

Seaweed Growth, Transcriptomics, and Defense Responses: Trends and Insights from Bibliometric Mapping

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ABSTRACT

Seaweeds (macroalgae) play a critical ecological role and hold growing promise for aquaculture, biotechnology, and the sustainable bioeconomy. Despite substantial advances in seaweed physiology, transcriptomics, and stress biology, current knowledge remains fragmented across physiological, molecular, and applied research domains. Here, we present a comprehensive bibliometric and critical synthesis of global seaweed research, integrating co-occurrence mapping with in-depth literature analysis. A dataset of 13,657 publications from Scopus and Web of Science (1970–2026) was analyzed using the Bibliometrix R-package (Biblioshiny) to identify research trends, thematic clusters, and knowledge gaps. Three dominant themes emerged: (i) growth and physiological regulation, (ii) stress responses and molecular adaptation, and (iii) cultivation and applied systems. Trend analysis indicates a clear shift from traditional ecological studies toward stress-related and application-driven research, including biostimulants and climate resilience. However, thematic mapping reveals a persistent disconnect between physiological and molecular approaches, alongside limited mechanistic insight in cultivation research. Our critical synthesis further uncovers inconsistencies in reported growth responses under environmental stress and a weak linkage between transcriptomic insights and practical aquaculture outcomes. These findings emphasize significant gaps in connecting gene expression with phenotypic performance and in translating laboratory-based molecular knowledge into field-scale cultivation systems. Collectively, the results suggest that interdisciplinary, multi-omics frameworks are essential for advancing seaweed growth and stress tolerance research, and that bridging fundamental and applied science is key to developing resilient, sustainable seaweed production systems.

Keywords: Bio-Stimulants, Environmental, Multi-Omics, Production, Seaweed, Sustainable

INTRODUCTION

Seaweeds, or macroalgae, have attracted growing scientific and industrial interest due to their ecological significance and diverse applications in aquaculture, food, pharmaceuticals, biorefineries, and biofuels (Yun *et al.*, 2015; De Saeger *et al.*, 2020; Aina *et al.*, 2022; Tirtawijaya *et al.*, 2022; Arias *et al.*, 2023). Their rapid growth rates and

marine adaptability position them as sustainable resources for bio-based products, while also contributing to nutrient cycling and water quality improvement (Mai *et al.*, 2010; Granada *et al.*, 2018). The cultivation of key species such as *Gracilaria* and *Macrocystis* has been progressively optimized to enhance yields and nutritional profiles for aquaculture systems (Yang *et al.*, 2015; Camus *et al.*, 2018).

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Advances in transcriptomics and metabolomics have begun to illuminate the molecular mechanisms underlying seaweed growth, stress responses, and defense. Transcriptomic analyses of species including *Ecklonia cava* and *Gracilaria* have revealed rapid defense responses to pathogenic threats, providing a foundation for breeding disease-resistant cultivars (Lee *et al.*, 2016; Camus *et al.*, 2018; Zhuang *et al.*, 2024; Lang *et al.*, 2025). Integrating metabolomics with transcriptomics further links metabolic pathways to growth and defense regulation, offering a more holistic view of seaweed physiology (Kumar *et al.*, 2016).

Under escalating environmental pressures, including climate change and pollution, understanding seaweed defense mechanisms has become increasingly critical. Seaweeds counter oxidative stress and resist pathogens through adaptive biochemical pathways (Poza *et al.*, 2018), and transcriptomic studies continue to identify key genes and metabolites that can be leveraged to optimize cultivation resilience (Camus *et al.*, 2018).

Despite these advances, knowledge remains scattered across physiological, molecular, and applied domains, with no comprehensive synthesis to date. This review addresses this gap by integrating bibliometric mapping with critical literature analysis to identify research trends, dominant themes, and knowledge gaps across seaweed growth, transcriptomic regulation, and defense responses. The findings aim to provide a structured foundation for future interdisciplinary research and sustainable seaweed biotechnology.

METHODS

This study combined scientometric (bibliometric) analysis with a systematic literature review (SLR) to evaluate research trends in seaweed growth, transcriptomics, and defense responses. This dual approach allowed quantitative mapping of scientific output alongside qualitative thematic synthesis, ensuring a rigorous and reproducible framework.

Data sources and search strategy

A systematic literature search was conducted in two major scientific databases, Scopus and Web of Science (WoS), due to their extensive coverage of high-quality peer-reviewed publications and compatibility with bibliometric analysis tools. The search query was designed to capture the intersection of physiological, molecular, and defense-related aspects of seaweed research:

("seaweed*" OR "macroalgae*" OR "marine macroalgae") AND (growth OR physiology OR cultivation OR transcriptom* OR RNA-seq OR "gene expression" OR defense OR "stress response" OR immunity)

Publications from 1970 to 2026 were retrieved without document-type restrictions. Initial searches yielded 1,360 records from Scopus and 15,226 from WoS. After retaining only English-language articles and proceedings papers, the dataset was reduced to 1,170 (Scopus) and 13,483 (WoS) documents.

Data screening and cleaning

The datasets obtained from Scopus and Web of Science were exported in compatible bibliographic formats and subsequently merged into a single dataset. Duplicate records were identified and removed through bibliometric data cleaning procedures, resulting in the elimination of 995 duplicate entries. The final dataset comprised 13,657 documents spanning the period from 1970 to 2026, sourced from 2,067 journals and other publication outlets. The document types were dominated by research articles (12,938), followed by proceedings papers (307) and article-proceedings papers (412). This large and comprehensive dataset provides a robust foundation for reliable statistical analysis and network-based bibliometric mapping.

Bibliometric analysis using R

Bibliometric analysis was conducted using the Bibliometrix R-package and its web interface,

Biblioshiny, which supports comprehensive science mapping and performance analysis (Zupic and Čater, 2015; Aria and Cuccurullo, 2017; Abafe *et al.*, 2022). The analysis encompassed several complementary dimensions. First, descriptive analysis was performed to evaluate annual scientific production, citation metrics, authorship, and collaboration patterns. Second, conceptual structure analysis was carried out using keyword co-occurrence networks to identify major thematic clusters and emerging research hotspots. Third, intellectual structure analysis was applied through co-citation networks to reveal influential publications and the underlying knowledge base of the field. Finally, thematic mapping was conducted to classify research themes based on their centrality (relevance within the field) and density (level of development), enabling the identification of motor, basic, niche, and emerging themes.

Systematic literature review and thematic synthesis

A systematic literature review (SLR) was conducted to interpret and contextualize the bibliometric findings. Relevant publications within each thematic cluster were screened and qualitatively synthesized to identify research consensus, contradictions, and knowledge gaps. Thematic clusters derived from keyword co-occurrence analysis directly structured the narrative review, ensuring coherent integration between bibliometric results and literature synthesis.

RESULTS AND DISCUSSION

The bibliometric dataset reflects a broad and well-established research landscape in seaweed science, characterized by sustained growth and increasing scientific impact. The field demonstrates a strong expansion trend, with an annual growth rate of 10.62%, reflecting a rapidly evolving research domain. The average citation per document (28.29) underscores a high level of scientific influence and knowledge accumulation across studies. The large number of contributing authors (35,952) highlights extensive global engagement, while the average of 5.52 co-authors per document reflects a highly collaborative research environment. An international

collaboration rate of 26.86% further confirms substantial cross-country scientific cooperation. Collectively, these patterns suggest that research on seaweed growth, transcriptomics, and defense responses has emerged as a dynamic, interdisciplinary, and globally interconnected field of increasing academic and practical relevance.

Bibliometric analysis

Most relevant sources

The most relevant publication sources identified through bibliometric analysis (Biblioshiny) are presented in Figure 1. The Journal of Applied Phycology stands out as the most dominant source, reflecting its central role as the primary outlet for seaweed-related research. Other prominent journals, including Marine Ecology Progress Series, Aquaculture, and Journal of Phycology, collectively underscore the strong interdisciplinary nature of the field, spanning marine ecology, aquaculture systems, and phycological studies. Journals such as Algal Research, Journal of Experimental Marine Biology and Ecology, and Frontiers in Marine Science further highlight the growing emphasis on applied research, biotechnology, and environmental interactions. This broad distribution across journals confirms that seaweed research is widely disseminated across ecological, physiological, and applied marine science disciplines, reinforcing its multidisciplinary character.

Trend topics (1970–2026)

The temporal evolution of research topics reveals a clear thematic shift over time (Figure 2). Early research (2000–2010) centered on ecological and physiological processes, including nutrient uptake, herbivory, chemical defenses, and population dynamics. Between 2010 and 2016, focus gradually expanded toward biochemical and physiological mechanisms—photosynthesis, secondary metabolites, and stress-related responses. Most recently (2017–2024), research has shifted toward applied and environmentally relevant topics, with increasing prominence of terms such as stress, temperature, response, cultivation, and growth. Emerging themes, including biostimulants, microbiome, and blue

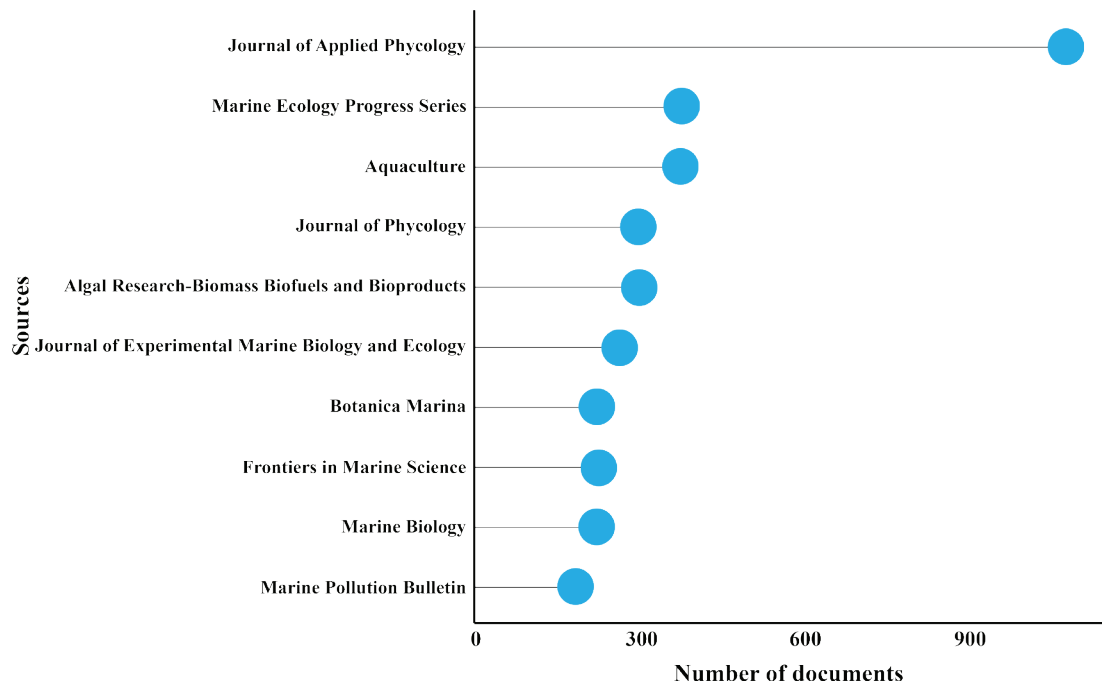


Figure 1. Most relevant publication sources ranked by document count, highlighting the journals that contributed the greatest number of publications to the dataset.

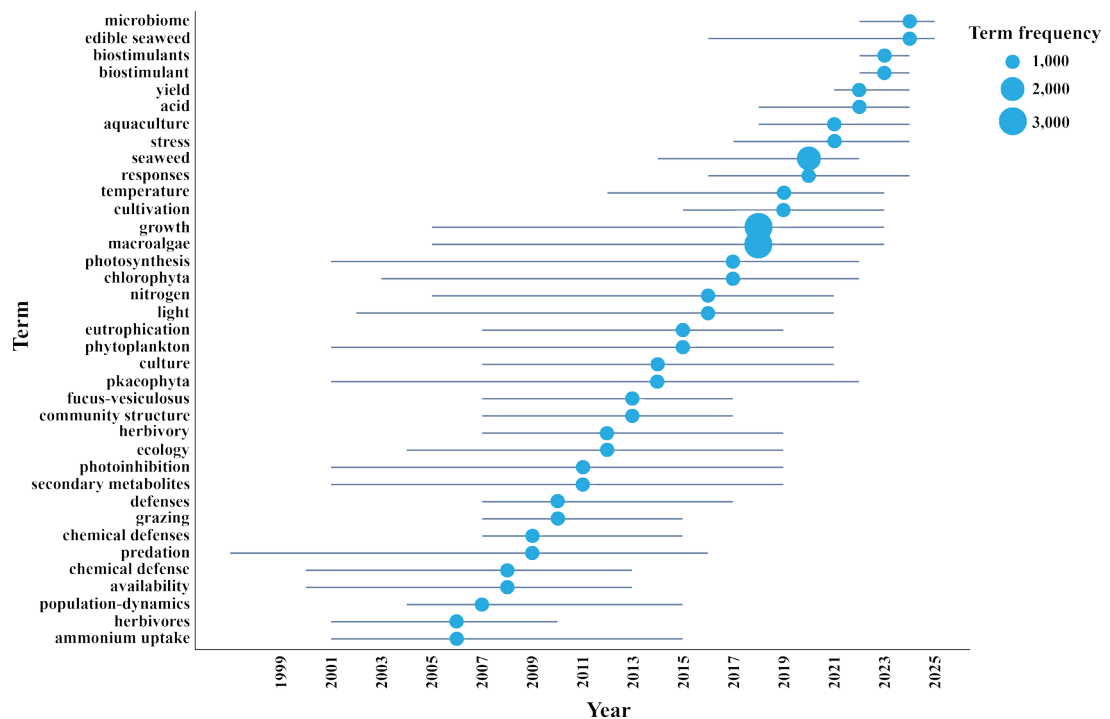


Figure 2. Temporal evaluation of trend topics over time. Bubble size represents term frequency, while the position of each bubble indicates the year in which the topic was most prominent.

Relevance degree (centrality) and development degree (density)

The bubble chart (Figure 4) classifies seaweed research themes by Relevance Degree (Centrality) and Development Degree (Density). Motor themes (upper-right quadrant), including growth, macroalgae, and nitrogen, are well-developed and highly relevant, driving productivity and nutrient dynamics research. Basic themes (lower-right) include broader terms such as seaweed, algae, and seaweeds, providing general context but remaining less developed. Niche themes (upper-left) are relatively specialized and well-developed but poorly integrated into mainstream discourse. Emerging or declining themes (lower-left), including Rhodophyta, cultivation, and aquaculture, may reflect either nascent research directions or areas of waning attention.

Intermediate themes such as photosynthesis, temperature, and responses appear near the center,

indicating their transitional role between fundamental and applied research. Overall, this distribution highlights a dynamic shift toward integrating physiological, environmental, and applied aspects. The bibliometric analysis identifies three dominant thematic clusters structuring the intellectual landscape: (i) growth and physiological processes, (ii) stress responses and biochemical mechanisms, and (iii) cultivation and applied aquaculture systems, which provide the conceptual framework for the following critical synthesis.

Environmental drivers of growth

Seaweed growth is strongly influenced by environmental factors such as temperature, light intensity, salinity, and nutrient availability (Teo *et al.*, 2009; Sangkia *et al.*, 2019; Kinnby *et al.*, 2020; O'Flynn *et al.*, 2023). However, findings across studies remain notably inconsistent and often species-specific. For example, while moderate temperature increases enhance growth rates in

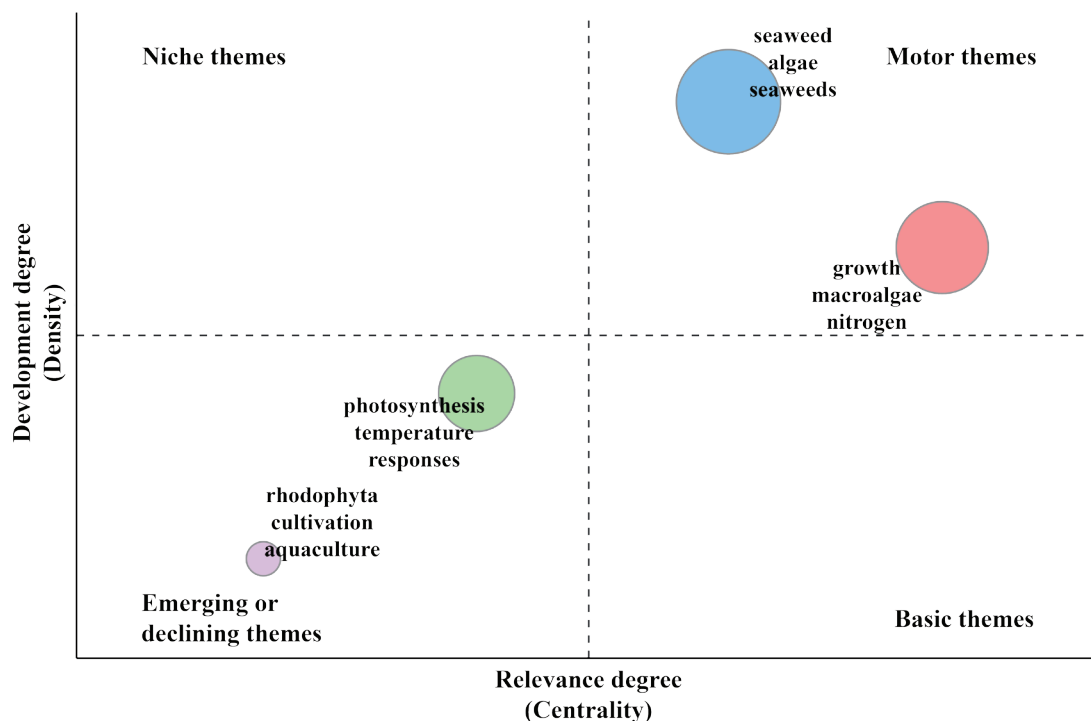


Figure 4. Thematic map showing the distribution of identified themes across four quadrants: motor themes, basic themes, niche themes, and emerging or declining themes, based on relevance degree (centrality) and development degree (density).

certain *Kappaphycus alvarezii* populations (Sangkia *et al.*, 2019; Syahrul *et al.*, 2023), other studies show that similar conditions induce physiological stress and reduce productivity (Kinnby *et al.*, 2020). This variability indicates that growth responses are governed not by single environmental factors but by their complex interactions and threshold effects, relationships that remain insufficiently characterized.

From a bibliometric perspective, the dominance of growth-related keywords confirms that biomass production and physiological performance remain central research priorities. However, limited integration with molecular-level analyses points to a gap in linking environmental drivers to underlying biological mechanisms, particularly the relationship between environmental variability and metabolic regulation (Charrier *et al.*, 2017). In applied contexts, integrated multi-trophic aquaculture (IMTA) shows potential for optimizing nutrient utilization and enhancing productivity (Granada *et al.*, 2018; Ashkenazi *et al.*, 2022), though scalability and long-term stability under fluctuating environmental conditions remain underexplored.

Genetic and molecular basis of growth

Advances in genomics and transcriptomics have provided valuable insights into the genetic regulation of seaweed growth, identifying genes associated with photosynthesis, carbon metabolism, and developmental processes (Beaulieu, 2019; Domozych *et al.*, 2012; Liu *et al.*, 2017). These approaches have enabled identification of regulatory pathways in growth and reproduction, such as tetraspore formation in *Gracilariopsis lemaneiformis* (Sun *et al.*, 2023). However, most studies remain focused on individual species or specific developmental stages, limiting cross-taxon generalization. A key limitation is the weak integration between growth-related studies and molecular research, transcriptomic approaches have been applied to specific developmental processes (Sun *et al.*, 2023), but their role in explaining growth performance variability under different environmental conditions remains limited.

Future research should therefore prioritize linking gene expression patterns with phenotypic traits such as growth rate, biomass yield, and nutrient uptake efficiency, integration that is essential for developing improved cultivars with enhanced productivity and resilience in large-scale aquaculture (Charrier *et al.*, 2017).

Stress responses and molecular adaptation

Abiotic stress responses

Seaweeds are routinely exposed to fluctuating conditions, including temperature shifts, salinity changes, and nutrient limitation, which significantly affect physiological performance (Teo *et al.*, 2009; Kinnby *et al.*, 2020; Rathor *et al.*, 2021; Seo *et al.*, 2023). Transcriptomic studies have identified key genes involved in stress tolerance, including those associated with antioxidant defense, osmotic regulation, and protein stabilization (Mao *et al.*, 2019; Rathor *et al.*, 2021; Seo *et al.*, 2023).

A critical limitation, however, is the inconsistency between physiological observations and molecular findings. While some studies report enhanced tolerance under moderate stress, others demonstrate significant metabolic disruption under similar stressors (Seo *et al.*, 2023), suggesting that stress responses operate at multiple regulatory levels, with molecular adaptations not always translating directly into improved growth performance.

The bibliometric trend analysis confirms a growing emphasis on stress-related topics, consistent with rising concern about climate change and environmental variability. Nevertheless, the limited prominence of explicit molecular keywords suggests that transcriptomic approaches remain incompletely embedded in mainstream seaweed research, despite their importance for understanding stress adaptation.

Biotic stress and defense mechanisms

Beyond abiotic factors, seaweeds are subject to biotic pressures such as herbivory and pathogen infection, which have driven the

evolution of diverse defense mechanisms, including secondary metabolite production and inducible chemical defenses (Hay *et al.*, 1988; Duffy and Hay, 1994; Vera *et al.*, 2011; Jones and Long, 2017). Transcriptomic analyses have identified genes involved in defense signaling and immune responses (Tian *et al.*, 2023). However, integration of these molecular findings with ecological and applied research remains limited, inducible defense responses documented in species such as *Fucus vesiculosus* (Flöthe *et al.*, 2014) have yet to be functionally characterized under aquaculture conditions.

The bibliometric network reveals relatively weak connections between defense-related and cultivation-related keywords, highlighting a disconnect between fundamental defense research and its practical application in seaweed farming, an interdisciplinary gap that warrants focused attention.

Cultivation systems and biotechnological applications

Seaweed cultivation has attracted increasing interest for sustainable biomass production and biotechnological applications (De Saeger *et al.*, 2020; Ali *et al.*, 2021). The bibliometric analysis classifies cultivation-related themes as emerging or underdeveloped, suggesting that despite practical importance, these topics remain insufficiently integrated into the broader research framework.

Current practices focus primarily on optimizing environmental conditions and species selection (Yang *et al.*, 2015; Supriyono *et al.*, 2022), with limited incorporation of molecular or physiological knowledge. While transcriptomic and metabolomic studies have generated insights into stress responses (Lewis *et al.*, 2022; Sujeeth *et al.*, 2022), their application to strain selection and cultivation performance remains largely unexplored.

In parallel, seaweed-derived compounds have emerged as promising biostimulants enhancing plant growth and stress tolerance (Omidbakhshfard *et al.*, 2020; Ali *et al.*, 2021; Borella *et al.*, 2023), with proposed roles in hormonal regulation,

metabolic pathways, and gene expression (Lewis *et al.*, 2022; Sujeeth *et al.*, 2022). However, a lack of standardized experimental approaches limits comparability across studies. Integrating cultivation practices with molecular insights thus represents a key research frontier, particularly for building resilient seaweed farming systems under changing environmental conditions.

Applications of seaweed-derived products

Seaweed extracts as biostimulants

The growing prominence of keywords such as biostimulants, extracts, and stress response in the bibliometric trend analysis reflects increasing research focus on seaweed-derived compounds in agriculture and biotechnology. Seaweed extracts are widely recognized for enhancing plant growth, improving nutrient uptake, and increasing abiotic stress tolerance (De Saeger *et al.*, 2020; Omidbakhshfard *et al.*, 2020; Ali *et al.*, 2021; Ma *et al.*, 2022; Tejasree *et al.*, 2024). These bioactive extracts contain phytohormones, polysaccharides, vitamins, and phenolic substances that collectively influence plant physiology (Omidbakhshfard *et al.*, 2020; Ali *et al.*, 2021). Extracts from *Ascophyllum nodosum*, for instance, enhance plant resistance to oxidative stress and improve tolerance to salinity and drought (Omidbakhshfard *et al.*, 2020; Borella *et al.*, 2023). Seaweed-based soil amendments, including compost and biochar, have also shown positive effects on crop productivity in marginal soils (Purwaningsih *et al.*, 2021). Despite these advances, the bibliometric analysis indicates that biostimulant research remains developing and incompletely integrated with molecular and physiological studies.

Mechanisms of action and molecular insights

Although the beneficial effects of seaweed extracts are well documented, their underlying mechanisms remain incompletely characterized. Current evidence implicates multiple pathways, including hormonal regulation, nutrient uptake enhancement, and modulation of gene expression

(De Saeger *et al.*, 2020; Lewis *et al.*, 2022; Sujeeth *et al.*, 2022). Recent transcriptomic and metabolomic studies have revealed activation of stress-related genes and metabolic pathways associated with plant defense and growth regulation (Lewis *et al.*, 2022; Sujeeth *et al.*, 2022). However, most findings derive from model plant systems rather than seaweeds themselves, indicating a critical gap in linking seaweed-derived compounds to their endogenous molecular mechanisms.

The bibliometric network further confirms limited connectivity between application-oriented and molecular-level research, underscoring the need for multi-omics approaches combined with applied experimentation to better understand and optimize seaweed-derived product use.

Research gaps and future directions

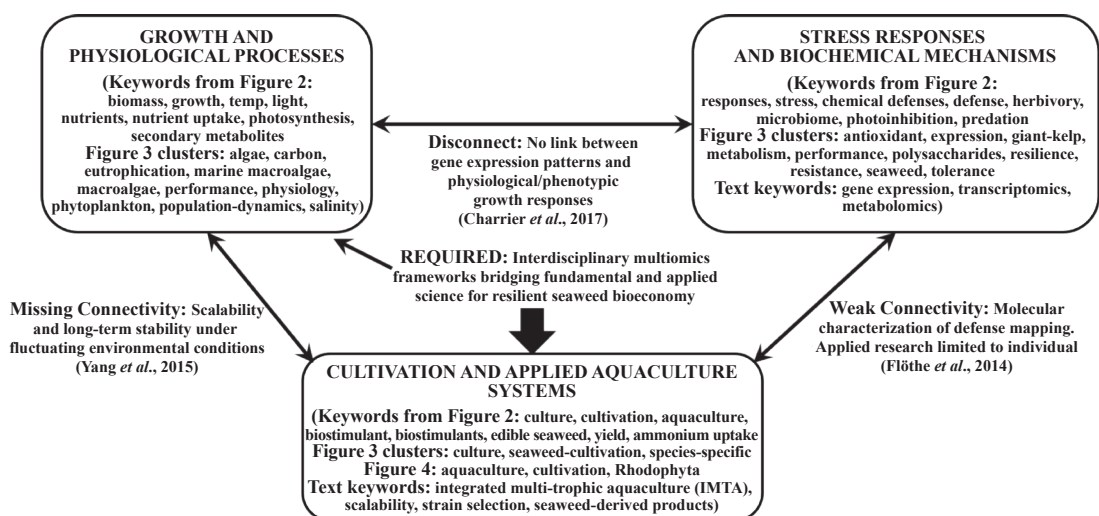
The integration of bibliometric mapping with literature synthesis reveals several critical gaps. First, there is a clear disconnect between physiological studies on growth and molecular investigations of gene expression (Charrier *et al.*, 2017). Second, the limited prominence of molecular keywords in trend analysis suggests that transcriptomic and multi-omics approaches

have yet to be fully embedded in mainstream seaweed research. Third, cultivation-related themes remain underdeveloped, particularly in terms of incorporating molecular and physiological insights into practical aquaculture systems (Yang *et al.*, 2015). Figure 5 synthesizes these gaps within a conceptual framework linking the three dominant research clusters and their key knowledge deficits.

These gaps collectively point to the need for interdisciplinary approaches that bridge physiology, molecular biology, and aquaculture. Future research should prioritize multi-omics integration, linking transcriptomic, metabolomic, and physiological data to advance understanding of stress tolerance and growth regulation (Kumar *et al.*, 2016). Bridging laboratory-based findings with field-scale applications remains equally essential for advancing sustainable seaweed cultivation.

Limitations of the study

Several limitations should be acknowledged when interpreting the findings of this study. First, the bibliometric analysis was restricted to publications indexed in Scopus and Web of Science, which may



Data sourced from Bibliometric analysis and Systematic literature review (SLR) (2000–2026)

Figure 5. Conceptual framework mapping research gaps.

exclude relevant contributions from other databases, grey literature, and regional journals not covered by these platforms. Second, only English-language publications were retained, potentially introducing language bias and underrepresenting research conducted in non-English-speaking countries, particularly across Asia and Latin America, where seaweed research is highly active. Third, findings are inherently shaped by the search query employed; although the query was designed to capture a broad thematic scope, studies using alternative or discipline-specific terminology may not have been retrieved. This keyword dependency is an inherent constraint of bibliometric approaches and should be considered when generalizing the results.

Beyond search-related limitations, bibliometric methods are primarily quantitative in nature, focusing on publication trends, citation patterns, and keyword co-occurrence rather than the depth or experimental rigor of individual studies. Although a systematic literature review was integrated to partially address this constraint, the interpretation of thematic clusters and the qualitative assessment of research development levels inevitably involve an element of subjective judgment. Readers should therefore treat thematic assessments as evidence-informed approximations rather than definitive measurements. Finally, the dynamic pace of scientific publishing means that recently indexed studies may not yet have accumulated sufficient citations to be fully represented in network-based analyses, and emerging topics may therefore appear less prominent than their actual research activity warrants.

CONCLUSIONS

This study delivers a structured synthesis of global seaweed research by combining bibliometric mapping with critical literature analysis. Three dominant themes were identified, growth and physiological regulation, stress responses and molecular adaptation, and cultivation and applied systems, reflecting a field that has expanded rapidly but unevenly. While growth-related research remains the most established, it is persistently disconnected from molecular investigations. Stress response research has grown considerably, yet transcriptomic

and multi-omics approaches remain underutilized in mainstream studies. Cultivation and aquaculture research, despite its applied urgency, is the least developed theme mechanistically.

Bridging these gaps requires interdisciplinary frameworks that integrate transcriptomics, metabolomics, and physiology, and that translate laboratory findings into field-scale cultivation systems. This study provides an evidence-based roadmap for that agenda, offering a foundation for advancing resilient, sustainable seaweed production and the broader seaweed-based bioeconomy.

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