



Metabolomics: an emerging frontier of systems biology in marine macrophytes



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ABSTRACT

Metabolomics is a rapidly emerging discipline within functional genomics which is increasingly being applied to understand biochemical phenotypes across a range of biological systems. Metabolomics measures all (or a subset) metabolites in a cell at a specific time point, reflecting a snapshot of all the regulatory events responding to the external environmental conditions. Although metabolomics and systems biology approaches have been applied to the study of terrestrial plants, few marine macrophytes have been examined using these novel technologies. Marine macrophytes (including seaweeds and seagrasses) are marine ecosystem engineers delivering a range of ecologically and economically valuable biological services; however they are under threat from a wide range of anthropogenic stressors, climate variation, invasive species and pathogens. Investigating metabolomic regulation in these organisms is crucial to understand their acclimation, adaptation and defence responses to environmental challenges. This review describes the current analytical tools available to study metabolomics in marine macrophytes, along with their limitations for both targeted and non-targeted workflows. To illustrate recent advances in systems biology studies in marine macrophytes, we describe how metabolites are used in chemical defence to deter a broad range of invasive species and pathogens, as well as metabolomic reprogramming leading to acclimation or adaptive strategies to environmental and anthropogenic stresses. Where possible, the mechanistic processes associated with primary and secondary plant metabolism governing cellular homeostasis under extreme environments are discussed. Further, we provide a comprehensive overview of an *in silico* plant metabolome database that can be utilized to advance our knowledge from a system biology approach to marine macrophytes. Finally, functional integration of metabolomics with the allied “omics” disciplines of transcriptomics and proteomics, as well as the emerging discipline of “fluxomics” are discussed in the context of developing biological system networks, the identification of unknown gene/protein functions and the analysis of metabolic pathways in marine plants exposed to stress.

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1. Introduction

Marine macrophytes include marine macroalgae (or seaweeds) and marine flowering plants called seagrasses, which are the dominant flora in coastal ecosystems worldwide. Both are considered as marine ecosystem engineers delivering a range of ecologically and economically valuable biological services such as nutrient cycling, carbon sequestration, sediment stabilization and habitat provision to a range of dependent marine fauna. Seaweeds have immense commercial importance for nutraceuticals, pharmaceuticals, human food, animal feed, soil conditioner, biofuels and hydrocolloids production [1] with annual market value US\$7 billion [2]. Seagrass meadows cover an area of 30–60 million km² of the coastal oceans, supporting 50% of the world's fisheries and providing essential nutrition for almost three billion people. Their nutrient cycling value alone is estimated to be three times higher than tropical rainforests, worth US\$2 trillion per year [3].

Marine macrophytes inhabit a unique aquatic environment and experience a diverse range of environmental fluctuations, anthropogenic stress and threats from invasive species and pathogens. Macrophytes experience chronic stresses including salinity fluctuations, light fluctuations, temperature, desiccation, eutrophication, light limitation from turbid water, hypoxia and/or anoxia, sediment discharge, heavy metal and industrial effluents, all of which affect the plant's health and thereby the ecosystem services that they provide [3–5]. To alleviate the stress imposed by extreme conditions and also in deterring their invasive species and pathogens, marine macrophytes must implement acclimation/adaptive strategies by re-programming their metabolite networks. The increasing amounts of transcriptomic based information on the acclimation of marine macrophytes to their extreme environment are being gathered [4]. However, very little is known about how transcriptomic changes translate into metabolite changes. Therefore, a global metabolomic profiling of marine macrophytes can provide a wide picture to understand the different biochemical pathways that maintain homeostasis under extreme perturbations within these plants [6,7].

Metabolomics is defined as the comprehensive and quantitative analysis of all (or a subset) metabolites in a biological system at a specific time point. Metabolomics is especially useful to understand how marine plants respond to highly dynamic environmental conditions that prevail in their unique ecological niches. Metabolites reflect the true integration of gene regulation and protein expression, whilst also incorporating the impact of the environment and/or other organisms. Therefore in a real sense, metabolites are a closer proxy of the phenotype, rather than mRNA transcripts or proteins alone, and thus metabolomics can provide an instantaneous snapshot of the physiological status of a biological system at any given time. A recent influx of genomic/transcriptomic resources of seaweeds (*Ectocarpus siliculosus*, *Chondrus crispus* and *Porphyridium purpureum*) and seagrasses (*Zostera marina*, *Z. noltii* and *Posidonia oceanica*) has dramatically altered the molecular horizons of marine macrophytes in studying their adaptive and tolerance strategies [4,8]. With the successful assembly and analysis of their complete genomes, several seaweeds species (*E. siliculosus*, *C. crispus* and *P. purpureum*) have already been considered as model organisms and are definitively more amenable for future molecular studies [9–11]. However, the decreased cost and increased sequencing efficiency of Next Generation Sequencing make possible the examination of different species of marine macrophytes besides

these model organisms, providing new opportunities for comparative genomics within the same group of seaweeds or seagrasses. In this respect, transcriptome-based analysis of marine macrophytes has provided novel insights into their successful propagation and adaptation to the highly dynamic marine environment [12–23]. Overall, these studies have inferred a complex regulation pattern for diverse gene networks; however, coherent explanation that connects these transcriptional responses to their functional phenotypic response has not yet been defined. The integration of metabolomics with a comprehensive transcriptomic and/or proteomic study can be used to validate the regulation of genes and/or proteins. Although, metabolite profiling in marine macrophytes has become a well-established discipline, most of the past work has been oriented towards examining the structural composition of cell wall matrices and identification of bioactive compounds for pharmaceutical purpose [7]. Relatively fewer investigations have examined the whole metabolomic response of marine macrophytes exposed to biotic and abiotic stress conditions [14–16,20,24–28].

Recent developments in analytical instrumentation and bioinformatics have advanced our capacity to measure numerous plant metabolites, evaluate metabolic changes in response to external stimuli and elucidate metabolic pathways. However, the analytical sensitivity and resolution required for the simultaneous separation and detection of 100s to 1000s of metabolites that are regulated under stress conditions have not yet been achieved [29]. Current studies are mostly restricted to targeted metabolomics, which focuses on amino acid and/or lipid metabolism [14,30,31]. Polyamines, oxylipins, floridosides and volatile organic compounds (VOCs) are other classes of targeted metabolites that are gaining interest in studies of the stress response in macrophytes [32–38]. Metabolomic database information generated for marine macrophytes is in its infancy [6,7] when compared to terrestrial plants where a range of metabolomic databases are available (Tables 1 and 2). The terrestrial plant KNApSack database [39] for example, contains ~50,000 plant metabolite entries. In comparison, the seaweed metabolite database (SWMD; <http://www.swmd.co.in>), the only macrophyte metabolomics database available, contains only 500 metabolites entries and mostly from the red seaweed *Laurencia* [40]; and there is currently no metabolic library available for seagrasses. This review provides a comprehensive overview of the use and capabilities of diverse metabolomic analytical tools in a targeted and non-targeted metabolomics workflow in marine macrophytes. Recent advances in understanding the chemical defence mechanisms of marine macrophytes used to deter a broad range of invasive species and pathogens are discussed. Further, we summarize the metabolite re-programming of marine macrophytes in response to extreme environments that provide new insights on their adaptation and/or acclimation mechanism to different stressors. The stress metabolites that are described include: amino acids, sugars, sugar alcohols, oxylipins, polyunsaturated fatty acids, polyamines, organic acids and phenolic compounds. The integration of metabolomics with the allied 'omics disciplines of transcriptomic, proteomic and fluxomics approaches are discussed in the context of developing biological systems networks, identification of unknown gene/protein functions, and metabolic pathways in marine plants exposed to stress conditions. Finally, we provide a comprehensive overview of in silico plant metabolome database information that can be utilized for the interpretation of marine plant metabolomic data sets.

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