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Genetic Basis and Breeding Strategies for Hybrid Kelp and Cultivated Microalgae

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Abstract The study's key discoveries include the identification of genetic traits that contribute to the heat resilience of kelp through intraspecific outbreeding, and the potential of hybridization to improve kelp traits such as growth and reproductive success under varying environmental conditions. Additionally, advancements in genetic engineering and synthetic biology have shown promise in optimizing microalgae for biotechnological applications, including enhanced biorefinery capabilities. The study also highlights the importance of maintaining genetic diversity and implementing strategic breeding programs to address challenges in kelp cultivation. The findings underscore the potential of genetic improvement and hybridization in developing robust kelp and microalgae cultivars. These strategies can significantly contribute to sustainable mariculture and biotechnological applications, ensuring high productivity and adaptability to changing environmental conditions.

Keywords Hybrid kelp; Cultivated microalgae; Genetic improvement; Breeding strategies; Heat resilience; Synthetic biology; Biorefinery; Mariculture

1 Introduction

Kelp and microalgae are pivotal components of marine ecosystems, serving as primary producers and forming the foundation of aquatic food webs. Kelps, large brown algae in the order Laminariales, are known for their role as ecosystem engineers, creating complex habitats that support a diverse array of marine life (Teagle et al., 2017; Weigel et al., 2022). They contribute significantly to nutrient cycling, energy capture, and provide biogenic coastal defense (Teagle et al., 2017). Microalgae, on the other hand, are microscopic algae that play a crucial role in aquatic ecosystems by producing a wide range of bioactive compounds, including fatty acids, carotenoids, and polysaccharides, which have applications in food and medicine (Sathasivam et al., 2017).

Genetic improvement of aquatic organisms, including kelp and microalgae, is essential for enhancing their productivity, resilience, and economic value. Hybridization and selective breeding can lead to the development of strains with superior traits, such as increased growth rates, disease resistance, and higher nutritional content. For instance, interfamilial hybridization between different kelp species has been shown to produce hybrids with unique morphological and metabolic characteristics, which could be harnessed for commercial and ecological benefits (Murúa et al., 2020). Additionally, understanding the genetic basis of these traits can facilitate the development of targeted breeding strategies to optimize the performance of cultivated species.

The primary objectives of this study are to explore the genetic basis of hybrid kelp and cultivated microalgae, and to develop effective breeding strategies for their improvement. The study investigates the genetic and metabolic characteristics of hybrid kelp species to identify key traits that can be enhanced through breeding. It also analyzes the genetic diversity and metabolic pathways of microalgae to pinpoint potential targets for genetic improvement. Furthermore, it hopes to develop breeding strategies that integrate genetic insights to produce high-yield, resilient, and nutritionally superior strains of kelp and microalgae.

2 Genetic Basis of Hybrid Kelp

2.1 Overview of kelp genetics

Kelp, a type of large brown algae, has a complex genetic structure that is crucial for its adaptation and survival in various marine environments. The genetic improvement of kelp has been a focus in regions like Asia, where heterosis (hybrid vigor) has been utilized to enhance productivity and quality (Goecke et al., 2020). The genetic architecture of kelp involves both sporophyte and gametophyte generations, which alternate in their life cycle, providing unique opportunities for genetic studies and breeding (Zhang et al., 2015).

2.2 Genetic diversity in kelp populations

Genetic diversity is a critical factor for the resilience and adaptability of kelp populations. Studies have shown that wild kelp populations exhibit higher genetic diversity compared to cultivated ones, which is essential for maintaining the ecological balance and potential for future breeding programs. For instance, the genetic diversity of *Saccharina japonica* has been significantly affected by domestication, leading to distinct genetic pools between wild and cultivated populations (Zhang et al., 2017). Additionally, regional genetic differences have been observed, such as between the Gulf of Maine and Southern New England populations of sugar kelp, which are separated by biogeographic barriers (Mao et al., 2020).

2.3 Hybridization techniques in kelp breeding

Hybridization is a key technique in kelp breeding, aimed at combining desirable traits from different species or populations. Techniques such as recurrent mixed hybridization and phenotypic selection have been proposed to enhance kelp breeding (Goecke et al., 2020). In China, hybridization-based breeding pipelines have been optimized to produce robust cultivars by introgressing novel alleles and expressing hybrid vigor (Hu et al., 2023). Intergeneric hybridization has also been explored, although it requires careful molecular confirmation to ensure the persistence and normal development of hybrid sporophytes (Druehl et al., 2005).

2.4 Molecular markers and genomic tools in kelp hybridization

The development of molecular markers and genomic tools has significantly advanced kelp hybridization efforts. High-density SNP linkage maps and RAD sequencing have been employed to identify genetic loci associated with important traits, such as sex determination and morphological characteristics (Zhang et al., 2015). Additionally, genome-wide markers have been used to assess population structure and detect selection signatures, providing valuable insights for selective breeding (Mao et al., 2020). The use of SSR markers has also been instrumental in understanding the genetic impact of domestication on kelp populations (Zhang et al., 2017).

2.5 Case studies on hybrid kelp breeding

Several case studies highlight the success and challenges of hybrid kelp breeding. For example, interfamilial hybridization between *Macrocystis pyrifera* and *Lessonia spicata* has been confirmed through morphological, genotypic, and metabolomic analyses, demonstrating the potential for hybrid vigor in natural populations (Murúa et al., 2020) (Figure 1). Another study on *Laminaria digitata* and *L. pallida* revealed that interspecific hybrids exhibited higher thermal tolerance compared to their parental species, indicating heterosis for thermal resilience (Martins et al., 2019). These case studies underscore the importance of hybridization in enhancing the adaptability and performance of kelp under changing environmental conditions.

3 Breeding Strategies for Hybrid Kelp

3.1 Traditional breeding methods

Traditional breeding methods for kelp involve the selection and recombination of desirable traits through controlled mating and hybridization. This approach has been widely used in Asia, where the genetic improvement of kelp has largely relied on the utilization of heterosis, or hybrid vigor, expressed in certain combinations of parental material, including species hybrids. The process typically involves recurrent mixed hybridization and phenotypic selection within local populations to enhance productivity and product quality (Goecke et al., 2020). However, traditional methods face challenges such as genetic erosion and loss of heterozygosity due to repeated selection and self-crossing (Hu et al., 2023).

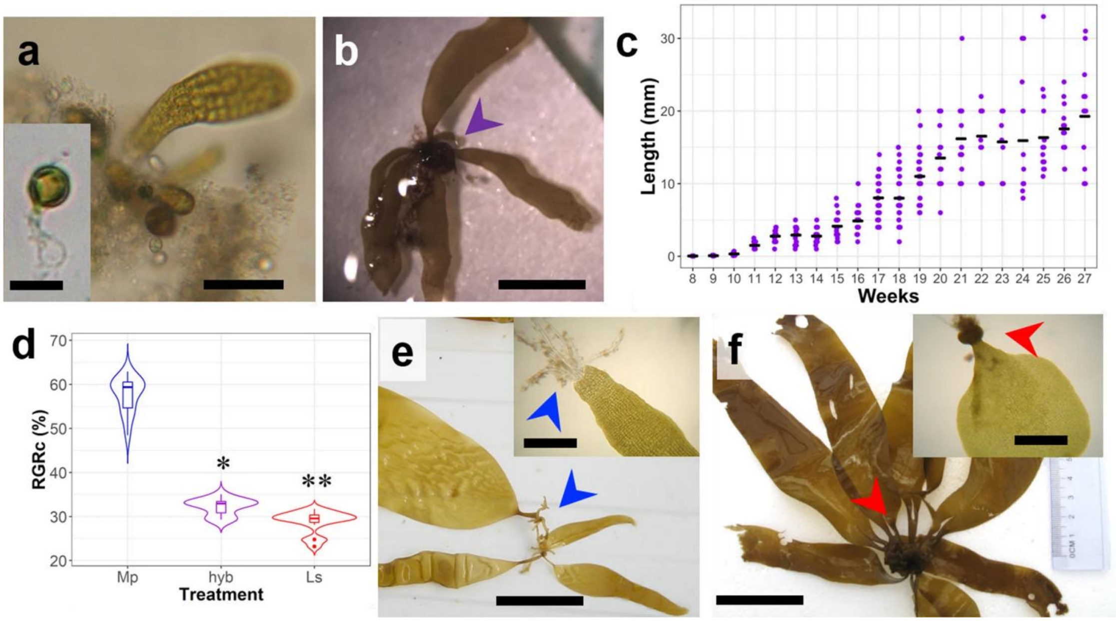

Figure 1 Development of the wild Macrocystis x Lessonia progeny in culture (Adopted from Murúa et al., 2020)

Image caption: (a) Emergence of early embryo from unicellular to few-celled female gametophytes. Scale bar: 14 µm. Inset: Germination pattern of the hybrid spores showing an empty embryospore and a primary cell of the gametophyte. Scale bar 8 µm. (b) Juvenile individual with fused-haptera holdfast (arrowhead). Scale bar: 1 cm. (c) Growth tendency of the hybrid progeny until 27 weeks, time point where they all suddenly died off. Segment = mean. (d) Corrected relative growth rate (RGRc) for the progeny from *M. pyrifera* (Mp), *L. spicata* (Ls) and the field hybrid (hyb). Boxes show median (horizontal bold line) ± 1.5 times the interquartile range (whiskers). Dots represent deemed outliers, and asterisks represent statistical groups after a Tukey's test ($p < 0.05$). (e,f) Morphology of juvenile *M. pyrifera* (e) and *L. spicata* (f) from Mar Brava after 40 weeks, showing their characteristic holdfast morphology (arrowheads). Scale bars: 2.5 cm. Insets: holdfast morphology of the same species at 15 weeks. Scale bars: 350 µm (Adopted from Murúa et al., 2020)

3.2 Marker-assisted selection (MAS) in kelp breeding

Marker-assisted selection (MAS) is a modern breeding technique that uses molecular markers to select for desirable traits, thereby accelerating the breeding process and improving accuracy. In kelp breeding, MAS has been employed to map and introgress genes associated with economically important traits. For instance, in *Saccharina japonica*, SSR markers have been used to construct genetic linkage maps and identify QTLs for traits like blade length and width, facilitating the selection of superior genotypes (Wang et al., 2023). MAS helps in the precise transfer of targeted QTLs, as demonstrated in other crops like cotton, where it has led to the development of cultivars with improved fiber quality (Darmanov et al., 2022).

3.3 Application of genomics and bioinformatics in kelp breeding

The integration of genomics and bioinformatics in kelp breeding represents a significant advancement over traditional methods. Genomic selection (GS) uses genome-wide markers to predict complex phenotypes, thereby accelerating breeding cycles and improving selection accuracy. This approach has been successfully applied in other fields, such as animal and tree breeding, and holds promise for kelp as well (Meuwissen et al., 2016; Grattapaglia et al., 2018). High-throughput genotyping and phenotyping, combined with machine learning and bioinformatics tools, can enhance the prediction models and facilitate the development of robust kelp cultivars (Sandhu et al., 2022). The enrichment of high-quality annotated reference genomes and functional analysis of trait-associated markers further supports the application of genomics in kelp breeding (Hu et al., 2023).

3.4 Challenges and opportunities in hybrid kelp breeding

Hybrid kelp breeding faces several challenges, including the management of germplasm diversity, technological innovations, and regional cooperation. Issues such as genetic erosion, loss of heterozygosity, and inter-cultivar accidental admixing need to be addressed to ensure sustainable breeding practices. However, there are also significant opportunities, such as the establishment of national germplasm repositories, the development of hybridization-based breeding pipelines, and the application of bioengineering strategies to enhance traits like thermal and disease resistance (Hu et al., 2023). The integration of ecological kelp-microbiome interactions and the use of synthetic biology approaches can further improve the adaptability and performance of hybrid kelp cultivars (Hlavová et al., 2015).

4 Genetic Basis of Cultivated Microalgae

4.1 Overview of microalgae genetics

Microalgae are photosynthetic microorganisms with a high degree of genetic diversity, enabling them to adapt to a wide range of environmental conditions. This genetic diversity is crucial for their role in global photosynthesis and CO2 sequestration, making them significant players in environmental sustainability. The genetic makeup of microalgae allows for the production of various primary and secondary metabolites, which have applications in pharmaceuticals, nutraceuticals, and industrial processes (Sreenikethanam et al., 2022).

4.2 Genetic variability in microalgae strains

The genetic variability among microalgae strains is a key factor in their adaptability and productivity. This variability can be harnessed through strain improvement techniques to enhance the yield and robustness of microalgae for industrial applications. Traditional methods such as random mutagenesis have been employed to create stress-tolerant and productive strains without introducing foreign genetic material (Trovão et al., 2022). Additionally, the availability of genome sequences and omics datasets from diverse microalgae species has provided a foundation for targeted genetic improvements (Kumar et al., 2020).

4.3 Genetic engineering approaches in microalgae

Genetic engineering has emerged as a powerful tool to enhance the metabolic capabilities of microalgae. Techniques such as CRISPR/Cas9, RNAi, ZNFs, and TALENs have been used to modify genes involved in lipid metabolism, fatty acid synthesis, and other metabolic pathways to increase the production of desired compounds (Fayyaz et al., 2020; Muñoz et al., 2021). These approaches have led to significant improvements in lipid content and altered fatty acid profiles, making microalgae more viable for biofuel production and other industrial applications (Muñoz et al., 2021). However, the application of these advanced genetic tools remains underutilized compared to other microorganisms (Kumar et al., 2020) (Figure 2).

4.4 Omics technologies in microalgae breeding

Omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, have revolutionized the breeding and genetic engineering of microalgae. These technologies provide comprehensive insights into the genome structure and metabolic pathways of microalgae, enabling the identification of key genes and regulatory networks involved in the production of high-value compounds (Salama et al., 2019; Kuo et al., 2022). Integrated omics approaches have been particularly effective in optimizing microalgal growth and biofuel production under various stress conditions (Salama et al., 2019). The use of multiomics datasets, big data analysis, and machine learning has further enhanced the ability to discover and manipulate traits for improved biorefinery capabilities and wastewater treatment (Kuo et al., 2022).

5 Breeding Strategies for Cultivated Microalgae

5.1 Selective breeding in microalgae

Selective breeding in microalgae involves the identification and propagation of strains with desirable traits. This traditional approach has been used extensively in agriculture and aquaculture to enhance production traits. However, many microalgae species do not possess the sexual characteristics required for traditional breeding, which limits the application of this method. Instead, selective breeding in microalgae often relies on the use of natural variants and mutants generated through chemical and physical mutagenesis (Hlavová et al., 2015).

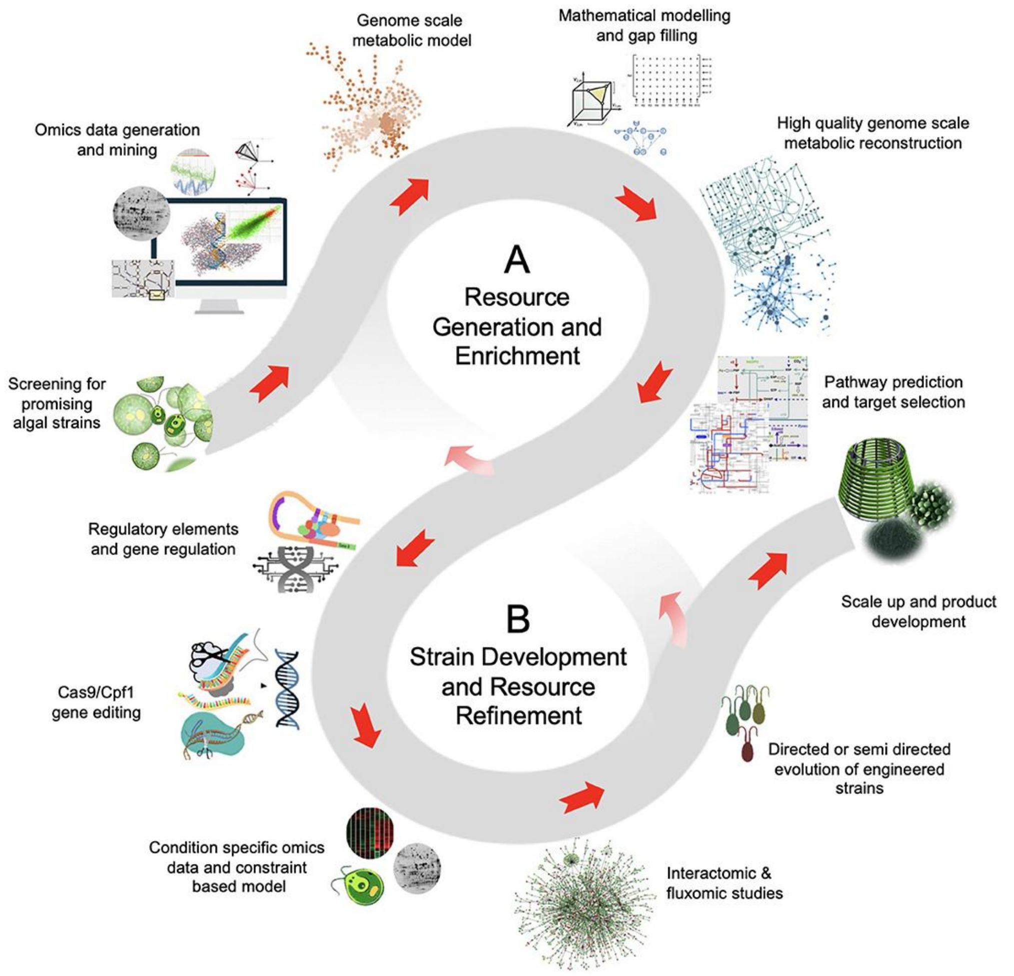

Figure 2 The schematic of data and resource driven strategy for microalgal bioengineering (Adopted from Kumar et al., 2020)

Image caption: (A) Resource generation and enrichment: The high-throughput technologies, intense computation and bioinformatic analysis, and the extensive research interest on microalgae can generate high-quality curated data. The genomic and transcriptomic data of model organisms provides a basic understanding of the biosynthetic pathway. This imperative information is aided by proteomics and metabolomics that offers functional insights for bioproduct discovery in microalgae. Also, the metabolomic data can be implemented to novel microbial isolates with limited genomic and transcriptomic information. (B) Strain development and resource refinement: The leads from metabolic models and the use of state-of-the-art technologies, such as genome-editing and high-throughput variant selection can be used for microalgae strain development. Often the metabolic flux shifts of the mutants implies an organism's evolution to optimize flux rearrangement. The objective of the flux balance shift can be biomass production or enhanced production of desired product. Moreover, the information obtained from fine-tuned modeling and genomic-editing experiments create resource avenues for further discoveries (Adopted from Kumar et al., 2020)

5.2 Genetic modification techniques

Genetic modification techniques have revolutionized the breeding of microalgae by enabling precise alterations to their genomes. These techniques include the use of RNA interference (RNAi), zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and CRISPR/Cas9 systems. These tools allow for the targeted modification of genes to enhance the production of desired metabolites, improve stress resistance, and optimize growth conditions (Ng et al., 2017; Zhang et al., 2019; Fayyaz et al., 2020). Genetic modification has shown promise in increasing biomass yield, carbon dioxide uptake, and the accumulation of high-value compounds (Fayyaz et al., 2020).

5.3 CRISPR-Cas9 and other gene editing tools

The CRISPR-Cas9 system has emerged as the most important genome editing tool due to its high efficiency and precision. This system allows for the targeted knock-in and knock-out of genes, as well as the modification of gene expression through CRISPR interference. The application of CRISPR-Cas9 in microalgae has been extensively studied, with successful examples of gene editing to enhance the production of biofuels, bioactive compounds, and other valuable products (Chen et al., 2019; Gratacap et al., 2019; Zhang et al., 2019). Other gene editing tools, such as ZFNs and TALENs, also play a significant role in microalgae breeding, although they are less commonly used compared to CRISPR-Cas9 (Ng et al., 2017).

5.4 Integration of metabolic engineering in microalgae breeding

Metabolic engineering involves the modification of metabolic pathways to optimize the production of specific compounds. In microalgae, metabolic engineering is often integrated with genetic modification techniques to enhance the yield of biofuels, bioproducts, and other valuable metabolites. This approach includes the overexpression or suppression of key enzymes, the introduction of novel biosynthetic pathways, and the optimization of regulatory networks. The integration of metabolic engineering with advanced gene editing tools has the potential to significantly improve the efficiency and productivity of microalgae-based biorefineries (Fayyaz et al., 2020; Teng et al., 2020).

5.5 Case studies on microalgae breeding for industrial applications

Several case studies highlight the successful application of breeding strategies in microalgae for industrial purposes. For instance, the use of CRISPR-Cas9 to develop thermo-sensitive genic male sterile lines in rice has been adapted to microalgae to enhance hybrid breeding and production efficiency (Zhou et al., 2016). Additionally, the application of artificial intelligence (AI) in conjunction with genetic modification has shown promise in optimizing microalgae cultivation and bioproduct yields (Teng et al., 2020). These case studies demonstrate the potential of advanced breeding strategies to overcome the challenges associated with microalgae production and to unlock new opportunities for industrial applications (Ng et al., 2017; Zhang et al., 2019; Fayyaz et al., 2020; Teng et al., 2020).

6 Comparative Analysis: Kelp vs. Microalgae Breeding

6.1 Genetic complexity and breeding challenges

Kelp and microalgae present distinct genetic complexities and breeding challenges. Kelp breeding has traditionally relied on heterosis and hybridization to improve traits such as productivity and quality. However, challenges such as genetic erosion, loss of heterozygosity, and accidental inter-cultivar admixing have been noted, particularly in regions like China (Hu et al., 2023). Additionally, the genetic diversity in wild kelp populations must be protected against genetic pollution, which can be managed by breeding local populations or developing non-hybridizing cultivars (Goecke et al., 2020).

In contrast, many microalgae species lack the sexual characteristics necessary for traditional breeding, making genetic improvement more challenging. Instead, microalgae are often improved through mutagenesis, which can be achieved using chemical and physical mutagens without creating genetically modified organisms (GMOs) (Hlavová et al., 2015). This approach, while effective, presents its own set of challenges, including the need for high-throughput screening to identify beneficial mutations (Trovão et al., 2022).

6.2 Technological advances and applications

Technological advancements have significantly impacted both kelp and microalgae breeding. For kelp, the development of hybridization-based breeding pipelines and the enrichment of high-quality reference genomes have been proposed to enhance breeding efficiency and cultivar robustness. Additionally, bioengineering strategies, such as priming for thermal and disease resistance, are being explored to meet future climate challenges (Hu et al., 2023).

Microalgae breeding has benefited from advances in genetic engineering and synthetic biology. Techniques such as site-directed mutagenesis and the use of gene editing tools have enabled the creation of tailor-made genotypes with enhanced traits (Trovão et al., 2022). Moreover, synthetic biology approaches are being employed to redesign metabolic pathways for the production of valuable secondary metabolites (Sreenikethanam et al., 2022). These advancements have the potential to accelerate the development of microalgae strains with improved productivity and stress tolerance (Hlavová et al., 2015).

6.3 Sustainability and environmental impact

Both kelp and microalgae offer sustainable solutions for food, feed, and bioenergy production, but their environmental impacts differ. Kelp farming can contribute to coastal ecosystem health by providing habitat and sequestering carbon. However, large-scale cultivation requires careful management to prevent genetic pollution and ensure sustainable practices (Mooney et al., 2018). The establishment of national germplasm repositories and strategic breeding programs can help mitigate these risks and promote sustainable kelp farming (Hu et al., 2023).

Microalgae cultivation is highly efficient in terms of resource use, with the potential to produce high yields of nutritionally complete food and feed products (Torres-Tiji et al., 2020). Additionally, microalgae play a crucial role in CO2 sequestration, contributing to global photosynthesis and reducing greenhouse gas emissions (Sreenikethanam et al., 2022). However, the high production costs associated with microalgae cultivation remain a significant barrier. Advances in strain improvement and high-throughput screening technologies are essential to overcome these challenges and enhance the sustainability of microalgae production (Trovão et al., 2022).

7 Future Prospects and Directions

7.1 Emerging technologies in aquatic breeding

The future of aquatic breeding, particularly for kelp and microalgae, is poised to benefit significantly from emerging technologies. Advances in genetic engineering, such as CRISPR-Cas9, offer precise tools for editing genomes to enhance desirable traits like growth rate, disease resistance, and environmental tolerance (Hlavová et al., 2015). Additionally, the integration of high-throughput sequencing and bioinformatics allows for the detailed mapping of genetic diversity and the identification of key genetic markers associated with beneficial traits (Camus et al., 2018; Hu et al., 2023). These technologies can streamline the breeding process, making it more efficient and targeted. Furthermore, synthetic biology approaches are being explored to create custom-designed microalgae strains that can produce high-value compounds, thereby expanding their biotechnological applications (Hlavová et al., 2015).

7.2 Potential for hybrid breeding programs

Hybrid breeding programs hold significant promise for improving the productivity and resilience of kelp and microalgae. The concept of heterosis, or hybrid vigor, has been successfully applied in kelp breeding to enhance traits such as thermal tolerance and growth rates (Martins et al., 2019; Goecke et al., 2020). For instance, hybridization between different kelp species has resulted in offspring with superior thermal tolerance, which is crucial in the face of climate change (Martins et al., 2019). Similarly, hybrid breeding strategies have been employed to maintain genetic heterozygosity and prevent inbreeding depression, as demonstrated in the development of the Dongfang no.7 kelp variety (Li et al., 2016). These programs can be further optimized by leveraging genetic and phenotypic data to select the best parental combinations, thereby maximizing the benefits of hybrid vigor (Camus et al., 2018; Murúa et al., 2021).

7.3 Policy and regulatory considerations

The expansion of hybrid breeding programs and the use of genetic technologies in aquatic breeding necessitate careful consideration of policy and regulatory frameworks. It is essential to establish guidelines that ensure the safe and sustainable use of genetically modified organisms (GMOs) and hybrids in aquaculture (Hu et al., 2023). Regulatory bodies must address concerns related to genetic pollution, particularly the potential for gene flow between cultivated and wild populations (Mooney et al., 2018). Policies should also promote the establishment of national germplasm repositories to preserve genetic diversity and support breeding programs (Hu et al., 2023). Additionally, there is a need for international cooperation to harmonize regulations and facilitate the exchange of genetic resources and breeding technologies across borders. This collaborative approach can help mitigate risks and maximize the benefits of advanced breeding strategies for global aquaculture (Mooney et al., 2018; Hu et al., 2023).

8 Concluding Remarks

The research on the genetic basis and breeding strategies for hybrid kelp and cultivated microalgae has highlighted several critical aspects. Firstly, the potential of kelp and macroalgae in providing food, feed, bioenergy, and raw materials for various industries is immense, but currently, only a few species are cultivated, primarily in Asia. The development of hybrid cultivars, such as *Saccharina japonica*, has shown promise in improving yield and quality through photoperiodic control and hybrid vigor. Additionally, the genetic improvement of microalgae through mutagenesis and synthetic biology offers significant potential for biotechnological applications. The genetic and phenotypic diversity in natural populations of kelp, such as Macrocystis pyrifera, underscores the importance of selecting appropriate source populations for breeding programs. Moreover, the challenges in kelp breeding in China, including germplasm diversity and management, highlight the need for strategic breeding programs and technological innovations.

The findings from these studies have several implications for aquaculture and biotechnology. The successful breeding and cultivation of hybrid kelp can lead to higher productivity and better quality of farmed products, which is crucial for meeting the growing demand for seaweed-based products. The ability to control the reproductive cycle of hybrid kelp through photoperiodic manipulation can enhance the efficiency of hatchery operations and ensure a steady supply of seedlings. Furthermore, the genetic improvement of microalgae through non-GMO methods can accelerate the development of strains with desirable traits, thereby expanding their use in various biotechnological applications. The preservation of genetic diversity through cryopreservation techniques can support sustainable breeding programs and help mitigate the impacts of climate change on natural populations.

Future research should focus on several key areas to advance the breeding and cultivation of hybrid kelp and microalgae. Firstly, there is a need to develop and optimize breeding protocols for a wider range of kelp species to enhance their cultivation potential in different regions. Investigating the genetic basis of important traits, such as thermal tolerance and disease resistance, can inform the selection of parent strains for hybridization. Additionally, integrating advanced genomic tools and bioinformatics can facilitate the identification of trait-associated markers and the development of DNA-based breeding technologies. Research should also explore the ecological interactions between kelp and their associated microbiomes to develop cultivars with enhanced performance and adaptability. Finally, expanding the use of cryopreservation techniques for the long-term conservation of genetic resources will be crucial for maintaining genetic diversity and supporting future breeding efforts.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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