

Volatile-mediated interactions with surface-associated microbes: A parallelism between phyllosphere of plants and eco-chemosphere of seaweeds

Mahasweta Saha¹  | Pauline Gilon^{1,2} | François Verheggen²

¹Marine Ecology and Biodiversity, Plymouth Marine Laboratory, Plymouth, UK

²Gembloux Agro-Bio Tech, TERRA, University of Liege, Liege, Belgium

Correspondence

Mahasweta Saha
Email: sahamahasweta@gmail.com

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Abstract

1. Both in terrestrial and aquatic realms, organisms communicate and interact with each other *via* volatile and non-volatile infochemicals. Terrestrial plants and seaweeds, known as prolific producers of volatiles, harbour a plethora of microbes on their surfaces like phyllosphere of plant leaves and eco-chemosphere of seaweeds, respectively, where complex ecological interactions are regulated through infochemicals.
2. Although plant leaf volatiles have been well-studied for their ecological functions in mediating microbial interactions, seaweed volatiles have been mostly investigated for their roles in climate regulation and with regard to climate change research. However, seaweed volatiles appear to be related to terrestrial plant volatiles both in terms of chemistry and ecology.
3. *Synthesis*. Evidence supports that seaweed volatiles can have important ecological functions in mediating interactions with microbes on their surface, just like plant leaf volatiles. Based on the existing vast literature on ecological interactions mediated by plant volatiles at phyllosphere and on the very few works on ecological roles of seaweed volatiles at eco-chemosphere, we advocate for the detailed investigation of volatile-mediated interactions regulating microbial colonisation processes on seaweed surfaces. Although of great ecological importance, this new field of research has remained largely unexplored. Thus, we also set directions for future research programs investigating the roles of seaweed volatiles at seaweed–microbe interface.

1 | INTRODUCTION

All living organisms including terrestrial plants and aquatic macrophytes like seaweeds (also known as marine macroalgae) produce **infochemicals** (see Glossary) for key eco-physiological processes and mediating ecological interactions (Saha et al., 2019; Vet & Dicke, 1992). Being emitted by one organism and perceived by the

other, infochemicals can influence growth, metabolic pathways and defence mechanisms of both the producer and the emitter (Kamio & Derby, 2017; Puglisi et al., 2019; Singh et al., 2017). These compounds originate from various biosynthetic pathways, have variable chemical structures, polarity and volatility (Mollo et al., 2017).

Volatiles produced by organisms [known as biogenic volatile organic compounds (BVOCs)], are a class of infochemicals which,

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GLOSSARY

Antifouling compounds: chemical compounds that inhibit the colonisation process of a solid surface (living or non-living).

Biofilm: surface-associated microbes (including bacteria, archaea and microalgae among others) united in a self-secreted matrix of extracellular polymeric substances (natural polymers of high molecular weight).

Biogenic volatile organic compounds (BVOCs): volatile organic compounds produced from biogenic processes.

Eco-chemosphere: A seaweed's surface layer which is a micro-hotspot of ecological interactions that are chemically mediated.

Epibacteria: Bacteria colonising the surface of the host organisms.

Holobiont: a collective biological system including the host, its microbiome and other associated symbionts.

Infochemicals: information-conveying chemicals (semiochemicals) including allelochemicals and pheromones that mediate interspecific and intraspecific communication, and population- and ecosystem-level interactions.

Phyllosphere: the aerial parts of plants, dominated by the leaves, whose surface refers to a vast habitat for microorganisms estimated at approximately 10^9 km², an area about twice as great as the land surface.

Volatile compounds: chemical compounds typified by a relatively high vapour pressure at room temperature so that they have a large propensity to escape from their liquid or solid form into the gas phase.

due to their low molecular weight and low hydrophilicity, can be perceived as 'scents' and are known to induce olfactory sensations (Breer, 2003). Volatiles are characterised by a relatively high vapour pressure at room temperature so that molecules of volatile compounds have a large tendency to escape from their liquid or solid form into the gas phase (Steinke et al., 2018). Thus, BVOCs have the ability to travel far from the emitter, allowing them to participate in both short- and long-distance interactions between organisms within and across all kingdoms of life (Kanchiswamy et al., 2015; Li et al., 2019) making them an important class of infochemicals (Moelzner & Fink, 2015) both in terrestrial and aquatic environments (Brown et al., 2019). However, diffusion is typically four orders of magnitude slower in water than in air (Steinke et al., 2018).

Both land plants and seaweeds are intimately associated with abundant and diverse microbes (Rosenberg & Zilber-Rosenberg, 2016). These microbes chemically interact with their hosts (Goecke et al., 2010) influencing growth, health and defence of the host (Carthey et al., 2018; Hassani et al., 2018; Saha & Weinberger, 2019; Schmidt & Saha, 2020), ultimately forming a single entity, that is the **holobiont**.

Plant foliage strongly contributes to global BVOC emissions (Wiedinmyer et al., 2004) including mostly of isoprene, monoterpenes, methanol and other BVOCs. As one of the most prevalent microbial habitats on earth, the **phyllosphere** of land plants harbours numerous micro-organisms that live on leaf surfaces (Bringel & Couée, 2015), where BVOCs are well known to chemically mediate microbial interactions (Vacher et al., 2016). The main constituents of phyllospheric communities are represented by bacteria which can reach densities of 10^7 cells/cm² of leaf surface (Farré-Armengol et al., 2016). The phyllosphere offers a heterogeneous environment to microbes where they colonise often stressful and fluctuating environments.

Like in phyllosphere of plants, and chemically enriched phycosphere of phytoplankton (Bell & Mitchell, 1972), seaweeds form an exo-metabolome of compounds known as chemosphere (Alsufyani et al., 2017; Wichard, 2016). Seaweed surfaces are colonised by epibiotic biofilms, also known as their 'second skin'. Epibiotic biofilms are mainly dominated by bacteria (Wahl et al., 2012). Their surface densities can reach from 10^2 to 10^7 cells/cm² (Paix et al., 2020), and their ecological role is of great importance (Thorner et al., 2016). Together with this second skin and an additional diffusive boundary layer of water on seaweed surfaces (Hurd, 2000), the surface of seaweeds represents a micro-niche or micro-hotspot of chemically mediated ecological interactions known as the '**eco-chemosphere**' (Schmidt & Saha, 2020).

Seaweed-bacteria interactions can be beneficial when **epibacteria** help the normal development of their host (Wichard, 2015; Wichard & Beemelmans, 2018) and provide protection against secondary biofouling (Salta et al., 2013), in return for nutrients (Alsufyani et al., 2017) and physical protection offered by their host. Epibacteria can also be beneficial to and even essential for seaweeds producing hormones and morphogens essential for seaweed growth (Alsufyani et al., 2020). Surface-associated bacteria can also provide defence against other fouling micro-organisms (Singh & Reddy, 2014). However, this association is not always beneficial. Uncontrolled surface colonisation by epibacteria can compromise the tissue and photosynthetic capability of their host and induce diseases that can endanger the health of the host (de Mesquita et al., 2019). However, like terrestrial plants, seaweeds are known to control this colonisation process *via* infochemicals including BVOCs (Figure 1).

Seaweeds modulate the structure of their surface-associated epibacterial communities either by releasing defence chemicals themselves (see review by da Gama et al., 2014; Saha et al., 2018) or *via* their epibacterial communities (e.g. Saha & Weinberger, 2019; Wiese et al., 2009). Like rhizosphere of land plants (Lebeis et al., 2015), the surface metabolites of the red seaweed holobiont *Agarophyton vermiculophyllum* can chemically 'garden' microbial colonisers, that is, attract beneficial microbes that protect the alga from a tip bleaching disease symptom and at the same time deter bacteria that induce such disease (Saha & Weinberger, 2019). Kessler et al. (2018) demonstrated for the green seaweed *Ulva mutabilis* (Chlorophyta) a 'gardening' role of the osmolyte DMSP (dimethylsulphoniopropionate) in the attraction of the beneficial bacterium *Roseovarius* sp. MS2, responsible for

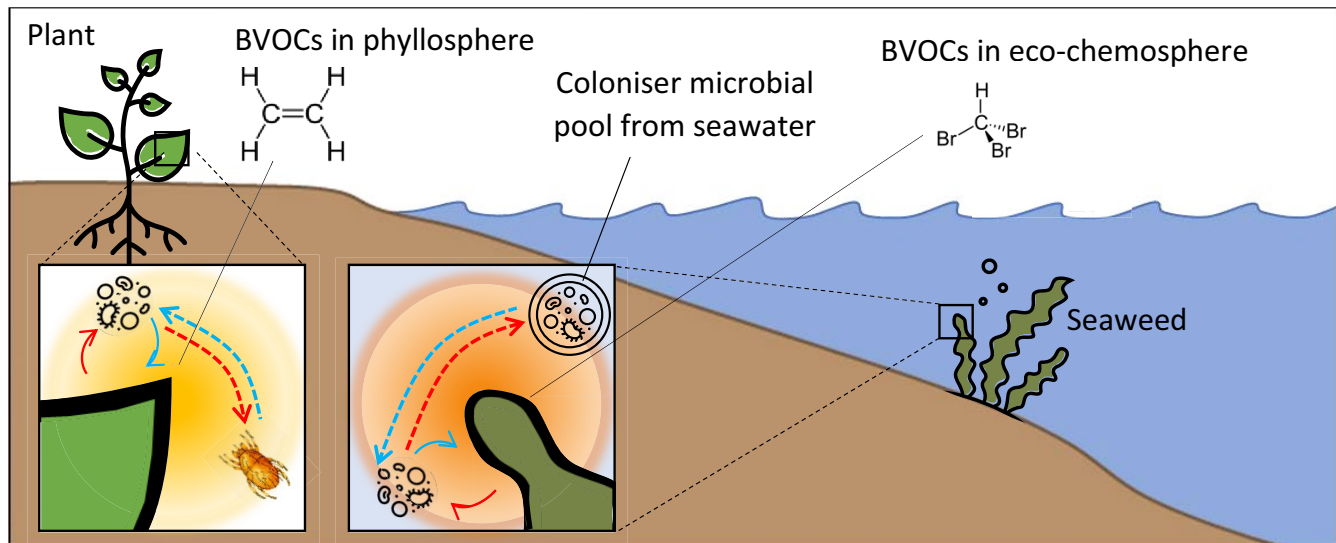


FIGURE 1 The schematic shows an analogy regarding BVOC-mediated primary (thin arrows; red = deterrence; blue = attraction) host-microbe interactions within the phyllosphere of land plants and the eco-chemosphere of seaweeds. The bold dotted arrows (red = deterrence; blue = attraction) indicate the secondary interactions, for example interactions with spider mites that can be mediated *via* this plant-microbe association in phyllosphere of plants. Similar is the case for seaweeds where BVOC-mediated host-microbe interaction can mediate secondary interactions, for example interactions with microbes from the coloniser pool present in seawater

the release of morphogenetic compounds that ensure proper algal morphogenesis. Thus, understanding crosstalk processes is fundamental to defining the type of relationship.

Naturally emitted BVOCs are mostly known for their roles in atmospheric processes (Matsumoto, 2014). Upon oxidation, BVOCs form secondary organic aerosols (SOAs), which act as cloud condensation nuclei (CCN) and thereby affect cloud formation and climate (Zhao et al., 2017). Therefore, the contributions to the global budget of these molecules, climate functioning roles as well as effect of abiotic factors on BVOC emissions are well-investigated for seaweeds (e.g. Kerrison et al., 2012; Rinnan et al., 2014). While many studies have demonstrated the ecological role of plant BVOCs at plant-microbe interface (Junker & Tholl, 2013), similar studies of seaweed BVOCs mediating seaweed-microbe interactions remain largely unexplored.

Rather than performing a comprehensive review on BVOC-mediated microbial interactions, we aimed at drawing parallelism on between plant leaves and seaweed surfaces using selected examples, in order to propose new research directions for volatile-mediated seaweed-microbe research. In this article, we briefly highlight some of the important volatile compounds from recent studies (between 2014 and 2020; for studies before 2013, see review by Junker & Tholl, 2013) that play ecological roles in phyllosphere of plants. While ecological interactions mediated by BVOCs are exceedingly well-studied in terrestrial plant-microbe systems, these have not yet been well-explored for aquatic ecosystems like seaweeds and are restricted to a small number of infochemicals. Thus, we list the very few volatile infochemicals (identified between 2006 and 2020) that have been reported so far in mediating ecological interactions among seaweeds and their surface-associated bacteria. Through this

article, we aim to bring attention to the importance of volatile infochemicals in mediating ecological interactions in eco-chemosphere of seaweeds and advocate for inclusion of volatile infochemistry research while investigating surface-associated seaweed microbe interactions. We also define key questions for future research which may allow us to understand how volatile infochemicals can influence the ecology and biology of seaweed holobionts.

2 | BVOC-MEDIATED INTERACTIONS IN PHYLLOSHERE OF PLANTS

Plant BVOCs are known to modulate density and composition of phyllospheric communities. Plant BVOCs can either promote or inhibit the growth of microbes and thus regulate their colonisation on leaf surfaces, by acting as carbon sources or through their antimicrobial effects (Chagas et al., 2018). Plant BVOCs can function as direct microbial defences and also as cues inducing antimicrobial responses in other parts of the same plant individual or in other plant individuals growing distant from the initial site of infection (Hammerbacher et al., 2019). Nevertheless, the generality of the antimicrobial effects of plant BVOCs is challenged by the ability of some microbes to tolerate and metabolise these volatile compounds (Junker & Tholl, 2013). Phyllospheric microbes can also produce their own BVOCs, which can affect plant physiology (Bitas et al., 2013) and can modulate BVOC emissions and affect interactions between plants and other organisms. Microbial BVOCs can enhance plant growth and stress resistance as well as prevent the colonisation by fungal and bacterial pathogens, and mediate microbial interactions that can have negative and neutral effects on plants (Farré-Armengol et al., 2016).

2.1 | Plant BVOCs as carbon sources for microbes

Biogenic volatile organic compounds from plant leaves can be important carbon sources for bacteria (Mercier & Lindow, 2000). Methylotrophs are prevalent colonists of the phyllosphere, and their typical capacity to grow on C₁ compounds provides them with a growth advantage in this habitat (Iguchi et al., 2015). An abundance of chloromethane-degrading bacteria also showed positive correlation with the production of CH₃Cl in *Arabidopsis thaliana* (Haque et al., 2017). Likewise, the phyllosphere of isoprene-emitting trees, such as poplar (Crombie et al., 2018) and oil palm (Larke-Mejia et al., 2019), harbours isoprene-degrading bacteria, typically equipped with isoprene metabolic genes and able to consume isoprene. Other microbes from the phyllosphere such as fungi can also use such compounds. The removal of fungi from the surface of *Brassica nigra* leaves led to the emission of four new BVOCs (cyclohexanone, cyclohexyl cyanide and two unknown compounds), suggesting the utilisation or inhibition of production of such compounds by fungi (Saurier et al., 2020).

2.2 | Plant BVOCs as defence chemicals

BVOCs from plant leaves can be important in structuring microbial communities (Junker et al., 2011). Ethylene, an important hormone involved in plant defence, contributes to structuring phyllospheric communities: ethylene-insensitive mutants of *Arabidopsis thaliana* showed quantitative differences in the community composition compared to wild-type plants (Bodenhausen et al., 2014). Jasmonic acid (JA), another important plant hormone involved in plant defence, is commonly known to induce the production of plant volatiles such as terpenes from leaf surfaces that can directly inhibit microbial growth (Kiryu et al., 2018; Yoshitomi et al., 2016) and induce resistance to microbes in plants (Taniguchi et al., 2014). Salicylic acid, a third hormone playing important roles in inducing defence such as via volatile terpene emissions, is produced upon pathogen infection of poplar leaves (Eberl et al., 2018).

2.3 | Epi-microbial BVOCs in promoting growth, providing associational defence and mediating tripartite interactions

Epiphytic methanol-utilising bacteria showed multiple plant growth-promoting activities, and foliar application of such bacteria and methanol improved the growth and yield performance of peanut plants (Gashti et al., 2014). Moreover, BVOCs mainly composed of esters, alcohols and S-containing compounds emitted from bacterial colonists of *Agave tequilana* and *Agave salmiana* increased the relative growth rate of their native plant hosts (Camarena-Pozos et al., 2019). Similarly, the fungal phytopathogen *Alternaria alternata* emits volatiles that promote growth and flowering in *Arabidopsis thaliana* (Sánchez-López et al., 2016). Furthermore, from the perspective of biocontrol, numerous microbial BVOCs emitted by phyllospheric microbes showed

antagonistic activities towards various foliar phytopathogens (Barakat et al., 2014; Thakur & Harsh, 2014). Epiphytic microbes from plant phyllosphere play a role in mediating tripartite interactions (Figure 1), for example plant–arthropod interactions (Noman et al., 2020). Depending on the hosted bacterial strain (either *Pseudomonas syringae* or *Pantoea ananatis* or *Pseudomonas putida*), colonised bean plants showed distinct emissions to which female spider mites reacted differently; leaf damage and oviposition preference were generally lower when compared to control plants (Karamanoli et al., 2020).

3 | BVOC-MEDIATED INTERACTIONS AT ECO-CHEMOSPHERE OF SEaweEDS

Seaweeds are a rich source of volatiles, especially halogenated hydrocarbons (Paul & Pohnert, 2011). However, ecological roles of seaweed BVOCs are woefully unexplored especially regarding their roles in the structuring of marine microbial communities when compared to phyllosphere of land plants. While epibacteria from seaweed surfaces can be a rich source of **antifouling compounds** deterring surface colonisation by competitors and invertebrate larvae (da Gama et al., 2014; Saha et al., 2018), all the research conducted so far has focussed mostly on non-volatile compounds either bound to the surface or released into the water column. On the contrary, the potential ecological role of volatiles originating both from the seaweed host and their epimicrobiota in modulating surface colonisation by further microbial colonisers is poorly understood, except for a very few surface-bound halocarbons.

3.1 | Seaweed BVOCs as defence and in structuring epimicrobial communities

Bromophenols are a class of BVOCs commonly found in red and brown seaweeds (Oh et al., 2008). The volatile halomethane bromoform has been found to be released through the surfaces of the red seaweeds *Corallina pilulifera*, *Lithophyllum yessoense* (Ohsawa et al., 2001) and *Asparagopsis armata* (Paul et al., 2006), and exhibits growth-inhibiting activities towards epiphytic marine microalgae and bacteria respectively. The volatile polyhalogenated 2-heptanone 1,1,3,3-tetrabromo-2-heptanone, a BVOC isolated from the surface of the red seaweed *Bonnemaisonia hamifera*, has growth-inhibiting effects against bacterial strains isolated from co-occurring red algae and demonstrated an ecologically relevant role as an antifoulant against bacterial colonisation. *B. hamifera* was found to be less fouled by bacteria relative to co-occurring seaweeds (Nylund et al., 2008). Evidently, 1,1,3,3-tetrabromo-2-heptanone would provide significant fitness benefits to *B. hamifera*. Bromoform and dibromoacetic acid from the red seaweed *Asparagopsis armata* reduce epibacterial density on the surface of the seaweed; individuals of *A. armata* lacking brominated metabolites harbour significantly higher densities of epiphytic bacteria than *A. armata* individuals that produced such metabolites (Paul et al., 2006).

Volatile emissions have also been linked to microbial colonisation as the red seaweed *Gracilaria* sp. released about eight times more BVOCs upon simulation of pathogen attack (Weinberger et al., 2007). Using similar simulations, the brown algal kelp *Laminaria digitata* produced volatile aldehydes (Goullitquer et al., 2009) and halocarbons (Palmer et al., 2005) upon oxidative stress. These compounds are chemically related to BVOC that act as airborne signals involved in the priming of defence responses in terrestrial plants (Cosse et al., 2011). Besides reducing the overall bacterial density, seaweed BVOCs can also structure the epimicrobial communities just like BVOCs from plant leaf surfaces. 1,1,3,3-Tetrabromo-2-heptanone compound from the red seaweed *B. hamifera* was found to shape the epibacterial community composition on the surface of *B. hamifera* (Persson et al., 2011). The brown seaweed *Taonia atomaria* produces two sesquiterpenes as surface-associated compounds that exhibited anti-adhesion properties towards non-epibiotic marine bacteria of the seaweed while being inactive towards epibiotic bacteria, which suggests their ability to regulate surface colonisation (Othmani et al., 2016). Moreover, the possibility that sesquiterpenes play a role in the selection of epibacterial communities is supported by Paix et al. (2020). In surface extracts (in contrast to total extracts), sesquiterpene concentrations were found to vary at a thallus scale with increasing concentrations from the holdfast to the blade and the surface metabolome drive epibiotic microbiota variations on the thallus of *Taonia* (Paix et al., 2020).

4 | FUTURE DIRECTIONS AND PERSPECTIVES

Volatile-mediated microbial interactions of seaweeds have only gained sporadic interest in the past few years. This field of research is quite unexplored when compared to that of volatile-mediated microbial interactions in land plants. Thus, below we discuss some of the potential future directions of research in this field.

4.1 | Investigating the role of seaweed BVOCs as carbon sources

Plant volatiles are known to be carbon sources for epibiotic microbes (e.g. isoprene-degrading and methylotrophic bacteria), which suggests that plant volatiles can act as colonisation inducers. Some studies indicate that a similar mechanism could be expected between seaweeds and marine bacteria. Isoprene degraders have been found in estuarine (Johnston et al., 2017) and marine (Alvarez et al., 2009) environments. Although seaweeds are known to be isoprene emitters (Broadgate et al., 2004), it is still unclear whether such isoprene-degrading bacteria are present on seaweed surfaces. Thus the role of isoprene as an infochemical mediating interactions with surface-associated microbes and other colonisers from the planktonic pool is unknown. Moreover, marine bacteria isolated from seawater have shown the ability to grow on volatile C₁ compounds such as

dimethylsulphide (DMS; Kim et al., 2007; Schäfer, 2007). DMS-degrading bacteria have also been found in association with corals, which are known to emit high levels of DMS (Raina et al., 2009). The identity and DMSP degradation capacity of the bacteria inhabiting the phycosphere and/or the chemical conditions (presence of other infochemicals) within the phycosphere of phytoplankton might regulate the direction of DMSP transformation and thereby influence the amount of DMS released into the atmosphere (Seymour et al., 2010). As DMS is of significant climatic importance, Seymour et al. (2017) argued that these microbial-scale ecological interactions acting within the phycosphere would have important implications for regional-scale climate regulation. Given seaweeds are known to release DMS in seawater as well (Bravo-Linares et al., 2010), DMSP has been detected on the surface of seaweeds (Saha et al., 2012) and similar ecological interactions also exist in the eco-chemosphere of seaweeds, it may be expected to find DMSP degraders in association with seaweeds—a hypothesis that deserves being tested in the future. Like phytoplankton, the presence of DMSP degraders on seaweed surfaces will have important implications for regional climate regulations.

Aquatic plant surfaces were also found to consume higher amounts of methane than those of terrestrial plants, and to harbour a number of methanotrophs quantitatively correlated with their methane consumption (Yoshida et al., 2014). Thus, it will be also interesting to investigate if seaweed thallus can act as a site for methane consumption and emission. To our knowledge, no study on associations between seaweeds and marine bacteria using seaweed volatiles as carbon sources has been published yet, although recent work suggests that seaweed BVOCs could effectively attract/repel marine bacteria to their surfaces (M. Saha, unpublished data).

4.2 | Investigating the role of seaweed BVOCs in direct antimicrobial defences and microbial 'gardening'

We already know that an infochemistry-dependent selection process leads to controlled enrichment of specific bacteria on seaweed surfaces (e.g. Paix et al., 2019; Saha & Weinberger, 2019). To better understand the complex seaweed-microbe interactions mediated by BVOCs on surfaces, future studies should characterise surface-associated seaweed BVOCs coupled with screening their roles in regulating microbial density on the surface of seaweeds. Techniques like solid phase micro extractions, and purge and trap, would allow collecting seaweed BVOCs before gas chromatography analyses. Evaluating the role of BVOCs on surface bacterial settlement and/or growth could be done in different ways: either testing each compound in isolation or a mix of all volatile compounds could be tested at ecologically relevant concentrations. Also, as desiccated seaweeds are known to accumulate a higher concentration of antifouling compounds on their surface (Brock et al., 2007), one should consider incubating the seaweed with and without seawater to analyse the

BVOCs released without and with desiccation and thereby test the resulting influence on epimicrobial communities.

Additionally, unlike BVOCs in phyllosphere of plants, the role of surface-associated seaweed BVOCs in the filtering process of environmental bacteria that may regulate community composition is unknown. To explore the ecological roles of seaweed BVOCs related to microbial surface colonisation, further research should compare how bacteria that colonise seaweeds (and those that do not because their settlement and growth is inhibited by BVOCs) impact seaweed health and fitness. As observed in phyllosphere bacteria, growth-promoting activities of seaweed BVOCs can be investigated in seaweed-associated bacteria, and positive response to seaweed BVOCs could be investigated. Additionally, seaweeds with artificially modified BVOC profiles could be used to study interactions mediated by volatile compounds between seaweeds and marine bacteria. To complement such experiments, tolerance/resistance to BVOCs could be searched in bacteria still present on seaweed surfaces emitting BVOCs, and eventually if such bacteria promote the growth and fitness of seaweeds as well.

4.3 | Investigating the role of seaweed BVOCs in indirect or tripartite defences

Large variety of BVOCs are emitted by terrestrial plants during infection by pathogenic microbes. These BVOCs function as defence against pathogenic microbes (Hammerbacher et al., 2019). Although the role of phytoplankton BVOCs in mediating tritrophic interactions was proposed by Steinke et al. (2002) more than a decade ago, studies performed on seaweeds are still very limited when compared to land plants. Thus, the potential role of seaweed BVOCs in seaweed–seaweed communication upon pathogen or herbivore attack has been not been investigated yet. As some seaweed BVOCs are chemically related to species which prime defence responses in terrestrial plants (Cosse et al., 2011), we may expect that seaweed BVOCs may act as induction signal for antimicrobial defence. It will be also interesting to investigate if microbes colonising seaweed surfaces can alter the BVOCs produced on the surfaces and thereby influence tritrophic interactions, as observed in the phyllosphere of terrestrial plants.

5 | CONCLUSIONS

In conclusion, seaweed volatiles appear to be related to terrestrial plant volatiles both in terms of chemistry and ecology regarding surface interactions with microbes. Ecological roles such as those of plant volatiles, which are intensively explored, could be expected for seaweeds as well. However, when compared to plants, currently our knowledge on volatile infochemicals in mediating seaweed–microbe interactions is still scarce, while rapid ongoing climate-driven changes (rising temperature, acidification, hypoxia, desalination) can potentially modify such BVOC-mediated interactions. Future studies

investigating seaweed volatiles in the context of seaweed–microbe interactions will thus contribute to our understanding of the ecological roles of these compounds in surface colonisation. Answering these fundamental questions in the near future will be essential to address how BVOC-mediated seaweed–microbe interactions may be altered at different spatial and temporal scales, under climate change-induced stressors and thereby alter further ecological interactions. Such alterations in ecological interactions may further influence the release of BVOCs into the atmosphere either qualitatively or quantitatively or both.

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AUTHORS' CONTRIBUTIONS

M.S. and P.G. wrote the paper; M.S. and F.V. supervised P.G.; M.S. conceived the idea, designed and planned the paper. All the authors approved the submitted version.

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ORCID

Mahasweta Saha  <https://orcid.org/0000-0001-9308-1054>

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