

Research Insight

Open Access

Epigenetic Regulation in Algae: Implications for Growth, Development, and Stress Response

Zhongxian Zhao, Guoping Chen, Linhua Zhang ✉

Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China

✉ Corresponding author: linhua.zhang@jicat.org

International Journal of Aquaculture, 2024, Vol.14, No.5 doi: [10.5376/ija.2024.14.0026](https://doi.org/10.5376/ija.2024.14.0026)

Received: 15 Aug., 2024

Accepted: 17 Sep., 2024

Published: 21 Oct., 2024

Copyright © 2024 Zhao et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Zhao Z.X., Chen G.P., and Zhang L.H., 2024, Epigenetic regulation in algae: implications for growth, development, and stress response, International Journal of Aquaculture, 14(5): 257-265 (doi: [10.5376/ija.2024.14.0026](https://doi.org/10.5376/ija.2024.14.0026))

Abstract This study provides an overview of the epigenetic mechanisms in algae and the role of non-coding RNAs in gene regulation. It offers an in-depth analysis of how these epigenetic mechanisms regulate the cell cycle, developmental stages, photosynthesis, and metabolism in algae. The study also focuses on the epigenetic regulation of algae in response to environmental stresses such as light, temperature, salinity, nutrient deficiency, and oxidative stress. Comparative studies reveal significant epigenetic variations between freshwater and marine algae, as well as between microalgae and macroalgae, suggesting that these differences may be closely related to their habitats. Case studies further confirm the potential of epigenetic regulation in enhancing stress tolerance in algae and optimizing biofuel production, highlighting the broad prospects of epigenetic mechanisms in algal cultivation and biotechnological applications. This research aims to promote sustainable algal farming practices and provide innovative solutions to address global environmental challenges such as climate change and resource scarcity.

Keywords Epigenetic regulation in algae; Non-coding RNAs; Cell cycle regulation; Environmental stress; Sustainable algal farming

1 Introduction

Epigenetics refers to heritable changes in gene expression that do not involve alterations in the DNA sequence itself. These changes are mediated through various mechanisms, including DNA methylation, histone modifications, chromatin remodeling, and non-coding RNAs. In eukaryotic cells, these epigenetic modifications play a crucial role in regulating gene expression in response to developmental cues and environmental stresses. DNA methylation, one of the most conserved epigenetic mechanisms, involves the addition of methyl groups to DNA, typically at cytosine residues, which can lead to changes in gene expression. Histone modifications, such as methylation, acetylation, and phosphorylation, alter the chromatin structure, thereby influencing gene accessibility and transcriptional activity (Agarwal et al., 2020). These epigenetic changes are often reversible, allowing organisms to adapt dynamically to changing environmental conditions (Wibowo et al., 2016).

Algae, as primary producers in aquatic ecosystems, play a vital role in global carbon cycling and are a potential source of biofuels and other valuable bioproducts. Understanding the epigenetic regulation in algae is crucial for several reasons. Firstly, it can provide insights into how algae respond to abiotic stresses such as changes in temperature, salinity, and nutrient availability, which are critical for their survival and productivity. Secondly, epigenetic modifications can influence the biosynthesis of metabolites, which are important for industrial applications. Thirdly, studying epigenetic mechanisms in algae can contribute to our understanding of evolutionary processes and the adaptation of these organisms to diverse and often extreme environments (Adhikar and Curtis, 2016; Singroha and Sharma, 2019). Given the increasing interest in sustainable and renewable resources, epigenetic research in algae holds significant promise for improving stress tolerance and enhancing biomass production (Akhter et al., 2021; Ferrari et al., 2023).

This study will provide a comprehensive overview of the current understanding of epigenetic regulation in algae, with a focus on its impact on growth, development, and stress responses. It will explore the effects of various epigenetic mechanisms and environmental factors on epigenetic modifications, as well as how these changes

promote adaptive responses to abiotic stress in algae. Additionally, the study will analyze recent advances in epigenetic research techniques and their applications in algal biology to identify key areas for future research and the potential biotechnological applications of epigenetic regulation in algae.

2 Mechanisms of Epigenetic Regulation in Algae

2.1 DNA methylation in algae

DNA methylation is a well-conserved epigenetic mechanism that plays a crucial role in regulating gene expression in response to various environmental stimuli. In algae, DNA methylation involves the addition of a methyl group to the cytosine residues in DNA, which can lead to gene silencing or activation depending on the context. This modification is pivotal for the organism's response to abiotic stressors such as heavy metals, nutrient availability, and temperature fluctuations. Stress conditions can induce changes in DNA methylation patterns, either through hypo- or hyper-methylation at specific loci or across the genome, which can have adaptive significance and influence genome evolution (Ferrari et al., 2023). The dynamic nature of DNA methylation allows algae to rapidly adjust their gene expression profiles to cope with environmental challenges, thereby enhancing their stress tolerance and overall fitness (Ji et al., 2023).

2.2 Histone modifications and chromatin remodeling

Histone modifications and chromatin remodeling are essential for the regulation of gene expression in algae. These processes involve post-translational modifications of histone proteins, such as methylation, acetylation, phosphorylation, and ubiquitination, which alter the chromatin structure and accessibility of DNA to transcriptional machinery. In algae, histone modifications are crucial for the regulation of stress-responsive genes, enabling the organism to adapt to changing environmental conditions. For instance, histone acetylation and deacetylation play significant roles in modulating gene expression in response to abiotic stresses such as drought, salinity, and extreme temperatures. Chromatin remodeling, facilitated by various chromatin-remodeling complexes, further contributes to the dynamic regulation of gene expression by altering nucleosome positioning and density, thereby influencing the accessibility of specific genomic regions to transcription factors and other regulatory proteins (Liu et al., 2022).

2.3 Role of non-coding RNAs in gene regulation

Non-coding RNAs (ncRNAs) are emerging as key regulators of gene expression in algae through their involvement in epigenetic regulation. These ncRNAs, which include microRNAs (miRNAs), small interfering RNAs (siRNAs), and long non-coding RNAs (lncRNAs), do not encode proteins but play critical roles in regulating gene expression at the transcriptional and post-transcriptional levels. In algae, ncRNAs are involved in various biological processes, including growth, development, and stress responses. They can modulate gene expression by guiding chromatin-modifying complexes to specific genomic loci, thereby influencing DNA methylation and histone modifications (Wei et al., 2017; Zhao et al., 2021). The interplay between ncRNAs and other epigenetic mechanisms adds an additional layer of complexity to the regulation of gene expression, enabling algae to fine-tune their responses to environmental changes and maintain cellular homeostasis (Chang et al., 2019).

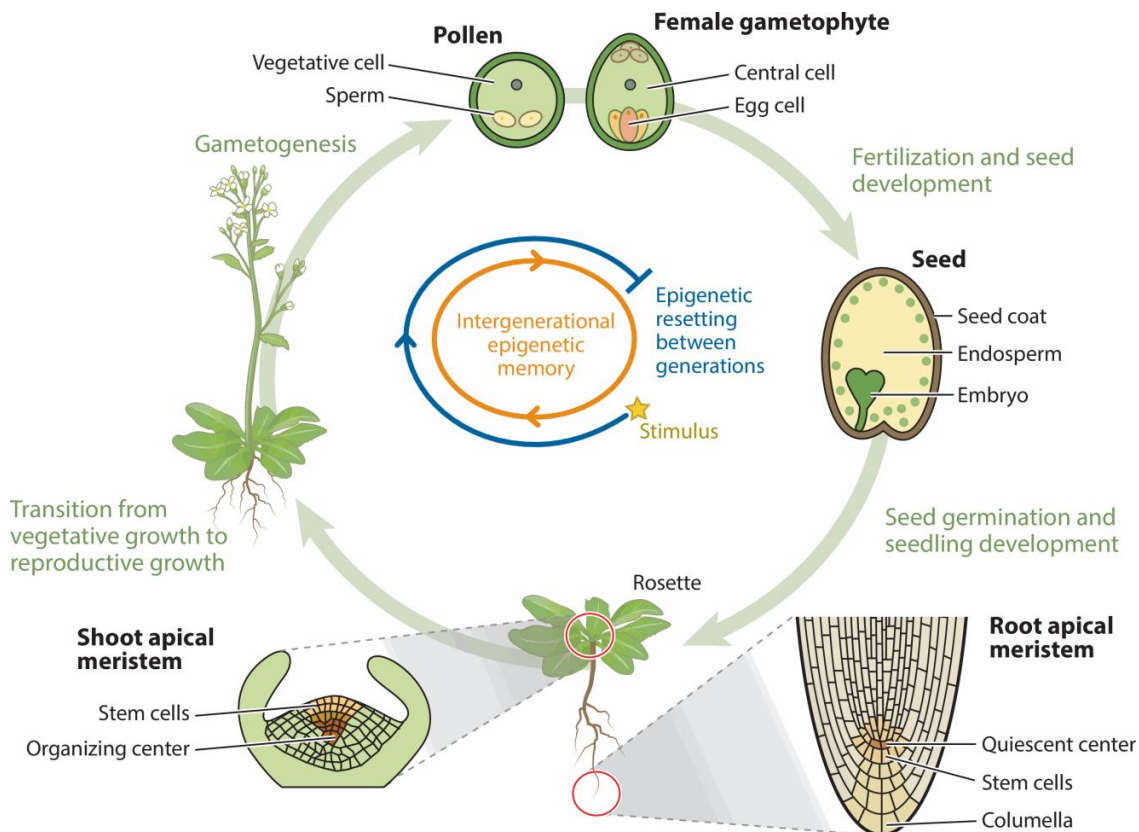
3 Epigenetic Influences on Algal Growth

3.1 Control of the cell cycle and growth regulation

Epigenetic factors such as DNA methylation and histone modifications are pivotal in regulating the cell cycle and growth in algae. Reactive oxygen species (ROS) and reactive nitrogen species (RNS), including hydrogen peroxide and nitric oxide, are significant in this context. These molecules act as signals that regulate the expression of proteins essential for completing the cell cycle, such as cyclins and cyclin-dependent kinases. The interaction of these signaling molecules with redox-sensitive transcription factors and various signaling pathways, including MAPK and G-protein pathways, underscores their role in algal cell development and growth regulation (Pokora et al., 2022). The modulation of DNA methylation patterns in response to environmental stressors can lead to changes in gene expression that support growth under adverse conditions (Ferrari et al., 2023).

3.2 Epigenetic modulation of algal developmental stages

Epigenetic modifications, including DNA methylation and histone modifications, provide an additional layer of regulation that controls developmental processes in algae. These modifications can be established, maintained, and removed to adapt to environmental changes and developmental cues (Figure 1). For instance, the reversible nature of these modifications allows algae to respond rapidly to stress and developmental signals, thereby influencing various stages of growth and development (Hewezi, 2017; Hemenway and Gehring, 2022). The establishment of epigenetic memory, where certain epigenetic states are maintained within an individual but reset between generations, also plays a role in the developmental plasticity of algae.



Hemenway EA, Gehring M. 2023
Annu. Rev. Plant Biol. 74:87–109

Figure 1 Epigenetic memory on different timescales (Adopted from Hemenway and Gehring, 2022)

3.3 Impacts on photosynthesis and metabolism

Epigenetic regulation significantly impacts photosynthesis and metabolism in algae. For example, the green alga *Chromochloris zofingiensis* can reversibly shut down photosynthesis and reprogram its metabolism in response to glucose availability. This process involves rapid and reversible changes in the photosynthetic apparatus, thylakoid ultrastructure, and energy stores, including lipids and starch. The addition of glucose leads to the repression of photosynthetic pathways and the upregulation of heterotrophic carbon metabolism, highlighting the role of epigenetic mechanisms in metabolic flexibility and adaptation (Roth et al., 2019). Histone modifications in industrial microalgae like *Nannochloropsis* spp. have been shown to influence photosynthetic carbon fixation and storage, underscoring the importance of epigenetic factors in optimizing algal metabolism for industrial applications (Wei and Xu, 2018).

4 Epigenetic Regulation in Response to Environmental Stress

4.1 Stress responses to light, temperature, and salinity

Epigenetic mechanisms play a crucial role in how algae respond to various environmental stressors such as light, temperature, and salinity. DNA methylation, a well-conserved epigenetic mark, is pivotal in regulating gene

expression in response to these abiotic stresses. Changes in DNA methylation patterns, either hypo- or hyper-methylation, can significantly impact the organism's ability to adapt to stressful conditions. For instance, temperature stress can induce genome-wide DNA methylation changes, which are essential for the adaptive response and can even direct genome evolution. Histone modifications and chromatin remodeling are also involved in the stress response, providing a dynamic and reversible mechanism to regulate gene expression under fluctuating environmental conditions (Hewezi, 2017; Chang et al., 2019).

4.2 Epigenetic mechanisms in nutrient starvation

Nutrient availability is a critical factor influencing the growth and development of algae. Under nutrient starvation, epigenetic modifications such as DNA methylation and histone modifications play a significant role in regulating gene expression to optimize resource utilization. These modifications can lead to the activation or repression of genes involved in nutrient uptake and metabolism. For example, nutrient stress can trigger specific histone modifications that alter chromatin accessibility, thereby modulating the expression of stress-responsive genes (Thiebaut et al., 2019). Moreover, the interplay between nutrient availability and epigenetic regulation is crucial for maintaining cellular homeostasis and ensuring survival under nutrient-limited conditions (Ferrari et al., 2023).

4.3 Role in oxidative stress and other environmental pressures

Oxidative stress, caused by an imbalance between reactive oxygen species (ROS) and antioxidant defenses, is another significant environmental pressure that affects algae. Epigenetic alterations, including DNA methylation and histone modifications, are critical in mediating the cellular response to oxidative stress. These modifications can influence the expression of antioxidant genes and other stress-responsive pathways, thereby enhancing the organism's ability to cope with oxidative damage. For instance, oxidative stress can lead to changes in histone post-translational modifications, which in turn affect the histone code and gene expression patterns. The interaction between oxidative stress and epigenetic regulation is essential for maintaining cellular homeostasis and preventing pathogenesis (García-Giménez et al., 2021; Huang et al., 2022; Rubio et al., 2023).

5 Comparative Epigenetics Across Algal Species

5.1 Differences in epigenetic patterns between freshwater and marine algae

Epigenetic mechanisms, particularly DNA methylation, play a crucial role in the adaptation of algae to their respective environments. Freshwater and marine algae exhibit distinct epigenetic patterns that reflect their unique environmental challenges. For instance, freshwater species often show domain-centric ontology enrichment for nuclear and nuclear membrane functions, while marine species are enriched in organellar and cellular membrane functions. Marine algae tend to have more viral families integrated into their genomes, which may contribute to their adaptive strategies in saline environments (Nelson et al., 2020; Dong and Jin, 2024). These differences highlight the role of epigenetic modifications in enabling algae to thrive in diverse habitats.

5.2 Epigenetic variations among microalgae and macroalgae

Microalgae and macroalgae also display significant epigenetic variations that influence their growth, development, and stress responses. In microalgae, such as *Dunaliella salina*, epigenetic mechanisms like DNA methylation are involved in the response to osmotic stress, although the extent of these changes can vary significantly between strains (Leung et al., 2021). In contrast, macroalgae may exhibit different epigenetic responses due to their larger and more complex structures. For example, the industrial microalga *Nannochloropsis* spp. shows specific histone modifications that are crucial for photosynthetic carbon conversion and storage (Wei and Xu, 2018). These variations underscore the diverse epigenetic landscapes across different types of algae.

5.3 Insights from model species vs. non-model algal species

Research on model algal species, such as *Chlamydomonas reinhardtii*, has provided valuable insights into the role of epigenetic modifications in adaptation and stress responses. Experimental evolution studies have shown that manipulating DNA methylation and histone acetylation can significantly impact the adaptation of *Chlamydomonas* to various environmental stresses (Kronholm et al., 2017). However, non-model species also offer important perspectives. For instance, the marine diatom *Phaeodactylum tricorutum* demonstrates how DNA

methylation can act cooperatively with gene transcription to regulate key metabolic processes under high CO₂ and warming conditions (Wan et al., 2023). These findings highlight the importance of studying both model and non-model species to fully understand the epigenetic mechanisms underlying algal adaptation.

6 Technological Advances in Algal Epigenetics Research

6.1 High-throughput sequencing for epigenomic analysis

High-throughput sequencing technologies have revolutionized the field of epigenomics by enabling comprehensive analysis of epigenetic modifications across the entire genome. These technologies, particularly next-generation sequencing (NGS), allow for the identification and quantification of DNA methylation, histone modifications, and chromatin accessibility at a genome-wide scale. The integration of NGS with bioinformatics tools has facilitated the generation and interpretation of large-scale epigenomic datasets, providing insights into the regulatory mechanisms underlying gene expression and cellular function (Han and He, 2016; Xu, 2024). This approach has been instrumental in uncovering the complex interactions between epigenetic marks and their role in health and disease, and it holds significant potential for advancing our understanding of algal biology and stress responses.

6.2 CRISPR-Cas9 and epigenetic editing tools

The advent of CRISPR-Cas9 technology has provided a powerful tool for precise epigenome editing, enabling targeted modifications of DNA methylation and histone marks. CRISPR-Cas9-based systems, such as dCas9-KRAB and dCas9-p300, allow for the recruitment of epigenetic modifiers to specific genomic loci, thereby modulating gene expression in a controlled manner (Goell and Hilton, 2021). These tools have been successfully used to dissect the functional roles of epigenetic modifications in gene regulation and to explore their potential applications in therapeutic contexts. In algae, CRISPR-Cas9-mediated epigenome editing could be employed to investigate the epigenetic regulation of growth, development, and stress responses, offering new avenues for enhancing algal productivity and resilience (Thakore et al., 2015; Qi et al., 2023).

6.3 Advances in bioinformatics and data integration

The rapid accumulation of epigenomic data necessitates advanced bioinformatics tools for data processing, integration, and interpretation. Recent developments in computational epigenomics have focused on creating robust algorithms and software platforms to analyze high-throughput sequencing data, identify epigenetic patterns, and correlate them with phenotypic outcomes (Han and He, 2016). These tools enable researchers to integrate epigenomic data with other omics datasets, such as transcriptomics and proteomics, providing a holistic view of the regulatory networks governing cellular processes. In the context of algal research, bioinformatics advancements are crucial for deciphering the complex epigenetic landscapes and their implications for algal growth, development, and response to environmental stresses.

7 Case Study: Epigenetic Changes in Stress-Adapted Algae

7.1 *Chlamydomonas reinhardtii* as a model for epigenetic studies

Chlamydomonas reinhardtii has emerged as a pivotal model organism for studying epigenetic modifications due to its genetic tractability and the wealth of available molecular tools. Research has demonstrated that *C. reinhardtii* employs various epigenetic mechanisms to adapt to environmental stresses. For instance, under osmotic stress, *C. reinhardtii* accumulates osmolytes and osmoprotective sugars, increases reactive oxygen species (ROS) scavenging mechanisms, and alters cell physiology, which are likely regulated by epigenetic modifications (Colina et al., 2020). Experimental evolution studies have shown that manipulating DNA methylation and histone acetylation can significantly impact the adaptation of *C. reinhardtii* to different stress conditions, such as salt stress, phosphate starvation, and high CO₂ levels. These findings underscore the role of transgenerational epigenetic effects in adaptive evolution (Kronholm et al., 2017).

7.2 Epigenetic adaptations in marine algal species under extreme conditions

Marine algal species, like their freshwater counterparts, exhibit remarkable epigenetic adaptations to survive under extreme environmental conditions. For example, *C. reinhardtii* has been shown to adapt to high salinity by

altering its transcriptome, which includes the upregulation of genes involved in maintaining lipid homeostasis and enhancing glycolysis metabolism (Figure 2) (Wang et al., 2018). Similarly, exposure to UV-B radiation triggers the downregulation of specific microRNAs, such as Cre-miR914, which in turn affects the expression of target genes like ribosomal protein L18 (RPL18), enhancing the organism's tolerance to UV stress. These adaptations are indicative of complex epigenetic regulation mechanisms that enable marine algae to thrive in harsh environments.

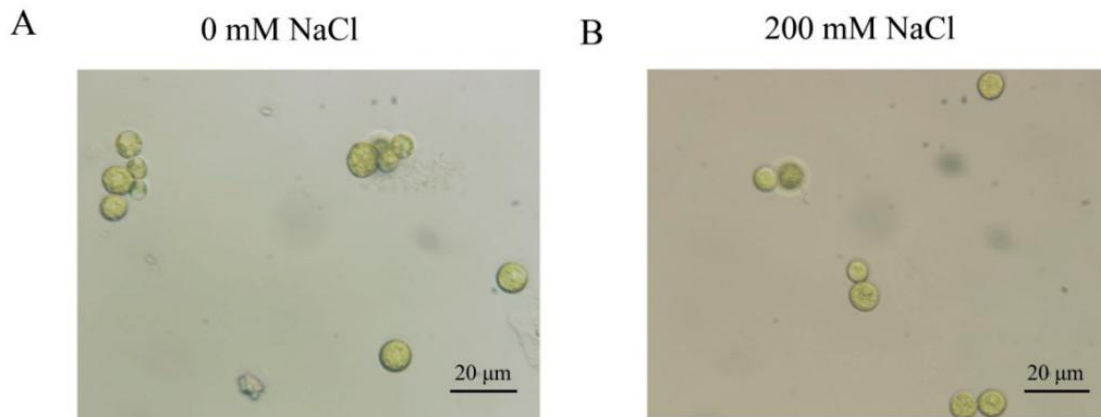


Figure 2 The morphology of *C. reinhardtii* cells without addition of NaCl (A) and the morphology of *C. reinhardtii* cells under 200 mM NaCl treatment (B) (Adopted from Wang et al., 2018)

7.3 Practical applications in improving algal stress tolerance

Understanding the epigenetic mechanisms underlying stress responses in algae has significant practical applications, particularly in the field of algal biotechnology. By targeting specific epigenetic pathways, it is possible to engineer algal strains with enhanced stress tolerance. For instance, manipulating the expression of genes involved in osmolyte accumulation and ROS scavenging could improve the resilience of algae to osmotic stress, making them more suitable for industrial applications (Colina et al., 2020). The insights gained from studying the epigenetic responses to UV radiation and salinity stress can be applied to develop algal strains that are more robust in fluctuating environmental conditions, thereby increasing their productivity and sustainability in biofuel production and other biotechnological processes (Wang et al., 2018; 2019).

8 Implications for Biotechnology and Algal Cultivation

8.1 Harnessing epigenetic mechanisms to enhance biomass production

Epigenetic mechanisms, such as DNA methylation, play a crucial role in regulating gene expression in response to environmental stimuli. By understanding and manipulating these mechanisms, it is possible to enhance biomass production in algae. For instance, DNA methylation patterns can be altered to improve stress tolerance, which in turn can lead to higher biomass yields under suboptimal conditions. Integrating chromatin signature analysis with transcriptomic data can identify key transcriptional regulators that control biomass production, providing targets for genetic engineering to boost algal growth (Ngan et al., 2015). These strategies can be combined with advanced cultivation techniques to maximize biomass output, making algal biofactories more efficient and economically viable (Benedetti et al., 2018).

8.2 Optimizing algal biofuel production through epigenetic modulation

Epigenetic modulation offers a promising avenue for optimizing biofuel production in algae. By targeting specific epigenetic marks, such as histone modifications and DNA methylation, it is possible to enhance lipid accumulation without compromising cell growth. For example, the transcription factor PSR1 has been identified as a key regulator of lipid biosynthesis in *Chlamydomonas reinhardtii*, and its manipulation can lead to increased lipid production (6). Moreover, metabolic engineering strategies that incorporate epigenetic insights can streamline the lipid biosynthesis pathways, thereby improving the overall efficiency of biofuel production (Xue et al., 2021). These approaches can be further refined through the use of genetic algorithms and response surface methodologies to optimize cultivation conditions, ensuring maximal lipid yield (Kumar et al., 2018).

8.3 Potential for developing stress-resistant algal strains

Developing stress-resistant algal strains is essential for sustainable algal cultivation, especially in the face of environmental challenges. Epigenetic mechanisms, such as DNA methylation, play a significant role in the adaptive responses of algae to abiotic stressors like heavy metals, nutrient deficiencies, and temperature fluctuations. By leveraging these mechanisms, it is possible to engineer algal strains that can withstand harsh conditions while maintaining high productivity. Genetic engineering and co-cultivation with growth-promoting bacteria can further enhance stress resistance and biomass yield (Zeraatkar et al., 2016; Berthold et al., 2019). These advancements not only improve the resilience of algal cultures but also reduce the costs associated with large-scale algal cultivation, making it a more viable option for biofuel and bioproduct production (Shurin et al., 2016).

Acknowledgments

We thank Ms. J. Wu from the Institute of Life Science of Jiyang College of Zhejiang A&F University for his reading and revising suggestion.

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.

Reference

- Adhikari S., and Curtis P., 2016, DNA methyltransferases and epigenetic regulation in bacteria, *FEMS Microbiology Reviews*, 40(5): 575-591.
<https://doi.org/10.1093/femsre/fuw023>
- Agarwal G., Kudapa H., Ramalingam A., Choudhary D., Sinha P., Garg V., Singh V., Patil G., Pandey M., Nguyen H., Guo B., Sunkar R., Niederhuth C., and Varshney R., 2020, Epigenetics and epigenomics: underlying mechanisms relevance and implications in crop improvement, *Functional and Integrative Genomics*, 20: 739-761.
<https://doi.org/10.1007/s10142-020-00756-7>
- Akhter Z., Bi Z.Z., Ali K., Sun C., Fiaz S., Haider F.U., and Bai J.P., 2021, In response to abiotic stress DNA methylation confers epigenetic changes in plants, *Plants*, 10(6): 1096.
<https://doi.org/10.3390/plants10061096>
- Benedetti M., Vecchi V., Barera S., and Dall'Osto L., 2018, Biomass from microalgae: the potential of domestication towards sustainable biofactories, *Microbial Cell Factories*, 17: 1-18.
<https://doi.org/10.1186/s12934-018-1019-3>
- Berthold D.E., Shetty K.G., Jayachandran K., Laughinghouse H.D., and Gantar M., 2019, Enhancing algal biomass and lipid production through bacterial co-culture, *Biomass and Bioenergy*, 122: 280-289.
<https://doi.org/10.1016/j.biombioe.2019.01.033>
- Chang Y.N., Zhu C., Jiang J.K., Zhang H., Zhu J., and Duan C.G., 2019, Epigenetic regulation in plant abiotic stress responses, *Journal of Integrative Plant Biology*, 62(5): 563-580.
<https://doi.org/10.1111/jipb.12901>
- Colina F., Carbó M., Cañal M., and Valledor L., 2020, A complex metabolic rearrangement towards the accumulation of glycerol and sugars consequence of a proteome remodeling is required for the survival of *Chlamydomonas reinhardtii* growing under osmotic stress, *Environmental and Experimental Botany*, 180: 104261.
<https://doi.org/10.1016/j.envexpbot.2020.104261>
- Dong B.H., and Jin L.F., 2024 Spatial and temporal dynamics of marine ecosystem structures in tropical oceans, *International Journal of Marine Science*, 14(3): 162-171.
<https://doi.org/10.5376/ijms.2024.14.0021>
- Ferrari M., Muto A., Bruno L., and Cozza R., 2023, DNA methylation in algae and its impact on abiotic stress responses, *Plants*, 12(2): 241.
<https://doi.org/10.3390/plants12020241>
- García-Giménez J., Garcés C., Romá-Mateo C., and Pallardó F., 2021, Special Issue "Redox regulation of the epigenetic landscape" "oxidative stress-mediated alterations in histone post-translational modifications", *Free radical Biology and Medicine*, 170: 6-18.
<https://doi.org/10.1016/j.freeradbiomed.2021.02.027>
- Goell J.H., and Hilton I.B., 2021, CRISPR/Cas-based epigenome editing: advances applications and clinical utility, *Trends in Biotechnology*, 39(7): 678-691.
<https://doi.org/10.1016/j.tibtech.2020.10.012>
- Han Y., and He X., 2016, Integrating epigenomics into the understanding of biomedical insight, *Bioinformatics and Biology Insights*, 10: 267-289.
<https://doi.org/10.4137/BBI.S38427>
- Hemenway E., and Gehring M., 2022, Epigenetic regulation during plant development and the capacity for epigenetic memory, *Annual Review of Plant Biology*, 74(1): 87-109.
<https://doi.org/10.1146/annurev-arplant-070122-025047>

- Hewezi T., 2017, Editorial: epigenetic regulation of plant development and stress responses, *Plant Cell Reports*, 37: 1-2.
<https://doi.org/10.1007/s00299-017-2233-x>
- Huang M., Wu Q., and Jiang Z., 2022, Epigenetic alterations under oxidative stress in stem cells, *Oxidative Medicine and Cellular Longevity*, 2022.
<https://doi.org/10.1155/2022/6439097>
- Ji J., Jing A., Geng T., Ma X., Liu W., and Liu B., 2023, Editorial: protein modifications in epigenetic dysfunctional diseases: mechanisms and potential therapeutic strategies, *Frontiers in Cell and Developmental Biology*, 11.
<https://doi.org/10.3389/fcell.2023.1216637>
- Kronholm I., Bassett A., Baulcombe D., and Collins S., 2017, Epigenetic and genetic contributions to adaptation in *Chlamydomonas*, *Molecular Biology and Evolution*, 34: 2285-2306.
<https://doi.org/10.1093/molbev/msx166>
- Kumar A., Guria C.D., and Pathak A.K., 2018, Optimal cultivation towards enhanced algae-biomass and lipid production using *Dunaliella tertiolecta* for biofuel application and potential CO₂ bio-fixation: Effect of nitrogen deficient fertilizer light intensity salinity and carbon supply strategy, *Energy*, 148: 1069-1086.
<https://doi.org/10.1016/j.energy.2018.01.042>
- Leung C., Grulois D., and Chevin L., 2021, Plasticity across levels: Relating epigenomic transcriptomic and phenotypic responses to osmotic stress in a halotolerant microalga, *Molecular Ecology*, 31: 4672-4687.
<https://doi.org/10.1111/mec.16542>
- Liu Y., Wang J., Liu B., and Xu Z., 2022, Dynamic regulation of DNA methylation and histone modifications in response to abiotic stresses in plants, *Journal of Integrative Plant Biology*, 64(12): 2252-2274.
<https://doi.org/10.1111/jipb.13368>
- Nelson D.R., Hazzouri K.M., Lauersen K.J., Jaiswal A., Chaiboonchoe A., Mystikou A., Fu W., Daakour S., Dohai B., Alzahmi A., Nobles D., Hurd M., Sexton J., Preston M., Blanchette J., Lomas M., Amiri K., and Salehi-Ashtiani K., 2020, Large-scale genome sequencing reveals the driving forces of viruses in microalgal evolution, *Cell host and Microbe*, 29(2): 250-266.
<https://doi.org/10.1016/j.chom.2020.12.005>
- Ngan C.Y., Wong C.H., Choi C., Yoshinaga Y., Louie K., Jia J., Chen C., Bowen B., Cheng H., Leonelli L., Kuo R., Baran R., García-Cerdán J., Pratap A., Wang M., Lim J., Tice H., Daum C., Xu J., Northen T., Visel A., Bristow J., Niyogi K., and Wei C., 2015, Lineage-specific chromatin signatures reveal a regulator of lipid metabolism in microalgae, *Nature Plants*, 1(8): 1-12.
<https://doi.org/10.1038/nplants.2015.107>
- Pokora W., Tułodziecki S., Dettlaff-Pokora A., and Aksmann A., 2022, Cross talk between hydrogen peroxide and nitric oxide in the unicellular green algae cell cycle: how does it work, *Cells*, 11(15): 2425.
<https://doi.org/10.3390/cells11152425>
- Qi Q., Hu B., Jiang W., Wang Y., Yan J., Ma F., Guan Q., and Xu J., 2023, Advances in plant epigenome editing research and its application in plants, *International Journal of Molecular Sciences*, 24(4): 3442.
<https://doi.org/10.3390/ijms24043442>
- Roth M., Gallaher S., Westcott D., Iwai M., Louie K., Mueller M., Walter A., Foflonker F., Bowen B., Ataii N., Song J., Chen J., Blaby-Haas C., Larabell C., Auer M., Northen T., Merchant S., and Niyogi K., 2019, Regulation of Oxygenic Photosynthesis during Trophic Transitions in the Green Alga *Chromochloris zofingiensis*, *Plant Cell*, 31: 579-601.
<https://doi.org/10.1105/tpc.18.00742>
- Rubio K., Hernández-Cruz E., Rogel-Ayala D., Sarvari P., Isidoro C., Barreto G., and Pedraza-Chaverri J., 2023, Nutriepigenomics in environmental-associated oxidative stress, *Antioxidants*, 12(3): 771.
<https://doi.org/10.3390/antiox12030771>
- Shurin J.B., Burkart M.D., Mayfield S.H., and Smith V., 2016, Recent progress and future challenges in algal biofuel production, *F1000Research*, 5.
<https://doi.org/10.12688/f1000research.9217.1>
- Singroha G., and Sharma P., 2019, Epigenetic modifications in plants under abiotic stress, *Epigenetics*, 2019: 10.
<https://doi.org/10.5772/intechopen.84455>
- Thakore P., D'Ippolito A., Song L., Safi A., Shivakumar N., Kabadi A., Reddy T., Crawford G., and Gersbach C., 2015, Highly specific epigenome editing by CRISPR/Cas9 repressors for silencing of distal regulatory elements, *Nature methods*, 12: 1143-1149.
<https://doi.org/10.1038/nmeth.3630>
- Thiebaut F., Hemerly A., and Ferreira P., 2019, A role for epigenetic regulation in the adaptation and stress responses of non-model plants, *Frontiers in Plant Science*, 10: 246.
<https://doi.org/10.3389/fpls.2019.00246>
- Wan J., Zhou Y., Beardall J., Raven J., Lin J., Huang J., Lu Y., Liang S., Ye M., Xiao M., Zhao J., Dai X., Xia J., and Jin P., 2023, DNA methylation and gene transcription act cooperatively in driving the adaptation of a marine diatom to global change, *Journal of Experimental Botany*, 74(14): 4259-4276.
<https://doi.org/10.1093/jxb/erad150>
- Wang B., Zhang F., Hu J., Gao X., Bian P., Liu Y., and Wang G., 2019, Cre-miR914-regulated RPL18 is involved with UV-B adaptation in *Chlamydomonas reinhardtii*, *Journal of Plant Physiology*, 232: 151-159.
<https://doi.org/10.1016/j.jplph.2018.11.021>

- Wang N., Qian Z.X., Luo M.W., Fan S.J., Zhang X.J., and Zhang L.Y., 2018, Identification of salt stress responding genes using transcriptome analysis in green alga *Chlamydomonas reinhardtii*, International Journal of Molecular Sciences, 19(11): 3359.
<https://doi.org/10.3390/ijms19113359>
- Wei J.W., Huang K., Yang C., and Kang C.S., 2017, Non-coding RNAs as regulators in epigenetics (Review), Oncology Reports, 37(1): 3-9.
<https://doi.org/10.3892/or.2016.5236>
- Wei L., and Xu J., 2018, Optimized methods of chromatin immunoprecipitation for profiling histone modifications in industrial microalgae *Nannochloropsis* spp, Journal of Phycology, 54(3): 358-367.
<https://doi.org/10.1111/jpy.12623>
- Wibowo A., Becker C., Marconi G., Durr J., Price J., Hagmann J., Papareddy R., Putra H., Kageyama J., Becker J., Weigel D., and Gutierrez-Marcos J., 2016, Hyperosmotic stress memory in *Arabidopsis* is mediated by distinct epigenetically labile sites in the genome and is restricted in the male germline by DNA glycosylase activity, eLife, 5: e13546.
<https://doi.org/10.7554/eLife.13546>
- Xu Q.B., 2024 Morphological classification species diversity and ecological functions of ciliate communities International Journal of Marine Science, 14(3): 172-181.
<https://doi.org/10.5376/ijms.2024.14.0022>
- Xue J., Balamurugan S., Li T., Cai J., Chen T., Wang X., Yang W., and Li H., 2021, Biotechnological approaches to enhance biofuel producing potential of microalgae, Fuel, 302: 121169.
<https://doi.org/10.1016/J.FUEL.2021.121169>
- Zeraatkar A., Ahmadzadeh H., Talebi A., Moheimani N., and McHenry M., 2016, Potential use of algae for heavy metal bioremediation a critical review, Journal of Environmental Management, 181: 817-831.
<https://doi.org/10.1016/j.jenvman.2016.06.059>
- Zhao Y.C., Chen Y.H., Jin M., and Wang J., 2021, The crosstalk between m6A RNA methylation and other epigenetic regulators: a novel perspective in epigenetic remodeling, Theranostics, 11(9): 4549-4566.
<https://doi.org/10.7150/thno.54967>



Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.