Biogeochemical significance of Intracellular calcification by Cyanobacteria

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Date: May 4th, 2020

EGU session SSP1.5

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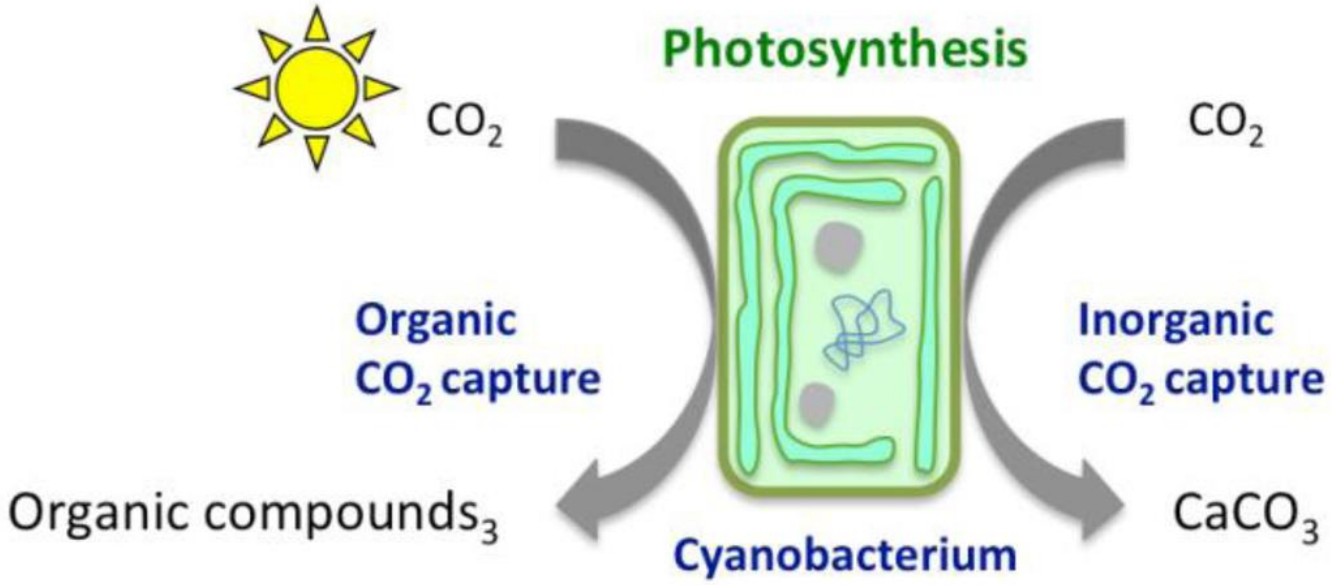
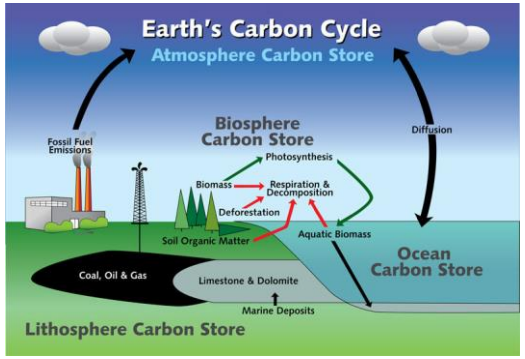
Credit: Top image Karim Benzerara and Stefan Borensztajn/CNRS,; Bottom: Emmanuelle Gérard, Nature, 2013

Traditionally, cyanobacterial calcification was strictly considered extracellular

- Cyanobacteria are known to promote the extracellular precipitation of Ca-carbonate minerals during the photosynthetic activity

- This process has resulted in the formation of carbonate deposits and a fossil record of importance for deciphering the evolution of cyanobacteria and their impact on the global carbon cycle.

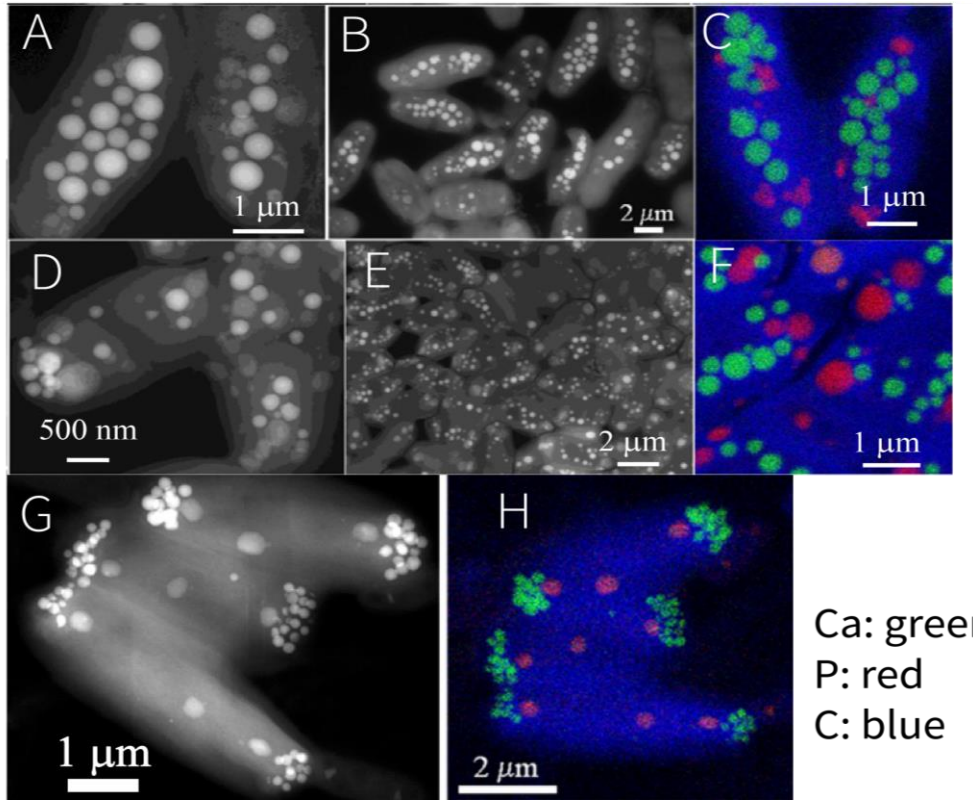




Reference: N Kamennaya et al. Minerals, 2012;
PC credits: https://www.sharkbay.org/place/hamelin-pool/; *NYS Department of Environmental Conservation*

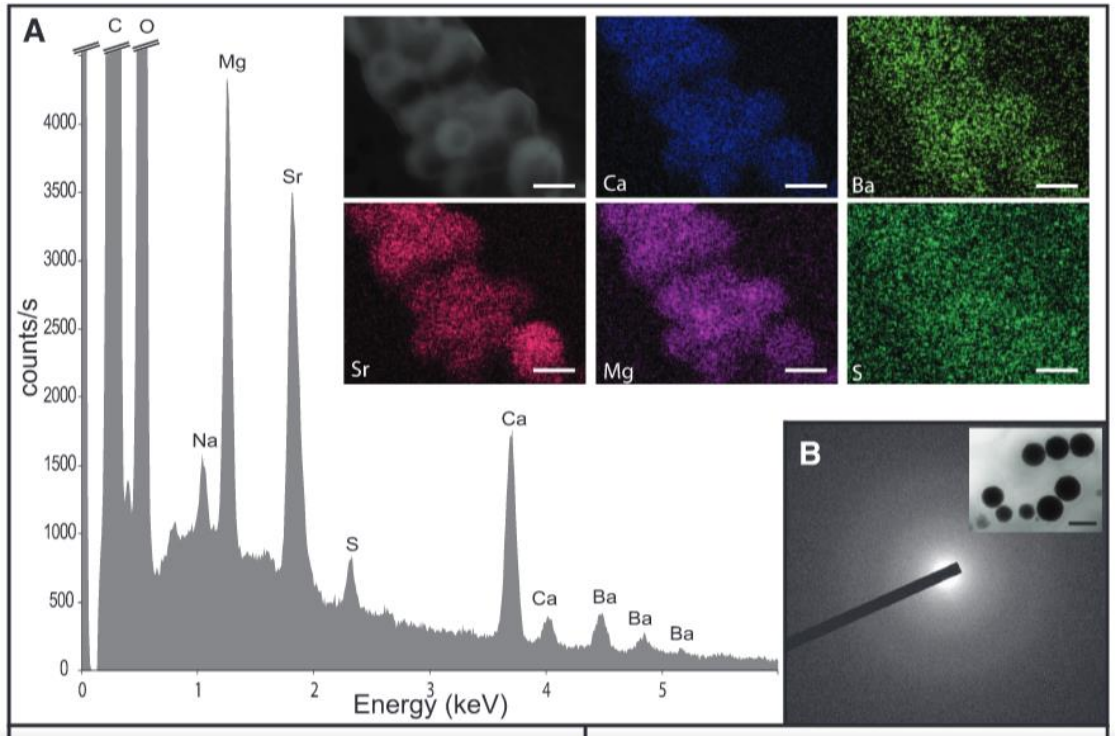
Detection of intracellular amorphous Ca-carbonate (iACC) inclusions in cyanobacteria *G. lithophora* challenged this paradigm

STEM-HAADF –EDXS of broad diversity of cyanobacteria forming iACC



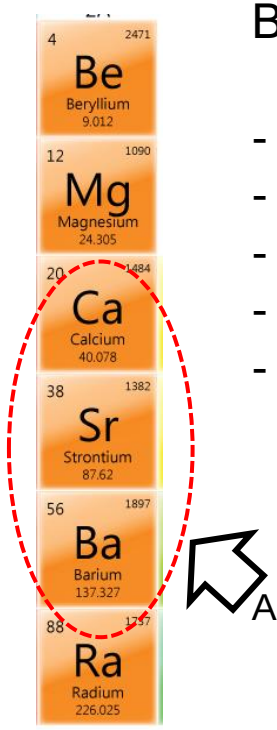
(A,B,C): *Cyanothece* sp. PCC 7425.
(D, E, F) Ca. *G. lithophora* strain D10.
(G,H): Ca. *S. calcipolaris G9* .

Intracellular Ca-carbonate inclusions enriched in Ca-Mg-Ba-Sr as shown in SEM-EDX spectrum (A) The inclusions measure 200-500 nm in diameter and are amorphous as shown in selected-area electron diffraction pattern (B)



Reference: Benzerara et al. PNAS, 2014; Couradeau et al. Science, 2012

Accumulation of alkaline earth elements (AEE) in cyanobacteria forming iACC is unique



AEE elements of interest

But first, let's look at the traditional understanding of role of AEE in cyanobacteria:

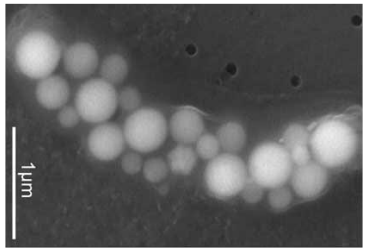
- Ca is biologically essential element
- Intracellular Ca concentrations are tightly regulated (~100nm)
- High cytosolic Ca, Ba, Sr and radioactive AEE concentrations are toxic
- Unlike Ca, Ba or Sr are not known to fill any biological role
- Micro-organisms rarely discriminate between AEE during uptake, owing to chemical similarity of AEE

Reference: Domínguez, Molecular Microbio, 2004; Torrecilla et al. Plant Physiology, 2000

Accumulation of alkaline earth elements (AEE) in cyanobacteria forming iACC is unique

Ba/Sr enrichment by *G. lithophora* not reproduced *in vitro*

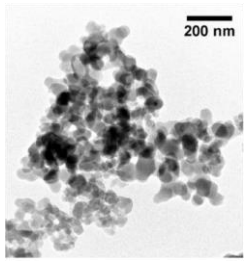
ACC in G. lithophora



$\frac{Ba}{Ca} = 1370$

$\frac{Sr}{Ca} = 86$

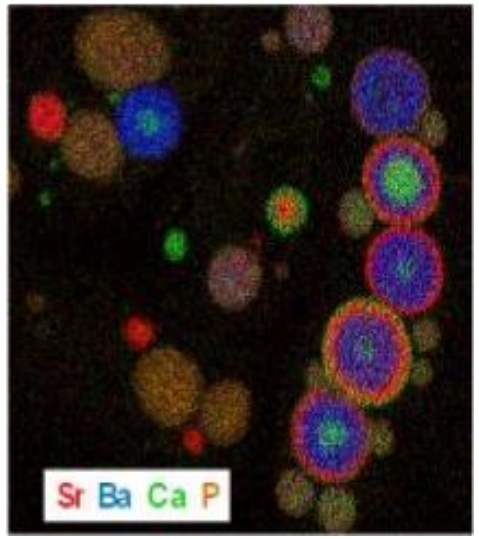
Synthetic ACC



$\frac{Ba}{Ca} = 0.5$

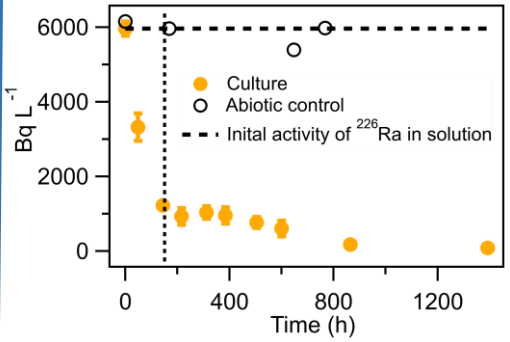
$\frac{Sr}{Ca} = 0.2$

Selective uptake of AEE by *G. lithophora*



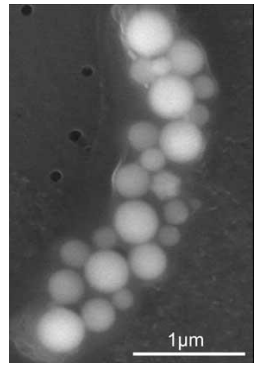
- Uptake order: Ba>Sr>Ca
- Selective uptake not a shared trait of all cyanobacteria forming iACC

Radioactive AEE uptake by *G. lithophora*



G. lithophora sequesters trace concentrations of Ra-226 and Sr-90 in presence of Ca

Ca requirement of Cyanobacteria forming iACC



Dissolution of all Ca accumulated within iACC estimated to release upto 3 M cytosolic Ca.

Q. What is the role of AEE accumulation in cyanobacteria forming iACC?

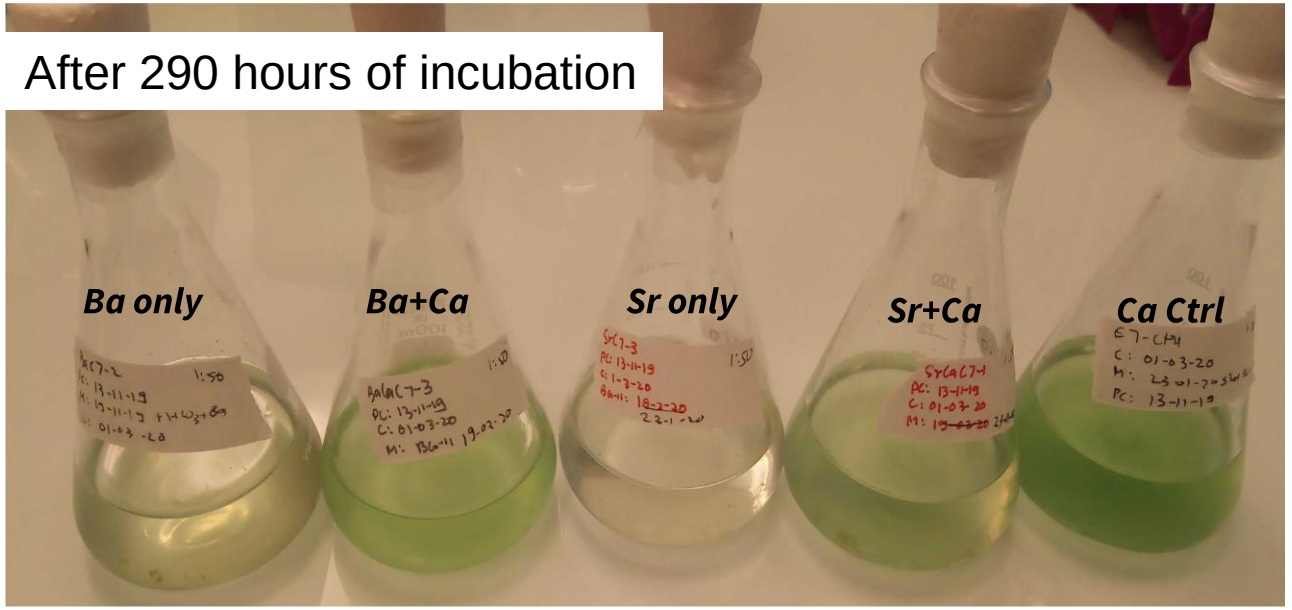
Reference: Cam et al. GCA, 2015 ; Cam et al, ES&T 2016; Mehta et al ES&T, 2019, Wever et al. Geobiology, 2019

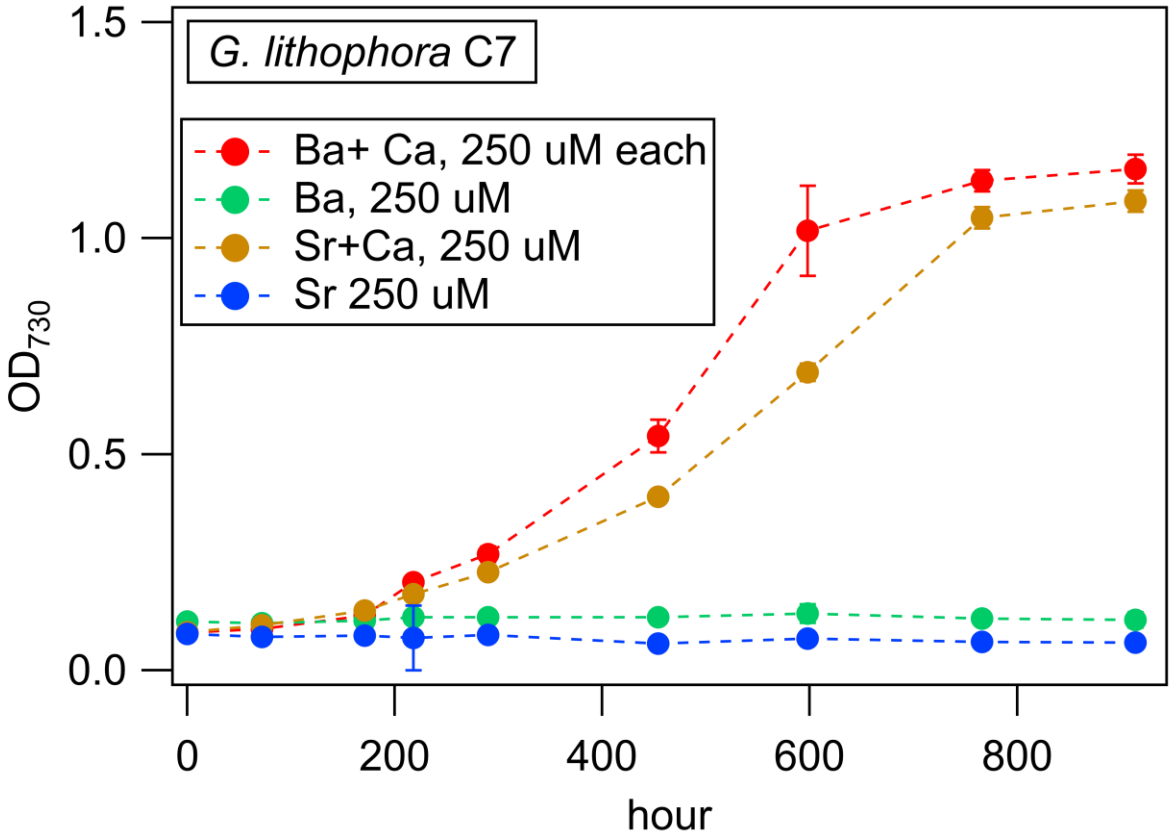
Findings

Results of batch incubations revealed that Ba/Sr alone couldn't replace Ca demand of *G. lithophora*

Parallel cultures of *G. lithophora* were set-up in BG-11 amended with:

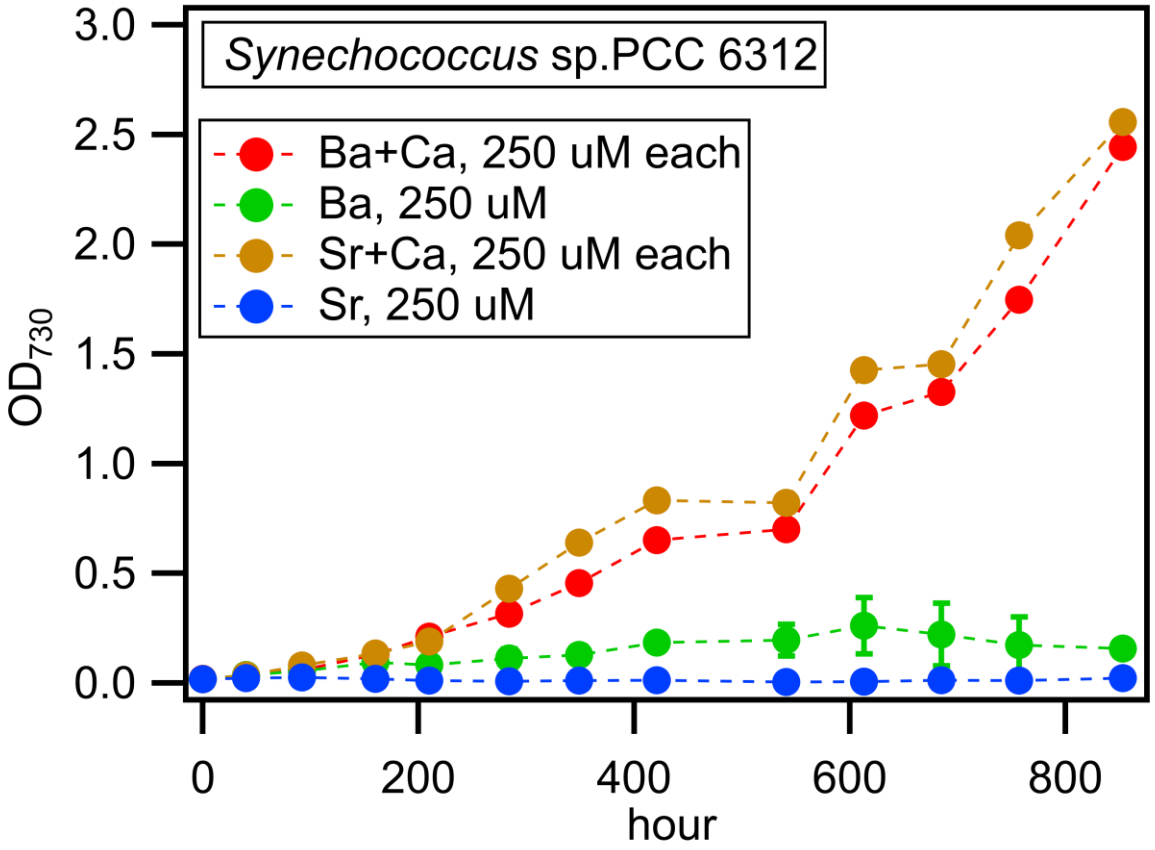
- Ba and Ca, 250 uM each, OR
- Ba, 250 uM, OR
- Sr and Ca, 250 uM each, OR
- Sr, 250 uM

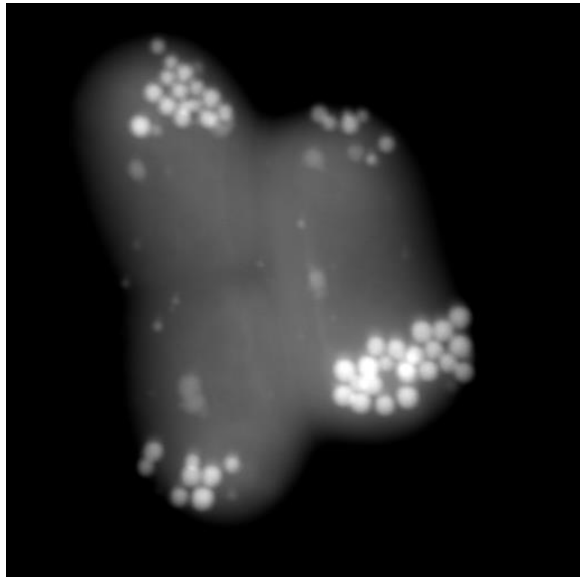




Reference: Mehta et al. in prep

Similar results in case of *Synechococcus* PCC 6312, which forms iACC but doesn't exhibit AEE selectivity…





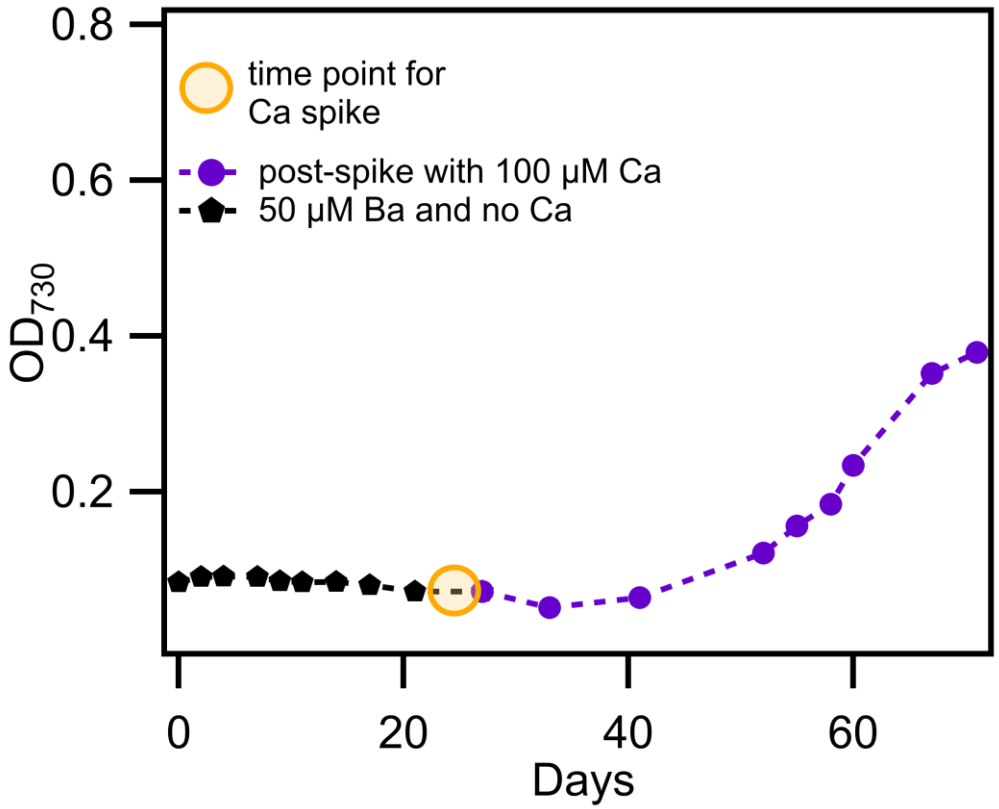
STEM image showing *Synechococcus* PCC 6312 grown in presence of Ca+Sr. The white spheres are iACC, enriched in Sr and Ca.

Reference: Mehta et al. in prep

The limited growth of *G. lithophora* in presence of Ba is recovered by addition of Ca

Experimental set-up:

G. lithophora grown in BG-11 modified with 50 uM Ba and no Ca→ After ~20 days, cell suspensions were spiked with 100 uM Ca

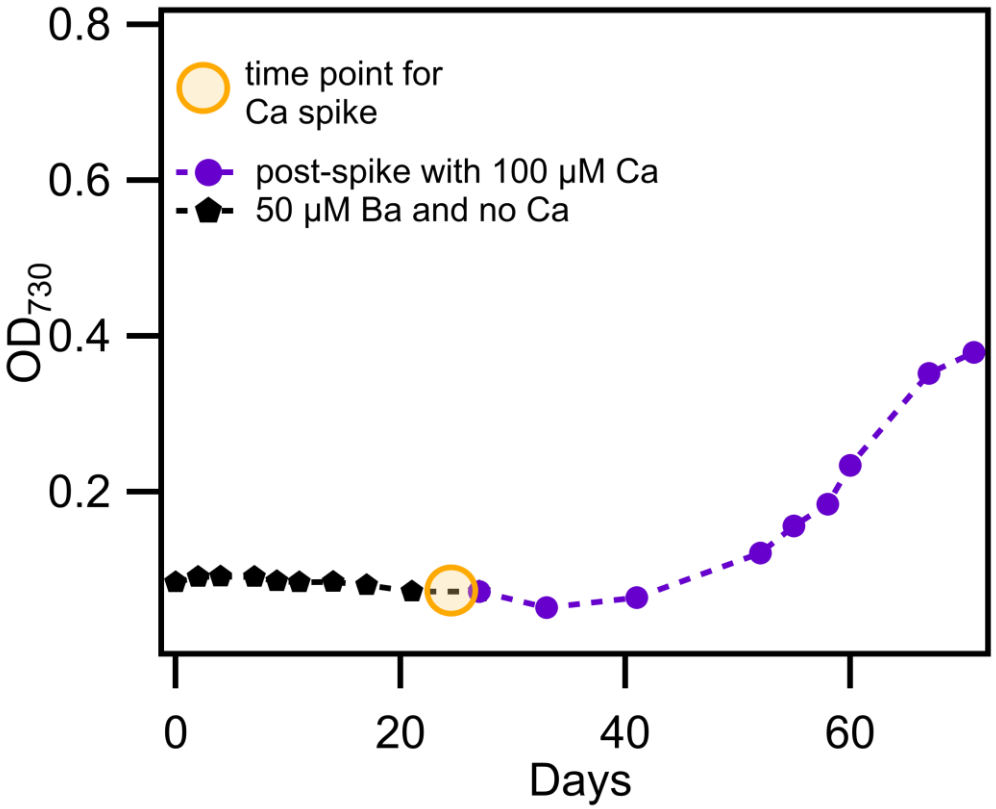


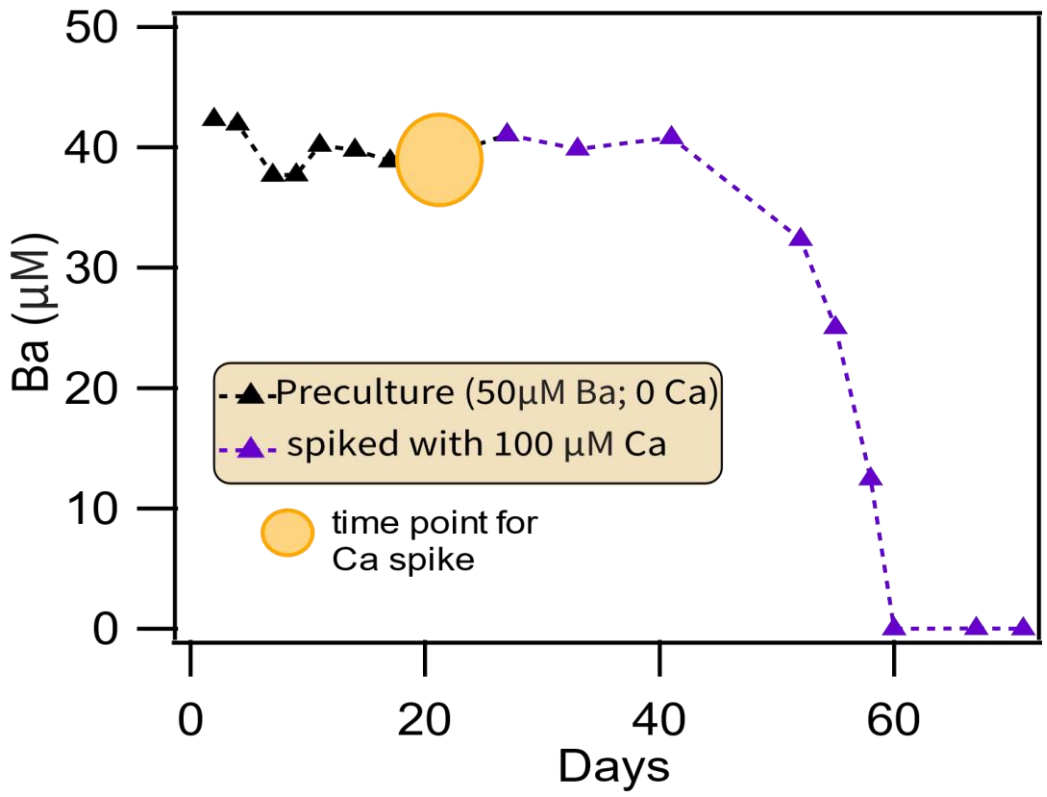
Reference: Mehta et al. in prep

Recovery of cellular growth upon Ca spike is accompanied by recovery of Ba uptake by *G. lithophora*

Experimental set-up:

G. lithophora grown in BG-11 modified with 50 uM Ba and no Ca→ After ~20 days, cell suspensions were spiked with 100 uM Ca





Reference: Mehta et al. in prep

What did we learn and not learn about the role of AEE in cyanobacteria forming iACC?

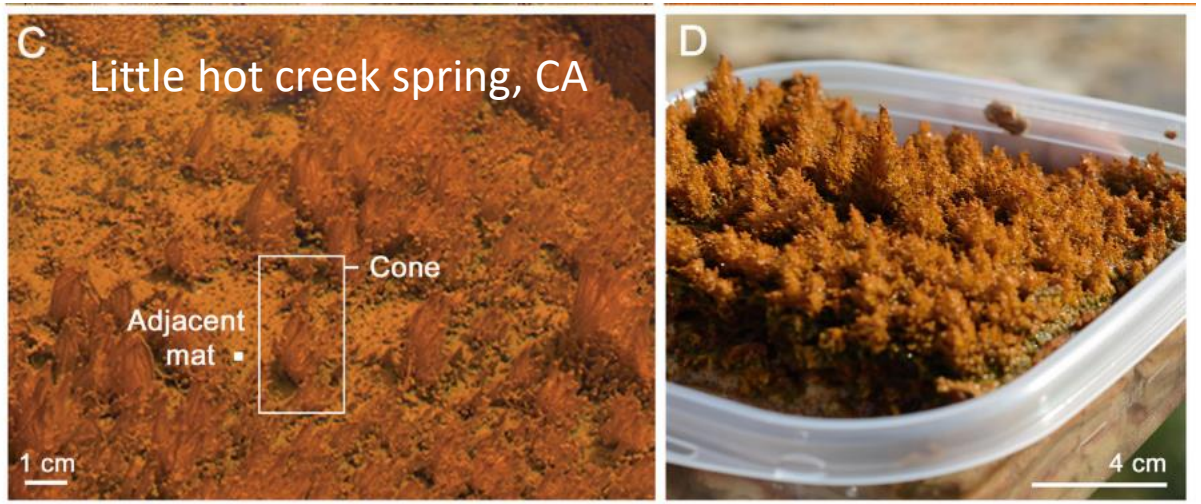
LESSONS LEARNED

- No direct evidence of any direct biological role of Ba or Sr in cyanobacteria forming iACC
- Intracellular pure Ba or Sr amorphous carbonates don't serve the same (biological) function as iACC
- Ca availability has a synergistic effect on growth and uptake of heavier AEE by *G. lithophora*

- **OPEN QUESTIONS**
- Why *G. lithophora* selectively accumulates Ba over Sr and Ca?
  - Environmental adaptation? Or some evolutionary pay-off from the process?
- Why only certain cyanobacterial strains show selective uptake of AEE?
  - Comparative genomics study may provide answers
- What is the purpose of iACC and how Ca-Ba-Sr-Mg-enriched carbonates differ in their function from pure Ca-carbonate inclusion?

Biogeochemical implications of intracellular calcification: A few examples

- Overlooked geochemical reservoir of Ba/Sr in certain ecological niche. Eg: Cone pool

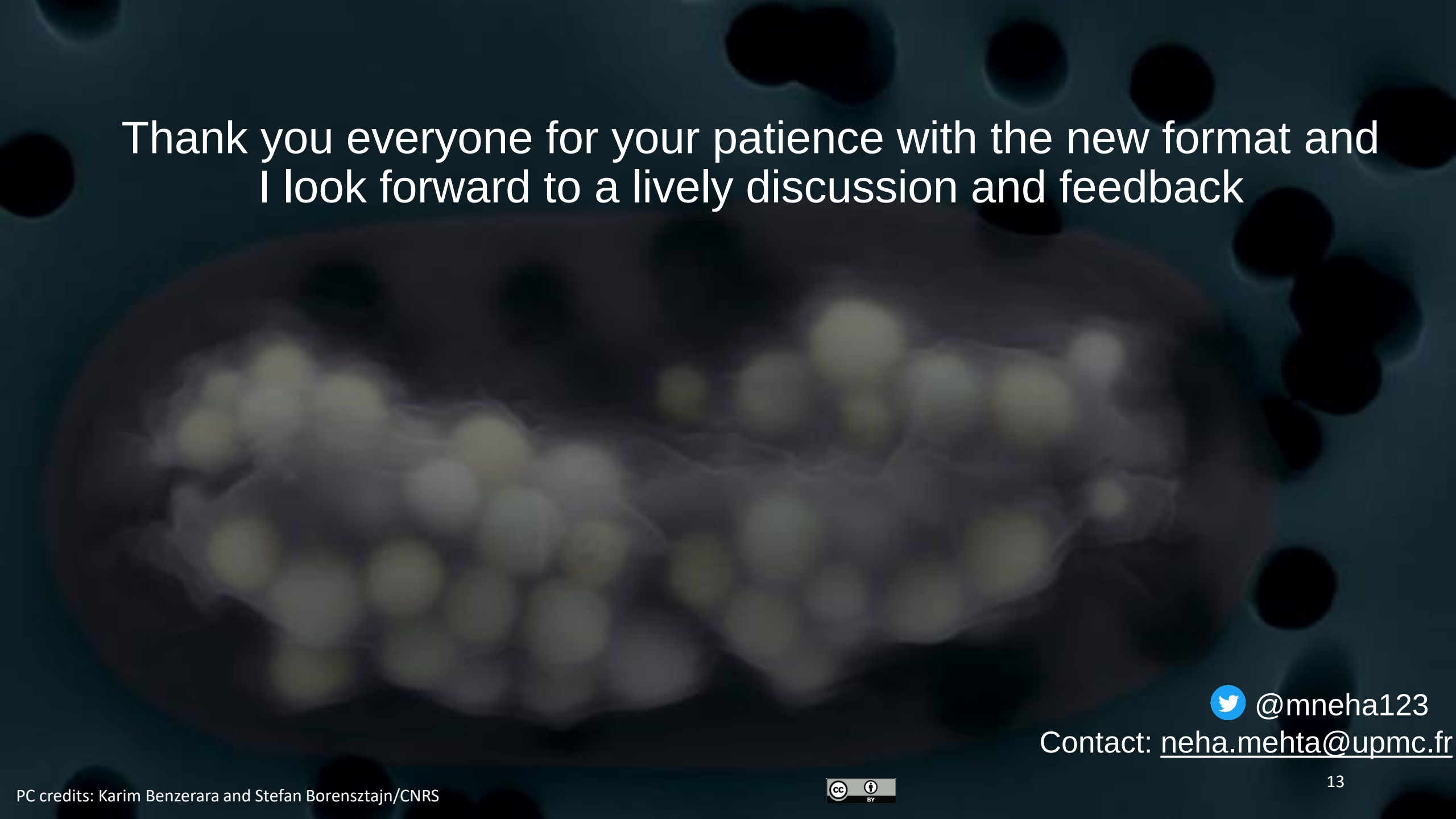


1- 10% of the bacterial community populating microbialites from cone pool at Little hot creek in California was accounted to close relatives of *G. lithophora*

- Ba/Ca and Sr/Ca ration may serve as biosignature of intracellular calcification in geologic record

Bioremediation of radioactive AEE

Reference: Bradley et al., 2017, npj Biofilms and Microbiomes



Thank you everyone for your patience with the new format and I look forward to a lively discussion and feedback

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PC credits: Karim Benzerara and Stefan Borensztajn/CNRS