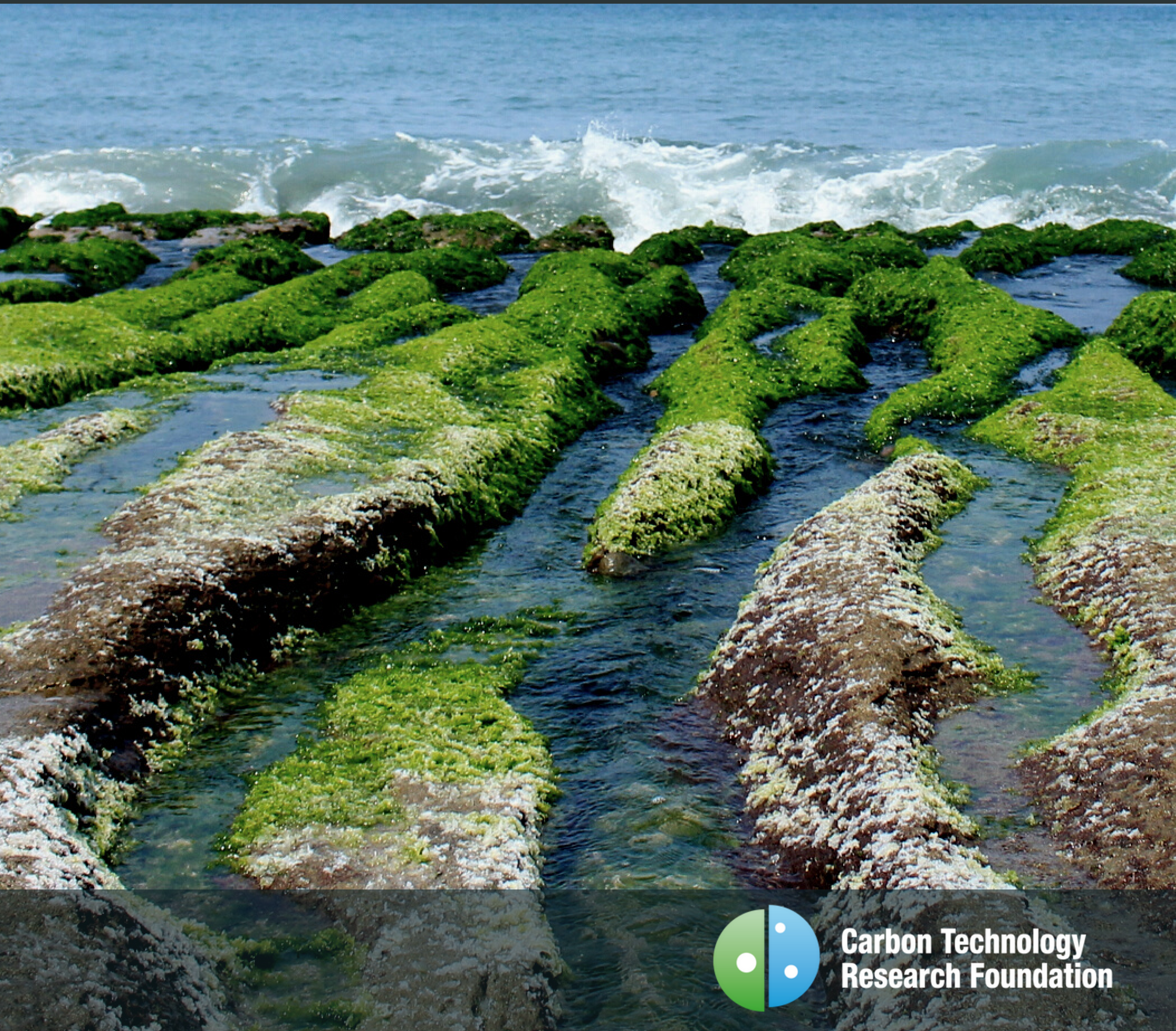
CARBON TECHNOLOGY RESEARCH FOUNDATION

Horizon Scan Report

on Opportunities for Further Research into the application of Biotechnology for Greenhouse Gas Removal



Carbon Technology
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Foreword

The IPCC AR6 Synthesis report is clear, we are highly likely to exceed the 1.5 degrees limit of warming in the near term and are currently on track to exceed 2 degrees of warming in mid-late 21st Century, reaching 3.2 degrees by 2100. With the deep emissions cuts required to stabilise temperatures currently far off track, it is increasingly clear that carbon dioxide removals (CDR) from the atmosphere are going to play a significant role in the efforts to stabilise the climate. The first State of CDR report recognises the large gap between what is required and what is currently being delivered. Virtually all current CDR (99.9% or 2 $GtCO_2$ per year) comes from conventional management of land, primarily via afforestation and reforestation. Only a tiny fraction results from novel CDR methods such as direct air capture, enhanced weathering or carbon capture and storage, with no proven methods yet available at scale. This represents a monumental challenge and this report seeks to explore one area of research and opportunity related to this.

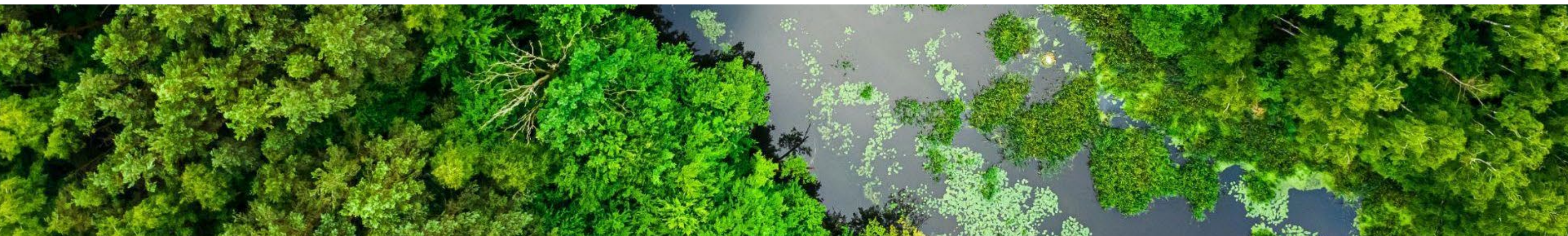
Commissioned by Carbon Technology Research Foundation (CTRF) in its first year of operation, we sought to understand where opportunities might lie to fund novel research into natural carbon removal pathways that could be enhanced or scaled up through the application of biotechnology. This review confirmed that there appears to be a number of opportunities that warrant further exploration and are currently underfunded. We have used this report to inform our initial priorities to offer funding to academic-led research projects targeting enhanced biological sequestration by microorganisms through to plant based systems.

We recognise the challenge and complexity of cutting edge research, but also the huge challenge in finding and deploying scalable carbon removal solutions. We will need rapid deployment and scaling of existing technologies as well as continued efforts to explore and deploy new solutions that could emerge in coming years and decades. We are hopeful that ground-breaking molecular techniques such as genomics and synthetic biology can be deployed to contribute to tackling the carbon removal challenge and look forward to seeing this develop in the years ahead. Under the guidance of our expert Advisory Council, we will support the research community to investigate these, and related topics, in order to gather further evidence and add to the current knowledge base for further exploration and investment.

I would like to offer sincere thanks to Dr. Ida Tarjem, Postdoctoral Associate at Cornell University, for completing this report and informing our research approach, as well as acknowledge the support of the CTRF team members who prepared this review for external publication.

D. Hillyard

Dave Hillyard, CEO



Summary

By 2050, an estimated 10 billion metric tonnes of CO_2 p.a. need to be removed from the atmosphere to meet the goals of the Paris climate agreement, with this number expected to double by the end of the century. Biosequestration, in which natural processes and biological systems are used for carbon capture and sequestration, offers several advantages over physical and chemical alternatives, including potentially being more cost-effective and sustainable. At its core, biosequestration relies on carbon fixation pathways, six of which have been identified in autotrophic organisms. The Calvin cycle, which is part of photosynthesis, is the primary pathway for fixing CO_2 in cyanobacteria, algae and higher plants.

Yet, the efficiency of carbon fixation pathways is constrained by several rate-limiting steps. Among others, the carboxylating enzyme of the Calvin cycle, Rubisco, poorly discriminates between CO_2 and O_2, which leads to photorespiration and loss of fixed carbon and nitrogen. However, with the advent of genome editing and synthetic biology, it is now feasible to improve existing or design entirely novel enzymes and biochemical pathways with more desirable properties, ultimately resulting in increased carbon fixation. Additionally, genome editing and synthetic biology enable improvements of other parts of the photosynthetic machinery beyond the Calvin cycle.

The Carbon Technology Research Foundation (CTRF) invests in research on biosequestration, with a particular emphasis on the use of biotechnology and biochemistry to enhance biosequestration of CO_2. The purpose of this horizon scan is to provide background information on biosequestration, along with an overview of ongoing and cutting-edge research taking place within this field, as well as gaps, underexplored avenues and future directions. The document will help inform communication and outreach strategies and investment focus and decision-making.

The horizon scan is structured according to the groups of organisms most relevant to biosequestration: bacteria, archaea, algae, fungi and higher plants. Additionally, we identify several research areas that may be of potential interest to CTRF in the future, namely reduced methane emissions in ruminants; biological nitrate inhibitors and enhanced nitrogen use efficiency; enhanced weathering; artificial ocean alkalinisation; cell-free, CO_2-fixing enzymatic systems; artificial leaves; and hybrid systems.

The findings demonstrate that bacteria (most notably cyanobacteria) and microalgae offer several benefits in terms of photosynthetic efficiency, growth rate, ability to grow in high-density cell cultures and hostile environments, as well as the possibility of producing value-added products (e.g., biofuels and bioplastics). The relatively high photosynthetic efficiency of bacteria and algae owes to their unique CO_2-concentrating mechanisms (CCMs), which include but are not limited to carboxysomes and pyrenoids, respectively, both of which are a type of microcompartments that help concentrate CO_2 around Rubisco.

Still, despite these benefits, there is room for improving the carbon sequestration capacity of bacteria and microalgae. In bacteria, this has been achieved in the lab through genetic

transformation of Rubisco and other enzymes involved in the Calvin cycle; installing additional bicarbonate transporters; introducing synthetic photorespiratory bypasses; and by designing and introducing synthetic pathways to augment the Calvin cycle. Another innovative approach is the use of synthetic biology to transform heterotrophic bacteria into autotrophs. Still, there is a need to broaden research beyond model species, which may otherwise limit fundamental discovery and applied research towards wider commercialisation. Furthermore, methods of cultivation remain laborious, which hampers scaling and commercialisation.

In microalgae, studies have identified over 300 candidate photosynthesis genes that can potentially be targeted through genetic engineering. Thus far, researchers have successfully engineered enzymes involved in the Calvin cycle and algal CCMs, as well as reduced the antenna size to minimise losses that occur through non-photochemical quenching and increased the absorption spectra of the photosystem. Other potential targets of interest include the Ci accumulation 5 regulator, which is a master regulator of algal CCMs; improvements to the electron transport chain; and a type of Rubisco present in some red algae, which demonstrates an unusually high CO_2/O_2 specificity factor. However, methods of genetic engineering need to be improved, including establishing systems that ensure efficient delivery of the CRISPR-Cas system into algal cells.

While interest in macroalgae has been growing in recent years, particularly with respect to the production of bio-products and ocean afforestation, the carbon sequestration potential of macroalgae is under debate. Furthermore, genetic transformation systems have been lacking, which partly owes to the complex morphology, sexual reproduction and life histories of macroalgae, as well as lack of functional genomics. Accordingly, research on macroalgae should not necessarily be considered a top investment priority.

Archaea are a group of extremophiles that are similar to, but evolutionarily distinct from, bacteria, of which several species play key roles in the global carbon cycle. Interestingly, some archaea exhibit a type III Rubisco enzyme which has been shown to be neither affected by nor inactivated by oxygen, and studies have demonstrated that the enzyme can also function at ambient temperatures. Still, our knowledge of the biology of archaea leaves much to be desired and genome editing systems remain time-consuming and challenging. Consequently, while archaeal biosequestration represents an intriguing and underexplored area of research, returns on investments may not be realised until the longer-term due to the need for fundamental research and discovery.

Filamentous fungi, most notably mycorrhizal fungi, are of interest from a biosequestration perspective given their significant contribution to the formation and stabilisation of soil organic matter. The cell wall of mycorrhizal fungi consists of complex and durable molecules such as melanin and chitin that prevent degradation, while secretions rich in glomalin help stabilise macroaggregates in the soil. Thus, these and related compounds represent potential genetic targets for transgene expression in other organisms, while the biosequestration capacity of mycorrhizae itself can be genetically enhanced. However, mycorrhizal biosequestration remains underexplored, which reflects a lack of understanding of the full carbon sequestration potential of mycorrhizal fungi and the mechanisms by which they sequester carbon. Furthermore, while genome editing is increasingly being applied in fungi, efficient systems have yet to be established across species. Limited research has been conducted in yeast. However, in a recently published study, heterotrophic yeast was transformed into a CO_2 assimilating autotroph, which may open the possibility of creating CO_2-fixing yeast factories.

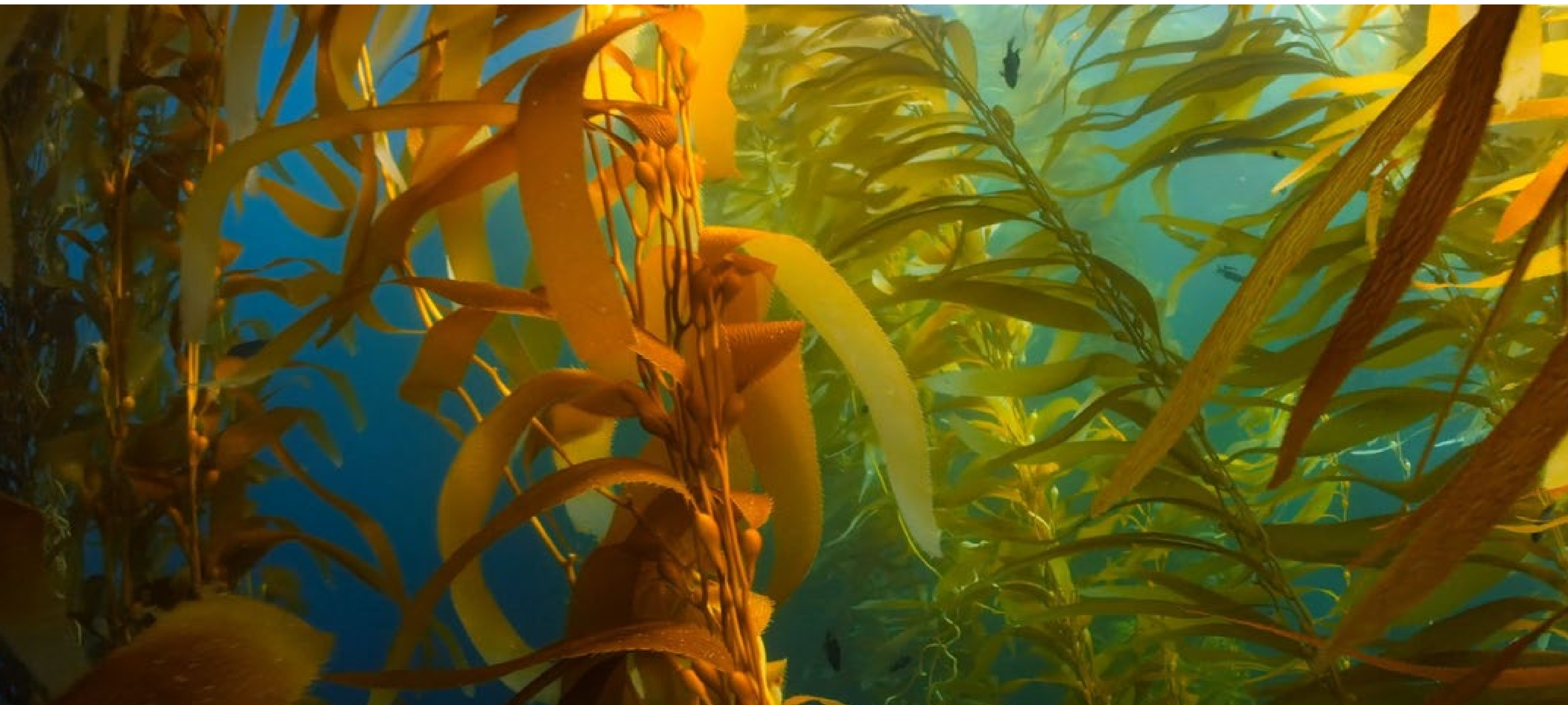
However, while bacterial and microalgal, and potentially also fungal and archaeal biosequestration offer advantages over plants, plant-based systems can be more rapidly deployed and remain the most well-researched, with well-established genetic transformation systems in several species. We identified eight main areas for biosequestration in plants: improving the Calvin cycle, bypassing photorespiration, engineering C_4 photosynthesis into C_3 plants, accelerating recovery from photoprotection, engineering aquaporins, increasing soil carbon sequestration, modifying canopy structure and enhancing trees as carbon sinks. We draw particular attention to research in which CCMs in algae, bacteria and C_4 plants, as well as synthetic enzymes and biochemical pathways and photorespiratory bypasses, are introduced into higher plants. Substantial progress to increase soil carbon sequestration and accelerating recovery from photoprotection is also being made. In turn, engineering of canopy structure and aquaporins remain less well-developed, but nevertheless potentially interesting opportunities for enhancing carbon sequestration.

Still, while several of these approaches show promise in the lab, technical, social and regulatory hurdles must be overcome before scaling and commercialisation can be realised. For instance, the complex nature of Rubisco makes manipulation of the enzyme challenging and a fuller understanding of the complex regulation between photorespiration and other metabolic pathways is needed. Some evidence even suggests that reducing photorespiration may not necessarily have beneficial effects. Furthermore, anatomical differences between C_4 and C_3 plants require fine-tuning of the biochemistry and anatomy of the latter. Additionally, while trees exhibit great potential for carbon sequestration and storage, their complex genomes and long generation times make genetic engineering more challenging compared to other photosynthetic organisms. Finally, to achieve full commercial viability and adoption by farmers and other end-users, crop varieties need to express traits of economic, nutritional and cultural relevance. In this respect, it is important to map any potential negative trade-offs between selecting for traits related to biosequestration and other important agronomic traits.

Of the other research areas of potential interest, engineering ruminant livestock, biological nitrate inhibitors and enhanced nitrogen use efficiency, and enhanced weathering are the most highly researched, while cell-free, CO_2-fixing enzymatic systems, artificial leaves and hybrid systems hold a lot of promise but are the most peripheral to the scope of CTRF. Artificial ocean alkalinisation is less well-explored, and some modelling studies indicate that artificial ocean alkalinisation can potentially have negative environmental impacts. As such, these should not be categorised as prioritised investment areas.

Acronyms

- 3HP/4HB: 3-hydroxypropionate/4-hydroxybutyrate cycle
- 3HP: 3-hydroxypropionate bicycle
- AOA: artificial ocean alkalinisation
- ATP: adenosine triphosphate
- BNIs: biological nitrification inhibitors
- CA: carbonic anhydrase
- CCM: CO_2-concentrating mechanism
- CH_4: methane
- CRISPR-Cas9: clustered regularly interspaced short palindromic repeats-CRISPR-associated protein 9
- CTRF: Carbon Technology Research Foundation
- DC/HB: dicarboxylate/4-hydroxybutyrate cycle
- ETC: electron transport chain
- EW: enhanced weathering
- FBPA: fructose 1,6-bisphosphate aldolase
- GHGs: greenhouse gases
- GMO: genetically modified organism
- H_2: hydrogen
- MCG: malyl-coA-glycerate
- MOG: Malonyl-coA-Oxaloacetate-Glyoxylate
- N_2O: nitrous oxide
- NAPDH: nicotinamide adenine dinucleotide phosphate
- NPQ: non-photochemical quenching
- pCO_2: partial pressure of carbon dioxide
- PSI: photosystem I
- PSII: photosystem II
- rTCA: reductive or reverse citric acid cycle
- Rubisco: ribulose-1,5-bisphosphate carboxylase/oxygenase
- RuBP: ribulose 1,5-bisphosphate
- SBPase: sedoheptulose 1,7-bisphosphatase
- TaCo: tartronyl-CoA pathway

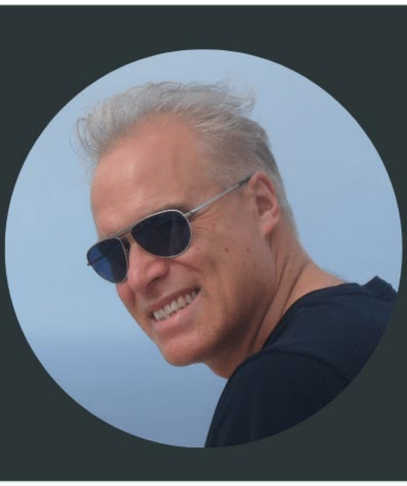


1. Introduction

Climate change is one of the greatest threats facing humanity. In addition to reducing emissions, there is a need to deliberately remove carbon dioxide (CO_2) from the atmosphere (i.e., negative emission), particularly considering the long atmospheric residence time of CO_2 (Minx et al., 2018). By 2050, an estimated 10 billion metric tonnes of CO_2 need to be pulled from the atmosphere to meet the goals of the Paris climate agreement, with this number expected to double by the end of the century (OSB & NASEM, 2019). Biosequestration, in which natural processes and biological systems are used for carbon capture and sequestration, offers several advantages over physical and chemical alternatives, including potentially being more cost-effective and sustainable (Onyeaka et al., 2021; Onyeaka & Ekwebelem, 2022; Prasad et al., 2021; Venkata Mohan et al., 2016). Despite its proposed benefits, however, biosequestration has been largely absent from high-level climate discussions, such as by the United Nations Framework Convention on Climate Change (Rodríguez-Martínez et al., 2022), and public investments have focused mostly on physical and chemical negative emission technologies (Giddings et al., 2020).

The Carbon Technology Research Foundation (CTRF) invests in research and development of biosequestration, with a particular emphasis on the use of biotechnology and biochemistry to enhance biosequestration of CO_2 and to a lesser extent other greenhouse gases (GHGs), such as methane (CH_4) and nitrous oxide (N_2O). The purpose of this horizon scan is to provide background information on biosequestration, along with an overview of ongoing and cutting-edge research taking place within this field, as well as gaps, underexplored avenues and future directions. The document will be used internally and together with the Advisory Council and selected partners and help inform communication and outreach strategies and investment focus and decision-making.

The document is structured as follows. First, the aims, methods and materials are presented, followed by background information on the global carbon cycle, limitations and opportunities of carbon fixation, genome editing and synthetic biology. Subsequently, the horizon scan provides an overview of ongoing and cutting-edge research categorised according to the different organisms relevant to biosequestration. The document ends with a conclusion and way forward.



"The scale of greenhouse gasses in the atmosphere has created the imperative to find cost-effective and scalable solutions for their removal. Solutions based on natural processes make sense and show great promise. This is where CTRF will focus its efforts."

Stig Arff, Founder, CTRF

2. Aims, methods and materials

The horizon scan was conducted with the aim of answering the following questions:

a. What research is taking place on the application of biotechnology and biochemistry to deliver enhanced/scalable natural solutions to carbon sequestration?
b. What potential gaps/opportunities are there for further or new research on the above?
c. What research universities/institutions are leading in this area of work?

Data were collected through a literature review using selected databases, most notably Google and Google Scholar, in August of 2022. The keywords included a combination of the organism in question (“plants”, “algae”, “cyanobacteria”, etc.), the technological tool of interest (“genetic engineering”, “genome editing”, “CRISPR-Cas”, “synthetic biology”, etc.) and words related to biosequestration (e.g., “carbon capture”, “carbon assimilation”, “carbon uptake”, “carbon sequestration”, “negative emission technology”, etc.). While we focused mostly on studies that explore ways to enhance biosequestration, we decided to include other research areas of potential interest from a climate change mitigation perspective, including research on ruminant livestock, biological nitrate inhibitors and enhanced nitrogen use efficiency, enhanced weathering, artificial ocean alkalisation, cell-free, CO_2-fixing enzymatic systems, artificial leaves and hybrid systems. While these are not prioritised investment areas, they all depend on or mimic natural processes and biological systems.

Note, however, that the primary objective of several of the identified studies was to enhance photosynthetic carbon fixation for the purpose of increasing yield and productivity (in plants) and feedstock for production of biofuels and other value-added products (algae and bacteria). Still, while the study objective was not climate change mitigation per se, we considered such studies of interest as the fundamental science is similar. Furthermore, we acknowledge the importance of coupling biosequestration (with the purpose of climate change mitigation) with commercial production of biomass as a way to lower net costs and provide an economic incentive to adopt biosequestration technologies.

3. Background

3.1. The global carbon cycle

The global carbon cycle describes the transfer (fluxes) of carbon between the four major carbon reservoirs (stocks): the atmosphere, land/terrestrial, the oceans and fossil fuels (Green & Byrne, 2004; Houghton, 2014). CTRF is particularly interested in the application of biotechnology and biochemistry to regulate the transfer of carbon between the atmosphere and land (the terrestrial carbon cycle) and between the atmosphere and oceans (the oceanic carbon cycle), as addressed next.[1]

The terrestrial carbon cycle is to a large extent determined by the balance between photosynthesis and respiration (Trumbore, 2006). Carbon-fixing autotrophic organisms, most notably photosynthesising plants and photo- and chemoautotrophic microbes (some bacteria, archaea and fungi), fix and transfer atmospheric carbon to the soil. Once fixed, carbon storage is controlled by autotrophic and heterotrophic respiration, as well as climatic, geological and geochemical processes and events (Gougoulias et al., 2014), along with soil erosion due to anthropogenic activities such as agriculture (e.g., tillage). Long-term storage can be achieved through association between carbon and soil minerals, via conversion to carbonate minerals or recalcitrant organic carbon (e.g., charcoal) and by reducing microbial respiration, among others (Jansson et al., 2021). Moreover, the deeper the carbon is stored in the soil, the longer its mean residence time, as decomposition rates decline with depth (Jansson et al., 2021; Jobbágy & Jackson, 2000).

The oceanic carbon cycle is largely controlled by differences in the partial pressure of CO_2 (pCO_2) between the atmosphere and surface ocean (Keller et al., 2018). The surface ocean pCO_2 is driven by the physical and biological carbon pumps (Heinze et al., 2015). The former refers to physico-chemical processes (e.g., temperature, carbonate chemistry and ocean circulation), while the latter refers to photosynthetic sequestration of carbon. For instance, carbon fixation by chemoautotrophic microorganisms, such as nitrite-oxidising bacteria, in the dark ocean has a substantial impact on carbon cycling (Pachiadaki et al., 2017). Macro- and microalgae bloom near the surface and subsequently sink to the deep ocean, thereby sequestering carbon into sediments for centuries or even longer (Smetacek et al., 2012). The role of fungi, in turn, is poorly understood. However, Orsi et al. (2022) recently confirmed the role of planktonic and benthic fungi in “helping to structure carbon flow from primary producers in marine microbiomes from the surface ocean to the subseafloor” (Orsi et al., 2022, p. 1245).

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[1] Importantly, it is “the interaction and feedbacks between carbon reservoirs that ultimately determines CDR [carbon dioxide removal] efficacy” (Keller et al., 2018, p. 250). For instance, if atmospheric CO_2 is removed (such as through biosequestration) to an extent where the atmospheric pCO_2 becomes lower than that of the ocean, carbon will be transferred from the ocean to the atmosphere (Keller et al., 2018). Thus, there is a need to better understand the carbon cycle responses to carbon dioxide removal.

3.2. Carbon fixation: Limitation and opportunities

Carbon fixation is the process by which CO_2 is incorporated into organic compounds. Hitherto, six biochemical pathways for carbon fixation have been identified in autotrophic organisms, of which the Calvin-Benson-Bassham pathway (hereafter the Calvin cycle) is the primary pathway for fixing CO_2 in cyanobacteria, algae and higher plants (Bar-Even, 2018; Bharti et al., 2014; Kumar et al., 2018).[2] The Calvin cycle, which is part of photosynthesis, consists of a series of enzymatic reactions divided into three main stages: carboxylation (carbon fixation), reduction and regeneration.[3] Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is responsible for catalysing the carboxylation of the CO_2 acceptor molecule ribulose 1,5-bisphosphate (RuBP) to initiate the Calvin cycle.

However, Rubisco is surprisingly inefficient and catalytically slow (Erb & Zarzycki, 2018; Parry et al., 2013; Tcherkez et al., 2006). Not least, Rubisco has a low specificity towards CO_2 and catalyses two competing reactions, namely carboxylation and oxygenation. The latter directs the flow of carbon through the photorespiratory pathway, which requires substantial amount of energy to get rid of toxic by-products (e.g., phosphoglycolate and glycolate), and results in the loss of 30-50% of the previously fixed CO_2 as well as nitrogen (Bar-Even et al., 2010; Raines, 2006). Furthermore, Rubisco's specificity for CO_2 decreases with an increase in temperature, which is alarming in a progressively warming world. In addition to the carboxylation capacity of Rubisco, photosynthetic CO_2 fixation is also dependent on the regenerative capacity of RuBP. As a consequence of these and other rate-limiting factors, the photosynthetic efficiencies in plants and algae range from 1-5% of available solar energy, while the theoretical efficiency is as high as 11% (Long et al., 2006).

Enzyme and metabolic engineering using genome editing and synthetic biology (as described in section 3.3. and 3.4) can help enhance CO_2 fixation in several ways. Given its central role in carbon fixation, Rubisco has been identified as a prime target for genetic manipulation to increase photosynthetic efficiency and carbon sequestration across a number of species (Parry et al., 2013; Parry et al., 2003; Satagopan & Tabita, 2016; Satagopan et al., 2019). These efforts include improvements in the carboxylation rate and reducing the oxygenation rate (Whitney

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[2] In addition to the Calvin cycle, two other pathways exist in aerobic autotrophs, namely the 3-hydroxypropionate (3HP) bicycle and the 3-hydroxypropionate/4-hydroxybutyrate (3HP/4HB) cycle. The 3HP bicycle is usually found in photosynthetic green non-sulphur bacteria, while 3HP/4HB is commonly present in extremely thermoacidophilic archaea (Andorfer & Drennan, 2021). Additionally, three carbon fixation pathways have been identified in anaerobic bacteria and archaea: the reductive or reverse citric acid (rTCA) cycle, the dicarboxylate/4-hydroxybutyrate (DC/HB) cycle and the Wood-Ljungdahl pathway (otherwise known as acetogenesis) (Berg et al., 2007).

[3] Photosynthesis, the process by which solar energy is used to convert atmospheric CO_2 and water into carbohydrates and oxygen, is divided into two stages referred to as the light and dark reactions. During the former stage, light energy is captured by the chlorophyll and associated pigments, ultimately yielding NAPDH and ATP that power the Calvin cycle during the latter stage.

et al., 2010; Wilson & Whitney, 2017).[4] Alternatively, studies indicate the possibility of splitting the catalysis of Rubisco across several enzymes, replacing Rubisco with alternative carboxylation enzymes, substituting the Calvin cycle with other pathways and engineering photorespiration bypass routes (e.g., Antonovsky et al., 2016; Bar-Even et al., 2010; Bar-Even, 2018; Claassens, 2017; Erb et al., 2017; Herz et al., 2017; Santos Correa et al., 2022; Schwander et al., 2016; Yu King Hing et al., 2019).

Additionally, other enzymes that control photosynthetic carbon flux besides Rubisco, such as fructose 1,6-bisphosphate aldolase (FBPA), sedoheptulose 1,7-bisphosphatase (SBPase), carbonic anhydrase (CA) and transketolase can also be genetically engineered (Raines, 2003; Tamoi et al., 2006; Uematsu et al., 2012).[5] Another possibility is to optimise other components of the photosynthetic machinery, such as the photosynthetic electron transport chain (ETC) that generates NADPH which, together with ATP generated by ATP synthase, helps drive the Calvin cycle (see footnote 3) (Chida et al., 2007; Rochaix, 2011; Takahara et al., 2010; Yamori et al., 2016). Other ways of enhancing carbon sequestration include enhancing light absorption, such as by expanding the photosynthetically active radiation spectrum to the infrared or change the morphology of the canopy (Allakhverdiev et al., 2016; Blankenship & Chen, 2013; Wolf et al., 2018), or to change the morphology and biochemical composition of root systems.

Notably, some organisms have evolved CO_2-concentration mechanisms (CCMs) that help increase the concentration of CO_2 around Rubisco, thus allowing Rubisco to overcome its affinity towards O_2 and limit photorespiration. These include carboxysomes in cyanobacteria and proteobacteria, pyrenoids in algae and diatoms and the C_4 system and Crassulacean acid metabolism (CAM) in higher plants (Tomar et al., 2017). CCMs can potentially be expressed in organisms that otherwise lack these.

3.3. Genome editing

Genome or gene editing is the use of molecular breeding approaches to alter the DNA of an organism and includes such tools as zinc finger nucleases, transcription activator-like effector nucleases and the clustered regularly interspaced short palindromic repeats – CRISPR-associated protein (CRISPR-Cas). Over the last

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[4] However, as noted by Lin et al. (2014): “the complex nature of Rubisco’s assembly has made manipulation of the enzyme extremely challenging” (p. 547). Santos Correa et al. (2022) further note how the improvement of Rubisco using bioengineering has been challenging due to two main aspects: “1) identification of the structural changes that promote performance and 2) identification of the ways to efficiently transplant these changes into RuBisCO within a target organism. Additionally, this task requires a satisfactory understanding of the regulatory pathways of the chloroplast gene, as well as the complex nature of catalysis and biogenesis promoted by this enzyme” (p. 11). Thus, “[t]he main challenge underlying the manipulation and modification of carbon-fixation routes is the insufficient understanding of how the pathways perform together within the studied organism” (Santos Correa et al., 2022, p. 13).

[5] Giri et al. (2020) contend that CA “is one of the most environmentally friendly and attractive biomimetic routes for carbon sequestration due to its economic viability and environmental compatibility” (p. 91). Thus, “[t]o reduce the greenhouse effect of carbon dioxide, further research should be devoted to the large-scale production, long-term performance of engineered CA, and developing highly efficient engineering strategies” (Giri et al., 2020, p. 91).

decade, the application of CRISPR-Cas has skyrocketed due to its specificity, versatility and efficiency, ushering in a new era in molecular biology. CRISPR-Cas involves the use of RNA-guided nucleases to introduce a double-stranded break at one or several targeted locations in the genome.[6] Subsequently, the double-stranded break is repaired by the cell's natural DNA repair mechanism, often resulting in single nucleotide changes or small deletions or insertions that resemble naturally occurring mutations.[7] Alternatively, repairs can be directed to introduce, delete or replace a part of the genome using a nucleic acid template. Combined with other genomic, transcriptomic and proteomic approaches, CRISPR can help improve our understanding of, and the ability to engineer, the genes controlling traits and metabolic pathways involved in biosequestration (Khumsupan et al., 2019; Naduthodi et al., 2018; Zhang, Y.-T. et al., 2019).

However, the use of CRISPR-Cas is more technically challenging than what is often portrayed in the popular and some of the scientific literature. Among others, biological differences between species make them more or less amenable to genetic engineering. For instance, the cells of algae and higher plants have a rigid cell wall that complicates the delivery of the CRISPR-Cas system to the cells. Other important factors to consider include the complexity of the genome, mode of reproduction, the reproductive rate, number of progeny per reproduction cycle and the generation time. Furthermore, whether it is possible to breed for a particular trait will depend on, among others, whether it is clearly defined and recordable, has sufficiently high heritability (i.e., a measure of the extent to which a trait is genetically controlled), if the trait is controlled by one or multiple genes, and any potential genetic correlations with other important traits (for instance, there might be a negative correlation between above and below-ground biomass in plants). Another determining factor is the cellular location of the DNA to be transformed (e.g., whether it is located in the nucleus, mitochondria or plastid). The rate of genetic improvement is also shaped by the politics, structure and organisation of the breeding sector in question (see, e.g., Van Eenennaam et al., 2021). For instance, climate change mitigation may not necessarily be part of national breeding goals nor may there be an incentive to include climate change goals, despite global warming being a high-level political priority (as seen in the case of methane emissions in dairy cattle breeding, see e.g., de Haas et al., 2017).

3.4. Synthetic biology

Synthetic biology attempts to make biology engineerable in order to “design and program biological systems to carry out prespecified functions” (DeLisi et al., 2020,

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[6] Several CRISPR-Cas systems exist, most of which are categorised as Class I or Class II, with each class containing several subtypes that exhibit particular advantages and drawbacks (Chaudhuri et al., 2022; Liu et al., 2020; Makarova & Koonin, 2015).

[7] As no foreign DNA is inserted in the genome, some regulatory authorities have decided that such genomic changes should not fall under the strict regulatory frameworks of genetically modified organisms (Lassoued et al., 2021; Schiemann et al., 2020; Schmidt et al., 2020; Smyth, 2019). Still, several political, regulatory and ethical hurdles remain.

p. 2). In contrast to genome editing, which commonly involves alterations to single nucleotides or smaller stretches of DNA, synthetic biology allows researchers to chemically construct genetic sequences (including entire genomes) so as to redesign and reconstruct existing or novel enzymes, metabolic pathways or biological systems. As noted by Gleizer et al. (2020), synthetic biology allows the disentanglement of "organisms and biosynthetic pathways from their evolutionary contingencies, potentially enabling improvements over natural systems by combining components that do not co-exist in nature (e.g., linking two pathways, localizing a pathway to an organelle)" (p. 1).

Thus, synthetic biology enables the creation of novel carbon fixation pathways that can help overcome the many reaction steps and low efficiencies of natural carbon fixation pathways (Andorfer & Drennan, 2021; Gong et al., 2016; Naseem et al., 2020; Santos Correa et al., 2022). For instance, Schwander et al. (2016) constructed a synthetic carbon fixation pathway that was up to five times more efficient than the Calvin cycle. The pathway consisted of 20 enzymes, three of which were engineered, while 17 were of natural origin (from nine different organisms). Additionally, a potential synthetic pathway known as Malonyl-coA-Oxaloacetate-Glyoxylate (MOG) may represent a better alternative to the Calvin cycle due to more efficient carboxylases (Salehizadeh et al., 2020). Similarly, Scheffen et al. (2021) recently developed a novel carboxylase able to catalyse the most difficult step of the theoretical tartronyl-CoA (TaCo) pathway, which would outcompete other pathways from both an energetic and carbon efficiency standpoint (Trudeau et al., 2018). Scheffen et al. (2021) also discovered two additional enzymes needed to fully reconstitute the TaCo pathway and were able to interface the TaCo pathway with photorespiration, ethylene glycol conversion and a synthetic CO_2 fixation pathway.

Consequently, synthetic biology is touted to play a key role in climate mitigation (DeLisi, 2019; DeLisi et al., 2020; Erb et al., 2021; Jatain et al., 2021). Still, synthetic biology has received limited attention in high-level discussions on CO_2 removal (DeLisi, 2019; DeLisi et al., 2020). Moreover, synthetic biology approaches are not without their limitations. For instance, synthetic pathways may interfere with endogenous metabolism, side-reactions and dead-end metabolites. Santos Correa et al. (2022) point out that "the development of artificial carbon-fixation pathways may be limited by the gap between theoretical predictions and their experimental realisation in synthetic biology. Moreover, attempts to synthesise new metabolic pathways in living organisms are challenging because of the limited understanding of the interactions between enzymes in heterologous systems" (Santos Correa et al., 2022, p. 10). However, some of these hurdles may be overcome with hermeting strategies (see Erb et al., 2017).

4. Horizon Scan

4.1. Bacteria

Many bacteria have the ability to efficiently sequester atmospheric CO_2 and play a key role in both the terrestrial and oceanic carbon (and methane and nitrogen) cycles (Barnett et al., 2021; Gougoulias et al., 2014; Jiao et al., 2010; Kandeler et al., 2005; Lechtenfeld et al., 2015; Naylor et al., 2020; Ogawa et al., 2001; Pomeroy et al., 2007). Notably, several bacterial species are currently being used to treat wastewater and in biomitigation of CO_2 in flue gases (de Morais et al., 2019). Moreover, bacteria reproduce rapidly, can exist in high-density cell cultures, have the ability to produce additive products (e.g., biofuels and bioplastics) and are relatively amenable to genetic engineering (Bharti et al., 2014). Then again, maintaining appropriate culturing conditions (in terms of pH, light, nutrients, temperature, contamination and so forth) requires significant labour (Costa et al., 2006; Goli et al., 2016; Jajesniak et al., 2014; Kumar et al., 2018; Saini et al., 2011). Consequently, Onyeaka and Ekwebelem (2022) argue that “[t]he major downside, from an economic standpoint, thus far has been related to methods for cultivation” (p. 1).

Cyanobacteria appear to be of particular interest from a biomitigation perspective, given that they account for 20-30% of the global CO_2 fixation (Pisciotta et al., 2010). Previously known as blue-green algae, cyanobacteria constitute a group of photoautotrophic bacteria that reside in a wide variety of marine and freshwater habitats (Flombaum et al., 2013; Pedersen & Miller, 2017; Puente-Sánchez et al., 2018). The relatively high CO_2 fixation efficiency of cyanobacteria owes to bacterial CCMs, including carboxysomes, which are protein microcompartments in which Rubisco and CA reside, and that help concentrate CO_2 around Rubisco (Long et al., 2018; Price et al., 2007). Moreover, cyanobacteria can convert CO_2 to recalcitrant calcium carbonate, which can be used as an agent for biomineralisation of CO_2 (Jansson & Northen, 2010). Additionally, cyanobacteria can be grown in hostile environments and be cultured on non-arable land with minimal nutrients (Lau et al., 2015; Pedersen & Miller, 2017; Puente-Sánchez et al., 2018).

Gene modification and editing have been reported in several species of cyanobacteria (Behler et al., 2018; Santos-Merino et al., 2019; Sun et al., 2018; Vijay et al., 2019; Zhang, Y. et al., 2019). This includes Synechoccus, which has been found to be particularly adept at carbon mitigation (Farrelly et al., 2013). Back in 2009, Atsumi et al. (2009) genetically modified S. elongatus PCC7942 to overexpress Rubisco, which doubled the productivity compared to the wild type. In a more recent study, Kanno et al. (2017) enhanced CO_2 fixation, glucose utilisation and chemical production in S. elongatus PCC 7942 by overexpressing and deleting genes involved in the Calvin cycle and the glycolysis pathway. De Porcellinis et al. (2018), in turn, demonstrated that overexpression of bifunctional fructose-1,6-biphosphatase/sedoheptulose-1,7-biphosphatase helped enhance photosynthesis in Synechococcus sp. PCC 7002. In another species of cyanobacteria, Synechocystis, Kamennaya et al. (2015) used genetic engineered to install additional BicA bicarbonate transporters, which is a family of low-affinity, high-flux transporters involved in cyanobacterial CCMs that help improve photosynthetic carbon fixation (Wang, C. et al., 2019). This led to a two-fold increase in carbon acquisition, growth and biomass accumulation (Kamennaya et al., 2015). Liang and Linblad (2017), in turn, overexpressed Rubisco in Synechocystis PCC 6803, demonstrating increased growth and photosynthetic rate.

Turning now to synthetic biology approaches, Shih et al. (2014) introduced a synthetic photorespiratory bypass based on the 3HP bicycle (see footnote 2) in S. elongatus sp. PCC 7942, which directly avoided the net loss of carbon and nitrogen. In 2018, Yu et al. (2018) designed a synthetic malyl-coA-glycerate (MCG) pathways to augment the Calvin cycle, which was functionally demonstrated in Escherichia coli, followed by implementation into S. elongatus PCC7942. “This work”, the authors concluded, “provides a strategy to improve carbon fixation efficiency in photosynthetic organisms” (Yu et al., 2018, p. 1). Of interest is also work by Antonovsky et al. (2016; 2017), in which the heterotrophic E. coli were transformed into autotrophs able to convert CO_2 into sugars and other biomass components.

However, Gale et al. (2019) note that, despite recent advances in synthetic biology and molecular tools for cyanobacterial research, most of the work published to date focuses on a small number of model species that are readily cultured under laboratory conditions, can be stored long-term by freezing and are amenable to genetic engineering (Elhai, 1993; Lea-Smith et al., 2016; Shestakov & Khyen, 1970; Stevens & Porter, 1980). This narrow focus “limits fundamental discovery and applied research towards wider commercialisation” (Gale et al., 2019, p. 1).

4.2. Archaea

Archaea are prokaryotic organisms that in many ways are similar to, albeit evolutionary distinct from, bacteria. Due to their special cellular membranes, archaea can withstand extreme environmental conditions, including high pressure, temperature, salinity, acidity and alkalinity. Importantly, many archaeal species play key roles in the global carbon cycle which, as noted by Nayak and Metcalf (2017), have “profound implications for climate change, yet our knowledge regarding the biology of these important organisms leaves much to be desired” (p. 2976). Interestingly, archaea are the only known organisms exhibiting so-called type III Rubisco enzymes. In Thermococcus kodakarensis, this version of Rubisco has been found to neither be affected nor inactivated by oxygen (Sato et al., 2007). Nishitani et al. (2010) have demonstrated that the enzyme also operates at ambient temperatures. Thus, Straub et al. (2018) note that “[t]he archaeal carbon fixation cycles provide an enzymatic toolkit to construct hybrid pathways that function over a wide range of temperature and pH. Since many of these enzymes retain significant activity at lower temperatures, their potential use is not limited to thermophile metabolic engineering, but may find use in photosynthetic plants and alga” (p. 548).

Wilson et al. (2016) transformed tobacco plants to express a Rubisco from the archaea Mehtanococcoides burtoni using conventional gene modification, which led to improvements in CO_2 fixation speed, CO_2 affinity and specificity for CO_2. In turn, De Almeida Camargo and Pereira (2022), Panicker (2022) and Lie et al. (2022) are among the first to report the use of CRISPR-Cas editing in archaea. However, genome engineering of extremophiles remains challenging and time consuming (Panicker, 2022). Thus, there is both a need to improve our understanding of carbon fixation in archaea with the intention of using this knowledge to enhance carbon fixation in plants, bacteria or algae (Nishitani et al., 2010), as well as to establish efficient genome editing systems.

4.3. Algae

4.3.1. Microalgae

Microalgae are a group of unicellular and simple multicellular photosynthetic organisms responsible for half of the total global primary productivity (Yang et al., 2020). They have a relatively high photosynthetic efficiency due to algal CCMs, including the presence of pyrenoids (Cheah et al., 2015; Kurano et al., 1995; Moreira & Pires, 2016; Packer, 2009; Sayre, 2010; Viswanaathan et al., 2022). Pyrenoids are cellular sub-compartments that help concentrate CO_2 around Rubisco, thus reducing photorespiration (Tomar et al., 2017).[8] In fact, microalgae can fix 10-50 times more CO_2 than terrestrial plants (Batista et al., 2015). Weerahandi et al. (2012) estimate that algae fix >65 Gt of carbon annually, which is equivalent to the carbon output of around sixty-five thousand 500 MW generating plants.[9] Microalgal photosynthesis can also result in the precipitation of calcium carbonate, a potentially long-term sink of carbon (Aresta et al., 2005; Olaizola, 2003). Moreover, algae can sequester CO_2 to bioenergy and other value-added bioactive compounds (e.g., proteins and vitamins) (Onyeaka et al., 2021).[10]

Microalgae offer additional advantages for high-performance reduction of CO_2: (i) rapid growth rates (Batista et al., 2015; Bennion et al., 2015; Brilman et al., 2013; Cheah et al., 2015); (ii) the ability to withstand harsh environmental conditions, thus allowing cultivation in saline-alkali water, wastewater and deserts, which reduces pressure on arable land (Moreira & Pires, 2016; Wang et al., 2008); (iii) the opportunity to utilise wastewater as a nutrient source (Farrelly et al., 2013; Onyeaka et al., 2021); and (iv) the capacity to directly convert flue gases from power plants and other

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[8] Research on pyrenoids is fragmented and more knowledge is needed to understand the physiological mechanism of microalgal carbon sequestration (Gayathri et al., 2021; Raven et al., 2008).

[9] However, Xu et al. (2019) note that “the analysis of carbon sequestration efficiency of existing microalgae is relatively simple. The main reason is that the existing data are not quantified, and there is a lack of standardized working framework and efficiency analysis model and process based on it” (p. 76).

[10] Diatoms, a type of silicified microalgae that contribute roughly 20% of global net primary productivity (Field et al., 1998; Nelson et al., 1995), remain a relatively underexplored group of microalgae with great potential and amenability for CO2 uptake and fixation at industrial scale (Sethi et al., 2020). Moving forward, there is a need to expand our knowledge about the carbon metabolism in diatoms, including the localisation and functionality of their enzymes (Sethi et al., 2020).

industrial exhaust gases into inorganic carbon (Arun et al., 2020; Wang et al., 2008), thus avoiding the cost of pre-treatment and CO_2 separation (Farrelly et al., 2013; Olaizola, 2003). Because of these advantages, microalgae are recognised as offering one of the most effective, environmentally friendly, economically feasible and sustainable approaches to carbon sequestration (Alami et al., 2021; Basu et al., 2014; Moreira & Pires, 2016; Quiroz Arita et al., 2016).

Still, microalgae do have relatively low photosynthetic capacity, which remains one of the most critical hurdles in moving towards scalable solutions, in addition to high costs associated with phototrophic cultivation, including cost of operations, infrastructure, maintenance, mass production and so forth. Encouragingly, studies have identified over 300 candidate photosynthesis genes in algae that can potentially be targeted through genetic engineering (Li, X. et al., 2019). The next subsections will address some of the attempts at enhancing photosynthetic carbon sequestration in microalgae (Barati et al., 2021; Grama et al., 2022). Note, however, that genetic engineering still remains challenging because the algal cell wall act as a barrier to vector delivery and due to high degrees of silencing, among other things (Jeong Br et al., 2002; Kim et al., 2015; Puchta & Fauser, 2013; Wu-Scharf et al., 2000).[11]

4.3.1.1. Engineering the Calvin cycle

Several attempts at engineering the Calvin cycle in microalgae have been carried out. For instance, Wei et al. (2017) enhanced the photosynthetic productivity in Nannochloropsis oceanica by overexpressing native Rubisco activase, which helps maintain Rubisco in its active configuration. The authors argued that the work “expands the reservoir of potential photosynthetic gene targets for plant biotechnology and provides a basis for constructing advanced microalgal cell factories for carbon sequestration and biofuel production” (p. 366). In a later study by Wei et al. (2019), they knocked down cytosolic CA in N. oceanica which resulted in ~45%, ~30% and ~40% elevation of photosynthetic oxygen evolution rate, growth rate and biomass accumulation rate under high carbon conditions, respectively. Another target for genetic transformation of the Calvin cycle is SBPase, which exerts strong metabolic control over RuBP regeneration at light saturation (Fang et al., 2012; Hammel et al., 2020). For instance, Fang et al. (2012) demonstrated that the overexpression of SBPase from Chlamydomonas improved the photosynthetic activity in Dunaliella bardawil.

Overexpression of aldolase, which also plays an important role in controlling the rate of RuBP regeneration (Iwaki et al., 1991), has also been found to increase the photosynthetic efficiency of microalgae (Fang et al., 2012; Ma et al., 2007; Ogawa et al., 2015; Work et al., 2012). For instance, Yang et al. (2017) improved the photosynthetic capacity of Chlorella vulgaris 1.2-fold by introducing FBPA from cyanobacteria (also see, e.g., Ogawa et al., 2015). The

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[11] However, digestion of the cell wall and preassembled Cas9 protein-gRNA ribonucleoproteins that do not require vector constructs appear to be promising approaches to overcoming the challenge of delivery.

authors assert that “aldolase is probably considered to be one of the most promising candidate targets for engineering to increase the photosynthetic CO_2 fixation” (p. 2). Another promising target is the Ci accumulation 5 regulator (Cia5) gene, which appears to be a master regulator of algal CCM activity (Asadian et al., 2022; Fukuzawa et al., 2001; Xiang et al., 2001). Finally, Naduthodi et al. (2021) note how the development of “techniques to assemble the red alga RuBisCO in microalgae could be an interesting approach towards enhancing CO_2 fixation” (p. 1024), owing to its high CO_2/O_2 specificity factor.

4.3.1.2. Reducing non-photochemical quenching, enhancing light absorption and engineering the electron transport chain

Algae lose absorbed solar energy through the process of non-photochemical quenching (NPQ), which is influenced by the lag in the adaptation of photosystem antenna sizes to light conditions.[12] Reducing the antenna size by genetic engineering has been explored as a strategy to reduce NPQ and improve photosynthetic efficiency (Beckmann et al., 2009; Cazzaniga et al., 2014; Friedland et al., 2019; Kirst et al., 2012; Masuda et al., 2003; Mussgnug et al., 2007; Naduthodi et al., 2021; Negi et al., 2020; Perrine et al., 2012; Verruto et al., 2018). Furthermore, the photosystem of plants and microalgae absorb light in the visible range (400-700 nm), meaning that only 50% of the available solar radiation is utilised (Blankenship et al., 2011). Thus, another approach is to introduce photosystems with higher light-harvesting efficiency or wider absorption spectrum (e.g., the infrared) (Gimpel et al., 2016), such as from bacteria (Vinyard et al., 2014).

Besides introducing novel photosystem complexes, the absorption range can be increased by introducing biosynthetic pathways for non-native pigments (Naduthodi et al., 2021). For instance, Koh et al. (2019; 2020) introduced the chlorophyllide a oxygenase gene from C. reinhardtii into N. salina to produce chlorophyll b, which is foreign to N. salina. While the purpose of the research was to increase cell number, cell dry weight and total lipid content, the results demonstrated the possibility of expressing non-native pigments to increase photosynthetic efficiency in microalgae. Naduthodi et al. (2021) identify the recently discovered chlorophyll f synthase, which produces the far-red light-absorbing chlorophyll f, as an interesting candidate gene (see, e.g., Trinugroho et al., 2020). It may also be possible to increase the light spectrum accessible to microalgae by expressing UV-absorbing pigments from Antarctic plants (Naduthodi et al., 2021; Post & Larkum, 1993). Finally, to

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[12] The photosystems are found in the thylakoid membranes (organelles within the chloroplasts in which the light-dependent reactions of photosynthesis take place) and are responsible for absorbing and transferring light energy (Yahia et al., 2019). The photosystems are composed of two basic operational units: the antenna complex and the reaction centre. The former consists of hundreds of pigment molecules that capture photons and transfer the light energy to the latter, which contains chlorophyll. When the chlorophyll becomes excited, electron transfer is initiated through the ETC (Yahia et al., 2019). We distinguish between photosystem I (PSI) and II (PSII).

improve ETC reactions, rate-limiting protein complexes in the ETC could be replaced with faster variants to improve the electron flow and reduce NPQ (Naduthodi et al., 2021; Saif Hasan & Cramer, 2012).

4.3.2. Macroalgae

A significant proportion of the net primary productivity of macroalgae (seaweed) is exported and sequestered directly to the deep ocean as dislodged seaweed tissue (Gallagher et al., 2022). Indirect measures indicate that macroalgae can sequester roughly around 173 TgC yr^{-1} globally (with a range between 61 and 268 TgC yr^{-1}) (Krause-Jensen & Duarte, 2016). Interest in macroalgae has been growing in recent years, mostly with regards to their use as a sustainable bioenergy feedstock or with respect to ocean afforestation (Chung et al., 2011; Laurens et al., 2020). However, genetic transformation of macroalgae has been lagging (Lin & Qin, 2014; Mikami, 2014; Qin et al., 2012; Robinson et al., 2013; but do see, e.g., Blomme et al., 2020). This partly owes to their complex morphology, sexual reproduction and life histories, as well as a lack of macroalgal functional genomics (Gupta et al., 2017). Moreover, there are reasons to question the amount of carbon that can be sequestered using macroalgae (in fact, seaweed farming may turn out to become a net source of CO_2) and the practicalities and economic and ecological implications of large-scale cultivation (Bach et al., 2021; Boyd et al., 2022; Gallagher et al., 2022; NASEM, 2021).

4.4. Fungi

Fungi, a group of heterotrophic eukaryotes, play a key role in both the marine and terrestrial carbon cycles (Malyan et al., 2019; Orsi et al., 2022; Pawłowska et al., 2019; Sellappan et al., 2022). Whereas several species of fungi are decomposers, thus releasing CO_2 to the atmosphere, other types of fungi contribute significantly to the formation and stabilisation of soil organic matter and have been found to store 26 times more carbon than bacteria (Six et al., 2006). For instance, mycorrhizal fungi, which form symbiotic relationships with the roots of most plants, help sequester carbon in the soil via several mechanisms (Averill & Hawkes, 2016; Clemmensen et al., 2013; Jastrow et al., 2007; Sellappan et al., 2022; Treseder & Holden, 2013). Among others, their cell walls are made up of complex and durable molecules such as melanin and chitin, which render fungal biomass and by-products recalcitrant to degradation (Guggenberger et al., 1999; Holland & Coleman, 1987). Additionally, the hyphae of mycorrhizal fungi and their secretions (including glomalin, which is an insoluble glue-like substance) also help stabilise macroaggregates in the soil (Jastrow et al., 2007). Ahmed et al. (2019) argue that glomalin “is the main factor that influences the carbon sequestration and storage in soil, either directly or indirectly by influencing other carbon sequestration factors” (p. 10). Consequently, some fungi are considered promising candidates for microbial inoculants to increase organic carbon in soils (Ahmed et al., 2019).[13]

Still, "the exact carbon sequential potential of mycorrhizal fungi still remains to be estimated" (Malyan et al., 2019, p. 287), and the mechanisms by which fungi sequester carbon are yet to be fully understood. Additionally, genetic engineering of filamentous fungi (such as mycorrhizae) has been challenging due to their more complex genetic background. However, while some technical hurdles remain (Alberti et al., 2020; Liao et al., 2021; Lichius et al., 2020; Song et al., 2019), the advent of CRISPR-Cas is changing the landscape of molecular breeding in filamentous fungi (Cho et al., 2014; Deng et al., 2017; Leisen et al., 2020; Nagy et al., 2017; Schuster & Kahmann, 2019; Song et al., 2019; Ullah et al., 2020; van Leeuwe et al., 2019; Wang & Coleman, 2019; Zou et al., 2021).[14] Still, we were unable to identify any studies applying biotechnology to enhance the carbon sequestration capacity of filamentous fungi. Thus, this remains an underexplored and intriguing field of research.

Yeast, in turn, are unicellular and heterotrophic eukaryotes that have been used as cellular factories for centuries, thanks to their easy culturing, rapid growth and readiness to genetic transformation. During the last few years, the CRISPR system has become widely applied in yeast (DiCarlo et al., 2013; Fraczek et al., 2018; Liao et al., 2021; Yang & Blenner, 2020), also for metabolic engineering (Gassler et al., 2019; Peña et al., 2018; Prielhofer et al., 2017; Weninger et al., 2016). While most of these studies have been carried out with the intention of improving food and quality traits, producing metabolites and other value-added compounds and fighting pathogenic fungi (e.g., in plants), could it be possible to genetically engineer yeast to function as cellular factories for carbon fixation?

In a study published in Nature, Gassler et al. (2020) used synthetic biology and gene editing to transform the heterotrophic yeast Pichia pastoris into an autotroph that grows on CO_2. This was achieved by engineering the peroxisomal methanol-assimilation pathway of P. pastoris into a CO_2-fixation pathway resembling the Calvin cycle. The authors argue that "[t]his engineered P. pastoris strain may promote sustainability by sequestering the greenhouse gas CO_2, and by avoiding consumption of an organic feedstock with alternative uses in food production" (p. 210).

4.5. Higher plants

While algal and bacterial, and potentially also archaeal and mycorrhizal, biosequestration systems offer advantages over plants, plant-based systems can be more rapidly deployed and remain the most well-researched (Giddings et al., 2020), with well-established genetic transformation systems in several species (Jansson et

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[13] Mycorrhizal fungi have also been tested for CH4 capture and studies indicate "an overlooked, potentially large role for fungi and their soil necromass in capturing and reducing CH4 emissions from soils in nature" (Liew & Schilling, 2020, p. 1467).

[14] We do not address macrofungi as we consider these to be of less relevance to biosequestration.

al., 2021).[15] Next, we address several approaches to enhanced biosequestration in plants: (i) improving the Calvin cycle; (ii) bypassing photorespiration; (iii) engineering C_4 photosynthesis into C_3 plants; (iv) accelerating recovery from photoprotection; (v) engineering aquaporins; (vi) increasing soil carbon sequestration; (vii) modifying canopy structure; and (viii) enhancing trees as carbon sinks.

4.5.1. Improving the Calvin cycle

Several modelling studies and transgenic experiments have demonstrated that overexpression of enzymes in the Calvin cycle, including Rubisco, can increase the photosynthetic rate in plants (e.g., Simkin, 2019; Simkin et al., 2019; Whitney et al., 2015; Zhu et al., 2007; Zhu et al., 2010). For instance, Cai et al. (2014) developed a mutant version of Rubisco, which resulted in an 85% increase in carboxylation activity and 45% increase in catalytic efficiency towards CO_2. Another approach includes replacing the native Rubisco enzyme with a variant from bacteria or algae that exhibit desirable properties, such as higher specificity towards CO_2 (Conlan & Whitney, 2018; Long et al., 2016; Zhu, X.-G. et al., 2004). Introduced alongside other components of bacterial or algal CCM (e.g., pyrenoids, carboxysomes or bicarbonate transporters), such approaches can help enhance photosynthetic carbon assimilation in higher plants (Atkinson et al., 2017; Fang et al., 2021; Hanson et al., 2016; Price et al., 2010; Price et al., 2012; Rae et al., 2017; Rolland et al., 2016).

For example, Lin et al. (2014) transformed tobacco plants to express Rubisco from the cyanobacterium S. elongatus PCC7942, which resulted in higher rates of CO_2 fixation. Long et al. (2018) used synthetic biology to construct a simplified synthetic carboxysome similar to the one found in the cyanobacterium Cyanobium marinum, which was subsequently introduced into the chloroplast of tobacco (also see, e.g., Long et al., 2016; Price et al., 2010; Rae et al., 2017). Long et al. (2018) considered their study “a critical and complex engineering milestone towards the longer-term goal of attaining a functional chloroplastic CCM in C_3 crop plants” (p. 6). Studies have also demonstrated that transgene expression of bicarbonate transporters from cyanobacteria (such as ictB) can enhance photosynthesis and growth in plants by reducing the oxygenation reaction of Rubisco (Hay, 2012; Hay et al., 2017; Lieman-Hurwitz et al., 2003; Lieman-Hurwitz et al., 2005; Price et al., 2010; Yang et al., 2008).

Other central proteins in the Calvin cycle, such as SBPase and FBPA, have also been genetically engineered (Ding et al., 2016; Driever et al., 2017; Lefebvre et al., 2005). Busch and Miller (2022) report that overexpression of these proteins resulted in increased carbon fixation in Arabidopsis thaliana (also see, e.g., Rosenthal et al., 2011; Simkin et al., 2015; Simkin et al., 2017). Alternatively, foreign SBPase, such as from cyanobacteria, has also been expressed in the chloroplast of higher plants to enhance photosynthetic carbon assimilation (Miyagawa et al., 2001; Tamoi et al.,

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[15] In a report by the McKinsey Global Institute, however, it is argued that while plants genetically engineered to sequester CO2 show promise in the laboratory, commercial viability and adoption by farmers and other end-users are further away in the future (Chui et al., 2020).

2006). Chida et al. (2007), in turn, achieved a 1.3-fold increase in the CO_2 fixation capacity in A. thaliana by expressing cytochrome C6 from algae. Cytochrome C6 is an electron carrier present in all microalgae that has been evolutionarily eliminated from the chloroplast of higher plants (replaced by plastocyanin). Similarly, López-Calcagno et al. (2020) transformed tobacco to express both algal cytochrome C6 and the cyanobacterial FBP/SBPase, which led to a notable increase in photosynthetic carbon assimilation.

4.5.2. Bypassing photorespiration

One way of increasing carbon assimilation is by bypassing the photorespiratory pathway (Peterhansel et al., 2013a; Xin et al., 2014), although the effectiveness of such approaches will depend on the complex regulation between photorespiration and other metabolic pathways (Ogren, 1984; Peterhansel et al., 2013b; Somerville & Ogren, 1982; Xin et al., 2014).[16] Photorespiratory bypass can be achieved in different ways, such as by modulating enzymes within the Calvin cycle and photorespiration, as addressed in the previous section (e.g., overexpression of SBPase). Additionally, naturally occurring and more efficient photorespiration routes and synthetic photorespiratory bypasses that do not release CO_2 can be introduced (Bar-Even, 2018).

As an example of the former, Kebeish et al. (2007) genetically modified A. thaliana to express the glycolate catabolic pathway found in E. coli, which helped reduce photorespiration (for similar studies, see e.g., Carvalho et al., 2011; Dalal et al., 2015). The authors argue that “[d]iverting chloroplastic glycolate from photorespiration may improve the productivity of crops with C_3 photosynthesis” (p. 593). As an example of the latter, South et al. (2019) used synthetic biology to engineer more efficient photorespiratory pathways in tobacco (also see, e.g., Maurino, 2019; South & Ort, 2017). Roell et al. (2021) recently introduced a synthetic bypass into A. thaliana, which was based on the β-hydroxyaspartate cycle present in marine proteobacteria. The authors contended that “our proof-of-principle study demonstrates an approach to turn a photorespiratory bypass into a carbon concentrating mechanism by synergistically coupling photorespiration and C4 metabolism” (p. 2).

4.5.3. Engineering C4 photosynthesis into C3 plants[17]

Three different types of photosynthesis exist in higher plants: C_3, C_4 and CAM (Packer, 2009; Poschenrieder et al., 2018).[18] C_3 is the most common, albeit least efficient and is found in several economically important crops such as wheat, rice and soybean. C_4 is found in only around 3% of land species, including maize, sorghum and sugarcane (Sage et al., 1999), and evolved as an adaptation to low

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[16] Some evidence suggests that reducing photorespiration may not necessarily have beneficial effects (Betti et al., 2016).

[17] Genes from halophytes, i.e., salt-tolerant plants, can also be transferred to C3 plants to improve carbon assimilation and stress tolerance (Yadav & Mishra, 2020).

[18] The names C3 and C4 refer to the number of carbon atoms in the compounds produced by photosynthesis (Jansson et al., 2010).

levels of O_2 in hot, arid regions (Osborne & Sack, 2012; Sage, 2004). In contrast to C_3 plants, in which Rubisco operates at around 25% of the maximum carboxylation rate (Maier et al., 2012), C_4 photosynthesis "allows Rubisco to operate closer to its maximal carboxylation rate, reducing the oxygenation reaction and thereby reducing carbon losses caused by photorespiration" (Raines, 2006, p. 334).

Thus, conferring some of the efficiency advantages from C_4 to C_3 plants is a major area of research (Covshoff & Hibberd, 2012; Edwards et al., 2001; Giddings et al., 2020; Leegood, 2002; Leegood, 2013; Li et al., 2017; Schuler et al., 2016; von Caemmerer et al., 2012; Whitney et al., 2011; Yadav & Mishra, 2020).[19] This can be achieved by introducing C_4 genes into C_3 plants (Yadav & Mishra, 2019), and/or by knocking out genes that suppress the C_4 cycle in C_3 plants (Patel & Mishra, 2019; Schuler et al., 2016). Overexpression of essential C_4 photosynthetic genes such as PEPC, PPDK and NADP-ME have been shown to enhance photosynthesis in tobacco (Laporte et al., 2002; Müller et al., 2018), potato (Häusler et al., 2001; Ishimaru et al., 1998), rice (Bandyopadhyay et al., 2007; Gu et al., 2013; Shen et al., 2015; Taniguchi et al., 2008) and wheat (Kershanskaya & Teixeira da Silva, 2010; Peng et al., 2018).

However, due to anatomical differences between C_3 and C_4 plants (the latter exhibit so-called Kranz anatomy), it is not only necessary to include C_4 genes, but indeed finetune the biochemistry and anatomy of the C_3 plants (von Caemmerer et al., 2012). As explained by Schuler et al. (2016): "in the age of synthetic biology, this still remains a monumental task, partially because the C_4 carbon-concentrating biochemical cycle spans two cell types and thus requires specialised anatomy" (p. 51). It is also important to note that C_4 genes may have negative genetic trade-offs with other economically important traits, which need to be mapped (Driever & Kromdijk, 2013). Thus, Cui (2021) argues that, while "[m]uch effort has been taken in the past to introduce the C4 mechanism into C3 plants, (…) none of these attempts has met with success" (p. 1).

4.5.4. Accelerating recovery from photoprotection

Plants have evolved several mechanisms, including NPQ (see section 4.3.1.2), to protect against excess sunlight and excessive heat that can otherwise cause photooxidative damage (particularly of PSII, see footnote 12), in which the photosynthetic machinery is turned off (Li et al., 2009). However, there is considerable lag in restoring photosynthesis. Thus, by accelerating the recovery time from photoprotection, photosynthetic CO_2 fixation can be enhanced (Kromdijk et al., 2016; Zhu, X. G. et al., 2004). This was successfully achieved by Kromdijk et al. (2016) in tobacco through transgenic expression of three genes from A. thaliana. Building on the work by Kromdijk et al. (2016), De Souza et al. (2022) recently published an article where they improved photosynthesis and yield in soybean by

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[19] The introduction of CAM, which allows nocturnal CO2 uptake, into C3 species have received less research attention than C4 engineering of C3 plants and is mostly considered with respect to the ability to increase water-use efficiency (Borland et al., 2014; Yang et al., 2015).

accelerating recovery from photoprotection through overexpression of three genes that encode proteins of the xanthophyll cycle, which is involved in the photoprotection of plants. Li et al. (2020), in turn, demonstrated that expression of the GOLDEN2-LIKE gene from maize, which is an important transcription factor that activates several photosynthesis-related proteins, reduced photoinhibition and improved photosynthesis in rice.[20]

Plants have also evolved repair mechanisms to prevent accumulation of damaged PSII. Surprisingly, when Chen et al. (2020) developed transgenic Arabidopsis plants expressing the psbA gene, which encodes a subunit of a protein involved in PSII repair, they found that this enhanced net CO_2 assimilation rates. The authors contend that the "findings represent a breakthrough in bioengineering plants to achieve efficient photosynthesis and increase crop productivity under normal and heat-stress conditions" (p. 570).

4.5.5. Engineering aquaporins

Aquaporins are water channel proteins involved in the transportation of, among others, water and CO_2 across the membranes of thylakoids and chloroplasts, and thus are essential for proper functioning of photosynthesis (Flexas et al., 2006; Gao et al., 2018; Hanba et al., 2004; Kawase et al., 2013; Patel & Mishra, 2021; Sade et al., 2009). Overexpression of genes encoding aquaporins have been suggested as targets to increase the availability of CO_2 and enhance stress tolerance and yield in crops (Ermakova et al., 2021; Shekoofa & Sinclair, 2018; Wang et al., 2017; Wang, X. et al., 2019).

4.5.6. Increasing soil carbon sequestration

In this section, we consider three main ways of increasing carbon sequestration in the soil by plants: (i) changing root architecture; (ii) changing the biochemical composition of roots; and (iii) turning annuals into perennials.

4.5.6.1. Changing root architecture

Several root traits have the potential to enhance carbon accumulation and lifetime in the soil. For instance, by engineering plants with deeper and more extensive root systems, it is possible to store fixed carbon for longer (Busch & Miller, 2022; Giddings et al., 2020; Paustian et al., 2016).[21] However, while several traits associated with root architecture are under genetic control and thus can be targeted using genetic engineering (Ogura et al., 2019; Uga et al., 2011; Uga et al., 2013), such traits are generally found to have low heritability (Chen et al., 2014; Malamy, 2005; Palta & Turner, 2019; Siddique et al., 1990). Moreover, while it is well known that root systems play a key role in soil

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[20] Photoinhibition refers to the process where excess light reduces photosynthetic efficiency.

[21] Breeding for certain root traits can also enable more efficient water and nutrient uptake (Abdolshahi et al., 2015; Lynch, 2013; Manschadi et al., 2006; Zhan et al., 2015; but do see Palta & Turner, 2019).

carbon sequestration, research is still needed to determine which root characteristics are, in fact, important for maximising sequestration and ensuring long-term storage (Jansson et al., 2021). Additionally, there is a lack of efficient methods for observing and quantifying root growth in the field (Waines & Ehdaie, 2007). Finally, potential trade-offs between breeding for traits related to root architecture and, for instance, above-ground biomass need to be evaluated.

Still, several research groups are engineering crops with enhanced soil carbon sequestration, including the Harnessing Plants Initiative at the Salk Institute. Additionally, a research team led by Pamela Ronald at the University of California, Davis, is currently screening thousands of rice strains with beneficial root traits. Once these have been identified, they will use CRISPR-Cas to further optimise the traits. At Stanford, a team led by Jennifer Brophy is designing a series of synthetic genetic circuits that allow them to modify, among others, root structures (Brophy et al., 2022).

4.5.6.2. Changing the biochemical composition of roots

Suberin, sporopollenin and lignin are all complex, recalcitrant compounds that may help increase the carbon content of roots and make roots more resistant to decomposition (Busch & Miller, 2022; Kell, 2012; Lorenz et al., 2007). Thus, by developing roots rich in such compounds, it may be possible to store carbon below ground for longer, with the potential added benefit of improved protection against abiotic and biotic stressors (Busch & Miller, 2022; Schweitzer et al., 2021). Thanks to studies in cork oak, several of the key enzymes involved in the biosynthesis of suberin have been identified (Wunderling et al., 2018). The Harnessing Plants Initiative mentioned above is seeking to increase suberin production in crops, including cover crops (Salk, n.d.).

Sporopollenin, in turn, is found in the outer wall of the spores and pollen grains of land plants and is extremely chemically inert as it helps protect the gametes against environmental stressors (Mackenzie et al., 2015).[22] Recently, Li et al. (2019) determined the molecular structure of pine sporopollenin, which is an important step in the direction of designing new biomimetic polymers with desirable inert properties (Li, F. S. et al., 2019). Researchers from the Whitehead Institute and MIT are currently investigating the possibility of enhancing carbon sequestration by genetically targeting sporopollenin as well as suberin.

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[22] Sporopollenin has been identified in the outer cell wall of some algal species, such as Auxenochlorella protothecoides. Living Carbon is currently genetically engineering microalgae to express higher levels of sporopollenin to increase biomass that can be used for durable carbon removal. In the long term, Living Carbon will expand their sporopollenin project to trees, grasses and other plants.

Finally, lignin is deposited in the secondary cell wall of all vascular plants, where it constitutes a kind of cellular glue that provides rigidity to the cell wall, and it serves key functions in abiotic and biotic stress tolerance as well as water transportation (Frei, 2013). While it has been suggested that lignin plays an important role in carbon cycling in soil (Tuomela et al., 2000; Zech et al., 1997), this is currently being debated in light of research suggesting that lignin-derived compounds have low accumulation in stable carbon pools (Carrington et al., 2012; Gleixner et al., 2002; Kiem & Kögel-Knabner, 2003; Marschner et al., 2008; Thevenot et al., 2010). This may be because lignin does not associate as readily with soil minerals (Thevenot et al., 2010). Thus, the role of lignin in long-term carbon sequestration remains to be fully elucidated.

4.5.6.3. Turning annuals into perennials

Several fruit, nut and forage crops, as well as some vegetable crops, are perennials, meaning that they live longer than one year and can be harvested repeatedly. In contrast, many cereals, oilseeds and legumes are annuals that must be sown each year, which not only disturbs the soil but leaves limited time for root systems to develop, thus contributing to carbon losses. Consequently, perennializing annual crops can help retain carbon in the soil, while also saving farm labour and cost related to replanting (DeHaan et al., 2020). The genetics of these major traits, however, are not well understood (Giddings et al., 2020). Still, while most of this research is at the laboratory or early pilot stage (Mulligan et al., 2020), a strain of perennial rice was commercialised in China in 2018 (Huang et al., 2018).

4.5.7. Modifying canopy structure

Canopy photosynthesis describes the photosynthesis of an entire crop field (the top and bottom layer leaves). In the canopy, the upper layer leaves commonly receive more light than their saturation level, while the lower level leaves are usually limited by available light (Song et al., 2017). Thus, improvement of canopy structure and light distribution inside the canopy has been an active area of research for at least two decades (Burgess et al., 2017; Drewry et al., 2014; Ort et al., 2010; Reynolds et al., 2000; Richards, 2000; Sakamoto et al., 2006; Sakamoto & Matsuoka, 2008; Song et al., 2017; Yamamuro et al., 2000). Ways in which to improve canopy photosynthesis include, most notably, manipulating the angle of the leaf and the leaf nitrogen distribution (Reynolds et al., 2000). More recently, genome editing has been used to change traits related to canopy structure (Fei et al., 2019; Fladung, 2021; Liao et al., 2019; Zhao et al., 2020).

Relatedly, albedo biogeoengineering aims to enhance canopy albedo by selecting for leaf glossiness and/or canopy morphologic traits that maximise solar reflectivity, thus theoretically reducing the temperature of the atmosphere. Ridgwell et al. (2009) quantified that such an approach could result in a summertime cooling of more than 1°C throughout much of central North America and midlatitude Eurasia.

4.5.8. Enhancing trees as carbon sinks

While trees are known to effectively and efficiently sequester CO_2, the rate at which this occurs is limited by C_3 metabolism (Tao et al., 2022). Genetic engineering of trees is challenging due to the complexity of their genomes and long generation times. Still, trees have been genetically modified to have greater growth rate, yield, wood quality and drought and disease resistance, among others (ISAAA, 2017). However, relatively little research and development have been conducted on enhanced carbon capture in trees. There are some notable exceptions, however, including the work by Living Carbon, which has genetically engineered seedlings of the poplar tree to reduce the transportation of glycolate, a by-product of photorespiration, out of chloroplast, along with a shunt pathway to metabolise the retained glycolate back to CO_2 for fixation through the Calvin cycle. In a non-peer-reviewed preprint, Living Carbon reports a 53% increase in the production of above-ground biomass in the best-performing seedlings (Tao et al., 2022).

However, the data were collected when the seedlings were harvested at five months. Thus, whether the trees will be able to store carbon in the long run (e.g., >50 years), as well as whether they will maintain high growth rates and health through their lifetime, remain to be seen. Indeed, DeLisi et al. (2020) argue that “[a] decade or more of research would likely be required just for proof of principle of a tree-based carbon drawdown strategy” (p. 4). The genetically engineered seedlings developed by Living Carbon are currently undergoing a four-year-long field trial in cooperation with Oregon State University, in addition to longer-term field testing together with farmers. Additionally, the company is developing a metal hyper-accumulating trait that slows down the rate of decomposition, thus extending the durability of the stored carbon.

4.6. Other research areas of potential interest

The following research areas currently fall outside the scope of CTRF but may represent potential investment opportunities in the future as they depend on or mimic natural processes.

4.6.1. Ruminant livestock

CH_4 is the second most important anthropogenically emitted GHG, with emissions having more than doubled since pre-industrial times (Wuebbles & Hayhoe, 2002). CH_4 is a potent GHG, with a global warming potential over 25 times that of CO_2 (Gerber et al., 2013).[23] CH_4 is also highly reactive and impacts the chemistry of both the

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[23] However, emissions of methane do not accumulate, and methane has an atmospheric lifetime of around 12 years, while CO2 has an atmospheric lifetime of centuries or even millennia (Cain et al., 2019; Collins et al., 2020; Smith et al., 2021). Accordingly, “even a very moderate reduction of global CH4 emissions at a rate of about 0.3% per year would stabilize warming from CH4 at approximately current levels” (Reisinger et al., 2021, p. 3). This has led some to argue that reducing CH4 emissions is not a necessary part of climate action. However, Reisinger et al. (2021) find “that failure to reduce livestock CH4 emissions would reduce the remaining carbon budget consistent with this temperature goal [limiting warming to 1.5°C] by almost one-quarter“ (p. 11). Additionally, De Haas (2021) argues that “[a] continuous reduction in CH4 intensity through breeding for low(er) emitting cows will help in reaching the targets set at the Paris COP meeting in 2015” (pp. 3-4).

troposphere and stratosphere (de Haas et al., 2017; Eckard et al., 2010; Wuebbles & Hayhoe, 2002). Livestock is the most significant anthropogenic source of methane (O'Mara, 2011), with CH_4 emissions expected to increase as the demand for animal protein grows (Mbow et al., 2019; 2018).[24]

Enteric fermentation is the process by which ruminant livestock (cattle, sheep, bisons, goats, deer and camels) digest fibrous plant materials (McAllister et al., 2015; Owens & Basalan, 2016). Thanks to a complex microbial community, which includes anaerobic bacteria and archaea (including so-called methanogens), protozoa and fungi, hydrogen (H_2) and CO_2 are converted to methane (de Haas et al., 2017).[25] 95% of this methane is belched by the ruminant (Murray et al., 1976). This represents a loss of energy which, in addition to nitrogen loss, is one of the main causes of inefficiency in ruminant production systems (Dijkstra et al., 2013; Johnson & Johnson, 1995).

Individual animal differences in methane production owe to several factors, including grazing behaviour, type of feed, anatomical and physiological differences in the gastrointestinal tract, fermentation conditions and microbial activity (Hegarty et al., 2010; Iqbal et al., 2008). Accordingly, several strategies have been employed to mitigate enteric CH_4 production by ruminants, including feed and feed additives and other nutritional interventions, animal-, soil- and fertiliser management, and vaccines, bacteriocins, phage therapy and probiotics to control methanogens (Eckard et al., 2010; Martin et al., 2010; Ouwerkerk et al., 2011).[26] However, such approaches have often yielded mixed or inconclusive results.

Growing evidence, however, suggests a link between animals genetics and the rumen microbial population (Guan et al., 2008; Pszczola et al., 2018; Wallace et al., 2019), digestive function (Hegarty, 2004), and feed intake and feed efficiency (Arthur et al., 2001; Richardson et al., 1996). Furthermore, studies indicate that, in addition to sizeable genetic variation, the heritability of traits associated with methane emission are within the range necessary for breeding (Breider et al., 2019; Donoghue et al., 2013; Lassen & Løvendahl, 2016; Lassen & Difford, 2020; Manzanilla-Pech et al., 2016; Pinares-Patiño et al., 2013; Pszczola et al., 2017; Zetouni et al., 2018). These findings indicate the possibility of selecting for lower-emitting cows, which comes with the added benefits of being cost-effective, permanent and cumulative (in contrast to other strategies for reducing ruminant emissions) (de Haas et al., 2021;

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[24] There are other agricultural species, such as rice, which emit substantial amounts of CH4. Thus, genetic engineering has been applied to develop lower-emitting rice (e.g., Su et al., 2015).

[25] Research is being conducted on developing biofilters containing bacteria that metabolise methane (see the Lidstrom Lab in the Appendix). Assuming installation at tens of thousands of emission sites, these biofilters could remove a total of 0.3 Gt methane by 2050 (Giddings, 2022).

[26] Efforts are underway to genetically edit plants used as livestock feed to reduce ruminant methane emission. Among others, researchers at Rothamsted have established a proof-of-concept using CRISPR-Cas9 to increase leaf oil content in A. thaliana, which has been shown to increase livestock productivity and suppress enteric methane emissions (Beechey-Gradwell et al., 2022; Bhunia et al., 2022; Winichayakul et al., 2020). Additionally, genome editing of methanogenic archaea has also been suggested to reduce CH4 production from ruminant livestock (de Almeida Camargo & Pereira, 2022; Nayak & Metcalf, 2017).

Hayes et al., 2013; Knapp et al., 2014). Conventional selection experiments in beef cattle and sheep demonstrate a decrease in CH_4 production when selecting for low CH_4 lines (Jonker et al., 2017; Pinares-Patiño et al., 2013).

However, more information is needed about the genetic correlation between traits related to CH_4 production and other economically important traits, such as milk yield, dry matter intake, fertility, health and body conformation (Wall et al., 2010; Weller et al., 2017; Zetouni et al., 2018). Encouragingly, some studies indicate minimal consequences of selection for reduced CH_4 emissions on traits related to reproduction and health (e.g., Lassen & Difford, 2020; López-Paredes et al., 2020). Still, "analyses of larger datasets are needed to confirm or deny the genetic correlation structure of other traits" (de Haas et al., 2021, p. 6).

While CRISPR-Cas has been employed in a wide variety of livestock, most studies focus on disease resistance, product quality and productivity, with a few exploring ways of making livestock more climate-smart (notably by making them more tolerant to heat) (Bellini, 2018; Laible et al., 2021; Nigam & Bhoomika, 2022). Thus, while genome editing to reduce CH_4 emission from ruminant livestock appears to be on the table (Giddings et al., 2020; Morrison, 2021; Osborne, 2019), little peer-reviewed literature has yet to be published on the topic.

4.6.2. Biological nitrate inhibitors and enhanced nitrogen use efficiency

Following CO_2 and CH_4, N_2O is the most potent GHG (Solomon et al., 2007), with a long atmospheric lifetime as well as being an ozone-depleting substance (Ravishankara et al., 2009). In 2012, Park et al. (2012) demonstrated that the "rise in atmospheric nitrous oxide levels is largely the result of an increased reliance on nitrogen-based fertilizers" (p. 261). Additionally, nitrogen-based fertilisers contribute to eutrophication of ground and surface waters and expansion of oxygen-depleted zones in coastal regions (Giddings, 2022). There are several ways in which to reduce nitrogen pollution, such as by genetically enhancing nitrogen-use efficiency in plants (Chen, K.-E. et al., 2020; Lebedev et al., 2021), or replacing chemical fertilisers with biological nitrification inhibitors (BNIs), which are based on "the natural ability of certain plant species to release nitrification inhibitors from their roots that suppress nitrifier activity, thus reducing soil nitrification and N2O emission" (Subbarao et al., 2013, p. 322). It has been estimated that BNIs can eliminate at least 30% of agricultural-related GHG emissions (Giddings, 2022). Another approach includes improved microbial inoculants that enhance nitrogen use efficiency.

4.6.3. Enhanced weathering

When rocks high in silicate, such as olivine, serpentine and basalt, are subject to chemical weathering, the dissolution process acts to bind atmospheric CO_2 in the form of bicarbonate that eventually ends up in the ocean where the carbon can be stored for millennia or longer, either as mineral sediments or dissolved in the water (Meysman & Montserrat, 2017; Moosdorf et al., 2014; OSB & NASEM, 2019). This process takes millions of years. However, by finely grinding silicate rocks and spreading the dust over large surface areas (such as beaches, forests and farmland), it is theoretically possible to increase carbon sequestration by as much as one billion tonnes of CO_2 annually (depending on the type of rock and material comminution technique) (Moosdorf et al., 2014). This is known as enhanced weathering (EW).

EW offers several other potential benefits, including reduction of N_2O and ocean acidification, the latter of which is beneficial for corals reefs and fisheries; remineralisation of the soil, which can support plant growth and reduce soil erosion and the need for fertilisers; it uses by-products of the aggregate and mining industry, which are abundant, accessible and inexpensive; and the technical infrastructure and know-how already exists (Zevenhoven et al., 2011). Among the drawbacks of EW is the presence of heavy metals that can accumulate in the soil (for instance, while olivine can sequester more carbon, it contains more heavy metals compared to basalt); the need for large amounts of rocks and land areas; and the need for substantial amount of energy to crush the rock (Beerling et al., 2018). Power et al. (2014) assert that “the costs of mineral pre-treatment and the energy economics of accelerating carbonation reactions from geological to industrial timescales remain serious obstacles” (p. 400). Moosdorf et al. (2014) further note that “[b]efore enhanced weathering could be applied on large scales, more research is needed to assess weathering rates, potential side effects, social acceptability, and mechanisms of governance” (p. 4809).

Several companies have ventured into EW. The Future Forest Company is currently doing tests in Scotland, employing basalt that is crushed using renewable energy. Un-do and Lithos Carbon also use basalt, which they are spreading on agricultural land areas. The former states that they “are working with climate scientists and carbon agencies to write the first methodology for enhanced weathering. Our model allows us to predict the rate at which carbon sequestration occurs, giving us data that will set the standard for the industry”. Project Vesta, in turn, uses olivine to enhance coastal carbon capture and decrease ocean acidification. They are currently conducting pilot studies in New York to monitor ecological impacts and carbon removal efficiency, with expected accreditation and scale-up to take place in 2023-2030.

Studies further suggest ways in which weathering and carbonation can be accelerated in the presence of microorganisms (Fathollahzadeh et al., 2018; Gadd, 2010; McCutcheon et al., 2016; Ng et al., 2016; Power et al., 2010; Power et al., 2014; Welch et al., 1999). For instance, the bacteria species Acidithiobacillus can potentially support acid leaching and thus enhance carbonate formation (Power et al., 2014). Fathollahzadeh et al. (2018), in turn, found that co-culturing of neutrophilic and acidophilic bacteria enhanced bioleaching of monazite. Studies have also shown that the presence of the fungus Knufia petricola accelerates dissolution of olivine seven times faster due to protons released by the fungus (Gerrits et al., 2021; Pokharel et al., 2019).

Sclarsic (2021) identifies several potential ways of biotechnologically enhancing rock weathering, such as by engineering microbes and fungi to produce silicases, oxalate, acetate and citrate, all of which can help speed up dissolution rates, as well as engineering microbial mechanisms for concentrating and nucleating carbonates to improve carbonate formation (Harrison et al., 2013; Power et al., 2010). However, Sclarsic (2021) notes that "[w]hether applied microbes would last long enough in the soil to meaningfully enhance rock weathering is an open question" (p. 38). Instead, bio-enhanced rock weathering could take place in mines and bioreactors (Sclarsic, 2021). However, despite these biotechnological opportunities, we have been unable to identify any peer-reviewed articles in which biotechnology is applied to EW. Still, Project Vesta reports that they are engineering microbes to sequester carbon by accelerating silicate-carbonate weathering (Giddings, 2022).

4.6.4. Artificial ocean alkalinisation[27]

Somewhat related to EW, artificial ocean alkalinisation (AOA) involves adding natural or artificial alkaline substances (e.g., olivine, lime or calcium hydroxide) to increase ocean pH, which results in enhanced carbon uptake and storage as well as reduced ocean acidification. Some scientists believe that AOA "presents some of the greatest potential in terms of CO_2 sequestration and co-benefits" (Burns & Corbett, 2020, p. 154). However, AOA remains poorly understood and underdeveloped (Burns & Corbett, 2020), and the CO_2 removal potential of AOA varies widely from model to model (Feng et al., 2017; González & Ilyina, 2016; Ilyina et al., 2013; Köhler, 2020; Lenton et al., 2018; Lenton & Vaughan, 2009). In fact, according to modelling conducted by González et al. (2018), rates of regional warming and ocean acidification would increase after termination of large-scale AOA, thus indicating higher environmental risks than previously thought (also see, e.g., Bach et al., 2019).[28]

4.6.5. Cell-free, CO2-fixing enzymatic systems

Researchers recently developed a cell-free, oxygen-insensitive and self-replenishing CO_2-fixing enzymatic system using synthetic biology and opto-sensing (allows monitoring and maintenance of the concentration of each cofactor in the synthetic cycles) (Luo et al., 2022). The aim of the study was to decouple CO_2 fixation from cellular physiology and growth that may otherwise reduce the CO_2 fixation rate, such as oxygen sensitivity. In principle, the rate of CO_2 fixation in in vitro cell-free enzymatic systems is scalable with enzyme concentrations up to physicochemical limitations. The system developed by Luo et al. (2022) consists of a synthetic reductive glyoxylate and pyruvate synthesis cycle and the MCG pathway. They report that they "accomplished sustained operation for 6 hours with a CO_2-fixing rate

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[27] We do not consider ocean iron fertilisation to be a viable solution as the predicted sequestration rates have proven disappointing and the approach is believed to pose significant ecological risks (Burns & Corbett, 2020).

[28] The research consortium RETAKE is currently assessing the potential, feasibility and possible side effects of various forms of marine alkalinity enhancement as a means to reliably and sustainably remove CO2 from the atmosphere.

comparable to or greater than typical CO_2 fixation rates of photosynthetic or lithoautotrophic organisms" (p. 154). However, Luo et al. (2022) note that "in vitro systems need to overcome a few challenges, including enzyme instability, metabolite instability and cofactor regeneration" (p. 154).

4.6.6. Artificial leaves

Researchers at the University of Illinois have developed an electrodialysis-driven artificial leaf that uses less power than a lightbulb to capture 100 times more carbon than other systems, including directly from the air (Prajapati et al., 2022). The artificial leaf works by absorbing atmospheric CO_2 via a dry organic solution to form bicarbonate ions, which migrate across a membrane and are dissolved in a liquid solution to concentrated CO_2.

4.6.7. Hybrid systems

The use of hybrid systems, i.e., a combination of biotic and abiotic components, can help enhance photosynthesis and carbon sequestration (Gleizer et al., 2020). For example, Sahoo et al. (2020) developed a hybrid microbe-metal interface, which consisted of an inorganic, semiconducting light-harvester material and bacteria, which assisted the microorganism in capturing energy from the sun (Sahoo et al., 2020). Su et al. (2020), in turn, were able to enhance CO_2 fixation by developing a nanowire-bacteria hybrid (Su et al., 2020). The start-up Ucaneo aims to capture 0.6 gigatonnes of global CO_2 emissions by 2035 using the world's first cell-free Direct Air Capture technology, leveraging a biocatalytic membrane to capture atmospheric CO_2.

5. Conclusion and way forward

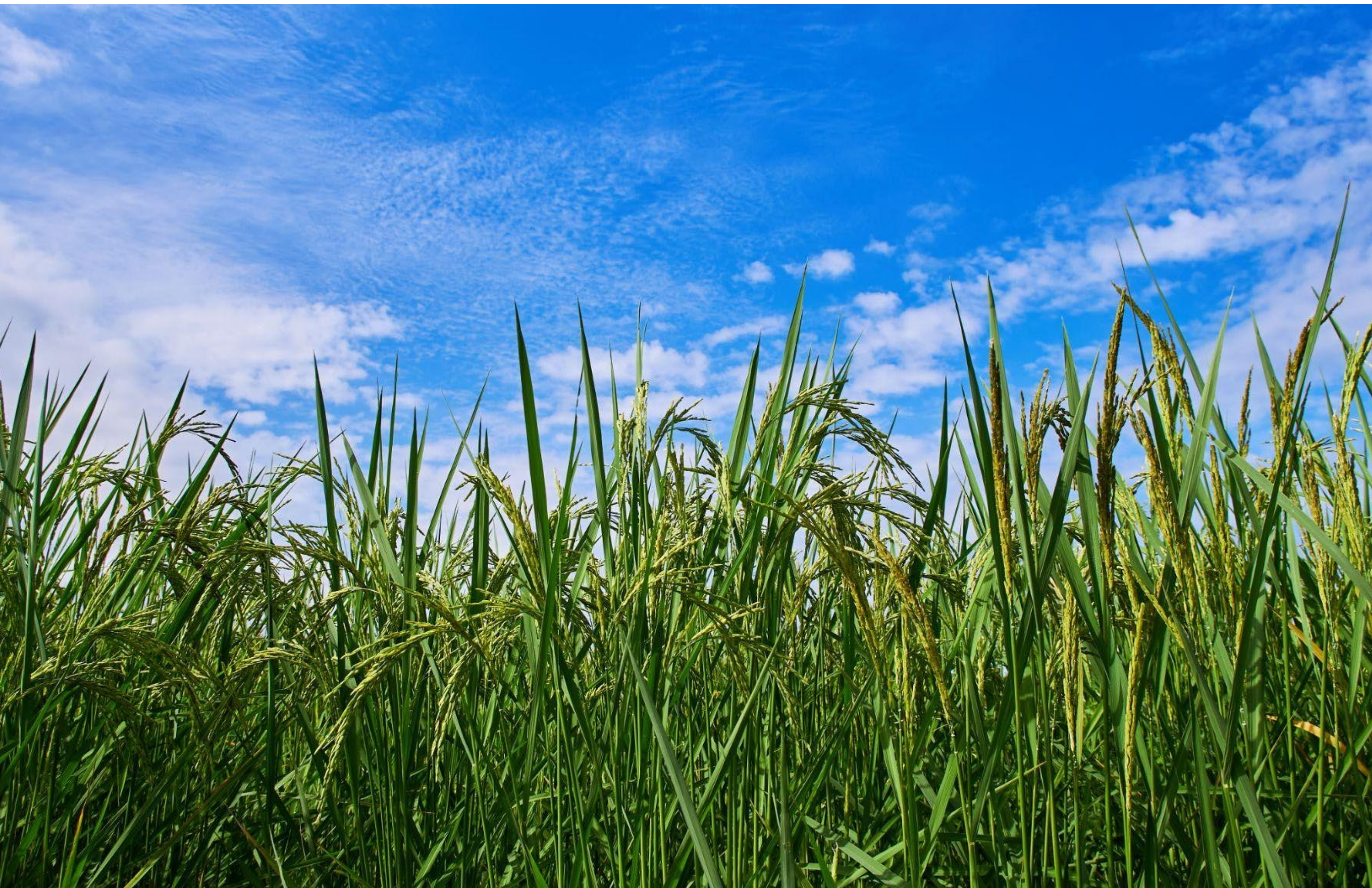
The horizon scan has identified on-going and cutting-edge research on the application of biotechnology and biochemistry to deliver enhanced/scalable natural solutions to carbon sequestration, as well as gaps and opportunities for further or new research. While bacteria and microalgae offer several advantages over higher plants, and should be prioritised in this respect, plants remain the most well-researched and can be more readily deployed. Additionally, research on microalgae and bacteria should expand beyond model species, especially with respect to cyanobacteria and diatoms, which may otherwise limit fundamental discovery and applied research toward commercialisation.

In bacteria, microalgae and higher plants, genetic engineering of Rubisco and other enzymes of the Calvin cycle (e.g., Rubisco activase, carbonic anhydrase, SPBase and FBPA), as well as other components of algal and bacterial CCMs (e.g., carboxysomes, bicarbonate transporters and pyrenoids), are active areas of research that show promise in laboratory settings. Additionally, genetic engineering of other parts of the photosynthetic machinery are being explored, such as accelerating recovery from photoprotection, increasing the absorption spectra of the photosystems and improving the electron flow in the ETC. Additionally, in higher plants, advances are being made with respect to engineering C_4 photosynthesis into C_3 plants, increasing soil carbon sequestration and modifying canopy structure. A potential but largely underexplored genetic target includes aquaporins.

Still, there is a need to improve our understanding of the complex nature of Rubisco and carbon fixation pathways in general, as well as of algal and bacterial CCMs, including so-called master regulator genes (e.g., Cia5). Moreover, knowledge of other types of Rubisco that exhibit particularly attractive properties, such as those present in red algae and archaea, needs to be expanded. In general, research aimed at understanding the biology and carbon sequestration capacity and mechanisms of archaea and mycorrhizal fungi is warranted, as well as establishing efficient genome editing systems. This will be important both in terms of increasing the sequestration potential of archaea and mycorrhizal fungi, as well as enabling transgene expression of relevant genes in other organisms (e.g., chitin and glomalin from fungi and type III Rubisco from archaea). However, returns on investments in archaeal and fungal research will likely not be realised until the long-term, as fundamental research and discovery are needed. Relatedly, biosequestration using trees holds promise, but also necessitates a longer-term perspective due to long generation times and complex genomics, which render genetic engineering more challenging. Macroalgae, in turn, should not necessarily constitute a top investment priority, given lack of functional genomics and efficient transformation systems, as well as contention about the net carbon sequestration capacity.

With respect to the other research areas of potential interest addressed in section 4.6, genetic engineering to reduce methane emission from ruminant livestock (as well as crops such as rice), biological nitrate inhibitors and enhanced nitrogen use efficiency, and enhanced weathering are the most well-researched. Notably, enhanced weathering seems to have caught the interest of several start-up companies. However, while various ideas on how to apply biotechnology to enhanced weathering exist, we have been unable to identify any peer-reviewed studies on the topic, and there also appears to be limited studies published on genome editing to produce lower-emitting ruminants. Artificial ocean alkalinisation is less well-understood and developed, and some modelling studies indicate potentially negative environmental impacts. As such, these should not necessarily be prioritised. In turn, cell-free, CO_2-fixing enzymatic systems, artificial leaves and hybrid systems hold a lot of promise but are the most peripheral to the scope of CTRF.

We would like to draw particular attention to synthetic biology, as it offers the most innovative, daring and next-generation approaches to carbon fixation, which goes beyond relatively simple modifications of endogenous metabolism (Bar-Even, 2018). A lot of exciting research is happening within the realm of synthetic biology in bacteria, microalgae and plants, in which enzymes, biochemical pathways and even entire organisms are reprogrammed to help overcome the many reaction steps and low efficiencies of natural carbon fixation pathways, including photorespiratory bypasses. For instance, in light of findings in which heterotrophic yeast and E. coli were transformed into autotrophs, can we imagine the creation of CO_2-fixing yeast and bacterial factories? Or could we simply decouple metabolism from the cell, as in the case of cell-free, CO_2-fixing enzymatic systems? Still, to fully realise the potential of synthetic biology, we must gain a better understanding of how biochemical pathways perform together within the studied organism, including how synthetic pathways may interfere with endogenous metabolism, side-reactions and dead-end metabolites.



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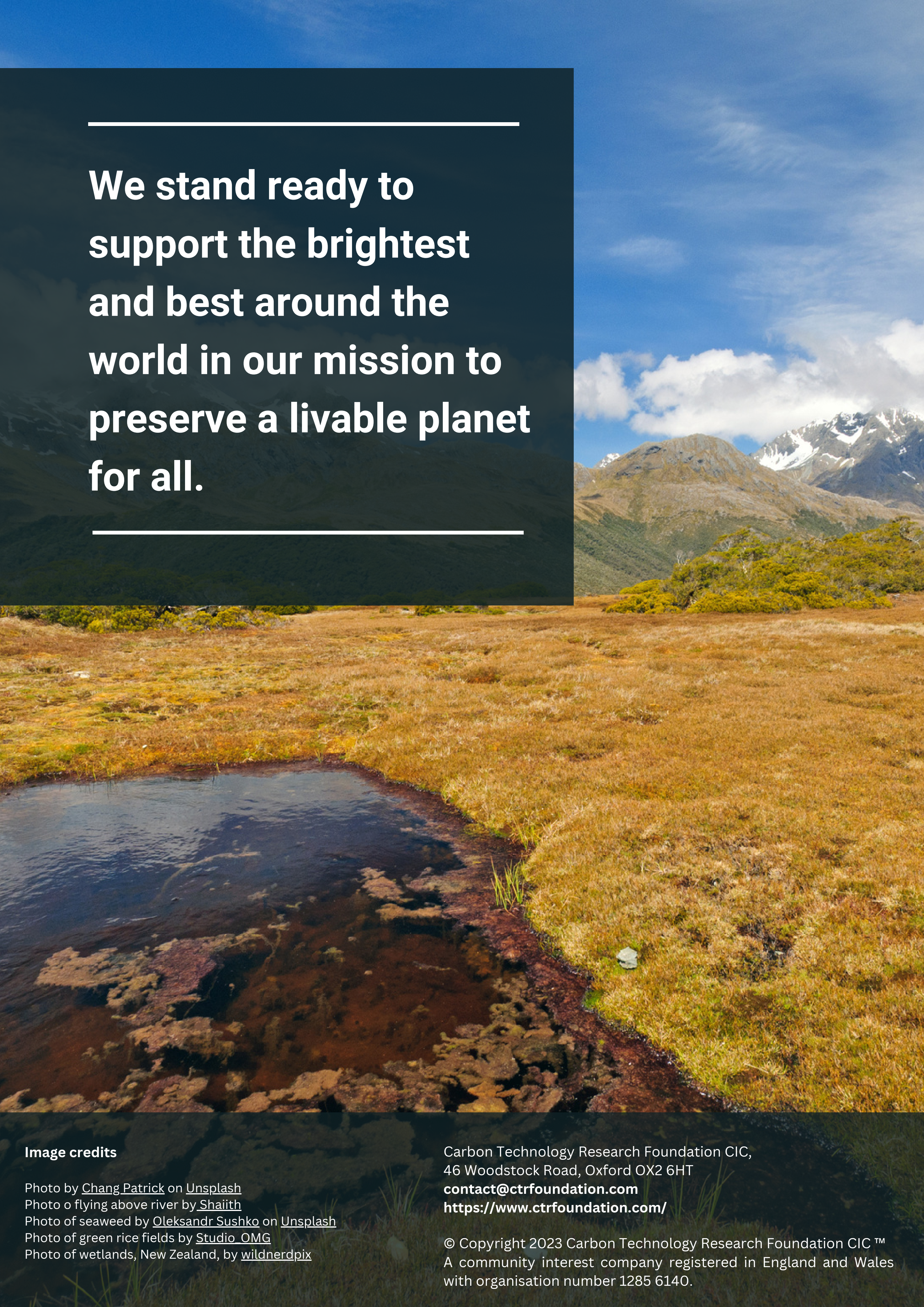

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