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NordAqua, a Nordic Center of Excellence to develop an algae-based photosynthetic production platform

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Abstract

NordAqua is a multidisciplinary Nordic Center of Excellence funded by NordForsk Bioeconomy program (2017–2022). The research center promotes Blue Bioeconomy and endeavours to reform the use of natural resources in a environmentally sustainable way. In this short communication, we summarize particular outcomes of the consortium. The key research progress of NordAqua includes (1) improving of photosynthetisis, (2) developing novel photosynthetic cell factories that function in a "solar-driven direct CO_2 capture to target bioproducts" mode, (3) promoting the diversity of Nordic cyanobacteria and algae as an abundant and resilient alternative for less sustainable forest biomass and for innovative production of biochemicals, and (4) improving the bio-based wastewater purification and nutrient recycling technologies to provide new tools for integrative circular economy platforms.

A rapid replacement of carbon-intensive infrastructures with net-zero carbon alternatives is vital for mitigation of the climate crisis. Current bioeconomy approaches have been focused mainly on the replacement of fossil raw materials for bio-based commodities. To this end, Nordic countries have largely invested in wood biomass which, for a number of reasons, cannot be considered sustainable or sufficiently available to effectuate a major change. The NordAqua research center has taken a different approach and focuses on aquatic photosynthetic organisms, which are characterized by fast growth rates and efficient photosynthesis, to convert solar energy and CO_2 into energy-rich chemicals. The NordAqua research largely relies on the natural abundance and diversity of Nordic cyanobacteria and algae, which provide a great opportunity for advancing research applicable to a Nordic blue bioeconomy. NordAqua makes use of algae biomass but, importantly, also develops direct photobiocatalytic processes that allow higher energy conversion efficiency to overcome the general insufficiency of biomass to drive low-carbon bioeconomies. Algae biotechnologies combined with a circular economy approach, achieved by the integrated removal of water pollutants and recycling of natural resources, drives the NordAqua research program. NordAqua is being delivered through a consortium of 10 Nordic universities and research institutes along with 10 industrial partners and several societal stakeholders (Figure 1A,B) and is financed by the NordForsk Bioeconomy program (2017–2022).

1 | ENHANCEMENT OF PHOTOSYNTHESIS OF AQUATIC PHOTOAUTOTROPHS

Photosynthesis-based algal/cyanobacterial bio-production can be considered a truly sustainable platform, since it utilizes the available natural resources of sunlight, CO_2, water and some minerals.

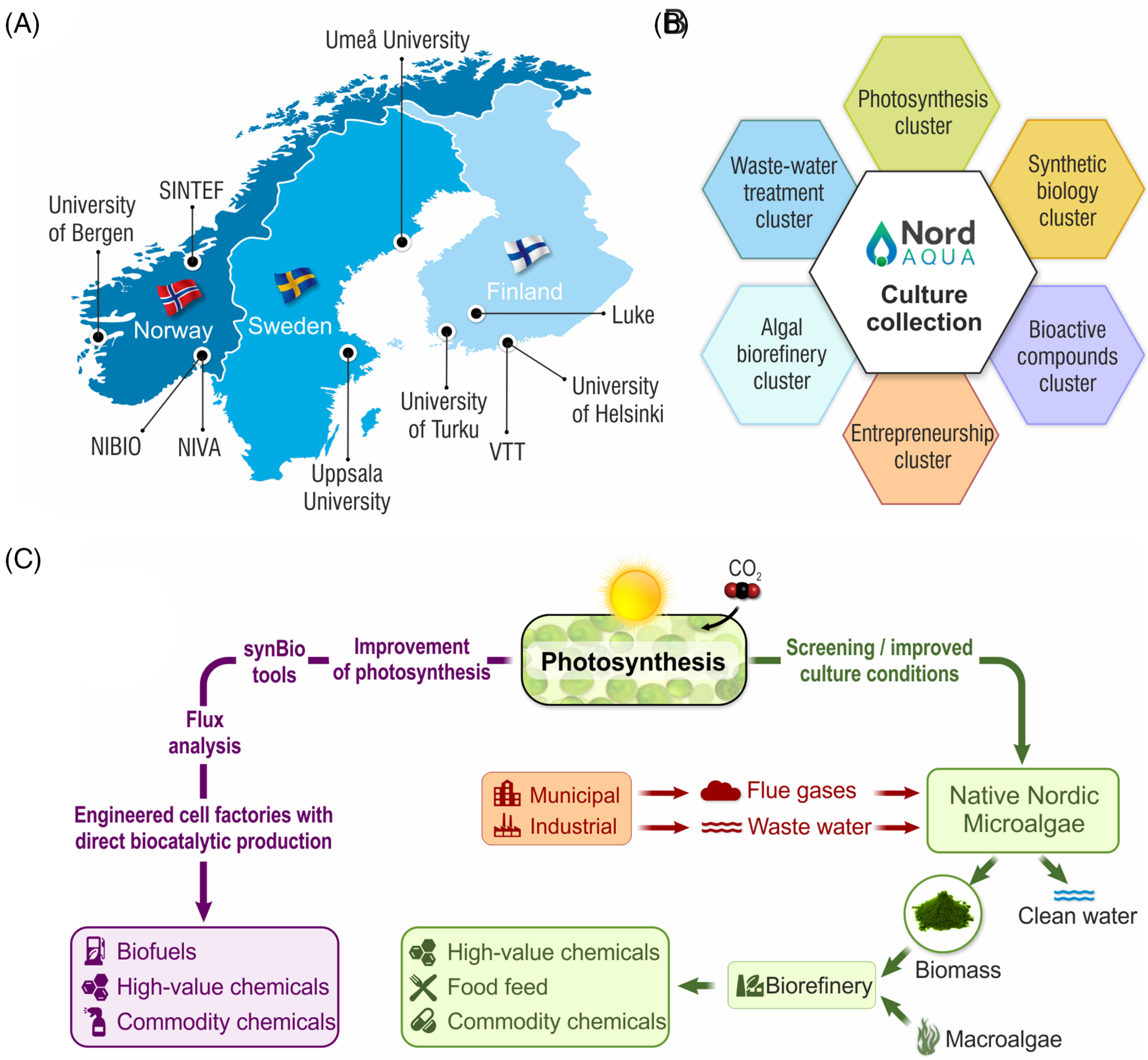

FIGURE 1 NordAqua consortium overview. NordAqua partner organizations (A), research clusters (B), and research concept (C). NordAqua concept includes (1) the production of cyanobacteria and algal biomass from specific Nordic species for biorefinery purposes, (2) the construction and use of photosynthetic cell factories for direct production of fine chemicals and biofuels, the cells functioning as biocatalysts

However, tight regulation of photosynthesis restricts product yield, constituting a major bottleneck for the employment of aquatic photoautotrophs on an industrial scale. Understanding the regulation of photosynthetic mechanisms and using this information to design more efficient photosynthetic energy transformation and carbon capture platforms is an emerging bio-production strategy. NordAqua has focused on auxiliary photosynthetic electron transport pathways in order to identify "waste points." Molecular mechanisms of flavodiiron proteins (FDP or Flv) 1-4-driven O_2 photoreduction have been elucidated and Flv1/3 was found to act as a rapid, strong, and transient electron sink in coordination with Flv2/4, which functions as a slow, steady-state sink downstream of Photosystem I. Importantly, in the presence of high CO_2, the Flv1/Flv3 hetero-oligomer is solely responsible for an efficient steady-state O_2 photoreduction, with *flv2* and *flv4* expression strongly downregulated (Nikkanen et al., 2020; Santana-Sanchez et al., 2019).

The removal of natural electron sinks has been used as an engineering strategy to enhance the yield of specific end-products. The elimination of flavodiiron proteins led to enhanced production of sucrose (Thiel et al., 2019) and improvement of light-driven biotransformation of 2-methylmaleimide (Assil-Companioni et al., 2020) in *Synechocystis* sp. PCC6803 as well as H_2 photoproduction in *Chlamydomonas reinhardtii* (Jokel et al., 2019). Photohydrogen production by green algae has also served as a case study for the calculation of light conversion efficiency (Kosourov et al., 2017) and validation of the improvement of photosynthetic light reactions. NordAqua researchers have developed a novel highly efficient "pulse illumination" protocol for sustainable H_2 photoproduction by *C. reinhardtii* (Kosourov et al., 2018, 2020). The research provides important information on avoiding "wasting" of already absorbed solar energy and, instead, channeling this energy safely and directly to useful bio-products, particularly H_2. Furthermore, it was demonstrated that by periodically switching between H_2 production and biomass accumulation phases, H_2 photoproduction can continue at least for 18 days (Jokel et al., 2019).

Photomixotrophy represents a commercially interesting platform where cyanobacteria and algae simultaneously perform photosynthesis and metabolize imported organic waste. However, the bioenergetics of photomixotrophy are not well known. We demonstrated that 3 days of photomixotrophic culturing hampers photosynthesis and CO_2 fixation in *Synechocystis* sp. PCC6803 (Solymosi et al., 2020). However, deletion of the small protein CytM counteracts this inhibition, thus enhancing photomixotrophic growth.

2 | PHOTOSYNTHETIC CELL FACTORIES

One of the key objectives of NordAqua is to explore new alternatives for sustainable large-scale photosynthetic bio-production using synthetic biology as the enabling technology (Figure 1C). To achieve this, NordAqua research focuses on the development of cyanobacterial chasses with improved photosynthesis (see above), advancing different synthetic biology toolboxes for fast and stable metabolic engineering and employing modular metabolic engineering strategies for the efficient production of various commodity chemicals (ethylene, isobutanol, sucrose), high-value chemicals (terpenoids), and biofuels (isobutene, 1-butanol, H_2) (Carbonell et al., 2019; Dienst et al., 2020; Durall et al., 2020; Liang et al., 2018; Liu et al., 2019; Miao et al., 2018; Mustila et al., 2021; Rodrigues & Lindberg, 2021; Thiel et al., 2018, 2019). To this end, a minimal synthetic promoter for heterocyst specific expression of protein has been developed (Wegelius, Li, et al., 2018), and the possibilities and limitations for regulating target genes at translational level using selected Ribosome Binding Site (RBS) sequences have been evaluated (Thiel et al., 2018). Specifically, the application of systematic modular engineering enabled the efficient biosynthesis of 1-butanol, an attractive commodity chemical and gasoline substitute, with a cumulative titer of 4.8 $g\,L^{-1}$ being the highest 1-butanol yield from CO_2 reported thus far (Liu et al., 2019). An enhanced production of ethanol was observed when overexpressing selected enzymes of CO_2 fixing Calvin-Benson-Bassham cycle (Liang et al., 2018; Roussou et al., 2021). Finally, a non-functional hydrogenase apoprotein, origin of green algae and expressed in living cells of a unicellular cyanobacterium, was successfully activated by introducing a synthetic complex mimicking the active site. The functional semisynthetic hydrogenase linked to the cell metabolism and generated a system with higher and longer lasting hydrogen production than the native system (Wegelius, Khanna, et al., 2018).

Suspension-based photosynthetic production systems suffer from low volumetric production and self-shading, which in turn lead to low light utilization, decreased production efficiency, and require energy intensive mixing. To overcome the bottlenecks of suspension-based cultures, NordAqua develops an alternative biofilm approach with algal or cyanobacterial cells entrapped in different solid-state carriers. Such engineered artificial photosynthetic biofilms decouple cell growth from production and function as long-lived tunable solar-driven biocatalysts in a direct "substrate in—product out" continuous production mode (Figure 1C). For this, NordAqua has built solid-state systems, where engineered photosynthetic production strains are immobilized in a bio-based alginate or nanocellulose framework (Heise et al., 2020; Jämsä et al., 2018; Kosourov et al., 2017; Vajravel et al., 2020; Volgusheva et al., 2019). This opens new possibilities for developing a novel technology platform based on nanocellulose templates with tailored pore-size and controllable surface charges that target sustainable chemical production by photosynthetic microorganisms. This will allow the control of production conditions, targeting the energy to desired products, transport of products and gases as well as the flux of electrons within the system.

3 | NORDIC CULTURE COLLECTIONS—AN UNEXAMINED TREASURE

The diversity of cyanobacteria and microalgae is enormous, with species adapted to, and thriving in, a multitude of habitats, from marine and fresh waters to very extreme environments. The algae and cyanobacteria strains studied in research laboratories and utilized in different industrial applications represent only a small portion of this diverse group of photosynthetic microorganisms. NordAqua exploits the abundance and diversity of microalgae isolated from the Nordic environment and inherently adapted to low light and low temperature conditions, in order to advance the development of Nordic blue biorefineries. NordAqua generated a joint database on Nordic microalgae and cyanobacteria culture collection, integrating valuable information from three collections in the Nordic region: (1) The HAMBI/UHCC collection of the University of Helsinki in Finland with roughly 1200 cyanobacterial strains; (2) the NORCCA collection with over 2000 microalgae and cyanobacteria strains and hosted the Norwegian Institute for Water Research; (3) A recently established Umeå University culture collection of cyanobacteria and microalgae isolated from Northern Sweden (62 strains). The NordAqua Culture Collection database (https://www.nordaqua.fi/our-culture-collection) will include information regarding the commercial potential of the native strains and will serve as valuable resource for biorefinery research in Nordic countries (e.g. limnology, aquaculture, wastewater treatment).

4 | NORDIC MICROALGAE AND CYANOBACTERIA AS A SOURCE OF NUTRACEUTICALS AND PHARMACEUTICALS

The NordAqua research center aims to generate multiple high-value products for full valorization of algal biomass. In collaboration with other projects, an analytical biochemistry platform for macro- and microalgae, enabling thorough characterization and -omics studies, was established at SINTEF. Recent advances in high-throughput rapid screening methods and microbial genomics enable to test the Nordic culture collections, present in the NordAqua network, for the production of anticancer, antifungal, antibacterial and antiviral compounds, enzyme inhibitors, medicinal peptides, highly antioxidative polyphenols, and carotenoids including UV-sunscreens. The anti-cancer activity of algal and cyanobacterial compounds was studied on different human cancer cell lines. Chemical and dereplication (identification of known compounds to prevent re-discovery of known or undesirable molecules) analyses revealed the presence of new cyanobacterial natural products (Shishido et al., 2020). A combination of chemical analyses with a computational strategy, such as molecular networking, opened wider possibilities to reveal new bioactive molecules from cyanobacteria and microalgae. Besides revealing natural bioactive compounds, NordAqua has also established action mechanisms for promising compounds. For example, in silico membrane modeling confirmed the experimental data showing that the presence of cholesterol is crucial for the insertion of the antifungal compound hassallidin into the membrane (Humisto et al., 2019). Peptides containing oxazoles show antibacterial, antiviral, and cytotoxic activity among others. Muscoride is an antimicrobial peptide alkaloid with two contiguous oxazoles and peptide termini protected by prenyl moieties. Muscoride biosynthetic gene clusters were identified through genome mining of *Nostoc* sp. PCC 7906 and *Nostoc* sp. UHCC 0398 and resulted in a discovery of a new muscoride variant. This work was important in expanding the cyanobactin family to include linear polyoxazole bisprenylated peptides (Mattila et al., 2019). Microcystin is one of the most commonly reported toxins in freshwater bodies around the world and constitutes a health risk in drinking water. The biosynthesis of rare variants of microcystin that contain a selection of homo-amino acids by the benthic cyanobacterium *Phormidium* sp. LP904c was also reported (Shishido et al., 2019). Benthic cyanobacteria are rarely considered in water management and this study clarifies how cyanobacteria make rare microcystin chemical variants and highlights the production of toxins by a benthic cyanobacterium isolated from a drinking water reservoir.

5 | NORDIC AQUATIC PHOTOTROPHS FOR THE PRODUCTION OF FOOD AND FEED

The biomass of the two North-Atlantic kelp species, sugar kelp *Saccharina latissima* and winged kelp *Alaria esculenta*, cultivated in Norwegian sea farms, is under investigation for the fast production of large amounts of biomass as a source of food and feed and for extraction of high-value compounds, for example, with anti-cancer activity. Varying cultivation conditions and harvesting strategies were shown to have a significant impact on the biomass yield and chemical composition. It was demonstrated that the farming of kelp integrated with salmon farms for anthropogenic fertilization gives 56% higher kelp biomass yield, yet the timing of the harvesting has a bigger impact on the composition and nutritional quality. For example, a significant decrease in omega-3 fatty acids and an increase in the monosaturated fatty acids was observed from April to May, the prominent harvesting period in mid-Norway (Monteiro et al., 2021). As large volumes of wet biomass are harvested over limited period, there is a strong need for cheap and efficient preservation methods. Effects of various storage methods and pre-processing on the chemical composition of cultivated kelps are thus under evaluation.

6 | WASTEWATER TREATMENT BY MICROALGAE AND CYANOBACTERIA

The integration of wastewater treatment with algal bio-production (biomass valorization) improves the economic feasibility and environmental sustainability of these two processes. There are a wide variety of wastewaters suitable to the cultivation of cyanobacteria and microalgae, and NordAqua has undertaken research to screen the suitability of Nordic Culture Collection strains for this purpose. Nordic strains were proven to be well suited to wastewater treatment, nutrient uptake and valuable biomass accumulation, and successful pilot scale studies have been performed. Besides strains from the culture collection (Ferro et al., 2020), indigenous algal-bacterial consortiums have also been evaluated for their ability to remove nutrients from wastewater at laboratory and pilot scale (Jämsä et al. 2017, Ferro et al., 2018). Analyzing the diversity of microbial communities and their seasonal dynamics throughout the growth period in a pilot-scale open pond using metabarcoding of 16S and 18S rRNAs revealed the fitness advantage of natural strains compared to non-native culture collection strains (Ferro et al., 2020).

Considering the challenging Nordic climate, NordAqua has addressed the opportunities of "cold-cultivation" (Jämsä et al. 2017) as well as the integration of microalgal cultivation within well-equipped Nordic greenhouses operating year-round (Salazar et al., 2021). The latter approach, providing controlled temperature, light and high CO_2, is an attractive "closed nutrient loop" approach. Pilot-scale cultivation in a real greenhouse environment demonstrated the potential of the biodiversity of Nordic culture collections in providing sustainable solutions to treat hydroponic effluents and demonstrated the feasibility of integrated microalgal wastewater reclamation and greenhouse cultivation in a Nordic climate (Salazar et al., 2021). Valorization of biomass through development of plant biostimulants or biopesticides is also under evaluation.

Microalgae and cyanobacteria were employed to remove pharmaceuticals (Gojkovic et al., 2019), heavy metals (Skrobonja et al., 2019), and recalcitrant organic pollutants present in water produced from oil and gas activities (Jaen-Gil et al., 2020). Of particular interest was the identification of transformation products, which in some cases might be more toxic than the contaminant compound.

Since light is a challenge in Nordic countries, Nordic strains were tested for their ability to grow heterotrophically or mixotrophically on waste substrates (Ferro, Colombo, et al., 2019). Mixotrophic cultivation of an algae-bacterium co-culture was successfully applied for wastewater reclamation in continuous mode, demonstrating its suitability for both summer and winter conditions in Nordic countries (Ferro, Gojkovic, et al., 2019). A Droop's mathematical model was generated to predict N assimilation and biomass composition under N starvation in Nordic algal species (Gojkovic et al., 2020).

Life cycle analysis (LCA) based on experimental data and modeling to assess the environmental impacts associated with specific processes and to identify possible bottlenecks is currently under progress.

7 | ALGAENEERS AND ENTREPRENEURSHIP

In all, NordAqua offers a commercially interesting production platform for the Nordic blue bioeconomy (Figure 1). However, the challenges of working between academia and business have been widely acknowledged (Creed et al., 2021). Therefore, entrepreneurship research conducted within the NordAqua framework focuses on understanding: (1) how scientists perceive and make sense of commercialization and entrepreneurship and (2) how scientists evaluate their own success, and barriers to it, in working at the interface of science and business (including interacting with industry and end-users).

Data have been collected during dedicated NordAqua entrepreneurship workshops (Hytti et al., 2020), through open-ended interviews of NordAqua researchers, and via a mentoring process set up for younger scholars. The preliminary findings indicate the tension researchers face when making sense of commercialization and entrepreneurship. As expected, the very tension between academia and business is further articulated in terms of value creation and goals (academic idealism vs. economic realism); identity conflicts (scientific, entrepreneurial, and personal identity); and the ways in which businesses and industries are to be approached (by a researcher or the third person). The findings suggest that these tensions are manifested differently depending on the researcher's phase of career and motivation as well as on the nature of research and its dependency on industry. This research continues and will further develop a better understanding of the studied phenomenon in order to open up new avenues for commercialization and entrepreneurship.

NordAqua initiated in 2018 the annual Nordic Algae Symposia (NAS) to promote blue bioeconomy, particularly emphasising the solving of bottlenecks in industrial applications of aquatic photosynthetic organisms. This discussion platform has already proved invaluable in strengthening the Nordic cooperation between excellent academic teams, facilitating interaction with algal industry.

8 | FUTURE PERSPECTIVES

A transition to successful bioeconomy requires significant changes not only in science and conduction of research, but also in society. To this end, NordAqua will further: (1) focus on strengthening Nordic and EU cooperation; (2) provoke discussion and increase awareness in society of sustainable bioeconomy as a safe way forward; (3) engage stakeholders, form strong relationships with end-users and advise decision makers on the benefits of a sustainable blue bioeconomy. NordAqua closely participated in the preparation of the EU CSA SUNRISE Technological Roadmap (2019) and currently actively collaborates with key European researchers and stakeholders from SunERGY network (https://www.sunergy-initiative.eu) in the promotion of emerging algal based biotechnologies for industrial applications.

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AUTHORS CONTRIBUTION

Drafting and coordination of writing the manuscript were done by Yagut Allahverdiyeva and Eva-Mari Aro. All the authors act as team and work package leaders, consequently involved in design, supervision and implementation of NordAqua research. The manuscript has been read and approved by all co-authors. Several members of the NordAqua consortium contributed to this special issue by individual papers.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

N/A

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