Chapter 7
Genome Editing of a Macroalgae with Possible Global Impacts

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Abstract Kelp forests are major marine ecosystems and key sources of biodiversity comparable to tropical forests, as pointed out by Darwin on the Beagle in 1834: *"Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp"*. Despite the key roles supporting marine life, our understanding of their biology lags far behind that of land plants. Kelp mitigates the effects of climate change, sequesters CO_2, reduces eutrophication while providing biomass for food, feed, and materials. Genome editing together with functional genomics can map genetic diversity potentials for temperature tolerance, important since they already face the upper tolerance limits in some regions. This chapter considers the major genome editing prerequisites; the transformation methods for introducing DNA/RNA and annotated genomes for predicting results. Risk assessments are discussed. These uses of genome editing show how widely applicable the techniques can be used from basic science to securing the global environment for our existence.

1 Genome Editing Prerequisites

Disappearance of species due to climate change is causing catastrophic changes to **biodiversity** within our ecosystems, affecting environmental and human health including threatening our survival. Policy makers recognize the need for actions to halt these losses and prevent extreme weather catastrophes, hopefully acting, leading to increased **science**-based activities **to secure our globe's future**. Species loss threatens human survival and quality of life directly by losing space, food/feed, and water resources and indirectly by reducing our health. Actions to halt or reverse planetary warming must involve policy leaders from across the globe and across the globe's environments. In the marine environment, **kelp forests** are highly relevant environments because they represent essential ecosystems supporting high levels of

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biodiversity that cover extensive regions of our coastlines. Kelp species have many uses from **harvested wild** habitats and **aquaculture** production globally, where sugar kelp is **facing extinction** from the warmer ranges of its habitat and arctic populations are challenged by melting ice caps and reduced sea salt content [1, 2]. Losses of kelp forests affects **whole ecosystems** because these environments are habitats for numerous species ranging from microorganisms through photosynthetic plants to a range of marine animals including mammals. Kelp forest disappearance would also be disastrous for the global ecosystem because kelp is highly efficient at sequestering CO_2. **Newly available technologies** provide tools to evaluate genetic diversity and resilience. Uses of kelp have a long history, however fundamental and applied research are underfinanced, and progress lags behind other fields of plant and animal sciences. This situation is improving with the advent of increasing numbers of annotated genome sequences for kelp and the development of associated genomics-enabled tools including **genome editing**. The **aquaculture potential** of kelps in the blue economy should ideally be kept in balance with and isolated from wild populations [3, 4]. In addition, cultivation of local strains as material for rewilding needs to be considered. However, Europe is still missing clear guidelines for macroalgae management ranging from harvesting wild populations, cultivation systems, and breeding strategies and methods including genome editing. The Phycomorph COST action produced a report [5] providing a background for the development of guidelines for good practice in macroalgae exploitation. This chapter presents an updated overview of the **potential of applying genome editing** to secure future benefits from **macroalgae for global health** in the face of climate change.

The CRISPR/Cas9 system, discovered from the adaptive immune system of bacteria, has revolutionized the field of genome editing by providing a simple, efficient, and precise method for targeted gene modification [6].

Genome editing for research and applied purposes still depends on (1) adapted **gene transfer methods** and (2) **annotated genomes** for efficient and safe predictable uses. To secure reliable results and predictable outcomes, independent of positional effects and additional genome variation caused by somaclonal variation due to time in vitro casing mutations, robust gene transfer methods with minimal time in vitro are paramount [7]. This gene transfer is still species dependent in plants. The gene transfer methods are mostly limited to two; particle bombardment and agrobacterial T-DNA transfer. The number, accuracy and annotation quality of plant genome sequences are rapidly increasing since the Arabidopsis genome was released in 2000 [8]. Since the techniques for sequencing whole genomes have improved massively this prerequisite is mostly met both regarding directing the location of gene transfer when using CRISPR/Cas9 and the means to do predictable high quality risk assessment of well characterized modified land-plants. However, some species are lagging behind such as macroalgae where the molecular characterization is just emerging with promising insights to basic biological understanding and correlated applied opportunities [9].

1.1 Genetic Transformation Methods

Gene transfer was first achieved by a range of techniques in the 1970s and 1980s [10]. The first GM bacteria were produced in 1973 [11], human insulin production from GM bacteria was achieved in 1978 and FDA approved 1982 and in 1994 the first GM crop plant was approved (see e.g. ISAAA statistics: https://www.isaaa.org/resources/publications/briefs/05/download/isaaa-brief-05-1997.pdf). Since then, transgenics and resulting plants have been established for most species including many economically important crops, generating over 30 GM crop plants which are approved in over 40 countries including the USA, Canada, Argentina, EU, Norway, UK and Switzerland covering over 190 million hectares.

The two preferred gene transfer routes are still agrobacterium transfection if it is adapted to the plant species and particle bombardment mostly when agrobacterium cannot be applied. Agrobacterium is preferred since it is a "cleaner" method transferring less transgene copies, and into more appropriate genome locations causing less unintended effects. This could be because of natural selection pressure favoring successful integration for Agrobacterium [12]. *Agrobacterium tumefaciens* is a plant pathogenic bacterium commonly found in soil, which has a long history of transferring a portion of its Ti-plasmid, the T-DNA segment into host genomes for infection and survival. In nature the T-DNA allow the introduction of exogenous genes and subsequent expression of the corresponding proteins [13]. This has been adapted for research and gene transfer purposes, by replacing the agrobacterium tumor causing T-DNA and introducing any DNA of interest. The cloned DNA in the T-DNA region is placed into a binary vector before being introduced to the *Agrobacterium* cells. As the plant tissue becomes infected, the T-DNA integrates itself into the host's genome, facilitating the stable expression of new genes [14].

Tobacco and tomato easily incorporate added DNA, while crop plants like cereals took decades of research before predictable transformation frequencies and reproducible results were achieved. Frequencies of regenerated transgenic plants have recently improved considerably for such recalcitrant species. This was partly due to an improved understanding of the cell cycles achieved by the introduction of related meristem developmental regulatory genes. Adding a growth regulating factor and a cofactor, greatly increased regeneration frequencies in wheat, triticale, rice and citrus [15]. CRISPR/Cas9 modifications of plant stem cells and the floral meristems have shown how the cell cycle and stem cells are related to growth and biomass production as well as yield from flowers, fruits and/or seeds [16–19]. As also seen in medical science, stem cell research is central to both basic and applied science, and plant breeding to meet sustainability goals for food production [20]. Further improvement by directing integration or integrating transgene constructs by homologous recombination by CRISPR/Cas9 has greatly improved predictability of targeted genome knock-out or transgene integration, while simultaneously reducing off-target effects by avoiding multiple inserted copies that are common when using particle bombardment for transgenesis.

Risk assessments and approval for commercialization of transgenic crops require characterization of the transgene integration, to secure single copy integration and detect possible unintended positional effects. This minimizes the risk of silencing the transgene as well as other parts of the genome. Somaclonal variation due to mutant effects of the transformation or time in tissue culture, has led to technological improvements that minimize time in culture, reducing unintended effects. Stable transfer depends on integration of transgenes into chromosomes. Some methods such as those to produce maximal amounts of transgene products, might have transgenes transiently active without nuclear integration or integration in organelles such as plastids.

1.2 Annotated Genomes

Genome sequences and analyses keep revolutionizing our understanding of basic biology such as stem cell functions and cell cycle implications, phylogeny, and evolution, providing a robust basis for deeper understanding of basic biological relationships and applications [21, 22]. This is because sequencing techniques have become increasingly accurate, efficient, and accessible. Also, shot-gun sequencing combined with long sequence reads provides reading through long repetitive sequences, such as centromeres, making it possible to identify unique regions for CRISPR/Cas9 specific alterations within any targeted genome part. This allows mapping the unknown parts of genomes, changing them from what some still refer as "junk-DNA" to informed molecular understanding [23]. Updated knowledge shows most of the genome is being transcribed to variable sized RNA molecules involved in gene regulation by RNAi like mechanisms [24, 25].

Specifically, such genomic methods are promising to fill the gaps in our understanding of microtubule directed cell cycle control, division planes, meristem functions and growth. The information generated is of great importance to medicine, food production and global health through allowing informed decisions for optimal sustainable uses of resources. Additionally, genome editing depends on well annotated genomes for risk assessments and applications. Thus, genome sequencing currently developed for new species allows adapting the CRISPR/Cas9 system in macroalgae. The other main limiting factor to applying genome editing to macroalgae are the gene transfer methods. Currently gene transfer is still only established for the green algae *Ulva* and the model brown algae *Ectocarpus*. This is expected to be extended to more species shortly like *S. latissima* from current efforts in Europe and Japan [9, 26].

1.3 Macroalgae Cultivation and Breeding

Macroalgae vegetate coastal and inshore areas and have been exploited by humans since prehistoric times. They are also important for providing a range of ecosystem services. Research is lagging behind land plants possibly partly because they are

positioned between land-based and fishery interests that are mainly further out at sea. They additionally compete with fish aquaculture e.g., the salmon industry, which often has higher financial significance in sea water areas. To secure native macroalgae populations from non-sustainable exploitation, some technology-based aquaculture production is developed for the dominant species such as the brown algae *S japonica* in the Eastern coastal regions of China, Japan, and Australia while *S latissima* occurs in the Atlantic cooler sea regions. Challenges for the exploitation of GM and GE algae are that sea regions interconnect and so cannot be easily contained as land plants. This means that regulations need to be established and agreed internationally.

Genome sequences are important to map genetic potential to survive strong selection pressures. Genome editing would be the best method to do both functional studies linking genes to temperature tolerance, and to enable breeding to meet requirements for sustainable algal strains that meet human needs.

The European Commission is responsible for EU's joint marine resources, but no regulatory frameworks and laws for macroalgae exploitation have been established at neither national nor European level [27]. The Phycomorph EU COST action FA1406 (2015–2019) drafted an extensive 200 page guideline "Pegasus" on sustainable aquaculture of seaweeds [5]. The impact of this on the EU Commission is unknown. An issue raised in several European countries is whether breeding can be applied to macroalgae being cultivated, where current cultivation of seaweed is largely carried out by local populations. Breeding would result in pre-cultivated gametophytes intercrossed in laboratory facilities to generate sporophyte "seedlings" for sea-based aquaculture cultivation of novel strains. So far only minimal breeding has been exploited, by crossing selected parental strains in *S. japonica*, and hardly any for *S. latissima* yet. Breeding might be needed to adapt sugar kelp for survival in warming sea locations; since temperature rise appears to be the main reason that sugar kelp populations have decreased.

2 Genome Editing – Important to Global Health for Mapping and Increasing Biodiversity to Survive Increasing Temperatures

Brown algae (*Phaeophyceae*) are ubiquitous, covering app. 25% of the world's coastlines and about half of them are in the Laminariales and Fucales. Kelps are efficient CO_2 sequesters and very efficient energy producers since they do not require terrestrial space, fresh water or added fertilizer. They therefore represent an important resource in the effort to mitigate the effects of global warming. In addition, kelps are effective purifying systems, removing organic pollutants from marine waters and they can also serve as monitors of the impact of climate change, particularly increased temperatures. Kelp growth is controlled by carbon allocation, primarily influenced by light, temperature, nutrient availability, and their genomic competence. The growth of the endemic Brazilian deep kelp *L. abyssalis*, for

example, is limited to the Austral summers while they tend to decrease in the Austral winter [1]. Consequently, little is known regarding the temporal variations in density and biomass of standing stock (individuals per m^2) for harvesting, commercial applications, or conservation of these species and, consequently, protecting the environment they inhabit. This is addressed in an ongoing Biodiversa+ project with 11 European and 2 Brazilian partners with some additional French and Norwegian associated partners in RESTORESEAS (https://www.restoreseas.net).

Generally, organisms can respond to changes in the environment by acclimation (phenotypic plasticity), or evolution (local adaptation). Local adaptation requires heritable genetic variation for traits that increase tolerance to the new environment, therefore, mapping the genetic variation for temperature tolerance is important to predict effects of rising seawater temperature and to possibly take actions to meet expected future sea water temperatures. Temperature tolerance in kelps has been shown to vary and is linked to genetic variation in the northern hemisphere for *Saccharina latissima* [28, 29] and *Laminaria digitata* [30]. For the cold-water kelps and the Laminaria pockets by the Brazilian and Moroccan coasts, the populations are declining and expected to disappear if they cannot adapt to warming sea regions. Comparative crosses within and between an arctic (Spitsbergen) and a temperate North Sea (Helgoland) population have shown heterosis effects positively affecting increased temperature tolerance in both populations, probably caused by increased heterozygosity. This even occurs if the introduced new alleles are from the northern population with less high temperature tolerance [30]. Previously genome sequencing in *Saccharina japonica* showed that the genetic variation within cultivated types were low compared to the genetic variation in the wild, since all cultivated populations descended from a few collected individuals from the wild [31]. This demonstrates that it is important to generate whole genome mapping/understanding to get accurate understanding of the genetic potential, also to avoid possible inbreeding depression in cultivated macroalgae due to accumulated reduced levels of genetic variation.

Pan genomes help anchoring newly sequenced individuals or closely related species as deeply sequenced and well annotated new accessions are generated, in addition to new genotypes from which to utilize the application of new tools including genome editing. Genome editing can facilitate fundamental functional studies to unravel seaweed biology from single genes to genomes and systems biology, including the kelps' coexisting biota. Annotated genomes will give us better mapping of genetic variation for important traits for survival of wild populations, as well as the productivity of cultivated populations. Mapping genetic variation for elevated temperature tolerance and variation in iodine content would build a solid foundation for selective breeding. The importance of understanding biodiversity was demonstrated when whole genomes of wild and cultivated *S. japonica* were re-sequenced in China, since that revealed existing genetic variation and the potentials from the populations [31].

A high quality annotated brown algae genome sequence is available for *Ectocarpus* (https://bioinformatics.psb.ugent.be/orcae/overview/EctsiV2). A chromosome-scale assembly of the *S. latissima* genome generated by the French

Genomique large-scale sequencing project Phaeoexplorer (https://phaeoexplorer.sb-roscoff.fr/home/) is expected to be released in early 2024 while the *L. ochroleuca* genome is currently being sequenced by the Restoresea project. This will add to the two available genomes: *S. japonica* and *Undaria pinnatifida* [32, 33], for interspecific comparisons. Genes that potentially play key roles in determining resilience to climate change, particularly climate warming, can be identified by combining results of the transcriptomic analyses with geographically correlated polymorphism information from the genomic analysis of population structure. Genes differentially regulated under temperature stress compared with control conditions and that show geographically correlated patterns of polymorphism, can be functionally assessed by CRISPR/Cas9 to select genes that are correlated with temperature tolerance. This approach may allow functionally annotate genes linked to resilience to temperature stress, with applied applications for breeding and survival in increasingly warmer seas [30].

3 Future Perspectives on Macroalgae Socioeconomics: From Ecology to Ecosystem Services

Genome editing is a powerful tool to meet important challenges in plant improvement that we face. GE allows **modelling** to predict the effects of temperature tolerance in wide crosses of kelp populations, to assess the effects of macroalgal growth on ecosystem dynamics [34, 35] and determine the potential for carbon sequestration under different climate scenarios [36]. The impact of climate change can be assessed based on no intervention on current kelp populations, a 2 °C temperature rise and the effects of above 2 °C increase in sea temperature [34, 37].

Growth as an integrative parameter of all physiological processes is controlled by carbon allocation that is primarily influenced by light, temperature, and nutrient availability, and their seasonal variations and interaction. Generally, most Northern Atlantic kelp species exhibit rapid growth from mid-winter to spring or early summer [38]. The pressure from anthropogenic activities on marine ecosystems have been driving severe changes in kelp distribution and abundance globally [39]. The decline in kelps forests can additionally affect a wide range of ecosystem services which are vital to human well-being (e.g., recreational and commercial fisheries activities). Examples of indirect influence on human well-being are: habitat provision for marine species, primary production, climate control, carbon storage, nutrient filtering and coastline protection [40].

Marine macroalgae (seaweed) net primary productivity (NPP) is of major ecological importance in the global carbon balance. Seaweeds form the largest and most productive underwater vegetated habitat on Earth, comparable to the terrestrial Amazon rain forest [36]. Global NPP datasets for 246 seaweed taxa from 429 individual sites distributed on all continents, from the intertidal to 55 m depth, underpin our increasing understanding of the importance of our ocean forests ecosystem

services. Their ecological contribution to annual aerial carbon production as well as to carbon production volumes are estimated to global averages of 656 and 1711 gC m^{-2} $year^{-1}$ in the subtidal and intertidal regions [41]. More than half of the macro algae species are brown algae; mainly Laminariales and Fucales. Brown algae (Phaeophyceae) are ubiquitous, dominating app. 25% of the world's coastlines and representing the major foundation of temperate coastal ecosystems, conservatively estimated to amount to an ecosystem value of $500,000–$1,000,000 per year per km of coastline [42]. The brown algae provide ecosystem services indirectly by increasing coastal production and habitat provision, and directly as fuel, feed, food and specialized products [43]. Well annotated genomes, functional genomics linking gene sequences with functions and application of this in breeding might be crucial for future survival of many macroalgae species and populations. GE is our best tool to answer fundamental questions about their biology, predict possibilities and generate solutions for their many services to the globe's ecology, climate, and more direct human interests.

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