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Engineering light-driven biomineralization for a sustainable carbonate economy

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Photosynthetic activity of cyanobacteria is a prominent driver of cell-surface catalysed extracellular calcium carbonate ($CaCO_3$) precipitation. This natural process termed "biomineralization" occurs only under specific circumstances but has given rise to significant carbonate rock formation throughout geological time. Engineering cyanobacterial cell surfaces for enhanced and constitutive biomineralization of abundant ocean-water dissolved Ca^{2+} and flue-gas CO_2 into $CaCO_3$ may allow for the biotechnological re-capture of CO_2 released by industrial processes such as thermal decarboxylation of $CaCO_3$. This may both limit net greenhouse gas emissions and transform $CaCO_3$ into a sustainable resource. Drawing from geological precedent and basic biological research, this perspective outlines promising synthetic biology strategies to convert cyanobacterial biomineralization into a cornerstone technology for a sustainable carbonate economy.

KEYWORDS

biomineralization and calcification, cyanobacteria, photosynthesis, cell surface engineering, CaCO3

1 Introduction

1.1 Oxygenic photosynthesis and carbonate rocks: from deep time to climate solutions

Oxygenic photosynthesis may have evolved as early as 3.8–3.5 Gya (Rosing and Frei, 2004; Tice and Lowe, 2004; Oliver et al., 2021) and has shaped the Earth more than any other physiological process. Light-driven water splitting has not only resulted in the enrichment of the atmosphere with molecular oxygen (Luo et al., 2016) but also affected the geological record through, *e.g.*, oxidation of ocean-water-dissolved iron, resulting in large-scale deposition of banded iron formations (Thompson et al., 2019). Beyond that, aquatic oxygenic photosynthesis is associated with the precipitation of carbonate minerals such as dolomite ($MgCa(CO_3)_2$) and calcite or aragonite (both $CaCO_3$) in a process called "biomineralization" (Merz, 1992; Riding, 1992). Biomineralization has given rise to most extant carbonate rocks (Vasconcelos et al., 1995), which consist of >50% carbonate minerals and make up for 20%–25% of all sedimentary rocks and as much as 10% of all rocks exposed at the Earth's surface (Parker, 1967). Such dolostones (dolomite) and limestones (aragonite and calcite) are estimated to store over 80% of the Earth's carbon (Falkowski et al., 2000), but limestone is being extensively sourced as raw material for industry and agriculture. Upon mining, limestone is commonly converted into quicklime (CaO) through thermal decarboxylation (Niu et al., 2022; Comes et al., 2024), with CaO extraction for cement production alone causing around 7% of global CO_2 emissions (Durastanti and Moretti, 2024). As less than half of this CO_2 is subsequently re-sequestered through cement carbonation

(Xi et al., 2016), CaO production contributes significantly to atmospheric CO_2 enrichment and anthropogenic climate change (Callendar, 1938; Jones et al., 2023). Mitigating the latter through reduction of net CO_2 emissions and opening up $CaCO_3$ as a sustainable resource could be achieved by coupling $CaCO_3$ thermolysis with microbial biomineralization that re-precipitates released CO_2 and abundant ocean-water-dissolved Ca^{2+} into $CaCO_3$, thus paving the way towards a more sustainable carbonate economy. While cyanobacterial biomineralization has been discussed as a potential means of cost-efficient CO_2 capture and sequestration (CCS) for more than a decade (Jansson and Northen, 2010; Kamennaya et al., 2012) and some inherently productive calcifying species could be identified (Lee et al., 2004; Liang et al., 2013) little practical progress has been made in this field. In this perspective, we suggest a new approach to reason-guided enhancement of light-driven, cell-surface catalysed $CaCO_3$ precipitation in planktonic cyanobacteria, allowing to harness this mechanism for future biotechnological applications.

1.2 Cyanobacterial cell-surface $CaCO_3$ precipitation: passive yet engineerable

Cyanobacteria are photolithoautotrophic prokaryotes and the only recent bacteria known to perform oxygenic photosynthesis. Cyanobacterial photosynthetic activity is assumed to have given rise to significant limestone sediments (Kaźmierczak et al., 1996; Altermann et al., 2006; Banerjee et al., 2006) such as stromatolites (*i.e.*, lithified laminated organosedimentary deposits) and micritic mudstones (Kaźmierczak et al., 1996; Suosaari et al., 2016). While in some cyanobacteria intracellular formation of $CaCO_3$ granules has been documented (Benzerara et al., 2014; Moreira et al., 2017), extracellular $CaCO_3$ precipitation is more commonplace and an arguably much more promising engineering target for light-driven biomineralization. This may technically allow to uncouple cell-surface catalysed carbonate precipitation from biomass production on which most approaches discussed for cyanobacterial CCS rely (Chen et al., 2012; Victoria et al., 2024).

Cyanobacterial $CaCO_3$ precipitation is widely considered a passive byproduct of light-driven metabolic activity (Obst et al., 2009), with $CaCO_3$ crystal formation being largely determined by alkaline conditions in the aqueous media, availability of Ca^{2+} cations, and presence of heterogenous crystallisation nuclei (Jroundi et al., 2022). Cyanobacteria in particular provide all these conditions in the microenvironment around their cells due to (i) media alkalization in the wake of photosynthetic carbon assimilation of CO_2 from HCO_3^- releasing hydroxide ions (OH^-) and thus increasing the extracellular pH to up to 10.5 (de Brito et al., 2022), and (ii) production of cell-surface components such as acidic exopolysaccharides (EPS) (Kamennaya et al., 2018; de Brito et al., 2022; Martinho De Brito et al., 2023) and negatively-charged surface-layer (S-layer) proteins (Schultze-Lam et al., 1992) attracting Ca^{2+} and nucleating $CaCO_3$ crystallisation. Further contributing to (bi-) carbonate ion availability, some cyanobacteria produce active extracellular carbonic anhydrase (eCA) enzymes which catalyse the hydration of water-dissolved CO_2 into HCO_3^-/H^+, presumably as a means of re-capturing CO_2 leaving the cell by diffusion (Soltes-Rak et al., 1997; Trimborn et al., 2009). While likely fostering extracellular $CaCO_3$ mineralisation (Kupriyanova et al., 2007; Hazarika and Yadav, 2023), no direct benefits of cyanobacterial eCA for carbon assimilation have been documented in so far (Kupriyanova et al., 2024), rendering its physiological relevance elusive. Light-driven processes underlying passive cell-surface catalyzed biomineralization (Obst et al., 2009; Görgen et al., 2021) and its intersection with anthropogenic biogeochemical carbon cycle contributions (Friedlingstein et al., 2025) are schematically summarized in Figure 1. With all relevant components being mechanistically understood, cyanobacteria are uniquely suited as synthetic biology chassis for engineered $CaCO_3$ production.

2 Perspective

2.1 Seawater Ca^{2+} availability might enable scalable CO_2 mineralization

Large-scale precipitation of water-dissolved CO_2 as $CaCO_3$ will require considerable amounts of Ca^{2+}. With ocean water containing approximately 10 mM Ca^{2+} (Millero et al., 2008; Emmanuel et al., 2012) and total ocean volume ranging around 1.35×10^9 km^3 (Charette and Smith, 2010) some 1.35×10^{20} mols of dissolved Ca^{2+} are available for $CaCO_3$ precipitation, corresponding to approximately 1.351×10^{19} kg of $CaCO_3$ or 4.985×10^6 km^3 of limestone (density ~2.71 g cm^{-3}). For reference, precipitation of all anthropogenically emitted CO_2 since the industrial revolution (*i.e.*, $\sim 1.5 \times 10^{15}$ kg) (Ritchie, 2019) as $CaCO_3$ would result in 1,260 km^3 of limestone equivalents, rendering ocean-water-dissolved Ca^{2+} a non-critical resource. Extracellular precipitation of seawater Ca^{2+} as $CaCO_3$ using marine or euryhaline cyanobacterial cell surfaces may thus provide a powerful tool for light-driven re-capture of CO_2 from $CaCO_3$ thermolysis or other industrial processes. Since most modern cyanobacteria do not precipitate relevant amounts of $CaCO_3$ for various reasons (Riding, 2006; Kamennaya et al., 2018), engineering their cell surface properties is likely required.

2.2 Promising engineering targets for enhanced $CaCO_3$ biomineralization

2.2.1 Cyanobacterial EPS remodelling

Bacterial EPS have been shown to be potent inducers of $CaCO_3$ precipitation (Ercole et al., 2007; Ercole et al., 2012). While cyanobacterial EPS production has been observed to be increased under elevated CO_2 partial pressures (Kamennaya et al., 2018) or through supplementing pH buffer substances to the culture media (de Brito et al., 2022), anionic EPS production has not yet been the target of directed genetic engineering attempts. This is likely due to the complexity of the underlying biosynthesis and secretion pathways, with more than 20 unique proteins being associated with cyanobacterial EPS biosynthesis (Pereira et al., 2015). In *Synechocystis*, a minimum of 16 genetic components are involved in sulfated EPS biosynthesis alone (Maeda et al., 2021). The genetic complexity underlying anionic EPS biosynthesis hence obstructs reason-guided improvement attempts, rendering engineering of

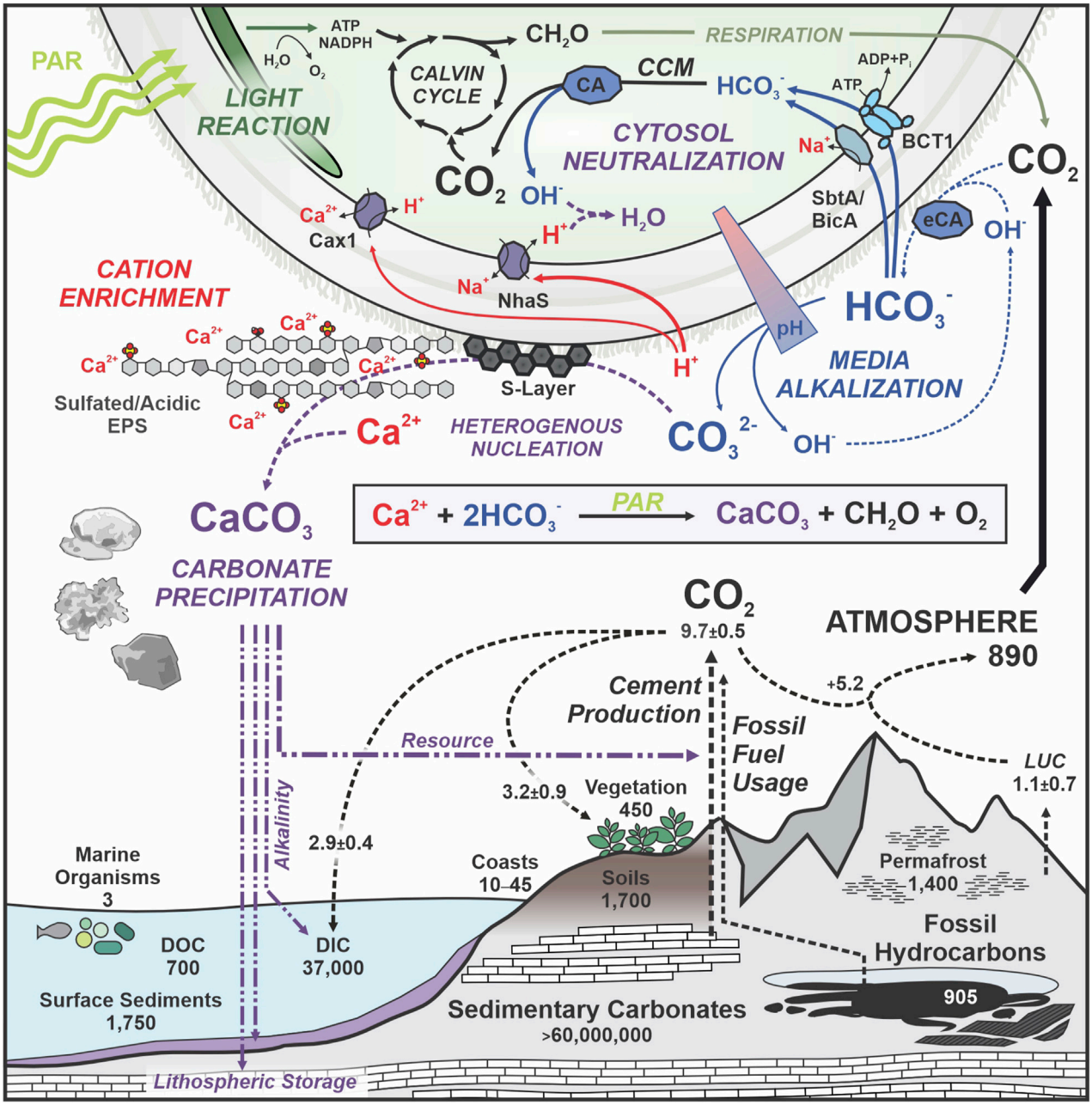

FIGURE 1
Cyanobacterial extracellular biomineralization and its connection to the biogeochemical carbon cycle. Top: metabolic processes and cellular components contributing to extracellular $CaCO_3$ precipitation in cyanobacteria. PAR, photo-synthetically active radiation. CCM, carbon concentrating mechanism. (e) CA, (extracellular) carbonic anhydrase. EPS, extracellular polysaccharides. Plasma-membrane localized bicarbonate importers (BCT1, SbtA, BicA) and proton/cation antiporters NhaS (H^+/Na^+) and Cax1 (H^+/Ca^{2+}) are indicated. Relevant active and passive processes are indicated in italics. The sum reaction formula of photosynthesis-assisted carbonate precipitation is indicated within the inset box. Bottom: anthropogenic carbon cycle contributions (dashed lines) and carbon reservoirs in Gt. DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; LUC, land use change. Natural destinations and possible applications of cyanobacterial $CaCO_3$ precipitates are indicated (purple). Quantitative data adapted from (Falkowski et al., 2000; Friedlingstein et al., 2025).

single gene encoded protein components a favourable target for altering the physicochemical properties of cyanobacterial cell surfaces.

2.2.2 Outer-membrane porins

Being Gram-negative bacteria, cells of cyanobacteria are enclosed by a second lipid bilayer membrane (*i.e.*, the outer membrane) which is commonly equipped with pore-forming beta-barrel proteins (porins) facilitating the uptake of small molecules (Vergalli et al., 2020). Such outer membrane porins have been engineering targets to alter cell surface properties in both *Escherichia coli* (Hogervorst et al., 1990; Xu and Lee, 1999; Chen et al., 2019) and the cyanobacterial model species *Synechococcus elongatus* PCC 7942 (Fedeson and Ducat, 2017).

As overexpression of *E. coli* porins OmpC, OmpF, and PhoE was found physiologically unproblematic, porins may present promising engineering targets for enhancing Ca^{2+} affinity of the cell surface in principle. However, cyanobacterial outer membranes have been found to naturally contain comparably few pore-forming proteins of low conductivity, likely facilitating the uptake of inorganic ions rather than small organic compounds (Hansel and Tadros, 1998; Kowata et al., 2017). Overexpression of modified porins may thus compromise cell viability as observed in *Synechococcus elongatus* PCC 7942 while also necessitating genetic removal of occluding factors such as EPS and S-layer proteins (Fedeson and Ducat, 2017), both of which serve as crystallization nuclei for $CaCO_3$. Cyanobacterial porin engineering may thus not be an optimal strategy towards facilitating $CaCO_3$ precipitation.

2.2.3 Surface display of synthetic Ca^{2+}-enriching polypeptides

Exposure of peptides on the surface of bacterial cells has been developed into a potent screening tool for affinity engineering (Rice and Daugherty, 2008; Kenrick and Daugherty, 2010). Relying on engineered variants of relatively small outer membrane proteins such as the beta-barrel proteins OmpX (Vogt and Schulz, 1999) and OmpA (Ruppert et al., 1994; Shi and Wen Su, 2001), these approaches are largely limited to extension of protein termini or exposed loops. This, however, bears the risk of compromising folding and insertion into the outer membrane. First successful engineering attempts of OmpA towards Ca^{2+} binding by insertion of an EF hand motif resulted in a binding capacity of one Ca^{2+} per OmpA (Johansson et al., 2007), which is likely insufficient for major enhancements of $CaCO_3$ precipitation capacity. Meanwhile, targeting fully synthetic oligopeptides with Ca^{2+} binding capacity provided through, *e.g.*, DXD, DXXD, DXDXDG, or DDXX (S/T) S motifs (Rigden and Galperin, 2004; Wu et al., 2008; Mishra et al., 2012) to the outer membrane via suitable secretion signal and transit peptides including palmitoylation sites for surface-exposed outer membrane anchoring (Wilson and Bernstein, 2016) may be a preferable alternative, but has not been achieved so far. Like porin engineering, synthetic peptide surface display likely requires genetic removal of obstructing EPS or S-Layer components, or the utilization of picoplanktonic strains inherently lacking such obstruction, like the emerging biotech chassis *Picosynechococcus* sp. PCC 7002 (Šmarda et al., 2002; Aikawa et al., 2014; Markley et al., 2015). Still, such an approach may prove fruitful and requires experimental validation.

2.2.4 Synthetic S-layers

Paracrystalline protein surface layers have been described in many phylogenetically distinct bacteria (Fagan and Fairweather, 2014) and all archaea (Rodrigues-Oliveira et al., 2017). While functionally similar, S-layer proteins are structurally highly diverse (Bahl et al., 1997; Hynönen and Palva, 2013) and thus likely products of multiple instances of convergent evolution. Many S-layer proteins have significant Ca^{2+} binding capacity due to aspartate-rich polypeptide sequences, and direct contribution of Ca^{2+} to protein lattice assembly and stability has been documented (Baranova et al., 2012; Bharat et al., 2017; Gambelli et al., 2019; Herdman et al., 2022). Being exposed on the very surface of the cell and known to facilitate $CaCO_3$ crystal nucleation (Schultze-Lam et al., 1992; Schultze-Lam and Beveridge, 1994), S-layer proteins are promising targets to engineer cell surfaces for optimal biomineralization. Related S-layer proteins have already been successfully transferred between cyanobacterial model species (Zu et al., 2020), indicating sufficient modularity. Exchanging endogenous S-Layers for or assembling highly Ca^{2+}-affine "synthetic" S-layers derived from, *e.g.*, the RsaA S-layer of *Caulobacter crescentus* binding up to 19 Ca^{2+} cations per protein subunit (Bharat et al., 2017) on inherently S-Layer free cyanobacteria thus represents a promising avenue towards cell-surface-proximal Ca^{2+} enrichment and facilitation of $CaCO_3$ crystal nucleation. As Ca^{2+} appears to be a structural component of many S-layer lattices, however, cell-surface recruited Ca^{2+} may not actually be available for $CaCO_3$ mineralization. Identification of naturally occurring S-layer proteins with high levels of loosely associated Ca^{2+} cations or *de novo* engineering of non-structural low-affinity binding sites may thus be required to effectively foster S-layer-driven $CaCO_3$ biomineralization.

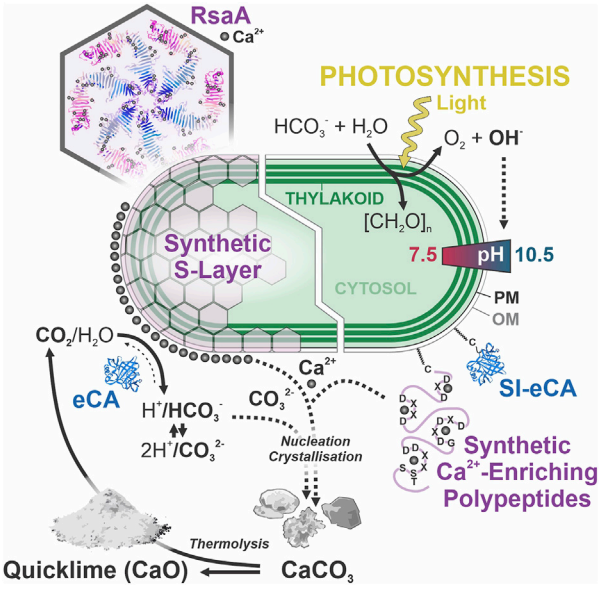

FIGURE 2
Enhancing light-driven $CaCO_3$ precipitation in engineered cyanobacteria. Hexameric symmetry and Ca^{2+} binding sites of the S-layer-forming RsaA protein from *Caulobacter crescentus*, adapted from (Bharat et al., 2017). The formation and strength of the photosynthesis-associated pH gradient are outlined. $[CH_2O]_n$, photosynthesized carbohydrates; (SI-) eCA, (surface-immobilized) extracellular carbonic anhydrase; PM, plasma membrane; OM, outer membrane. OM-tethering of SI-eCA and synthetic Ca^{2+}-enriching polypeptides with candidate Ca^{2+}-binding motifs through S-palmitoylation via cysteine (C) is indicated. Curved arrows indicate relevant chemical reactions and fluxes involved in biomineralization. Separate cell engineering strategies resulting in enhanced micrite formation are indicated (white boundary).

2.2.5 Overexpression and surface-immobilization of eCA enzymes

In vitro, eCA activity has been shown to foster $CaCO_3$ mineralization under high CO_2 partial pressures (Srivastava et al., 2015; Heuer et al., 2022). As of now, precise localization studies on enzymatically active cyanobacterial eCAs distinguishing periplasmic

and truly extracellular localization, *e.g.*, in the glycocalyx, are sparse. Here, *Cyanothece* sp. ATCC 51142 EcaA and *Sodalinema gerasimenkoae* IPPAS B-353 CahB1 represent noteworthy exceptions (Kupriyanova et al., 2011; 2019; 2022), although the native secretion mechanism of the latter remains elusive (Minagawa and Dann, 2023). While likely not essential for $CaCO_3$ mineralization *per se*, eCA activity near the extracellularly exposed surface of the outer membrane is likely to enhance $CaCO_3$ precipitation *in vivo*. Overexpression of free eCA in S-layer harbouring strains, or eCA-anchoring to the outer membrane in strains expressing synthetic Ca^{2+}-enriching polypeptide through, *e.g.*, a palmitoylation motif (Wilson and Bernstein, 2016), are thus to be considered.

2.3 Drafting optimal light-driven $CaCO_3$ biomineralization in cyanobacteria

Omitting the seemingly impractical engineering of cyanobacterial EPS, the previous considerations culminate in two promising strategies towards reason-guided enhancement of light-driven biomineralization. A schematic overview of engineered strains following both strategies, relying on modified S-layers and free eCA on the one hand, or synthetic Ca^{2+}-enriching polypeptides and surface-immobilized eCA on the other hand, is provided in Figure 2.

3 Discussion

3.1 Small is beautiful – why cyanobacteria may outshine eukaryotic biomineralizers

Storing CO_2 in the form of stable carbonate minerals faces fewer engineering and environmental challenges than other sequestration approaches like deep sea storage or deep ground injection, while maintaining minimal leakage risk as demonstrated by its natural counterpart (Ma et al., 2024). In natural systems, carbonate rocks are predominantly formed through biological and biologically induced processes, commonly summarized in the notion that *carbonates are born, not made* (James and Jones, 2016). Nowadays, photosynthetic plankton constitutes the most prolific carbonate factory, with recently evolved coccolithophore haptophyte algae producing around 50% of Holocene marine $CaCO_3$ sedimentation (Broecker and Clark, 2009). Due to their large contribution to pelagic $CaCO_3$ production *in situ* (Ziveri et al., 2023), these algae are being discussed as promising biotechnological CCS platforms. As these organisms remain hardly accessible to genetic engineering tools (Flavin and Chatterjee, 2024), any application remains largely limited to preexisting strains and their maximum productivity, however. A pronounced sensitivity to changes in carbonate chemistry and water acidification in most species (Beaufort et al., 2011; Meyer and Riebesell, 2015; Vázquez et al., 2023) and a general preference for growth temperatures below 30 °C (Gafar and Schulz, 2018; von Dassow et al., 2021) furthermore limit coccolithophore utility and application potential for CO_2 capture from, *e.g.*, hot cement industry flue gasses commonly containing 10%–20% CO_2 (Camargo and Lombardi, 2018). Lastly, coccolithophore formation involves active transport and Ca^{2+} concentration within the cell (Sviben et al., 2016), rendering it more energetically taxing than passive extracellular $CaCO_3$ precipitation. Cyanobacteria meanwhile are highly accessible to genetic engineering and tailoring to harsh growth conditions through adaptive laboratory evolution (Tillich et al., 2012; Dann et al., 2021), their photosynthetic activity results in more pronounced media alkalization than that of eukaryotic algae (Touloupakis et al., 2016; Zepernick et al., 2021; de Brito et al., 2022), and their smaller cells provide a favourable surface-to-volume ratio for cell-surface catalysed $CaCO_3$ precipitation. This renders engineered cyanobacteria a likely superior platform for any future work on light-driven $CaCO_3$ precipitation, and marks cyanobacterial cell-surface engineering a promising pathway towards flexible and scalable biotechnological $CaCO_3$ recovery.

3.2 Towards geobiologically inspired carbon recovery and storage

In accordance with their large contribution to the geological record, the utilization of cyanobacterial biomineralization for CCS was suggested before (Jansson and Northen, 2010), but no significant upscaling or commercial application has been achieved so far. Owing to a focus on EPS and the practical inaccessibility of complex anionic EPS biosynthesis to genetic and metabolic engineering, previous studies have near-exclusively focused on the identification of inherently productive calcifying species (Lee et al., 2004; Liang et al., 2013) and conductive cultivation methods (McCutcheon et al., 2014). A single genetic engineering attempt to increase calcification capacities was limited to the knockout of *cax1* (Ca^{2+}/H^+ antiporter) in the mesophilic freshwater model species *Synechocystis* sp. PCC 6803, resulting in enhanced BCT1 (Ca^{2+}-dependent HCO_3^- transporter) activity, increased CCM activity, and thus increased $CaCO_3$ precipitation (Jiang et al., 2013). Despite these first successes, biomineralization yields remain insufficient for large-scale applications. With documented rates of cyanobacterial Ca^{2+} precipitation from saltwater media corresponding to approximately 120–240 mg of $CaCO_3$ per liter of batch culture over a 2-week cultivation cycle (Lee et al., 2004; Yang et al., 2023), precipitation of 1 metric ton (t) of $CaCO_3$ would require the equivalent of two Olympic swimming pools (*i.e.*, ~$5*10^6$ L). This corresponds to approximately 5.8 t of CO_2 sequestration capacity per Olympic swimming pool equivalent per year, valued around 430 € worth of CO_2 certificates at current EU Emissions Trading System pricing. Hence, an increase in biomineralization capacity by several orders of magnitude is likely required to attain economic viability. Although no comprehensive understanding of the modulation of $CaCO_3$ crystallization through biological agents has been achieved to date, mechanic deformation of heterogenous nucleation sites alone has been reported to increase $CaCO_3$ nucleation rate by one order of magnitude (Taylor et al., 2020). Meanwhile, calcite and aragonite nuclei were found the only nuclei capable of markedly catalyzing $CaCO_3$ precipitation in natural surface seawater (Pan et al., 2021), highlighting the crucial importance of crystallization nuclei surface properties for efficient $CaCO_3$ mineralization. As crystallization rates in more complex biogenic systems such as supersaturated lysozyme solution have been found to increase by 8-10 orders of magnitude upon exposure to suitable heterogenous

nuclei (Filobelo et al., 2005), ample room for major improvement of bio-mediated $CaCO_3$ precipitation appears conceivable.

As opposed to previous attempts, engineering cyanobacterial cell surface properties through the introduction of modified or synthetic protein components and simultaneous genetic removal of obstructive features can be expected to allow for enhanced cell-surface catalysis of $CaCO_3$ precipitation. Especially recent breakthroughs in protein structure prediction and engineering (Watson et al., 2023) render this new approach worth pursuing. Here, a two-pronged empirical approach of introducing a re-engineered S-layer *or* disorganized synthetic cell-surface peptides with Ca^{2+} binding capacity appears a reasonable choice to determine the most conductive strategy, while EPS engineering remains prohibitively complex and porin/OMP engineering likely too functionally constrained for large-scale Ca^{2+} attraction and nucleation site provision. Finally, utilization of thermophilic chassis strains accessible for genetic engineering such as *Thermosynechococcus elongatus* BP-1 which strives at cultivation temperatures as high as 55 °C (Yamaoka et al., 1978; Iwai et al., 2004), or adaptive laboratory evolution for enhanced thermotolerance of mesophilic strains (Tillich et al., 2012) can likely enhance $CaCO_3$ precipitation efficiency due to reduced solubility of aragonite and calcite in warmer solutions, specifically enabling CO_2 capture from hot thermolysis or flue gasses. This should eventually allow for efficient light-driven re-routing of CO_2 emissions into carbonate resource production and lithospheric carbon storage.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

MF: Writing – original draft, Conceptualization, Funding acquisition, Writing – review and editing. MD: Conceptualization, Funding acquisition, Visualization, Writing – review and editing, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

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