

## Viewpoint

# Infochemicals in terrestrial plants and seaweed holobionts: current and future trends

### Summary

Since the holobiont concept came into the limelight ten years ago, we have become aware that responses of holobionts to climate change stressors may be driven by shifts in the microbiota. However, the complex interactions underlying holobiont responses across aquatic and terrestrial ecosystems remain largely unresolved. One of the key factors driving these responses is the infochemical-mediated communication in the holobiont. In order to come up with a holistic picture, in this Viewpoint we compare mechanisms and infochemicals in the rhizosphere of plants and the eco-chemosphere of seaweeds in response to climate change stressors and other environmental stressors, including drought, warming and nutrient stress. Furthermore, we discuss the inclusion of chemical ecology concepts that are of crucial importance in driving holobiont survival, adaptation and/or holobiont breakdown. Infochemicals can thus be regarded as a 'missing link' in our understanding of holobiont response to climate change and should be investigated while investigating the responses of plant and seaweed holobionts to climate change. This will set the basis for improving our understanding of holobiont responses to climate change stressors across terrestrial and aquatic ecosystems.

### Introduction

Ten years ago, a paradigm shift across the life and medical sciences brought awareness to the importance of the holobiont concept (see Table 1 Glossary). The term holobiont was first introduced by Lynn Margulis (Margulis, 1991) and describes the host and its associated community of microorganisms. Since then, several studies have addressed the complex interactions of host-associated microbes that influence many eukaryotic holobionts, including marine (e.g. the sponge, coral and seaweed holobionts; Thompson *et al.*, 2015; Webster & Thomas, 2016; Pita *et al.*, 2018; van der Loos *et al.*, 2019) and terrestrial holobionts (e.g. the plant and insect holobionts; Vandenkoornhuysen *et al.*, 2015; Dittmer *et al.*, 2016). In the plant and seaweed holobiont (also known as marine macroalgae), these interactions with microbes can result in improved host health (Longford *et al.*, 2019), increased growth (Berendsen *et al.*, 2012), disease suppression (Mendes *et al.*, 2011;

Chapelle *et al.*, 2016; Ritpitakphong *et al.*, 2016; Saha & Weinberger, 2019) and adaptation towards abiotic stressors (Dittami *et al.*, 2016). However, these interactions can also have negative effects, such as loss of morphology without the presence of beneficial bacteria (Wichard, 2015; Compant *et al.*, 2019) or can cause diseases as a result of dysbiosis between microbes with plant-health supporting functions and plant pathogenic microbes (Mendes *et al.*, 2013; Durán *et al.*, 2018; Yu *et al.*, 2019). Thus, responses of both plants and seaweeds to climate-change-induced stressors and environmental stress may be driven by shifts in their microbiota (Naylor & Coleman-Derr, 2018; Timm *et al.*, 2018; van der Loos *et al.*, 2019).

Surfaces of plants and seaweeds are characterised by strong chemical gradients due to exudation of organic and inorganic compounds (collectively called infochemicals), which can attract or deter microbes. Bacteria use quorum sensing (QS) to co-ordinate collective behaviours through cell-to-cell communication. QS relies on the production, release, and group-level detection of infochemicals called auto-inducers (reviewed in Papenfort & Bassler, 2016). Thus, infochemicals drive much of the host-microbial and microbe-microbe interactions and are suggested as one of the key ecological drivers in terrestrial and marine holobiont interactions (Hassani *et al.*, 2018; Saha *et al.*, 2019; Schmidt *et al.*, 2019). Yet, infochemicals are often overlooked in studies investigating the effect of climate change on the plant and seaweed host-microbe relationship. In this viewpoint, we aim to bring attention to the importance of infochemicals in climate change responses by comparing mechanisms and compounds that play key roles in both, plant and seaweed holobionts. Consequently, we call for the inclusion of chemical ecology concepts in holobiont research, which can provide essential key aspects in understanding responses of plant and seaweed holobionts to climate change stressors and other environmental stressors.

### Infochemicals of the rhizosphere in the plant holobiont

In the plant holobiont, the rhizosphere represents a hotspot of chemically mediated interactions (Mendes *et al.*, 2013; Mhlongo *et al.*, 2018) in which millions of chemical compounds are being exchanged between the plant and its microbiota (Mhlongo *et al.*, 2018). Therefore, we focus here on the interactions taking place in the rhizosphere. Infochemicals in the rhizosphere are largely composed of low-molecular weight, high-molecular weight and volatile organic compounds (VOCs) (Ortíz-Castro *et al.*, 2009; Schenkel *et al.*, 2015; Tyc, *et al.*, 2017). Depending on their diffusion ability infochemicals have different action ranges, with VOCs diffusing further in the soil environment than non-volatile compounds (de la Porte *et al.*, 2020). This gradient can guide either chemo-attraction of beneficial bacteria in the rhizosphere that sense infochemicals via as yet unknown receptors (Schulz-Bohm *et al.*,

Table 1 Glossary.

Antifoulant	Chemical compounds that inhibit the colonization process of a solid surface (living or non-living).
Dysbiosis	The shift in the microbiome from a stable state to disturbed state where commensal or new colonizers may become detrimental.
Epibacteria	Bacteria colonizing the surface of the host organisms.
Holobiont	Host and its associated communities of microorganisms (i.e. microbiota, including mutualistic to parasitic interactions).
Infochemicals	Chemical compounds (organic and inorganic) released by microbes, animals and plants into their environment and used as cues and signals, where chemical cues are unintentionally released compounds and chemical signals are intentionally released compounds that supply specific information.
Microbiota	The collection of microorganisms in interaction with their host, ranging from mutualistic to parasitic interactions.
Quorum sensing	A cell-density dependent mechanism by which bacteria communicate and collectively regulate gene expression.
Rhizosphere	The region of the soil under the direct influence of plant root activities, including water and nutrient uptake, rhizodeposition, and gas dynamics.
Volatile organic compounds (VOCs)	Small, carbon based molecular weight compounds with low molecular mass, high vapor pressure, low boiling point and a lipophilic moiety.

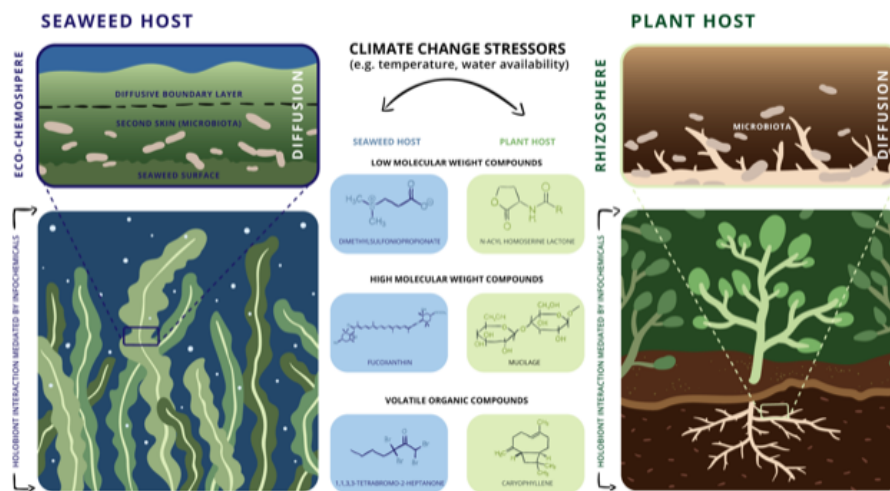
2018), or deterrence of pathogens (Weisskopf, 2013; Raza *et al.*, 2016) and other predators (Schulz-Bohm *et al.*, 2017). Infochemicals produced on the root surface can also act as chemical defence against pathogens and other microorganisms that compete for nutrients (Bais *et al.*, 2004; Raaijmakers & Mazzola, 2012). Low-molecular weight root exudates, including sugars, amino acids and organic acids (e.g. malic acid or fumaric acid), phenolics (e.g. flavonoids) and other secondary metabolites serve as substrates and signaling molecules for microbes (Bais *et al.*, 2006). Microbial low-molecular weight compounds with direct and indirect beneficial properties for the plant host include siderophores (Aznar & Dellagi, 2015) and quorum sensing signals, like N-acyl-homoserine lactones (AHLs, Schikora *et al.*, 2016). AHL-based quorum sensing is a well described mechanism of chemical communication that acts in a cell density-dependent manner (Eberl, 1999). Quorum sensing is likely an important mechanisms for the communication between the plant holobiont by serving as a universal language for bacterial communication (for more details we refer to the review by Hassani *et al.* (2018)). Microbe-associated molecular patterns (MAMPs) and pathogen-associated molecular patterns (PAMPs) may also be classified as low-molecular weight infochemicals that are sensed by the plant host and trigger innate immunity responses (Ranf, 2017). These include the protein flagellin, the Elongation Factor Tu (EF-Tu) or the receptor-like protein ReMAX (for a more in-depth review on innate immunity and the plant microbiota we refer to the review by Hacquard *et al.* (2017)). High-molecular weight root exudates primarily include mucilage (high molecular weight polysaccharides) and proteins that mostly serve as carbon-based nutrients for microbes and

regulate microbial diversity and activity in the rhizosphere (Bais *et al.*, 2008; Mendes *et al.*, 2013). Root and microbial derived volatile infochemicals belong to several chemical classes, including alkenes, alcohols, ketones, benzenoids, pyrazines, sulfides, and terpenes (Schulz & Dickschat, 2007; Schmidt *et al.*, 2015; Bouwmeester *et al.*, 2019) and generally act in a concentration dependent manner (Nemcovic *et al.*, 2008; Schmidt *et al.*, 2016). VOCs that maintain soil health, promote plant growth and drive resistance of pathogens include 2-3-butanediol (Ryu *et al.*, 2003; Kong *et al.*, 2018), dimethyl-disulfide (DMDS) (Meldau *et al.*, 2013; Chinchilla *et al.*, 2019), and indole (Bailly *et al.*, 2014). Terpenes are one of the most important volatile infochemicals that mediate belowground-interactions between plants and microbes, such as (E)- $\beta$ -caryophyllene (Rasmann *et al.*, 2005; Schulz-Bohm *et al.*, 2017). While plant roots release a wide range of unique terpene compounds via the mevalonate (MVA) or non-mevalonate (MPE) pathways (Huang & Osbourn, 2019) with terpene synthases (TPSs) being the key gatekeepers in terpene biosynthesis (Karunanithi & Zerbe, 2019). Since the recent discovery that TPSs are widely distributed in bacteria too (Yamada *et al.*, 2015; Dickschat, 2016), TPSs encoding for several common plant root and fungal emitted terpenes, like the (E)- $\beta$ -caryophyllene synthase (Fig. 1) have been also been found in soil bacteria (Rabe *et al.*, 2013).

Apart from infochemicals being individually produced by the plant host and the microbiota, the microbiota can induce plant infochemicals and modulate plant hormone levels and the pathways they steer (Ravanbakhsh *et al.*, 2018). For example, the microbial VOC acetoin and 2,3-butanediol and the quorum sensing signals AHLs (reviewed in Sharifi & Ryu, 2018b) can elicit the plant hormonal signals salicylic acid and jasmonic acid/ethylene that trigger plant defense mechanisms. Similarly, the plant growth promoting hormones auxin or cytokinin can be induced by bacteria producing infochemicals like indole (Ryu *et al.*, 2003; Bailly *et al.*, 2014; Bhattacharyya *et al.*, 2015). Some of these volatile infochemicals are suggested to act in similar ways as the previously described MAMPs (Sharifi & Ryu, 2018a); however no experimental evidence has supported this hypothesis so far. Overall, the hormonal regulation by the microbiota illustrates one of the core concepts of the holobiont theory, namely that plants and microbes form an ecological unit that adapts plant responses to specific situations (Vandenkoornhuys *et al.*, 2015) (for a review on ethylene signaling as a model system for holobiont evolution we refer to Ravanbakhsh *et al.* (2018)).

### Infochemicals of the eco-chemosphere in the seaweed holobiont

Communication via infochemicals is mainly mediated through the seaweed surfaces which, together with their 'second skin' of microbes (dominated mainly by epibacteria; Wahl *et al.*, 2012) and an additional diffusive boundary layer of water (Hurd, 2000) represents a micro-niche analogous to the rhizosphere of plant roots or the phycosphere of phytoplankton cells (Seymour *et al.*, 2017). Rich in infochemicals, a seaweed's surface layer is a micro-hotspot of ecological interactions that are chemically mediated. Therefore,



**Fig. 1** Seaweed (left) and plant (right) holobiont interactions driven by infochemicals in the eco-chemosphere and rhizosphere, respectively. Infochemicals are either produced by the microbiota, by the host or both. E.g. DMSP (Dimethylsulfoniopropionate) is produced by both, the seaweed host and the microbiota. Similarly, in the plant holobiont, E- $\beta$ -caryophyllene is produced the host and the microbiota, while quorum sensing molecules like N-acyl homoserine lactones are produced only by the microbiota. Climate change stressors, such as increasing temperature in water or soil or water availability in soil can affect the infochemical-driven interactions taking place in the holobionts, leading to either 1) holobiont adaptation or 2) holobiont breakdown depending on the balance of beneficial and pathogenic members of the microbiota and the infochemicals produced. Figure by illustrator Ariana Sauder.

we propose a new term, the ‘eco-chemosphere’ for this layer (Fig. 1), which could be also applied to other marine macro-organisms like sponges or corals. Similar to the rhizosphere, gradients of infochemicals within this sphere can guide chemotaxis of bacteria in microscale interactions (Seymour & Raina, 2018), where motile bacteria can sense infochemicals using transmembrane chemoreceptors that allow them to direct their movement towards or away from the chemical gradients. The radius of influence of this sphere, for example, would be dependent of properties of the living surface (including infochemicals release rate, wettability, microtopography) as well as of the properties of the infochemical itself (e.g. polarity, molecule persistence in the medium). Infochemicals from the surface of seaweeds can also act as a chemical defence against other microbial colonizers as excessive microbial colonization followed by colonization of macro-organisms (e.g. mussels, bryozoans) might not only hinder nutrient uptake, but also reproduction and photosynthesis among other processes (reviewed by da Gama *et al.*, 2014; Saha *et al.*, 2018). Moreover, this defence can be provided by associated microbes (Nasrolahi *et al.*, 2012). Yet, until the development of surface extraction method about two decades ago, identifying infochemicals that are present at (or near) the surface of the seaweed host and the boundary layer was a major challenge. Compared to terrestrial plants, surface associated infochemicals mediating interactions with bacteria have only been identified from a handful of seaweeds so far and include VOCs like halogenated furanones (Dworjanyn *et al.*, 2006), bromoform and dibromoacetic acid (Paul *et al.*, 2006), polybrominated 2-heptanone (Nylund *et al.*, 2008) from red seaweeds. The halogenated furanones act as a specific antagonist of the acylated homoserine lactone (AHL) regulatory system (quorum sensing) present in bacteria, thereby inhibiting bacterial colonization (Manfield *et al.*, 2002). Bromoform and dibromoacetic acid were found to reduce epibacterial colonization on the surface of the red seaweed *Asparagopsis armata*. The volatile

polyhalogenated 2-heptanone (1,1,3,3-tetrabromo-2-heptanone) isolated from the surface of the red seaweed *Bonnemaisonia hamifera* had growth-inhibiting effects against bacterial strains isolated from co-occurring red algae and demonstrated an ecologically relevant role as an antifoulant against bacterial colonization (Nylund *et al.*, 2008). Thus, 1,1,3,3-tetrabromo-2-heptanone could provide significant fitness benefits to *B. hamifera*. Besides reducing the overall bacterial density, this compound was found to control the density and composition of seaweed-associated bacterial communities (Persson *et al.*, 2011). Other VOCs like sesquiterpenes (Othmani *et al.*, 2016b) are known to be produced by the brown seaweed *Taonia atomaria*. *T. atomaria* produces two sesquiterpenes as surface-associated compounds that exhibited anti-adhesion properties towards non-epibiotic bacteria of the seaweed while being inactive towards epibiotic bacteria isolated from the surface of *T. atomaria*, which suggests their ability to regulate surface colonization (Othmani *et al.*, 2016a). Surface associated seaweed compounds also include low molecular weight compounds like dimethylsulfoniopropionate (DMSP; Saha *et al.*, 2012), and high molecular weight compounds like fucoxanthin (Saha *et al.*, 2011) from the brown seaweed *Fucus vesiculosus*. Infochemicals like DMSP, fucoxanthin and proline identified from the surface of *F. vesiculosus* that are known to have both anti and pro-biotic effect depending on the bacterial strains tested, were found to affect the overall bacterial community composition associated with *F. vesiculosus*. Tendencies for insensitivity towards all three compounds were reported among bacterial taxa that were found to typically dominate the epibacterial communities of the *F. vesiculosus* holobiont (Saha *et al.*, 2014).

As described earlier for the plant holobiont, infochemicals in the seaweed holobiont can be also produced by the host, the microbiota or both. For example, transcriptomic analysis of the red seaweed *Laurencia dendroidea* and its microbiome demonstrated biosynthesis of terpenoids, such as (–)-elatol through the MEV pathway

by the seaweed itself (de Oliveira *et al.*, 2012). By contrast, DMSP can be emitted by both the seaweed host and the surface associated bacteria (Fig. 1) as marine bacteria are also known to be DMSP producers (Williams *et al.*, 2019) and can contribute to the production of DMSP along with the seaweed host. Thus, contribution towards the chemical cocktail of surface associated infochemicals will depend on the abundance and thickness of epibacteria in the 'second skin' as well as their metabolic activity (Wahl *et al.*, 2010). Epibacteria on seaweeds also have core functions related to protection against pathogens (Saha & Weinberger, 2019) and in morphogenesis via the release of morphogenetic compounds (Wichard *et al.*, 2015). Moreover, epibacteria from seaweeds are known to offer functions like chemical defence as they can produce antibacterial compounds that can protect seaweeds from further colonization (Kumar *et al.*, 2011).

Vesicle transportation along membranous tubular collection and cell death events of *corps en cerise* (or cherry bodies) was found to be responsible for exudation of halogenated compounds to the thallus surface of the red macroalgae *Laurencia obtusa* with defensive role against colonizers (Salgado *et al.*, 2008). Molecular mechanism regulating morphogenesis in the green macroalgae was deciphered recently when demonstrated that thalassin released by *Maribacter* sp. induced rhizoid and cell wall formation. The authors showed that gametes acquired the iron complex of thalassin thereby linking morphogenetic processes with intracellular iron homeostasis.

### Current trends: infochemicals across plant and seaweed holobionts in response to climate change stressors and other abiotic factors

Climate-change-induced stressors, such as warming and increased CO<sub>2</sub>, can alter the production and composition of infochemicals with profound effects on terrestrial and marine ecosystems. In the plant holobiont, abiotic stress such as water (flooding, drought) and nutrient stress (changes in nitrogen and phosphorus availability) can alter chemical composition of root exudate profiles and root morphology, which in turn affect the assembly, composition and metabolic functioning of the microbiota (Hartman & Tringe, 2019). A widely observed phenomenon in water-limited soils is an increase in the ratio of Gram-positive to Gram-negative bacteria, with increases in bacteria of the phylum *Actinobacteria* and *Firmicutes* (Naylor *et al.*, 2017; Fitzpatrick *et al.*, 2018); an effect that can be partially explained by a physiological advantage that makes these phyla more adapted to dry conditions in soil. Often these changes are driven by one or a few members of a phylum with observed small shifts in response to drought (Barnard *et al.*, 2013). *Actinobacteria*, including *Streptomyces* sp. are known emitters of VOCs that belong to a range of chemical classes, including alcohols, ketones, esters, and nitrogen- and sulfur-containing compounds, and their VOC profiles are typically strain specific (Cordovez *et al.*, 2015; Choudoir *et al.*, 2019). Changes in the abundance of *Actinobacteria* suggests an effect on the emission of infochemicals and the resulting chemically mediated interactions in the plant holobiont on a fine-scale level.

Indirect or direct changes in microbial chemical compounds in the rhizosphere have already been shown to influence the health and fitness of the plant host in response to abiotic changes (Hartman & Tringe, 2019). Root exudates seem to be one of the key class of infochemicals in shaping plant holobiont responses to climate change by contributing to the structure of rhizosphere communities. A recent study showed that root exudation is coupled with microbial substrate-use preferences that contributes to the assembly of the rhizosphere microbiome, enabling the use of metabolite interaction traits to engineer favorable microbial communities on roots (Zhalnina *et al.*, 2018). This suggests that plants regulate their metabolic interactions with microorganisms, thus potentially recruiting beneficial communities (Zhalnina *et al.*, 2018). A controlled mechanism of the plant holobiont to maintain microbial activity during drought recovery also stems from root exudates that can trigger more soil respiration (priming of soil carbon), thus facilitating regrowth through stimulating microbial activity in the rhizosphere (Vries *et al.*, 2019). Similarly, microbial VOCs like 2,3-butanediol and DMDS can induce abiotic stress tolerance consequently preventing the suppression of plant growth and reduction in crop yields (Ryu *et al.*, 2004; Tyagi *et al.*, 2020). The same compound, 2,3-butanediol was shown to induce drought tolerance by stimulating the plant production of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) and nitric oxide (NO) (Cho *et al.*, 2013). Other protecting mechanisms triggered by infochemicals include the accumulation of antioxidants and osmo-protectants in plants via microbial VOCs (Zhang *et al.*, 2010), facilitation of iron uptake under iron deficiency via microbial VOCs and coumarins (Zhang *et al.*, 2009; Voges *et al.*, 2019), plant growth by microbial VOCs (Ryu *et al.*, 2003; Bailly & Weisskopf, 2012; Bitas *et al.*, 2013) and immunity via MAMPs (Stringlis *et al.*, 2018). Infochemicals can also serve as nutrients when the plant is under starvation. Under conditions of sulfur starvation, plants can directly take up and assimilate the S-containing compounds like DMDS emitted from some plant-growth promoting bacteria (Meldau *et al.*, 2013) (for more details we refer to the review by Liu & Zhang, 2015).

Increasing CO<sub>2</sub> levels are largely absorbed by the oceans, decreasing pH of the surface water impairing functionality of marine infochemicals (e.g. volatile infochemicals cause chemotactic reactions among invertebrates associated with the seagrass community. Such behaviour was found to differ between current and high CO<sub>2</sub> conditions treated seagrass (Zupo *et al.*, 2015). Diseases are also an emerging threat to ocean ecosystems due to increasing anthropogenic stressors, like increased water temperatures. In heat stressed coral holobiont fragments, concentrations of the infochemical DMSP increased five-fold, correspondingly increasing the chemotactic response of the pathogen *Vibrio coralliilyticus* towards heat stressed coral (Garren *et al.*, 2014). However, compared to marine animal holobionts like corals, the impact of climate change stressors on infochemicals mediating interactions within the seaweed holobiont remains underexplored (see Saha *et al.*, 2014).

Warmer waters have been positively correlated with higher frequencies of bleaching in the red seaweed *Delisea pulchra*. Bleached thalli of the alga not only had low levels of antibacterial defence compared to healthy individuals but the microbial

community associated with bleached thalli were also distinct from those on surfaces of healthy *Delisea* individuals (Campbell *et al.*, 2011). Bleached individuals had significantly lower level of the antimicrobial infochemical furanones than co-occurring healthy individuals. Contradictory to *Delisea*, temperature stressor up to 25°C using indoor mesocosms leads to a very limited effect upon antibacterial infochemical (dimethylsulphoniopropionate (DMSP), fucoxanthin and proline) concentrations of the brown seaweed *Fucus vesiculosus* (Saha *et al.*, 2014). Interestingly, while proline and fucoxanthin rarely reached surface concentration ranges necessary to deter epibacterial colonization, DMSP was found to be sufficiently concentrated on the surface of the alga to inhibit epibiotic bacterial colonization under all temperature treatments.

### Future trends: Integration of chemical ecology in holobiont under climate change studies

In order to recruit beneficial microorganisms, plants release infochemicals (see section 'Infochemicals of the rhizosphere in the plant holobiont') into their root's surroundings that selectively stimulate beneficial microorganisms for plant growth and health (Reinhold-Hurek *et al.*, 2015; Sasse *et al.*, 2018), but also microbes produce infochemicals as a direct response to changes in their environment which helps the plant to adapt to stressors. As a result, in the past few years lots of focus has been put towards investigating the protective functions of the microbiota for the health of the plant host in response to biotic and abiotic stresses (Vannier *et al.*, 2019). Yet, we do not know how abiotic changes affect the production of infochemicals of microorganisms that show a higher abundance in response to stressful conditions.

Variation in abiotic factors due to changes in temperature and soil moisture have been shown to induce a shift in chemically-mediated interactions in the plant holobiont that further led to shifts in the community composition (see section 'Current trends: infochemicals across plant and seaweed holobionts in response to climate change stressors and other abiotic factors') (Xu *et al.*, 2018). In plants, in addition to temperature, water availability is an important factor that controls microbial activity in soil (Insam & Seewald, 2010), and the production of infochemicals depending on their physico-chemical properties (e.g. water solubility). For example, monoterpene emission by soil microbes, including  $\alpha$ -pinene and limonene was shown to increase with decreasing soil moisture (Asensio *et al.*, 2007). It seems likely that chemically-mediated interactions in the plant holobiont are affected by soil warming and lower water availability (Asensio *et al.*, 2007; Meisner & de Boer, 2018), thus modulating the plant hosts' response to drought.

Almost a decade ago, it was demonstrated for the first time that an entire suite of surface associated metabolites from the surface of the brown seaweed *Fucus vesiculosus* can play a strong selective role in recruiting epibacteria on the surface of seaweed (Lachnit *et al.*, 2010). However, no evidence could be demonstrated for the beneficial role of such microbes and the purpose of chemically mediated recruitment of microbes. Recently, infochemicals from the surface of the red seaweed holobiont *Agarophyton vermiculophyllum* were shown to engage in chemically mediated

microbial 'gardening' by specifically attracting beneficial microbes while deterring detrimental pathogens (Saha & Weinberger, 2019). Although it is evident that seaweed holobiont infochemicals play a strong selective role in structuring the seaweed holobiont, how these seaweed holobiont infochemicals may change under stressors has not yet been well addressed while investigating responses of seaweed holobionts under climate change.

Variation in abiotic factors due to changes in season or location can cause a variation in such chemically mediated interactions at the surface of seaweeds (Saha & Wahl, 2013). Recent work by (Paix *et al.*, 2019), demonstrated that temporal factors like seasonality can be positively correlated to the presence of certain infochemicals on the surface of the brown macroalga *Taonia atomaria*. While the 'spring period' cluster was mainly characterized by dipeptides and positively correlated with a single bacterial taxon of the Alteromonadaceae family, the 'summer period' cluster was dominated by epibacterial taxa (including Erythrobacteraceae, Rhodospirillaceae, Oceanospirillaceae and Flammeovirgaceae) and showed positive correlations with a few metabolites like DMSP and proline, known as seaweed antimicrobial compounds. Climate change induced regional stressors, like for example low salinity, can cause an altered bacterial community composition on the surface of seaweeds. Thus, acclimation can be mediated by changes in the microbiota. For example, in brown algae the genus *Ectocarpus*, presence of certain specific bacteria was found to facilitate adaptation to low salinity environment (Dittami *et al.*, 2016). The authors found that the *Ectocarpus* strain 371 (originally isolated from freshwater) was unable to survive in diluted seawater medium (DSWM) upon removal of bacteria through an antibiotic treatment. Cultures treated with antibiotics in seawater medium did not survive the transfer to DSWM, even after several weeks of recovery. To re-establish the capacity of antibiotic-treated strain 371 to acclimate to DSWM, the strain was re-inoculated with medium from non-antibiotic treated cultures. Bacterial strains specifically responsible for this adaptation to low salinity treatment were not identified. Similarly, in plants, increased abundance and activity of monoderm bacteria, which lack an outer cell membrane and contain thick cell walls was shown to be correlated with the adaptation to drought (Xu *et al.*, 2018). Given that surface microbiota can change in response to the surface infochemistry in terrestrial plants (as evidenced above), like terrestrial plants, we do not know yet whether this altered microbiota may assist the seaweed with regard to adaptation to climate change stressor via the production of infochemicals.

### Perspectives

Given that environmental factors like season and location can drive changes in the infochemistry and thereby drive responses of the microbiota, we hypothesize that climate-change-induced stressors like increased mean temperature can also induce quantitative or qualitative changes in the host and or microbiota emitted infochemicals of plants and seaweeds. Such changes have already been observed for DMSP in corals, where increased production of DMSP in thermally stressed corals attracted the pathogenic bacteria *Vibrio coralliilyticus* (Garren *et al.*, 2014). Seaweeds are

also known to be prolific producers of DMSP (Van Alstyne & Puglisi, 2007), which can be both catabolized and metabolized by marine bacteria. This serves as an example of how increased temperatures may lead to an increased exudation of DMSP on the surface of seaweeds (and also released DMSP into the water column), which may not only attract beneficial bacteria (Kessler *et al.*, 2018) but also pathogenic microbes, thus leading to dysbiosis and ultimately resulting in diseased holobionts. Climate change stressors, like increased mean temperature or ocean acidification have been found to cause shifts in microbial communities of seaweeds (Minich *et al.*, 2018) or maintain stable communities i.e. microbiota did not change with pCO<sub>2</sub> levels (Cavalcanti *et al.*, 2018). However, unlike terrestrial plants we do not know how these altered epibacterial profiles may result in an alteration of the infochemicals produced by these surface microbiotas. We also do not know how such an alteration in the infochemistry of plants and seaweeds under climate-change-induced stressors may affect the tritrophic ecological interactions mediated by these plant and seaweed holobiont infochemicals.

Both plant and seaweed holobiont research is currently aimed at understanding how holobionts adapt to climate change stressors (Classen *et al.*, 2015; Duarte *et al.*, 2017; Simon *et al.*, 2019). However, it is currently not known who is responding first to climate change stressors: the host or the microbiota, or both simultaneously? Infochemicals from microorganisms seem to play a pivotal role in enabling plants to increase their environmental tolerance. But, unlike terrestrial plants, this aspect has not been studied so far in seaweeds as mentioned earlier (section 'Future trends: Integration of chemical ecology in holobiont under climate change studies'). We also do not know for both plant and seaweed holobionts if there are key infochemicals or specific classes of infochemicals (e.g. terpenes) that drive climate change adaptation and if so, can they be induced, for example through microbiome engineering, in order to support holobiont survival/adaptation?

The underlying infochemical-mediated mechanisms driving changes in host–microbe interaction are strikingly unexplored despite sufficient evidence (described earlier). Infochemicals can thus be regarded as a 'missing link' in our understanding of holobiont responses to climate change and should be investigated while investigating the responses of plant and macroalgal holobionts to climate change. There is an obvious need to prioritize the inclusion of chemical ecology in plant and seaweed holobiont research. This will lead to a better understanding and assessment of how climate-change-induced stressors affect interactions in plant and seaweed holobionts. Understanding these interactions and underlying mechanisms will allow us to harness the goods and services provided by terrestrial and marine holobionts that are imperative to the health of ecosystems and to human health.


## Acknowledgements


MS acknowledges Plymouth Marine Laboratory for a PML fellowship. RS acknowledges Mitacs for a postdoctoral fellowship. We gratefully appreciate the valuable input and comments from Paolina Garbeva and three anonymous reviewers.

## Author contributions

RS and MS conceived the idea, designed, and planned the research and wrote the manuscript. RS and MS contributed equally to this work.

## ORCID

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

Ruth Schmidt  <https://orcid.org/0000-0003-2491-0706>

**Ruth Schmidt<sup>1</sup>**  **and Mahasweta Saha<sup>2\*</sup>** 

<sup>1</sup>Department of Microbiology and Biotechnology, Institut Armand Frappier, Montreal, H7V 1B7, Canada;

<sup>2</sup>Marine Ecology and Biodiversity, Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, UK

(\*Author for correspondence: [sahamahasweta@gmail.com](mailto:sahamahasweta@gmail.com))

## References

- Asensio D, Peñuelas J, Filella I, Llusà J. 2007. On-line screening of soil VOCs exchange responses to moisture, temperature and root presence. *Plant and Soil* 291: 249–261.
- Aznar A, Dellagi A. 2015. New insights into the role of siderophores as triggers of plant immunity: what can we learn from animals? *Journal of Experimental Botany* 66: 3001–3010.
- Bailly A, Groenhagen U, Schulz S, Geisler M, Eberl L, Weiskopf L. 2014. The inter-kingdom volatile signal indole promotes root development by interfering with auxin signalling. *The Plant Journal* 80: 758–771.
- Bailly A, Weiskopf L. 2012. The modulating effect of bacterial volatiles on plant growth. *Plant Signaling & Behavior* 7: 79–85.
- Bais HP, Broeckling CD, Vivanco JM. 2008. Root exudates modulate plant–microbe interactions in the rhizosphere. In: Karlovsky P, ed. *Secondary metabolites in soil ecology*. *Soil biology*, vol. 14. Berlin, Heidelberg: Springer, 241–252.
- Bais HP, Fall R, Vivanco JM. 2004. Biocontrol of *Bacillus subtilis* against infection of *Arabidopsis* roots by *Pseudomonas syringae* is facilitated by biofilm formation and surfactin production. *Plant Physiology* 134: 307–319.
- Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology* 57: 233–266.
- Barnard RL, Osborne CA, Firestone MK. 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME Journal* 7: 2229–2241.
- Berendsen RL, Pieterse CMJ, Bakker PAHM. 2012. The rhizosphere microbiome and plant health. *Trends in Plant Science* 17: 478–86.
- Bhattacharyya D, Garladinne M, Lee YH. 2015. Volatile indole produced by rhizobacterium *Proteus vulgaris* JBSL202 stimulates growth of *Arabidopsis thaliana* through auxin, cytokinin, and brassinosteroid pathways. *Journal of Plant Growth Regulation* 34: 158–168.
- Bitas V, Kim H-S, Bennett JW, Kang S. 2013. Sniffing on microbes: diverse roles of microbial volatile organic compounds in plant health. *Molecular Plant–Microbe Interactions* 26: 835–843.
- Bouwmeester H, Schuurink RC, Bleeker PM, Schiestl F. 2019. The role of volatiles in plant communication. *The Plant Journal* 100: 892–907.
- Campbell AH, Harder T, Nielsen S, Kjelleberg S, Steinberg PD. 2011. Climate change and disease: bleaching of a chemically defended seaweed. *Global Change Biology* 17: 2958–2970.
- Cavalcanti GS, Shukla P, Morris M, Ribeiro B, Foley M, Doane MP, Thompson CC, Edwards MS, Dinsdale EA, Thompson FL. 2018. Rhodoliths holobionts in a changing ocean: host-microbes interactions mediate coralline algae resilience under ocean acidification. *BMC Genomics* 19: 701.

- Chapelle E, Mendes R, Bakker PAH, Raaijmakers JM. 2016. Fungal invasion of the rhizosphere microbiome. *ISME Journal* 10: 265–268.
- Chinchilla D, Bruissin S, Meyer S, Zühlke D, Hirschfeld C, Joller C, L'Haridon F, Mène-Saffrané L, Riedel K, Weiskopf L. 2019. A sulfur-containing volatile emitted by potato-associated bacteria confers protection against late blight through direct anti-oomycete activity. *Scientific Reports* 9: 18778.
- Cho S-M, Kim YH, Anderson AJ, Kim YC. 2013. Nitric oxide and hydrogen peroxide production are involved in systemic drought tolerance induced by 2R,3R-butanediol in *Arabidopsis thaliana*. *The Plant Pathology Journal* 29: 427–434.
- Choudoir M, Rossabi S, Gebert M, Helmig D, Fierer N. 2019. A phylogenetic and functional perspective on volatile organic compound production by actinobacteria. *mSystems* 4: e00295-18.
- Classen AT, Sundqvist MK, Henning JA, Newman GS, Moore JAM, Cregger MA, Moorhead LC, Patterson CM. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial–plant interactions: what lies ahead? *Ecosphere* 6: 130.
- Compant S, Samad A, Faist H, Sessitsch A. 2019. A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. *Journal of Advanced Research* 19: 29–37.
- Cordovez V, Carrion VJ, Etalo DW, Mumm R, Zhu H, van Wezel GP, Raaijmakers JM. 2015. Diversity and functions of volatile organic compounds produced by *Streptomyces* from a disease-suppressive soil. *Frontiers in Microbiology* 6: 1081.
- Dickschat JS. 2016. Bacterial terpene cyclases. *Natural Product Reports* 33: 87–110.
- Dittami SM, Dubocq-Bidot L, Perennou M, Gobet A, Corre E, Boyen C, Tonon T. 2016. Host–microbe interactions as a driver of acclimation to salinity gradients in brown algal cultures. *ISME Journal* 10: 51–63.
- Dittmer J, van Opstal EJ, Shropshire JD, Bordenstein SR, Hurst GDD, Brucker RM. 2016. Disentangling a holobiont – recent advances and perspectives in nasonia wasps. *Frontiers in Microbiology* 7: 1478.
- Duarte CM, Wu J, Xiao X, Bruhn A, Krause-Jensen D. 2017. Can seaweed farming play a role in climate change mitigation and adaptation? *Frontiers in Marine Science* 4: 1–8.
- Durán P, Thiergart T, Garrido-Oter R, Agler M, Kemen E, Schulze-Lefert P, Hacquard S. 2018. Microbial interkingdom interactions in roots promote arabidopsis survival. *Cell* 175: 973–983.e14.
- Dworjanyn S, de Nys R, Steinberg P. 2006. Chemically mediated antifouling in the red alga *Delisea pulchra*. *Marine Ecology Progress Series* 318: 153–163.
- Eberl L. 1999. N-Acyl Homoserinylactone-mediated gene regulation in gram-negative bacteria. *Systematic and Applied Microbiology* 22: 493–506.
- Fitzpatrick CR, Copeland J, Wang PW, Guttman DS, Kotanen PM, Johnson MTJ. 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. *Proceedings of the National Academy of Sciences, USA* 115: E1157–E1165.
- da Gama BAP, Plouguerné E, Pereira RC. 2014. The antifouling defence mechanisms of marine macroalgae. In: Jacquot J-P, Gadal P, ed. *Advances in botanical research*. Oxford, UK: Elsevier, 413–440.
- Garren M, Son K, Raina J-B, Rusconi R, Menolascina F, Shapiro OH, Tout J, Bourne DG, Seymour JR, Stocker R. 2014. A bacterial pathogen uses dimethylsulfoniopropionate as a cue to target heat-stressed corals. *ISME Journal* 8: 999–1007.
- Hacquard S, Spaepen S, Garrido-Oter R, Schulze-Lefert P. 2017. Interplay between innate immunity and the plant microbiota. *Annual Review of Phytopathology* 55: 565–589.
- Hartman K, Tringe SG. 2019. Interactions between plants and soil shaping the root microbiome under abiotic stress. *Biochemical Journal* 476: 2705–2724.
- Hassani MA, Durán P, Hacquard S. 2018. Microbial interactions within the plant holobiont. *Microbiome* 6: 58.
- Huang AC, Osbourn A. 2019. Plant terpenes that mediate below-ground interactions: prospects for bioengineering terpenoids for plant protection. *Pest Management Science* 75: 2368–2377.
- Hurd CL. 2000. Water motion, marine macroalgal physiology, and production. *Journal of Phycology* 36: 453–472.
- Insam H, Seewald MSA. 2010. Volatile organic compounds (VOCs) in soils. *Biology and Fertility of Soils* 46: 199–213.
- Karunanithi PS, Zerbe P. 2019. Terpene synthases as metabolic gatekeepers in the evolution of plant terpenoid chemical diversity. *Frontiers in Plant Science* 10: 1166.
- Kessler RW, Weiss A, Kuegler S, Hermes C, Wichard T. 2018. Macroalgal–bacterial interactions: role of dimethylsulfoniopropionate in microbial gardening by *Ulva* (Chlorophyta). *Molecular Ecology* 27: 1808–1819.
- Kong HG, Shin TS, Kim TH, Ryu C-M. 2018. Stereoisomers of the bacterial volatile compound 2,3-butanediol differently elicit systemic defense responses of pepper against multiple viruses in the field. *Frontiers in Plant Science* 9: 90.
- Kumar V, Rao D, Thomas T, Kjelleberg S, Egan S. 2011. Antidiatom and antibacterial activity of epiphytic bacteria isolated from *Ulva lactuca* in tropical waters. *World Journal of Microbiology and Biotechnology* 27: 1543–1549.
- Lachnit T, Wahl M, Harder T. 2010. Isolated thallus-associated compounds from the macroalga *Fucus vesiculosus* mediate bacterial surface colonization in the field similar to that on the natural alga. *Biofouling* 26: 247–255.
- Liu X-M, Zhang H. 2015. The effects of bacterial volatile emissions on plant abiotic stress tolerance. *Frontiers in Plant Science* 6: 774.
- Longford SR, Campbell AH, Nielsen S, Case RJ, Kjelleberg S, Steinberg PD. 2019. Interactions within the microbiome alter microbial interactions with host chemical defences and affect disease in a marine holobiont. *Scientific Reports* 9: 1363.
- van der Loos LM, Eriksson BK, Falcão Salles J. 2019. The macroalgal holobiont in a changing sea. *Trends in Microbiology* 27: 635–650.
- Manefeld M, Rasmussen TB, Hentzer M, Andersen JB, Steinberg P, Kjelleberg S, Givskov M. 2002. Halogenated furanones inhibit quorum sensing through accelerated LuxR turnover. *Microbiology* 148: 1119–1127.
- Margulis L. 1991. Symbiosis as a source of evolutionary innovation. In: Margulis L, Fester R, ed. *Symbiosis as a source of evolutionary innovation: speciation and morphogenesis*. Cambridge, MA, USA: MIT Press, 454.
- Meisner A, de Boer W. 2018. Strategies to maintain natural biocontrol of soil-borne crop diseases during severe drought and rainfall events. *Frontiers in Microbiology* 9: 2279.
- Meldau DG, Meldau S, Hoang LH, Underberg S, Wunsche H, Baldwin IT. 2013. Dimethyl disulfide produced by the naturally associated bacterium *Bacillus* sp B55 promotes *Nicotiana attenuata* growth by enhancing sulfur nutrition. *The Plant Cell* 25: 2731–2747.
- Mendes R, Garbeva P, Raaijmakers JM. 2013. The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiology Reviews* 37: 634–663.
- Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider JHM, Piceno YM, DeSantis TZ, Andersen GL, Bakker PAHM *et al.* 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* 332: 1097–1100.
- Mhlongo MI, Pieter LA, Madala NE, Labuschagne N, Dubery IA. 2018. The chemistry of plant–microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. *Frontiers in Plant Science* 9: 112.
- Minich JJ, Morris MM, Brown M, Doane M, Edwards MS, Michael TP, Dinsdale EA. 2018. Elevated temperature drives kelp microbiome dysbiosis, while elevated carbon dioxide induces water microbiome disruption. *PLoS ONE* 13: e0192772.
- Nasrolahi A, Stratil SB, Jacob KJ, Wahl M. 2012. A protective coat of microorganisms on macroalgae: inhibitory effects of bacterial biofilms and epibiotic microbial assemblages on barnacle attachment. *FEMS Microbiology Ecology* 81: 583–595.
- Naylor D, Coleman-Derr D. 2018. Drought stress and root-associated bacterial communities. *Frontiers in Plant Science* 8: 2223.
- Naylor D, DeGraaf S, Purdom E, Coleman-Derr D. 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME Journal* 11: 2691–2704.
- Nemcovic M, Jakubíková L, Viden I, Farkas V. 2008. Induction of conidiation by endogenous volatile compounds in *Trichoderma* spp. *FEMS Microbiology Letters* 284: 231–236.
- Nylund G, Cervin G, Persson F, Hermansson M, Steinberg P, Pavia H. 2008. Seaweed defence against bacteria: a poly-brominated 2-heptanone from the red alga *Bonnemaisonia hamifera* inhibits bacterial colonisation. *Marine Ecology Progress Series* 369: 39–50.

- de Oliveira L, Gregoracci G, Silva GG, Salgado L, Filho G, Alves-Ferreira M, Pereira R, Thompson FL. 2012. Transcriptomic analysis of the red seaweed *Laurencia dendroidea* (Florideophyceae, Rhodophyta) and its microbiome. *BMC Genomics* 13: 487.
- Ortíz-Castro R, Contreras-Cornejo HA, Macías-Rodríguez L, López-Bucio J. 2009. The role of microbial signals in plant growth and development. *Plant Signaling & Behavior* 4: 701–712.
- Othmani A, Briand JF, Ayé M, Molmeret M, Culioli G. 2016a. Surface metabolites of the brown alga *Taonia atomaria* have the ability to regulate epibiosis. *Biofouling* 32: 801–813.
- Othmani A, Bunet R, Bonnefont J-L, Briand J-F, Culioli G. 2016b. Settlement inhibition of marine biofilm bacteria and barnacle larvae by compounds isolated from the Mediterranean brown alga *Taonia atomaria*. *Journal of Applied Phycology* 28: 1975–1986.
- Paix B, Othmani A, Debroas D, Culioli G, Briand J. 2019. Temporal covariation of epibacterial community and surface metabolome in the Mediterranean seaweed holobiont *Taonia atomaria*. *Environmental Microbiology* 21: 3346–3363.
- Papenfort K, Bassler BL. 2016. Quorum sensing signal–response systems in Gram-negative bacteria. *Nature Reviews Microbiology* 14: 576–588.
- Paul N, de Nys R, Steinberg P. 2006. Chemical defence against bacteria in the red alga *Asparagopsis armata*: linking structure with function. *Marine Ecology–Progress Series* 306: 87–101.
- Persson F, Svensson R, Nylund GM, Fredriksson NJ, Pavia H, Hermansson M. 2011. Ecological role of a seaweed secondary metabolite for a colonizing bacterial community. *Biofouling* 27: 579–588.
- Pita L, Rix L, Slaby BM, Franke A, Hentschel U. 2018. The sponge holobiont in a changing ocean: from microbes to ecosystems. *Microbiome* 6: 46.
- de la Porte A, Schmidt R, Yergeau É, Constant P. 2020. A Gaseous Milieu: extending the boundaries of the rhizosphere. *Trends in Microbiology* 28: 536–542.
- Raaijmakers JM, Mazzola M. 2012. Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annual Review of Phytopathology* 50: 403–24.
- Rabe P, Citron CA, Dickschat JS. 2013. Volatile terpenes from actinomycetes: a biosynthetic study correlating chemical analyses to genome data. *ChemBioChem* 14: 2345–2354.
- Ranf S. 2017. Sensing of molecular patterns through cell surface immune receptors. *Current Opinion in Plant Biology* 38: 68–77.
- Rasmann S, Köllner TG, Degenhardt J, Hiltbold I, Toepfer S, Kuhlmann U, Gershenzon J, Turlings TCJ. 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434: 732–737.
- Ravanbakhsh M, Sasidharan R, Voeselek LAJ, Kowalchuk GA, Jousset A. 2018. Microbial modulation of plant ethylene signaling: ecological and evolutionary consequences. *Microbiome* 6: 52.
- Raza W, Ling N, Liu D, Wei Z, Huang Q, Shen Q. 2016. Volatile organic compounds produced by *Pseudomonas fluorescens* WR-1 restrict the growth and virulence traits of *Ralstonia solanacearum*. *Microbiological Research* 192: 103–113.
- Reinhold-Hurek B, Bünger W, Burbano CS, Sabale M, Hurek T. 2015. Roots shaping their microbiome: global hotspots for microbial activity. *Annual Review of Phytopathology* 53: 403–424.
- Ritpitakphong U, Falquet L, Vimoltust A, Berger A, Métraux J-P, L'Haridon F. 2016. The microbiome of the leaf surface of *Arabidopsis* protects against a fungal pathogen. *New Phytologist* 210: 1033–1043.
- Ryu C-M, Farag MA, Hu C-H, Reddy MS, Kloepper JW, Paré PW. 2004. Bacterial volatiles induce systemic resistance in *Arabidopsis*. *Plant Physiology* 134: 1017–1026.
- Ryu C-M, Farag MA, Hu C-H, Reddy MS, Wei H-X, Paré PW, Kloepper JW. 2003. Bacterial volatiles promote growth in *Arabidopsis*. *Proceedings of the National Academy of Sciences, USA* 100: 4927–4932.
- Saha M, Berdalet E, Carotenuto Y, Fink P, Harder T, John U, Not F, Pohnert G, Potin P, Selander E *et al.* 2019. Using chemical language to shape future marine health. *Frontiers in Ecology and the Environment* 17: 530–537.
- Saha M, Goeckel F, Bhadury P. 2018. Minireview: algal natural compounds and extracts as antifoulants. *Journal of Applied Phycology* 30: 1859–1874.
- Saha M, Rempt M, Gebser B, Grueneberg J, Pohnert G, Weinberger F. 2012. Dimethylsulphopropionate (DMSP) and proline from the surface of the brown alga *Fucus vesiculosus* inhibit bacterial attachment. *Biofouling* 28: 593–604.
- Saha M, Rempt M, Grosser K, Pohnert G, Weinberger F. 2011. Surface-associated fucoxanthin mediates settlement of bacterial epiphytes on the rockweed *Fucus vesiculosus*. *Biofouling* 27: 423–433.
- Saha M, Rempt M, Stratil SB, Wahl M, Pohnert G, Weinberger F. 2014. Defence chemistry modulation by light and temperature shifts and the resulting effects on associated epibacteria of *Fucus vesiculosus*. *PLoS ONE* 9: e105333.
- Saha M, Wahl M. 2013. Seasonal variation in the antifouling defence of the temperate brown alga *Fucus vesiculosus*. *Biofouling* 29: 661–668.
- Saha M, Weinberger F. 2019. Microbial “gardening” by a seaweed holobiont: Surface metabolites attract protective and deter pathogenic epibacterial settlement. *Journal of Ecology* 107: 2255–2265.
- Salgado LT, Viana NB, Andrade LR, Leal RN, da Gama BAP, Attias M, Pereira RC, Amado Filho GM. 2008. Intra-cellular storage, transport and exocytosis of halogenated compounds in marine red alga *Laurencia obtusa*. *Journal of Structural Biology* 162: 345–355.
- Sasse J, Martinoia E, Northen T. 2018. Feed your friends: do plant exudates shape the root microbiome? *Trends in Plant Science* 23: 25–41.
- Schenkel D, Lemfack MC, Piechulla B, Splivallo R. 2015. A meta-analysis approach for assessing the diversity and specificity of belowground root and microbial volatiles. *Frontiers in Plant Science* 6: 707.
- Schikora A, Schenk ST, Hartmann A. 2016. Beneficial effects of bacteria–plant communication based on quorum sensing molecules of the N-acyl homoserine lactone group. *Plant Molecular Biology* 90: 605–612.
- Schmidt R, Cordovez V, de Boer W, Raaijmakers J, Garbeva P. 2015. Volatile affairs in microbial interactions. *ISME Journal* 9: 2329–2335.
- Schmidt R, Etalo DW, de Jager V, Gerards S, Zweepers H, de Boer W, Garbeva P. 2016. Microbial small talk: volatiles in fungal–bacterial interactions. *Frontiers in Microbiology* 6: 1495.
- Schmidt R, Ulanova D, Wick LY, Bode HB, Garbeva P. 2019. Microbe-driven chemical ecology: past, present and future. *The ISME Journal* 13: 2656–2663.
- Schulz S, Dickschat JS. 2007. Bacterial volatiles: the smell of small organisms. *Natural Product Reports* 24: 814.
- Schulz-Bohm K, Geisen S, Wubs ERJ, Song C, de Boer W, Garbeva P. 2017. The prey's scent – volatile organic compound mediated interactions between soil bacteria and their protist predators. *ISME Journal* 11: 817–820.
- Schulz-Bohm K, Gerards S, Hundscheid M, Melenhorst J, de Boer W, Garbeva P. 2018. Calling from distance: attraction of soil bacteria by plant root volatiles. *ISME Journal* 12: 1252–1262.
- Seymour JR, Amin SA, Raina J-B, Stocker R. 2017. Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships. *Nature Microbiology* 2: 17065.
- Seymour JR, Raina J-B. 2018. Swimming in the sea: chemotaxis by marine bacteria. *Microbiology Australia* 39: 12.
- Sharifi R, Ryu C-M. 2018a. Sniffing bacterial volatile compounds for healthier plants. *Current Opinion in Plant Biology* 44: 88–97.
- Sharifi R, Ryu C-M. 2018b. Revisiting bacterial volatile-mediated plant growth promotion: lessons from the past and objectives for the future. *Annals of Botany* 122: 349–358.
- Simon J-C, Marchesi JR, Mougél C, Selosse M-A. 2019. Host-microbiota interactions: from holobiont theory to analysis. *Microbiome* 7: 5.
- Stringlis IA, Proietti S, Hickman R, Van Verk MC, Zamioudis C, Pieterse CMJ. 2018. Root transcriptional dynamics induced by beneficial rhizobacteria and microbial immune elicitors reveal signatures of adaptation to mutualists. *The Plant Journal* 93: 166–180.
- Thompson JR, Rivera HE, Closek CJ, Medina M. 2015. Microbes in the coral holobiont: partners through evolution, development, and ecological interactions. *Frontiers in Cellular and Infection Microbiology* 4: 176.
- Timm CM, Carter KR, Carrell AA, Jun S-R, Jawdy SS, Vélez JM, Gunter LE, Yang Z, Nookaew I, Engle NL *et al.* 2018. Abiotic stresses shift belowground *populus*-associated bacteria toward a core stress microbiome. *mSystems* 3: e00070-17.
- Tyagi S, Lee K-J, Shukla P, Chae J-C. 2020. Dimethyl disulfide exerts antifungal activity against *Sclerotinia minor* by damaging its membrane and induces systemic resistance in host plants. *Scientific Reports* 10: 6547.
- Tyc O, Song C, Dickschat JS, Vos M, Garbeva P. 2017. The ecological role of volatile and soluble secondary metabolites produced by soil bacteria. *Trends in Microbiology* 25: 280–292.



- Van Alstyne KL, Puglisi MP. 2007. DMSP in marine macroalgae and macroinvertebrates: distribution, function, and ecological impacts. *Aquatic Sciences* 69: 394–402.
- Vandenkoornhuysen P, Quaiser A, Duhamel M, Le Van A, Dufresne A. 2015. The importance of the microbiome of the plant holobiont. *New Phytologist* 206: 1196–1206.
- Vannier N, Agler M, Hacquard S. 2019. Microbiota-mediated disease resistance in plants. *PLoS Path* 15: e1007740.
- Voges MJEEE, Bai Y, Schulze-Lefert P, Sattely ES. 2019. Plant-derived coumarins shape the composition of an Arabidopsis synthetic root microbiome. *Proceedings of the National Academy of Sciences, USA* 116: 12558–12565.
- Vries FT, Williams A, Stringer F, Willcocks R, McEwing R, Langridge H, Straathof AL. 2019. Changes in root-exudate-induced respiration reveal a novel mechanism through which drought affects ecosystem carbon cycling. *New Phytologist* 224: 132–145.
- Wahl M, Goecke F, Labes A, Dobretsov S, Weinberger F. 2012. The second skin: ecological role of epibiotic biofilms on marine organisms. *Frontiers in Microbiology* 3: 292.
- Wahl M, Shahnaz L, Dobretsov S, Saha M, Symanowski F, David K, Lachnit T, Vasel M, Weinberger F. 2010. Ecology of antifouling resistance in the bladder wrack *Fucus vesiculosus*: patterns of microfouling and antimicrobial protection. *Marine Ecology–Progress Series* 411: 33–48.
- Webster NS, Thomas T. 2016. The sponge hologenome. *MBio* 7: e00135-16.
- Weisskopf L. 2013. The potential of bacterial volatiles for crop protection against phytopathogenic fungi. In: Méndez-Vilas A, ed. *Microbial pathogens and strategies for combating them: science, technology and education*. Badajoz, Spain: Formatex Research Center, 1352–1363.
- Wichard T. 2015. Exploring bacteria-induced growth and morphogenesis in the green macroalga order Ulvales (Chlorophyta). *Frontiers in Plant Science* 6: 86.
- Wichard T, Charrier B, Mineur F, Bothwell JH, De Clerck O, Coates JC. 2015. The green seaweed *Ulva*: a model system to study morphogenesis. *Frontiers in Plant Science* 6: 72.
- Williams BT, Cowles K, Bermejo Martínez A, Curson ARJ, Zheng Y, Liu J, Newton-Payne S, Hind AJ, Li C-Y, Rivera PPL *et al.* 2019. Bacteria are important dimethylsulfoniopropionate producers in coastal sediments. *Nature Microbiology* 4: 1815–1825.
- Xu L, Naylor D, Dong Z, Simmons T, Pierroz G, Hixson KK, Kim Y-M, Zink EM, Engbrecht KM, Wang Y *et al.* 2018. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *Proceedings of the National Academy of Sciences, USA* 115: E4284–E4293.
- Yamada Y, Kuzuyama T, Komatsu M, Shin-ya K, Omura S, Cane DE, Ikeda H. 2015. Terpene synthases are widely distributed in bacteria. *Proceedings of the National Academy of Sciences, USA* 112: 857–862.
- Yu K, Pieterse CMJ, Bakker PAHM, Berendsen RL. 2019. Beneficial microbes going underground of root immunity. *Plant, Cell & Environment* 42: 2860–2870.
- Zhalnina K, Louie KB, Hao Z, Mansoori N, da Rocha UN, Shi S, Cho H, Karaoz U, Loqué D, Bowen BP *et al.* 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nature Microbiology* 3: 470–480.
- Zhang H, Murzello C, Sun Y, Kim M-S, Xie X, Jeter RM, Zak JC, Dowd SE, Paré PW. 2010. Choline and osmotic-stress tolerance induced in Arabidopsis by the soil microbe *Bacillus subtilis* (GB03). *Molecular Plant–Microbe Interactions* 23: 1097–1104.
- Zhang H, Sun Y, Xie X, Kim M-S, Dowd SE, Paré PW. 2009. A soil bacterium regulates plant acquisition of iron via deficiency-inducible mechanisms. *The Plant Journal* 58: 568–577.
- Zupo V, Maibam C, Buia MC, Gambi MC, Patti FP, Scipione MB, Lorenti M, Fink P. 2015. Chemoreception of the seagrass *Posidonia oceanica* by benthic invertebrates is altered by seawater acidification. *Journal of Chemical Ecology* 41: 766–779.

**Key words:** climate change, holobiont, infochemicals, plant, seaweeds.

Received, 2 June 2020; accepted, 15 September 2020.