to 3 ATP molecules, depending on the H^+/ATP stoichiometry of ATP synthase (Kramer and Evans, 2011).

Potassium (K) is involved in numerous plant processes, including transmembrane transport and enzyme activation. For example, ion transporters and K^+ channels are integrated into the thylakoid. Energy conversion may be affected by modulation of acidification by way of thylakoid and lumen K^+ and Cl^-channeling. Thus, in the thylakoid membrane, the K^+ channel activates PQ, while a K^+/H^+ antiporter stimulates e^- transport (Tränkner et al., 2018; Galvis et al., 2020). Also, K facilitates CO_2 diffusion into chloroplasts and it is involved in the transport of photosynthates throughout the plant (Tränkner et al., 2018).

2.3 Secondary macronutrients

Calcium (Ca) is part of the Mn_4CaO_5 cluster, the site of water splitting and production of O_2 on the e^- donor side of PSII

(Avramov et al., 2020). Also, it is involved, by still unknown mechanisms, in the regulation of e^- transfer and overall photosynthesis (Brahmachari et al., 2017). Calmodulin interacts with K^+ channel domains and glutamate decarboxylase (Yang and Poovaiah, 2003). In the C-reactions of photosynthesis, Ca is a structural element in lectin (Nonomura et al., 2020).

Magnesium (Mg) is not only at the center of all chlorophyll molecules in the antenna used for harvesting sunlight and transferring excitation energy to the reaction center (Weber et al., 2025), but also is in the reaction center chlorophylls in both PSI and PSII, which drive the e^- transfer from water to $NADP^+$ (Adriaje, 2025). Moreover, metalloenzymes of the CBB cycle and all reactions involving ATP require Mg^{2+}. For example, the initial CO_2 link to rubisco is activated by Mg^{2+} and transketolase and phosphoribulokinase are central to the regeneration of ribuose-5-phosphate (e.g., Castro et al., 2021). In addition, Mg is involved in translocation of photosynthates (see, for example, Ishfaq et al., 2021).

Sulfur (S) is associated with iron forming iron-sulfur (FeS) clusters in the Rieske FeS-protein of the Cyt b_6f complex and is part of several PSI components (F_X, F_A, F_B; and in ferredoxin (Fd)). Also, S is a component of methionine and cysteine, two important amino acids that are part of several protein complexes in photosynthesis (de Vitry et al., 2004; Astolfi et al., 2021).

2.4 Micronutrients

Iron (Fe) is part of the structure of several e^- carriers in the system, including bound FeS clusters in Cyt b_6f (FeS of Rieske iron-sulfur protein), PSI (F_x, F_A, F_B), and Fd, see above for S. Further, iron (with bound HCO_3^-; see above) regulates e^- transport in PSII (Müh and Zouni, 2013; Schmidt et al., 2020). In chloroplasts, the biosynthesis of thiamine, a coenzyme for transketolase involved in the C-reactions of photosynthesis (Luo et al., 2026), requires the essential FeS protein (Raschke et al., 2007). For photorespiration, the Fd-dependent glutamine oxoglutarate aminotransferase gene encodes glutamate synthase (Klimpel et al., 2025).

Zinc (Zn) has indirect roles in photosynthesis, primarily as a cofactor in the Cu/ZnSOD, the superoxidase used for the delivery of Cu to plastocyanin (PC) and carbonic anhydrase (Castillo-González et al., 2018).

Manganese (Mn) is the key constituent of the photosynthetic water-splitting catalyst, the Mn_4CaO_5 cluster (Kern et al., 2018; Umena et al., 2011). Both Mn and Ca are involved in the modulation of glycoregulation by lectins (Naithani et al., 2021). Mn is a cofactor in a broad range of catalytic reactions in plants and may be involved in photorespiration (Castro et al., 2021).

Copper (Cu) is a part of PC, which is a mobile carrier transferring electrons from the Cyt b_6f complex to PSI. It is a cofactor of oxidative phosphorylation and is involved in the biosynthesis of alkaloids, flavins and peptides. Further, it is a cofactor of the Cu/ZnSOD, involving both the Cu chaperone for the Cu/ZnSOD in the stroma and the plastid chaperone of the intermembrane space (Schmidt et al., 2020).

Boron (B) is required for the regulation of carbohydrate metabolism in the C-reactions of photosynthesis (Li et al., 2017). Its participation in the light reactions of photosynthesis is not known.

Molybdenum (Mo) is present in four metalloenzymes that catalyze redox reactions in plants involving FAD, FeS or molybdopterin e^- transport chain prosthetic groups (Mendel and Hänsch, 2002). Mo improves chloroplast configuration, increases chlorophyll content (Imran et al., 2019), and conducts crosstalk with iron (Bittner, 2014).

Chlorine (Cl) occurs in plants in the form of chloride ions (Cl^-). It is involved in the regulation of proton (H^+) transfer during photosynthetic water oxidation at the Mn_4CaO_5 cluster in PSII and, more broadly, Cl^- acts as an essential micronutrient for PSII photoassembly and photosynthetic oxygen evolution (Raven, 2020; Imaizumi and Ifuku, 2022). In the thylakoid membrane, the Cl^- channel/transporter may regulate e^- transport in photosynthesis (Dukic et al., 2019).

Nickel (Ni) and Cobalt (Co) play indirect roles in photosynthesis, mainly as cofactors of the nickel/cobalt transporter-permease (NiCo-PIC1), an enzyme that transports Fe^{2+} through the inner membrane of the chloroplast (Schmidt et al., 2020). Co is a chaperone of Cu in the Cu/ZnSOD (Zhu et al., 2000).

3 Photosynthesis

3.1 The light reactions

From an historical viewpoint, the majority of depictions of photosynthesis are shown as in Figure 1A, which classically emphasize the input of light, water (H_2O) and CO_2 to the process of oxygenic photosynthesis. This process has long been known as the principal producer of molecular oxygen on earth in which sunlight that reaches the chloroplast inside of a cell in a leaf is absorbed by the green chlorophylls (for a discussion on the reason for the choice of chlorophyll a, see Björn et al., 2009). Located in the thylakoid membranes, the two pigment systems, PSI and PSII, involve light absorption, excitation energy transfer, primary photochemistry, e^- transfer, oxidation of water, and reduction of $NADP^+$ to NADPH. In addition to e^- transfer, among the complexes in the membrane, protons (H^+) are released into the lumen of the thylakoids, providing an H^+ gradient, which also is utilized to produce ATP via ATP synthase, located in the thylakoid membrane of the chloroplast. Thereafter, NADPH and ATP are used to convert CO_2 into carbohydrates, via C_3 and C_4 pathways, packing energy into sugar bonds (Shevela et al., 2019; Blankenship, 2021).

In this perspective, we show the complexes in photosynthesis as simplified structures of the chloroplast. Protein complexes and cofactors are shown only on the upper side of the thylakoid membrane, while the ion channels are shown on the bottom side. At the top of the diagram, the chloroplast outer membrane is shown with graphic summaries of sugar transport and N-assimilation in the cytoplasm (outside of the chloroplast) to further feature the light reactions. Indeed, the inner membrane of the chloroplast depicts delivery of copper ions via the Cu/ZnSOD and transport of iron ions via the NiCo-PIC1 enzyme complexes. Other activities are not shown here.

The above Figure 1A serves to identify the sites in the light reactions of photosynthesis upon which the related elements will be

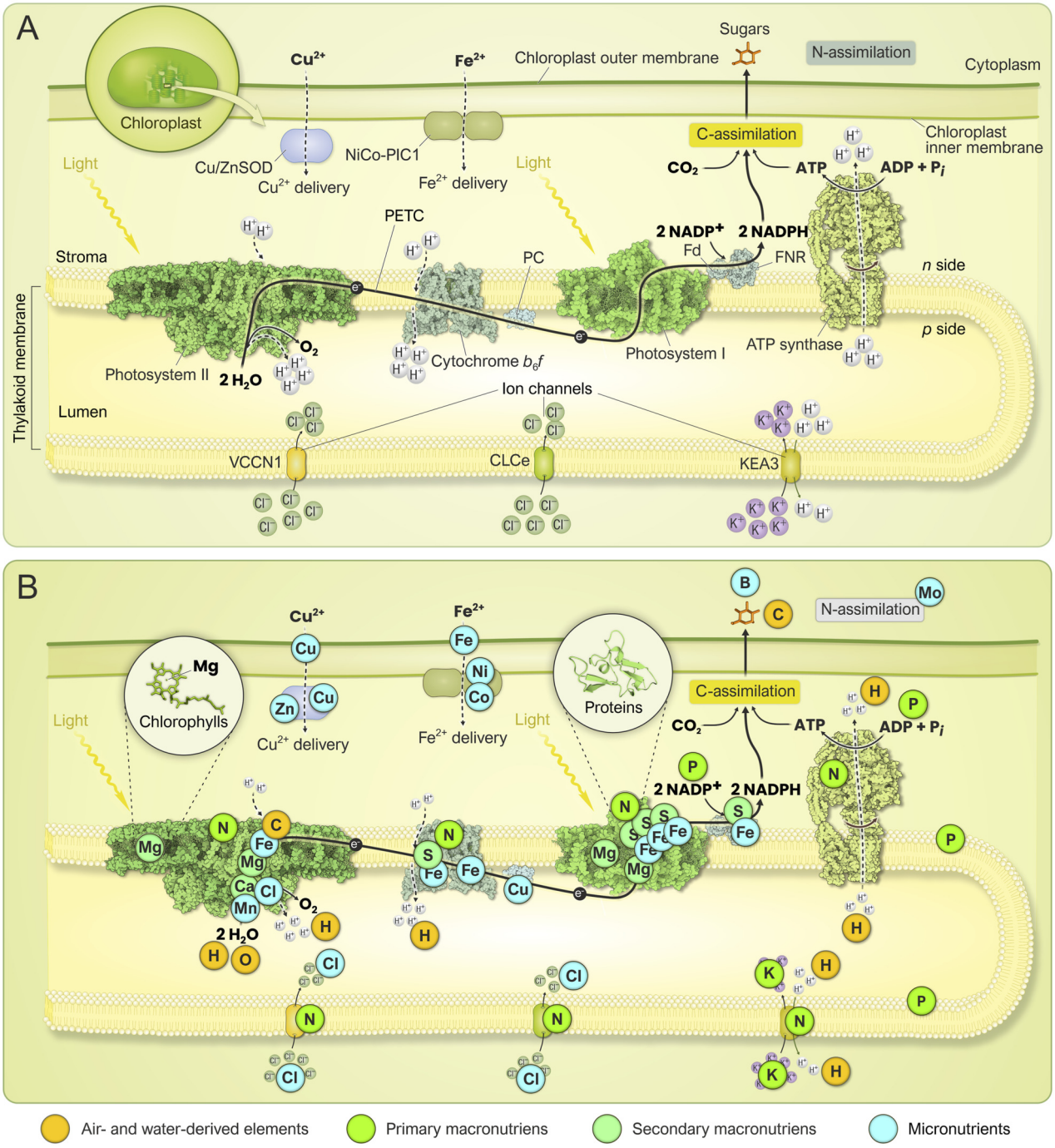


FIGURE 1
(A) A generalized schematic of the photosynthetic electron transport chain (PETC) and major protein complexes of the thylakoid membrane involved in oxygenic photosynthesis. The ion channels are depicted in this membrane at the bottom of this panel. Further, the chloroplast membranes with the Cu/ZnSOD and the NiCo-PIC1 are shown at the top of the diagram, as well as carbon and nitrogen assimilation inside and outside of the chloroplast. The complexes shown here were generated with *Protein Imager* using coordinates from the following PDB entries: 5xnl, 6b8h, 1vf5, 4y2b, 3w5u, and 1ag6. Note that the complexes are not represented at a 1:1 ratio. Abbreviations: ADP/ATP, adenosine diphosphate/triphosphate; CLCe, Cl^-channel/transporter; Cu/ZnSOD, Cu/Zn superoxide dismutase; Cyt b_6f, Cytochrome b_6f complex; e^-, electron (or electrons); Fd, ferredoxin; FNR, ferredoxin-NADP oxidoreductase; H^+, proton (or protons); KEA3, K^+/H^+ antiporter; n- and p-sides, stromal and lumen sides of the thylakoid membrane; $NADP^+$/NADPH, oxidized/reduced nicotinamide adenine dinucleotide phosphate; NiCo-PIC1, a Ni/Co transporter-permease in chloroplasts; PC, mobile plastocyanin copper protein; PQ, mobile plastoquinone; SOD, superoxide dismutase; rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase; VCCN1, a voltage-dependent Cl^-channel. **(B)** Overlay of elements on the key protein complexes of the thylakoid and chloroplast membranes. Shown are locations for various roles of the essential plant nutrient elements, with emphasis on their key functions in the light reactions of photosynthesis.

overlain, as next shown, in Figure 1B. Indeed, essential nutrient elements in relation to their role(s) in photosynthesis are shown in Figure 1B, located at their corresponding sites in the membranes. Of these critical elements, the majority are involved as components of the light reactions of photosynthesis: C, H, O, N, P, K, Ca, Mg, S, Fe, Mn, Cu, and Cl. The remaining essential elements, Zn, B, Mo, Ni and Co, function indirectly in various photosynthetic processes as cofactors, catalysts, and transporters. As an example, pathways of Mo are connected to Fe metabolism (Bittner, 2014). Near the top of the diagram, Zn, Cu, Ni and Co are shown with their respective enzymes.

Figure 1 of the Z-Scheme and the location of elements is provided in this open-source issue for education and lectures. Note that detailed illustrations of photosynthetic processes are available in Govindjee's educational poster series online[1].

3.2 The carbon reactions

With respect to the C-reactions of photosynthesis, the general emphasis in the past had been directed towards the uptake of CO_2 and H_2O–the building blocks of carbohydrates. Further, we note that it is important to consider C- and N-assimilation as integrated processes (Bloom, 2015; Thompson et al., 2017). In fact, Bloom et al. (2002) showed that co-application of elevated CO_2 with N promoted the synthesis of nitrogenous products that are key to growth, while Mo played key roles in N-assimilation, resulting in amino acids and proteins important for all aspects of plant growth and development (see, e.g., Mendel, 2007). Furthermore, to the degree that photosynthesis in a leaf is related to N-content, it is because the enzymes in the CBB cycle and in the membranes of the chloroplast represent the majority of leaf N (Evans and Clarke, 2019) and, when pinpointed to a ratio of 155 mol electrons mol^{-1} Cyt f s^{-1}, the capacity for e^- transport is directly proportional to Cyt f. Magnesium, at the heart of chlorophyll, also is known to be involved in the activation of the metalloenzymes in the carbon reactions of photosynthesis starting with ribulose-1,5-bisphosphate carboxylase/oxygenase (see, for example, Carmo-Silva and Sharwood, 2023), and in the essential reactions involving ATP. Consequently, the CBB cycle is activated by Mg as a cofactor in the metalloenzymes, aldolase, transketolase, fructose-1,6-biphosphotase (for example, see Adriaje, 2025), and sedoheptulose-1,7-bisphosphatase (Le Moigne et al., 2025).

Several enzymes in the path of carbon are activated by the reduction of disulfide bonds on conversion *in light* of Fd that is reduced in PSI to a thiol signal. That is to say, the light and C-reactions employ S to transmit signals in the process of photosynthesis (Pasquini et al., 2017). Another essential nutrient element, B (*e.g.,* Li et al., 2017), plays transport roles here. Further, as C- and N-metabolism are tightly related, Mo is shown here because it is required for inorganic N-assimilation mainly as a cofactor in the assembly of nitrate reductase (Imran et al., 2019).

In this section of the C-reactions, we include the structural requirement of legume lectins for Ca and Mn ions at the reversible binding site for specific carbohydrates because they share a role in the modulation of the lectin cycle in plants (Nonomura et al., 2020; Naithani et al., 2021). Specifically in the Jack Bean, Ca and Mn ions serve to stabilize cis-peptide linkages and loop-folding in the lectin at the glycan binding site of Concanavalin A. However, these metal ions do not interact with the carbohydrate that is bound to the lectin (Lisacek et al., 2025).

3.3 Transporters

The actions of metal transporter families enable uptake and movement of nutrients and they include the following: ABC, CAX, CCX, CDF/MTP, ECA, HMA, NRAMP, OPT, VIT and ZIP (Huang et al., 2024). Notably, numerous metalloenzymes are mobile and involve co-transporters and membrane permeases. For example, uptake and transport have been determined for P (Wang et al., 2020), K (Lhamo et al., 2021; Luo et al., 2026), Ca (Wang et al., 2023), S (Gigolashvili and Kopriva, 2014), Mg (Hosseini Pouya and Abdullah and Heidari, 2026), B (Colak and Aydın, 2025; Li et al., 2017; Zhou et al., 2025), Fe (Ning et al., 2023), Mg (Meier et al., 2025), Cu (Xu et al., 2024; Akhtar et al., 2026), Mo (Weber et al., 2023), Ni and Co (Mackievic and Demidchik, 2023; Wang et al., 2025). Transporters coordinate the interplay of compounds, metals and metalloids—from ammonia (Porras-Murillo et al., 2025) to Zn (Krämer, 2025; Ochoa Tufiño et al., 2025) — that regulate the acquisition, distribution and efficient utilization of essential plant nutrients. We consider the "team" relationships of the above elements within a protein complex equally essential–such as for Fe and S, in a Rieske protein; Ca and Mn, in a Mn_4CaO_5 cluster; Ca and Mn in lectins; Co, Zn and Cu, *e.g.,* the Cu/ZnSOD; and Fe, Ni and Co, *e.g.,* the NiCo-PIC1 – because every team of elements works together to support plant life.

The activity of Co in chloroplast functions supports its classification as an essential element, and like Ni, its optimal foliar dose may be in the nanomolar range. Crop advisors currently recognize Co as essential (for example, see online: Essential elements for plant nutrition, Cornell NRCCA Certified Crop Advisor Study Resources (Northeast region).pdf[2]). Moreover, for some state regulatory codes in the USA, Co is labeled an essential mineral element (see online, CSR 250–11.030[3]) and we concur. Today, the requirement for Co is further supported by evidence of its involvement in plants as a cofactor in the metalloenzyme Ni/Co transporter-permease (NiCo-PIC1) in chloroplasts (Schmidt et al., 2020) and as a chaperone for the metalloenzyme Cu/Zn superoxide dismutase (Cu/ZnSOD) (Zhu et al., 2000). Coincidentally, in artificial photosynthesis (see, for example, Mori et al., 2025) Co and other transition metal nanostructures have been investigated at length (Sun et al., 2025). Based on these findings of Co, as well as for the other elements (B, C, Ca, Cl, Cu, H, Fe, Mg, Mn, Mo, N, Ni, O, P, K, S, and Zn) in specific relation to chloroplast function in the plant cell, we recommend that the transfer of photosynthesis-related

1 www.life.illinois.edu/govindjee/newposters.html

2 https://nrcca.cals.cornell.edu/nutrient/CA1/CA010102.php

3 https://casetext.com/regulation/missouri-administrative-code/title-6-department-of-higher-education-and-workforce-development/division-250-university-of-missouri/chapter-11-administration-of-missouri-fertilizer-law/section-6-csr-250–11030-labeling-additional-plant-nutrients

technologies to agriculture regard the fundamental roles of the essential nutrient elements for plants to process light. In the future, the essentiality of other beneficial minerals may be investigated. For example, Frew et al. (2018) highlighted interactions of silicon (Si) with photorespiration and Pavlovic et al. (2021) has shown beneficial interactions in pathways that may indicate a critical role for Si.

3.4 Signaling

Photosynthesis in the foliage of crops relies on nutrient elements from air, water and minerals because, in their absence, reactions cannot be completed. It follows that failures of critical functions are inseparably associated with loss of viability. Of all the metabolic processes in plants, including those in the agricultural crops, providing for this essentiality is particularly important for energy transformations, here exemplified by photosynthesis, whereby light energy is transformed into chemical energy (see, for example, Shevela et al., 2019; Blankenship, 2021). A deficiency in any of the elements may inhibit one or more metabolic pathways (see, for example, the model of Carstensen et al. (2018) for the impact of deficiency in P on the PETC and inhibition of ATP synthase activity) and may shunt to alternate pathways in plants.

In the event of midday deficiency of C-assimilation, photorespiration may occur, but plants with Kranz anatomy may utilize C_4 metabolism, for the most part, avoiding high rates of photorespiration (Lundgren et al., 2014). As compared to C_3 metabolism alone, shunting to C_4 photosynthetic pathways may reduce photorespiration and with it, the costs of photorespiration that may involve ammonia release and its reassimilation by a photorespiratory N-cycle that includes glutamine synthetase and glutamine:2-oxoglutarateaminotransferase. These pathways involve multiple metabolic steps across the chloroplast, peroxisome, mitochondria, and cytosol that utilize ATP (and other redox agents) to the loss N, H_2O, and CO_2. Therefore, both N-use efficiency and water use efficiency are greater in plants with C_4 than those with C_3 metabolism, particularly under high light and temperature conditions (see, for example, Sage and Pearcy, 1987; Sage et al., 1987; Evans and Clarke, 2019).

Recently, Fan et al. (2021) showed that signaling between N, P, S, Zn, and Fe may involve complex crosstalk processes in response to nutrient deficiency. Also, research focusing on signaling networks shows multifaceted roles that connect sugar, nitrate and phosphate nutrients in controlling molecular pathways (Li et al., 2021). Add to that, deficiencies of secondary fertilizers, such as Ca, Mg, and S, in lateritic and leached acid soils, are growing concerns for farm production (see, for example, Ishfaq et al., 2021) because these minerals are vital to photosynthesis. In regions where a deficiency of any of the elements are diagnosed, supplementation by foliar applications is recommended, and based on the sites in the light reactions shown in Figure 1, it may be important to place the nutrients at the site of the photosynthetic processes. Crop nutrient levels may be monitored via sap analysis of plant shoots to support photosynthesis and deficiencies may be corrected by formulating essential plant nutrient elements, as needed. In cases where primary fertilizers, secondary fertilizers and micronutrients may be applied to supplement the deficiencies obviated by sap and soil analyses, foliar uptake of nutrient elements (see, for example, Eichert and Fernández, 2012) may be considered. That would be because the light reactions of photosynthesis are measured in picoseconds (Eaton Rye, 2019) and, to be true, nutrients cannot be drawn up from roots in the soil to the shoot with such rapidity.

3.5 Crosstalk

Technology transfer from the laboratory to the field is likely to benefit from evaluations of crosstalk and signaling networks in biochemical pathways (Mattoo and Upadhyay, 2019). We note that in the case of upregulated farm production, whether by PGRs or through endogenous genetic manipulations, successful future advancements may rely on biorational approaches such that there is a sufficiency of the essential plant nutrient elements to secure high efficiency photosynthesis. Indeed, when treating crops with PGRs, N-input plays integral roles in C-partitioning (Naithani et al., 2021). For instance, in consideration of the correlation of photosynthetic capacity to N-content (Hymus et al., 2001; Jin et al., 2015) and the implications of N-use efficiency for drought relief in crops by elevated CO_2 (Sekhar et al., 2021), applications of nitrogenous plant nutrients with PGRs may carry the potential to benefit vegetative productivity. In agriculture, there are more than forty active ingredients that are registered PGRs (see, for example, Rademacher, 2015) and the metabolons of these diverse chemical compounds are involved in complex signaling pathways (Mattoo and Upadhyay, 2019), including those of photosynthesis and other vital processes involved in signaling networks (Li et al., 2021). For example, Yoshida et al. (2011) showed that light regulates auxin and cytokinin for the initiation of lateral organs of plants. Also, note the role of HCO_3^- in the PETC or in field applications of metabolites of photosynthesis, such as thiamine pyrophosphate, for a heightened perspective at eliciting upregulated processes in photosynthesis (Luo et al., 2026). Recently, Klimpel et al. (2025) discovered that crosstalk between brassinosteroids and amino acid synthesis in photorespiration regulate plant physiology. Thus, it follows that crosstalk may be enhanced by formulation of several commercial PGRs such as cytokinins, auxins, and α-mannosides for optimization of signaling events (*e.g.,* kinetin, indole butyric acid, and the like) and with the essential plant nutrient elements that support heightened photosynthesis. Metabolic shifts of primary plant nutrient elements, such as the C:N ratios, are involved in changes of phases (see, for example, Shah et al., 2024) and, therefore, co-application of a PGR with the essential nutrient elements may benefit photosynthesis goals. The processes that drive the C-reactions may be crucial for achieving consistent field results and this is true for methyl-α-D-mannopyranoside (αMeM), a PGR for photosynthesis (Nonomura et al., 2020; Naithani et al., 2021) for which a role for Mn and Ca in the lectin cycle is recognized (Nonomura and Benson, 2014) and wherein co-application of essential plant nutrient elements with αMeM were found to enhance yields as compared to nutrient controls (Benson et al., 2009; Nonomura and Benson, 2014; Nonomura et al., 2018). Lectins have roles in the C-reactions of photosynthesis, the sugar code, and cell signaling, and ongoing studies of the plant

lectome may lead the field with glycomimetics, molecules that emulate the structure and function of natural glycans (Osterne et al., 2025). We look to the future when glycomimetics with high binding coefficients and high specificities may provide the field with carbohydrate interactions in the plant lectin cycle that may improve the efficiency of photosynthesis.

4 Discussion

Photosynthesis depends on the presence of essential mineral elements at their sites of photosynthesis (see Table 1; Figure 1), for the most part, in the leaves and green stems of crop plants. Most of the reactions in photosynthesis are catalyzed by enzymes, activators, and cofactors in chloroplasts, and close to a third of all known enzymes are associated with the metal elements: Ca, Mg, Fe, Mn, Zn, Cu, Ni, and Co. Moreover, these elements are required for the activity of their respective metalloenzymes (Castro et al., 2021). Transition elements are of particular importance (Yruela, 2013), for example, Fe is essential for the light reactions of photosynthesis (Müh and Zouni, 2013), as well as is the Rieske FeS protein subunit of the Cyt b_6f complex in the chloroplast. As energy transformation in all green plants involves proteins, we recommend further investigations, especially for cultivated plants, by means of biocuration for the elucidation of ever more complex pathways with genetic tools including transcriptomics, metabolomics, proteomics, genomics, epigenomics, ionomics, and lipidomics. Such investigations would seek information about the specificity of metalloenzymes to corresponding organelles, such as those of chloroplasts, peroxisomes, and vacuoles. In the future, a broader purview of the interactive requirements (Schmidt et al., 2020) of the nutrient elements, however complex, may give us insights that bring clarity to their work in photosynthesis.

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Conflict of interest

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