Gergely MARÓTI
Institute of Plant Biology, Biological Research Centre, ELKH

Molecular actors and mechanisms of inter-kingdom algal-bacterial interactions. Discovering the potential of these interactions.

Background

Microalgae are microbial photosynthetic organisms with polyphyletic origin. They are ubiquitously found across different ecosystems as primary producers and account for approximately 40% of the global photosynthesis. Consequently, they display a substantial diversity in shape, size, life history, environmental ranges (salinity, pH and temperature gradients) and functional potential. Their relative small size and high affinity to nitrogen and phosphorus enable microalgae to take up large amounts of nutrients at a faster rate compared to terrestrial plants or macroalgae. They also have a 20% higher photosynthetic efficiency rate compared to the land plants, show high carbon capturing efficiency through the CO_2 concentrating mechanism (CCM) and can be grown and harvested throughout the year. These advantages, coupled with the immense diversity, make these organisms the ideal candidates for industrial cultivation for the production of algal based biomass, bioproducts and bioenergy.

Most eukaryotic organisms maintain symbiotic relations with beneficial microbes. These interactions affect in the host nutrient acquisition, defense against enemies and immunity, development or reproduction. In most cases, the benefit to the microorganism is a privileged acquisition of nutrients and a growth niche. The interacting partners can develop various levels of interactions from simple co-localization to endosymbiotic lifestyle. The specific project focused on a group of so far rather neglected but ubiquitous mutualistic interactions developed between unicellular eukaryotic green algae strains (various members of the *Chlamydomonas*, *Chlorella* and *Coelastrella* genera) and their natural bacterial partners. We have also generated engineered synthetic algal-bacterial communities to investigate the physiological, cellular and molecular level interactions between the partners and the possible utilization of the communities.

Main achievements

The scientific programme resulted in **17 international peer-reviewed** scientific publications in the 4 year and 9 months (see the full list below). The total impact factor of these project-related publications is **74.27**. (one additional project-funded publication is under review at the moment). Our research group participated in other related projects as cooperation partner, these projects resulted in further publications (more than 15). Thus, the specific NKFI project supported the publication of more than 30 scientific publications in total.

The results were obtained in the following fields:

- **algal-bacterial communities in biohydrogen production**
  Important new results were obtained in the field to prove the direct role of partner bacteria in generating excess electrons (for both direct and indirect photolytic ways) for the algal hydrogenase enzymes.

- **algal-bacterial communities in wastewater treatment and bioremediation**
  The roles of algae were shown in the efficient use of dissolved nitrogen and phosphorous compounds of wastewater. The specific effects of algae addition on the restructuring of wastewater microbial communities were investigated in detail.

- **use of algae as plant biostimulants and source of antimicrobial agents**
  Clear plant biostimulatory activities of selected algae were described on both model and plants and crops (tomato). The significance of algal EPS molecules, which can be regulated by partner bacteria was described.

1. Algal-bacterial communities in biohydrogen production

Algal hydrogen production is a promising candidate for being a future environmental friendly solution to replace fossil fuel utilization. The application of algal-bacterial consortia has a number of advantages over using axenic algae cultures for hydrogen evolution. The main benefit of this method is the easy implementation, since no pre-growth of algal biomass is necessary for hydrogen production. Also, there is no need to pay attention to the otherwise highly costly culture purity, the appropriately selected algal-bacterial partners form stable consortia. Beside hydrogen evolution, the excess biomass can be harvested to continuously maintain the optimal co-culture density for the maximum hydrogen production rate and the biomass can be used for various further purposes. The application of bacterial partners can support the oxygen consumption also in nutrient deprived cultures and enhance the rate of hydrogen production in these combined systems as well. Bacterial respiration accelerates the oxygen consumption rate and reduces the time needed for reaching anaerobiosis to approximately 4 hours depending on the experimental setup (from 1 to 8 days observed in nutrient-depleted axenic algae cultures). Acetic acid is a key component in our approach to ensure anaerobic environment. By purging of the culture headspace for a few minutes each day with a designed gas mixture containing less than 5% (v/v) oxygen the important period of acetic acid consumption can be prolonged, the carbon dioxide production might be reduced and the maximum hydrogen production rate can be kept at constant high level. The required frequency of the gas purging is estimated for between 4 to 24 hours depending on the experimental setup. Using a light intensity of 50 μmol m^{-2} s^{-1} for illumination of the batch co-cultures

the most promising initial algae concentration density is around OD 1 measured at 750 nm, however, higher algae concentrations might also be effective in case light distribution in the co-culture is solved. The highest accumulated hydrogen yields were observed for the different algal partners under similar experimental setup. The combination of a gas-to-liquid phase ratio of 1/1 with an algae cell density of 3.96 * 10^8 algae cell ml^{-1} (OD_{750}: 1) resulted in the highest accumulated algal hydrogen yields. Accumulated hydrogen yield was also strongly influenced by the algal cell size, smaller cell size correlated with higher hydrogen evolution rate. The highest accumulated algal hydrogen yield (88.98 ± 2.19 ml H_2 l^{-1} d^{-1}) was obtained with *Chlorella* sp. MACC 360 - *E. coli* Δ*hypF* co-culture.

In another study our specific goal was to achieve sustainable, continuous algal hydrogen production through photofermentation using starch as the sole carbon source. To reach this objective, it was essential to select appropriate eukaryotic green algae strains for the co-cultivation with *B. amyloliquefaciens*, to optimize algal–bacterial ratio and density of the starting co-cultures, as well as to fine-tune the gas-to-liquid ratio in the applied fed-batch lab-scale photobioreactors. It is important to note that, in our system, the specific algal hydrogen production was in the focus. The lack of hydrogenase enzymes in the partner bacterium was an important criterion, so that the applied *B. amyloliquefaciens* did not directly contribute to the photofermentative hydrogen yield.

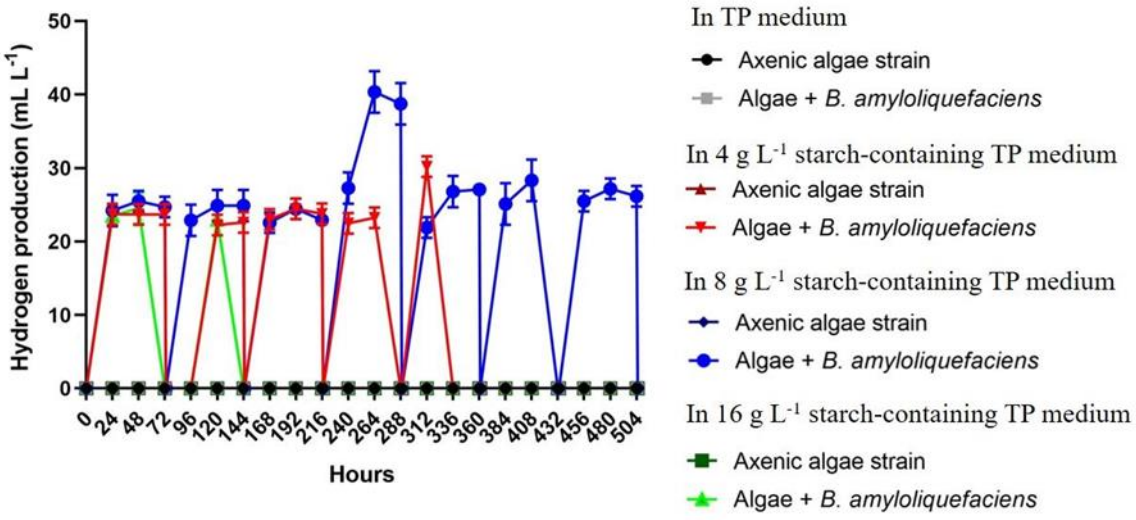

Figure 1. Continuous hydrogen production of *Chlorella* sp. MACC-360 in acetate-free TP medium supplemented with elevated amount of bacterial partner (the initial bacterial OD_{600} of 0.175). Hydrogen was measured in the headspace at every 24 h. Bottles were aerated for 5 min after hydrogen measurement at every 72 h.

We utilized two green algae species from the *Chlamydomonas* and *Chlorella* genera to engineer stable synthetic communities by incorporating a starch-degrading bacterium from the *Bacillus* genus into the inter-kingdom consortium. Continuous photoheterotrophic biohydrogen production was achieved by elaborating an appropriate algal–bacterial ratio and fine-tuning the culture conditions for the synthetic consortia. Medium with starch as only carbon source served as a simple model of cheap substrate for algal hydrogen generation. The engineered pairwise algal–bacterial associations showed increased biomass and biohydrogen yield compared to the axenic control conditions. *Chlorella* sp.

MACC-360 produced a significantly higher amount of hydrogen when both the bacterium partner and starch were added to the media compared to the axenic algae. Continuous, elevated algal hydrogen production was achieved in media supplemented with 8 g L^{-1} starch as sole carbon source when carefully selected initial cell number values were used for the *Chlorella* sp. MACC-360–*B. amlyloliquefaciens* co-cultures.

Our results indicated that algal biohydrogen production is directly impacted during co-cultivation with specific bacterial members. We also identified that co-cultivation with all, but one bacterium led to an improvement in *C. reinhardtii* cc124 growth. *Bacillus* species isolated from different environments can reproducibly improve biohydrogen production across two other species of green algae: *Chlorella* MACC-360 and *Parachlorella* MACC-38. Co-cultivation of *C. reinhardtii* with different *Bacillus* species also improved algal lipid accumulation and biohydrogen production, while co-cultivation with *Methylobacterium* sp. led to greater carbohydrate accumulation and very low hydrogen production.

We also carried out transcriptome studies to look at gene expression of *C. reinhardtii* under axenic cultivation and co-cultivation with *Bacillus cereus*, *Bacillus thuringiensis*, and *Methylobacterium* sp. There was an increased expression of NDA2 only in algae co-cultivated with both *Bacillus* species.

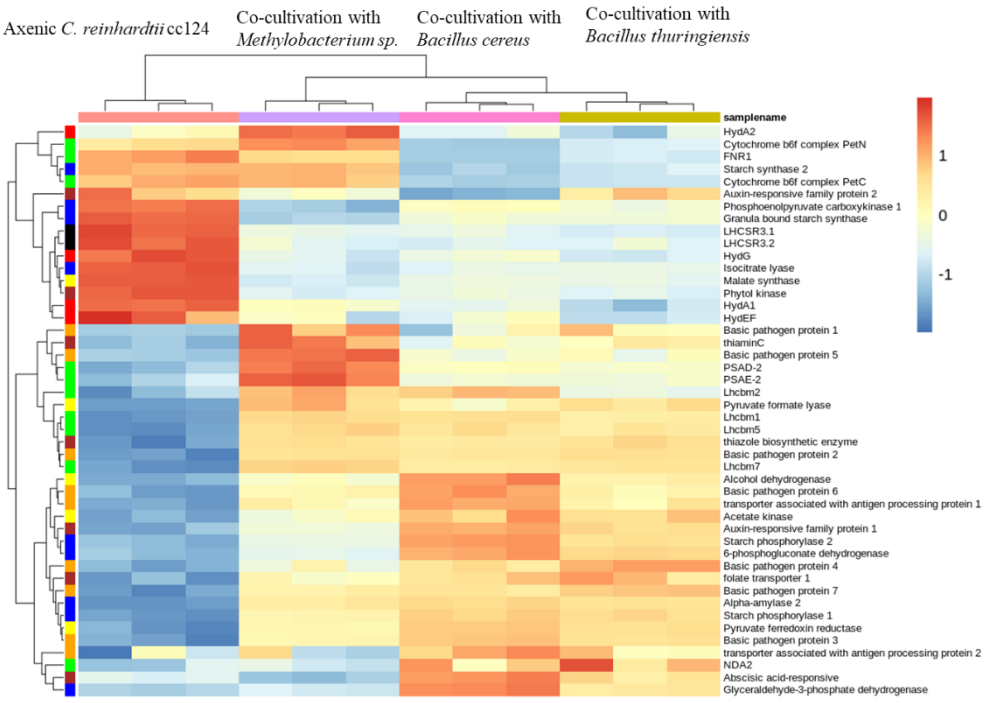

Figure 2. Heatmap of important algal genes showing significant differential expression across different samples.

NDA2 is a type II NADH dehydrogenase involved in the transfer of electrons from the breakdown of carbohydrates to ferredoxin. We also observed the *hyda2* transcript being upregulated only in algae co-cultivated with *Methylobacterium* sp. The *hyda2* isoform of exhibits a greater predilection for consuming hydrogen. This could be another reason for low hydrogen production. On

the other hand, *C. reinhardtii* co-cultivated with *Bacillus* had upregulated genes involved in fermentation. Enzymes such as pyruvate formate lyase (PFL) and pyruvate ferredoxin reductase (PFR), both of which are directly involved in breaking down pyruvate with concomitant release of biohydrogen had greatly increased expression under bacterial co-cultivation. Improved biohydrogen generation may result from the upregulation of genes involved in fermentation processes. We also identified a low expression of stress-related light-harvesting complexes under bacterial co-cultivation. These results coupled with the phenotypic observation of high lipid and carbohydrate accumulation provide a compelling argument for the need to investigate and cultivate algae with bacterial partners.

2. Algal-bacterial communities in wastewater treatment and bioremediation (and combined biohydrogen production)

There are a number of difficulties that arise while operating biodegradation systems (like wastewater treatment plants) in constantly changing microenvironments. These issues must be resolved to create and execute viable solutions for effective biological wastewater treatment and combined energy production. Several green algae-based photoheterotrophic strategies were used in this study. The major objective of our research was to assess the potential of dark fermentation effluent as a source of photoheterotrophic algae biomass. We combined these efforts with biohydrogen generation, which was discussed above. Changes in total nitrogen, total phosphorous, and BOD (biological oxygen demand) reflected the efficiency of biodegradation (treatment) during the photo-fermentation phase and demonstrated the crucial role played by green algae in the process. The presence of green algae was indispensable for efficient N and P consumption as well as BOD decrease in the photo-fermentation stage. The role of the enriched microbial inoculum (which is a mix of dark fermentative bacteria) in photoheterotrophic stage appeared to be marginal in further element uptake and degradation of organic molecules. Enriched microbial inoculum had around 10–20% biodegradation efficiency on the dark fermentation effluent compared to that of the green algae being around 35–50%. This finding is intriguing because it suggests that the nutrient composition of the dark fermentation effluent is presumably more accessible to the photosynthetic green algae than to the bacterial communities developed during anaerobic dark fermentation. Thus, the metabolic functions performed by dark fermentation communities already involved in biodegradation during the first dark fermentation phase can be complemented by *Chlorella* metabolism. The bacterial community was impacted to a greater degree by the addition of enriched microbial inoculum compared to the addition of algal inoculum. *Chlorella* green algae did not have a strong effect on shaping the community, instead, the various interactions taking place between different bacterial species might have made the changes. The low impact of *Chlorella* on changing the microbiome structure could very well be due to the short duration of the photoheterotrophic stage, which was only 3 day-long. Further research is needed to elucidate the complex metabolic interactions among the main identified bacterial groups and the photosynthetic green

algae. Our results indicated promising perspectives for the combined approach of wastewater treatment and concomitant biohydrogen evolution using a two-stage pipeline of dark and photoheterotrophic fermentation.

Algal cultivation in agricultural and municipal effluents is an attractive goal for algal studies. This is because these wastewater effluents are typically rich in nutrients required to support algal growth and development, while also exploring the possibility to convert the recovered algal biomass into medium or low-value products. There also have been several studies exploring the use of food-waste effluents as cultivation media. However, to arrive at this destination we need a meticulous understanding of how cultivated algal species will interact with both the native microbiome and invading microbial contaminants. This is a requirement even for the industrial cultivation of green algae. We made use of synthetic wastewater media to simulate municipal wastewater effluents and co-cultivated *C. reinhardtii* with twenty-eight different bacterial members, representing three different phyla and isolated from different environments. We investigated the utility of bacterial partners in maintaining a microoxic environment, enabling algae to thrive in high-nutrient wastewater, and treating wastewater while producing copious amounts of biohydrogen. Our studies with brewery wastewater effluents revealed that *Chlorella* MACC-360 could photoheterotrophically grow while bioremediating the effluents. The concentration of wastewater played a major role in nutrient uptake. Algae grown in undiluted wastewater effluent had a high rate of nutrient uptake, despite accumulating lower biomass. Furthermore, we found that the presence of algae is necessary for effective nutrient uptake and that heat pre-treatment is a key step in maintaining high biohydrogen production. Samples with heat-treated microbial inoculum along with algae produced the highest amount of biohydrogen, while samples without heat-treated microbial inoculum produced the lowest amount of biohydrogen. Finally, we also identified that filter sterilization did not lead to the removal of all bacteria from the effluent.

Heat treatment and photofermentation both exhibited significant effects on the microbial community, according to metagenomic analyses. Heat treatment changed the microbiome community structure. Bacteria from the *Lactobacillus* genus reduced in abundance while bacteria from *Clostridium* increased in abundance. On the other hand, the three-day photofermentation led to a significant increase in bacteria from the genus *Prevotella, Clostridium,* and *Veillonella*. Complete pathways for the biosynthesis of vitamins were found in the whole genome assembled bins of *Prevotella* and *Veillonella*, which may help increase the algal growth rate. Finally, we discovered that although bacterial taxonomy varies across samples, the corresponding function does not. We showed that it was feasible to produce biohydrogen in addition to contaminant removal using current algal-based remediation technologies. Although most of the biohydrogen production strategies have, theoretically, low energy requirements and could utilize various organic wastes as substrates, the practical applications are still far from being economically feasible. One way to address this economic issue could be the development of novel hybrid approaches. An overall increase in both the H_2 yields and the efficiency of wastewater treatment could

be achieved by using the remaining effluents of dark fermentation in a microalgae-based photoheterotrophic degradation system. However, only a handful of studies tackled the biohydrogen production potential of microalgae-driven photoheterotrophic degradation. The successful development of a novel hybrid dark fermentative – photoheterotrophic biohydrogen production approach required a deep understanding of the microbial communities likely performing these metabolic processes in a tight synergy. Thus, in order to render this combined approach a viable alternative to the classic single-stage biohydrogen production methods, the metabolic waste-products generated during the dark fermentation step had to be readily available as substrates for algal biomass generation in the second step. A novel

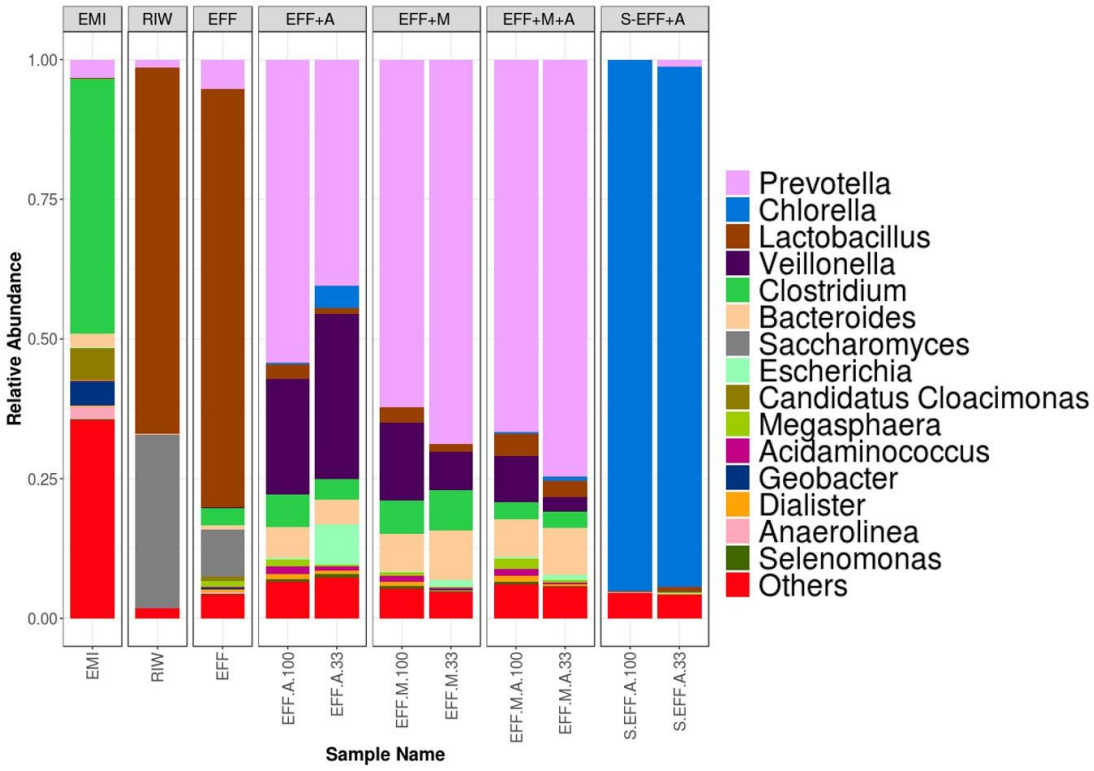

Figure 3. Taxonomic profiles for all samples at the genus level. Enriched microbial inoculum (EMI) has a different profile of microbial genera compared to both the raw initial wastewater (RIW) and dark fermented wastewater (EFF). However, during photo-fermentation all the samples have a very similar profile and abundance of genera. Higher *Ch. vulgaris* abundance is seen in diluted samples compared to undiluted samples. This correlates well with cell count assays. The top 15 genera are shown below.

hybrid biohydrogen evolving system was investigated in our studies using a two-stage biodegradation approach (microbial dark fermentation followed by photoheterotrophic treatment using *Chlorella vulgaris* green algae). We focused on the second photo-fermentative stage of this biodegradation process. A series of outputs ranging from nitrogen and phosphorous removal through biological oxygen demand to the composition of the biodegradation communities were carefully monitored during the photo-fermentation experiments. Special attention was paid to the correlations between the rearrangements of the involved bacterial-algal communities and the performance of the biodegradation system. We used whole metagenome shotgun sequencing to characterize the microbial community

during different stages of wastewater treatment and applied this approach to track how the major functions changed across the different stages.

The bioremediation capacity of microalgae was investigated for specific contaminating agents, especially nitrate was in our focus. *Chlamydomonas* sp. MACC-216 and *Chlorella* sp. MACC-360 were studied for their growth and nitrate removal properties using various concentrations of nitrate. We aimed to understand the influence of nitrate on the growth and to assess the nitrate removal capacity of the two selected microalgae using modified tris-acetate-phosphate (TAP) medium and synthetic wastewater (SWW). The effects of different nitrate concentrations on the accumulation of proteins, carbohydrates and lipids were also investigated in the microalgae. Both microalgae were shown to have the capacity to remove nitrate with high efficiency. High nitrate concentrations led to lipid accumulation in *Chlamydomonas* sp. MACC-216, while protein and carbohydrate contents were not affected. We also revealed that high nitrate concentrations in synthetic wastewater improved the growth of *Chlorella* sp. MACC-360 in comparison to *Chlamydomonas* sp. MACC-216. Both selected axenic green microalgae performed well in removing nitrate from synthetic wastewater. The nitrate removal capacity of these microalgae are being studied in real wastewater, initial data revealed, that algal–bacterial interactions further increased the nitrate removal efficiency.

3. Use of algae as plant biostimulants and source of antimicrobial agents

Green algae possess a largely undiscovered biomolecule composition, a high number of candidate biostimulatory, antimicrobial and anticancer molecules are expected to be encoded in algal genomes. Our research group mostly focused on the plant biostimulant activities of selected eukaryotic green algae, and we were successful in discovering novel algal treatment approaches, conditions and algae isolates efficient in promoting the growth and yield of model and agricultural plants.

Our study aimed to investigate the specific effects of selected green eukaryotic microalgae on *Medicago truncatula* grown under controlled greenhouse conditions. We conducted a comparative study of the growth-promoting effects of two *Chlorella* strains and one *Chlamydomonas* strain on *M. truncatula* when administered as live cells via the soil drench method. Our main focus was on parameters that additively determined yield and quality. These included plant structure/morphology, height, flower number, biomass and pigment content. The tested eukaryotic green microalgae exerted growth stimulating effects on *Medicago truncatula*, a phenomenon attributable to phytohormones and algal EPS production. The algae application on plants influenced leaf size, biomass accumulation, pigment content and pod/flower production. *Chlorella* MACC-360 had the most significant impact on *Medicago* plants. However, the treatment with *C. reinhardtii* cc124 persistently increased both chlorophyll and carotenoid contents of the plant contrary to the applied *Chlorella* species. These results inspire insightful studies to elucidate the mechanism of the different microalgae on plants at the molecular level. Our studies

employing the combination of microscopy and genomics/transcriptomics techniques to elucidate the status of the interaction between the microalgae and plant roots, including the microbiome of the rhizosphere, are still in progress. The differential expression of selected genes was also studied via targeted molecular techniques, namely quantitative polymerase chain reaction (qPCR) to obtain better insight into the effects of microalgae treatments on plants at the molecular level. We have directly confirmed that a number of plant genes showed clear and specific response to the microalgae treatment.

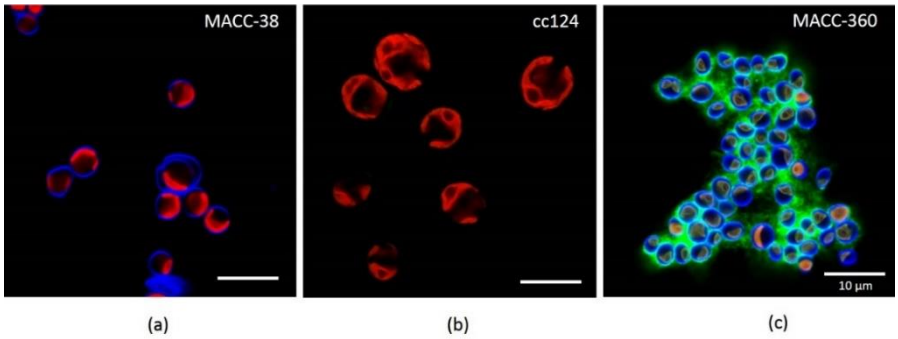

Figure 4. CLSM (confocal laser scanning microscopy) pictures of live microalgae cells on the 7th day after inoculation; (**a**) *Chlorella* MACC-38; (**b**) *C. reinhardtii* cc124; (**c**) *Chlorella* MACC-360 stained with calcofluor white (CFW) and concanavalin A (Con A). The blue fluorescence is CFW dye, which stains the cell walls, red is the chloroplast autofluorescence of live cells and green fluorescence is Con A dye, which binds to extracellular polysaccharides (EPS).

We also aimed at evaluating the efficacy of two green microalgae strains as biostimulants on tomato under controlled conditions (without stress). Living cells suspended in distilled water as well as culture suspensions (living cells plus spent media) were applied via soil drenching. Algal extracts prepared by crushing the cells under liquid nitrogen and resuspension of the slurry in water were also applied by foliar spraying. Microalgae from both *Chlorella* and *Chlamydomonas* genera had biostimulating effects on tomatoes irrespective of the selected portion of algae cultures administered to plants. When compared against the controls, *Chlorella sp.* MACC-360 treatment significantly affected fruit diameter, fruit weight, chlorophyll b and carotenoids irrespective of age of plants. In contrast, *C. reinhardtii* cc124 significantly affected fruit diameter and chlorophyll a content relative to control irrespective of age of plants.

This study proved that the biostimulant action of microalgae influenced photosynthetic performance and is dependent on algal strain. The differences between the two algal treatments were significant for some of the important parameters such as maximum quantum yield and regulated energy loss. Although it is difficult to point out a single reason explaining the observed biostimulant action of microalgae, the presence of EPS again had a strong implication on the algal biostimulant action. Nonetheless, a more thorough characterization of the composition of the microalgae portions (cells, supernatant/spent media, isolated EPS and total extract from destroyed cells) can provide more insight into the molecular mode of action of the algae.

NKFI FK-123899 publications

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Total Impact Factor: 74.27

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