

MINIREVIEW – Incubator

The seagrass holobiont: understanding seagrass-bacteria interactions and their role in seagrass ecosystem functioning

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One sentence summary: The proposed minireview uses the holobiont concept to highlight the importance of seagrass microbiome in sustaining seagrass ecosystems and the need to include microbiome in future seagrass management and/or restoration plans.

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ABSTRACT

This review shows that the presence of seagrass microbial community is critical for the development of seagrasses; from seed germination, through to phytohormone production and enhanced nutrient availability, and defence against pathogens and saprophytes. The tight seagrass-bacterial relationship highlighted in this review supports the existence of a seagrass holobiont and adds to the growing evidence for the importance of marine eukaryotic microorganisms in sustaining vital ecosystems. Incorporating a micro-scale view on seagrass ecosystems substantially expands our understanding of ecosystem functioning and may have significant implications for future seagrass management and mitigation against human disturbance.

INTRODUCTION

Seagrasses are marine flowering plants which colonised the aquatic environment about 100 million years ago (den Hartog 1970; Les, Cleland and Waycott 1997; Orth et al. 2006), and are present in coastal areas of all continents except Antarctica (Hemminga and Duarte 2000; Green 2003). Seagrasses are important benthic ecosystem engineers and, where canopy meadows are present, provide a variety of ecological services (Costanza et al. 1997; Orth et al. 2006). They are highly productive primary producers (Duarte and Cebrian 1996; Duarte and Chiscano 1999)

that represent an important source of food and a habitat for a number of organisms (Beck et al. 2001; Heck, Hays and Orth 2003; Valentine and Duffy 2006). They also support different ecosystems through the export of their organic material (Heck et al. 2008; Hyndes et al. 2014), and are extremely important for coastal protection due to their capacity to reduce wave intensity and turbulence (Gambi, Nowell and Jumars 1990; Ackerman and Okubo 1993). Moreover, seagrass meadows are critical in the sequestration of carbon dioxide (blue carbon), thus mitigating the effects of ocean acidification (Fourqurean et al. 2012; Duarte et al. 2013).

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Seagrasses, similar to terrestrial plants, harbour diverse communities of epi- and endophytic bacteria associated with their leaves and roots (Weidner et al. 2000; Uku et al. 2007; Garcias-Bonet et al. 2016). From our knowledge of terrestrial plant-microbial interactions, it is clear that the presence of a specific set of microorganisms can have significant consequences for plant growth, health and productivity (Compant et al. 2005; Rodríguez et al. 2006; Hayat et al. 2010). There is substantial field and laboratory-based evidence showing that seagrasses, while supporting their epiphytic microbial communities through the exudation of nutrients (Brylinsky, 1971; Kirchman et al. 1984; Wang et al. 2014), obtain a number of advantages in return from these communities (O'donohue et al. 1991; Ugarelli et al. 2017). The intimate relationship between seagrasses and their microorganisms (Kirchman, 1984; Welsh 2000; Holmer et al. 2001; Kurilenko, Ivanova and Mikhailov 2007; Garcias-Bonet et al. 2012) supports the idea that these organisms together constitute a 'holobiont' (Thompson et al. 2014; Bordenstein and Theis 2015), where the holobiont is defined as a 'host' organism ('biont') that builds symbiotic relationships with a variety of other organisms, including prokaryotes and eukaryotes (Margulis 1991). The organism and its symbiotic partners, together ('holo', meaning whole) represent an integrated community that support each member for its success of survival (Margulis 1991).

In this review, we present the unique diversity of seagrass epiphytic and endophytic bacteria, providing examples of how they differ from the microbial communities inhabiting surrounding environments, as well as among different seagrass species. We review the various positive and negative interactions that occur between seagrasses and their colonising bacteria, and the role of epi- and endophytic microorganisms in sustaining plant fitness. Finally, we highlight literature gaps such as the relevance of the seagrass holobiont in seagrass ecosystem functioning, and suggest the manipulation of seagrass associated microorganisms as alternative solution to enhance seagrass restoration efforts and management.

SEAGRASS-ASSOCIATED MICROORGANISMS

Seagrass tissues provide a physical substrate for a great variety of epiphytic organisms belonging to both prokaryotic and eukaryotic domains, including autotrophs (diatoms, cyanobacteria, encrusting algae; e.g. Borowitzka, Lavery and van Keulen 2007; Piazzini et al. 2007; Hamisi et al. 2013), and heterotrophs (microorganisms, fungi, invertebrates; e.g. Weidner et al. 2000; Devarajan, Suryanarayanan and Geetha 2002; Sakayaroj et al. 2010). Both the above- and below-ground tissues host a high abundance of microorganisms, ranging between 10^6 cells cm^{-2} for leaves (Kirchman et al. 1984) and 10^5 to 10^6 cells cm^{-2} for roots and rhizomes (Blaabjerg and Finster 1998).

In general, seagrass leaves and roots seem to possess a core of epiphytic bacteria, which differ from the microbial strains present in the surrounding environments (e.g. the SAR11 cluster, which dominates the water column; Weidner et al. 2000; Pfister, Gilbert and Gibbons 2014; Roth-Schulze et al. 2016). For example, Jensen, Kühl and Priemé (2007) describe Epsilonproteobacteria (in particular sulphur-oxidizing bacteria –SOB– genus *Arcobacter* and *Sulfurimonas*), Gammaproteobacteria and Actinobacteria as important colonisers of *Zostera marina* roots, while Deltaproteobacteria appears to dominate the rhizosphere (Table 1). Also, Cúcio and colleagues (2016) found that root epiphytic bacterial assemblages of seagrass (*Z. marina*, *Zostera noltii* and *Cymodocea*

nodosa) significantly differed from the communities of surrounding sediment and seawater. In accordance with these results, Fahimipour et al. (2017) showed that eelgrass root microbial communities strongly differed from sediment communities due to a high abundance of SOB (genus *Sulfurimonas*) on the root surface compared to the sediment. However, they also found contrasting results related to the seagrass leaf communities whereby bacterial composition of leaves was highly variable among replicates and similar to the surrounding seawater communities. This suggests a possible recruitment of leaf bacteria epiphytes from the water column. However, further studies are needed to clarify the discrepancies between these results which may be due to different sampling and laboratory methodology.

It is also clear that a difference exists among the microbial community of marine autotrophs related to the type of host (Martin et al. 2017). For example, Roth-Schulze and colleagues (2016) assessed the diversity of microorganisms associated with two seagrasses (*Posidonia australis* and *Halophila ovalis*) and six macroalgal species (green, red and brown seaweeds) and found that taxonomic diversity was unique to each type of host analysed. However, based on existing studies, it is not clear yet whether differences among seagrass epiphytic microbial communities are related to seagrass phylogeny or influenced by specific physico-chemical conditions present on the seagrass surface. For example, the epiphytic cyanobacteria of *Cymodocea serrulata* had similarities among plants collected at different sites (dominated by genera *Lyngbya* and *Cyanosarcina*), but clear differences as compared to the epiphytic cyanobacteria of *Thalassia hemprichii* from the same location (genus *Synechococcus*; Uku et al. 2001). Similarly, the epiphytic communities of the aquatic plants *Stuckenia pectinata* and *Potamogeton perfoliatus* in close proximity were highly divergent (Crump and Koch 2008) and a recent study (Martin et al. 2018) has highlighted the high diversity of root microorganisms of three seagrass species (*H. ovalis*, *Halodule uninervis* and *C. serrulata*). Also, two out of five bacterial taxa from the eelgrass *Zostera marina* roots and leaves collected at Chesapeake Bay (USA) were closely related to taxa associated with *Z. marina* roots in a study conducted in Denmark (Europe), suggesting the presence of cosmopolitan *Z. marina* microorganisms (Crump and Koch 2008).

Yet, the possibility exists that generalist microorganisms may be associated with more seagrass species. For example, Crump and Koch (2008) identified members of the Proteobacteria, Spirochaetes and Bacteroidetes that were associated with more than one submerged plant species (*P. perfoliatus*, *Z. marina* and *S. pectinata*). These were generally the most abundant microorganisms associated with each plant species, suggesting a dominance of only a few bacteria adapted to live a plant-epiphytic life. Bacteria belonging to the family Rhodobacteraceae have been consistently detected on leaves and roots of *Halophila stipulacea* in the red sea (Mejia et al. 2016), and seem to be part of the root microbial community of *Z. marina* and *Z. noltii* (Cúcio et al. 2016; Ettinger et al. 2017). Moreover, Roth-Schulze and colleagues (2016) found a high variability between bacterial communities associated with the same host type with a large proportion of taxa uniquely associated with one replicate of a particular host species. However, this distinction does not seem to be related to the host phylogeny, but is instead better explained by the physicochemical properties of the host (Burke et al. 2011b; Miranda et al. 2013; Stratil et al. 2013). In fact, Roth-Schulze and colleagues (2016) also demonstrated a high functional redundancy of microbial communities shared among host types due to microorganisms experiencing similar physicochemical characteristics on biotic surfaces. These results further support the

Table 1. Summary of the main epiphytic and endophytic bacteria phylum or class associated with above- and below-ground tissues of different seagrass species, based on published literature.

Seagrass species	Seagrass compartment	Epiphytic bacteria phylum/class	Endophytic bacteria phylum/class	Reference
<i>Zostera japonica</i>	Leaf	Bacteroidetes		Inaba et al. 2017
<i>Zostera marina</i>	//	//		Crump and Koch 2008
//	Root	//		Crump and Koch 2008
<i>Halophila stipulacea</i>	Leaf	γ -proteobacteria		Weidner et al. 2000
<i>Zostera japonica</i>	//	//		Inaba et al. 2017
<i>Zostera marina</i>	//	//		Crump and Koch 2008
//	Root	//		Crump and Koch 2008
<i>Halophila stipulacea</i>	Leaf	α -proteobacteria		Weidner et al. 2000
<i>Zostera marina</i>	Leaf	//		Crump and Koch 2008
//	Root	//		Crump and Koch 2008
<i>Zostera marina</i>	Root	δ -proteobacteria		Crump and Koch 2008
<i>Halophila stipulacea</i>	Leaf	β -proteobacteria		Weidner et al. 2000
<i>Zostera marina</i>	Root	Epsilonbacteria		Crump and Koch 2008
<i>Zostera marina</i>	Leaf	Actinobacteria		Crump and Koch 2008
//	Root	//		Crump and Koch 2008
<i>Halophila stipulacea</i>	Leaf	Verrucomicrobia		Weidner et al. 2000
//	//	Planctomycetes		Weidner et al. 2000
<i>Cymodocea rotundata</i>	//	Cynobacteria		Hamisi et al. 2013
<i>Posidonia oceanica</i>	Rhizome		α -proteobacteria	Uku et al. 2007
//	Root		//	Garcias-Bonet et al. 2012
//	Leaf		//	Garcias-Bonet et al. 2012
<i>Cymodocea serrulata</i>	Root		//	Garcias-Bonet et al. 2012
<i>Halophila uninervis</i>	//		//	Martin et al. 2018
<i>Cymodocea serrulata</i>	Root		γ -proteobacteria	Martin et al. 2018
<i>Posidonia oceanica</i>	Rhizome		δ -proteobacteria	Venkateswaran et al. 2003
<i>Cymodocea serrulata</i>	Root		Actinobacteria	Garcias-Bonet et al. 2012
<i>Thalassia hemprichii</i>	//		//	Venkateswaran et al. 2003
<i>Halophila ovalis</i>	//		//	Wu et al. 2012
<i>Cymodocea serrulata</i>	Root		Firmicutes	Martin et al. 2018
<i>Posidonia oceanica</i>	Rhizome		Bacteroidetes	Jose, Sivakala and Jebakumar 2014
//	Leaf		//	Garcias-Bonet et al. 2016
				Garcias-Bonet et al. 2016

'host effect' hypothesis, whereby the settlement of bacteria that share general traits for a host-associated life may be influenced by specific parameters (e.g. surface pH, specific nutrients exuded) on host tissue surface (Rawls et al. 2006; Martin et al. 2018).

Microorganisms can also live endophytically within leaf tissues (Garcias-Bonet et al. 2012), and in the case of roots, between and inside epidermal, exodermal and cortex cells (Kuo 1993; Küsel et al. 1999; Nielsen, Liesack and Finster 1999). Few studies have investigated the diversity of seagrass leaf and root endophytes. For *Posidonia oceanica*, the low number of bacterial operational taxonomic units observed in internal tissues suggests a high level of specialisation to an endophytic life (Table 1; Garcias-Bonet et al. 2012, 2016). Some bacteria (belonging to *Desulfovibrionaceae*, *Rhodobacteraceae* and *Actinobacteria*) seem to be common endophytes of seagrasses (*P. oceanica*, *Z. marina*), while others have only been found in tissues of specific seagrasses. For example, *Marinomonas* species are associated with the endophytic microbial community of *P. oceanica* (Espinosa et al. 2010), but have not been found in the tissue of *Z. marina* or *C. serrulata* (Jensen, Kühl and Priemé 2007; Jose, Sivakala and Jebakumar 2014).

SEAGRASSES SHAPE THEIR MICROBIAL COMMUNITY

The development of specific seagrass microbial communities depends on the ability of plants to shape their epiphytic microbial communities through a series of positive (such as the release of nutrients from plant surface; McRoy and Goering 1974; Kirchman et al. 1984; Wang et al. 2014) or negative (the production of antimicrobial defences; Zidorn 2016) interactions (Fig. 1, Table 2) interactions. In terms of the positive effects of seagrasses on microbes, seagrass leaves and roots exude nutrients that can attract bacteria to the plant surface (Wood and Hayasaka 1981; Perry and Dennison 1999), and bacteria isolated from the roots of *Z. marina* demonstrate chemotaxis towards amino acids exuded by the eelgrass roots (Wood and Hayasaka 1981; Krutz et al. 2003). This may also explain the patchy bacterial distribution on the root surface, where bacteria congregate near areas of radial oxygen loss and/or nutrient release (Nielsen et al. 2001). In terms of plant tissue colonisation, it seems that epiphytic bacteria on seagrasses may be able to use the organic substrates excreted by marine plants. In support of this hypothesis, Kurilenko, Ivanova and Mikhailov (2007) inoculated *Z. marina* leaves and two abiotic surfaces (glass and metal) with two epiphytes isolated from the seagrass itself and three free-living bacteria, in oligotrophic media. The two seagrass epiphytic bacteria

Table 2. Positive and negative interactions between seagrass and colonising bacteria.

Process	Process description	References
Seagrass positive (+) effects on bacteria		
Nutrient exudation	Seagrass leaves and roots exude nutrients that can be metabolised by resident bacteria. Nutrients exuded by seagrasses include amino acids, vitamins, iron and sulphur compounds, such as DMSP	Wood and Hayasaka 1981 Perry and Dennison 1999
Seagrass negative (-) effects on bacteria	Seagrass defences are activated when plant membrane receptors recognise and bind specific molecules originating from pathogens. A process of defense responses begins with the production of secondary metabolites and ROS	Bent 1996 Boller and Felix 2009
Secondary metabolites	Plant secondary metabolites can be divided into three chemically distinct groups: terpenes, phenolics, and nitrogen-containing compounds. Their defence mechanism is related to the ability of degrade bacterial QS molecules	Manefield et al. 2002 Bauer and Mathesius 2004 Zidorn 2016
ROS	ROS include superoxide anion radical, O_2^- , hydrogen peroxide, H_2O_2 and the highly reactive hydroxyl radicals, $\bullet OH$, that target DNA, RNA, proteins and lipids of many bacteria	Cabiscol Català, Tamarit Sumalla and Ros Salvador 2000 Torres, Jones and Dangel 2006 Zhao and Drlica 2014
Bacterial positive (+) effects on seagrass		
Nutrient enhancement	Aerobic nitrogen (N) fixation. Diazotrophic bacteria support seagrass N demand through nitrogen fixation Anaerobic N fixation. SRB significantly contribute to anaerobic N fixation which occurs in seagrass-inhabited sediments and/or seagrass root surface Mineralization of organic N and phosphorus (P). SRB can enhance nutrient availability for seagrass root uptake by mineralising organic matter Solubilization of P. Seagrass leaf epiphytes, such as cyanobacteria <i>Anabaena</i> sp., <i>Calothrix braunii</i> and <i>Nostoc</i> sp., may increase P availability for seagrass uptake by solubilising P compounds to inorganic forms	Welsh 2000 Nielsen et al. 2001 Pereg-Greg, 2002 Hamisi et al. 2009 O'donohue et al. 1991 Hansen et al. 2000 Powell, Kenworthy and Fourqurean 1989 Evrard et al. 2005 Sharma et al. 2013 Sharma et al. 2013
Increasing plant growth and development	Seagrass leaf epi- and endophytic microbiome and root endophytic microbes produce phytohormones, such as IAA and cytokinins, which are suspected to play a pivotal role in plant growth and development	Kurtz et al. 2003 Werner and Schmülling 2009 Celdrán et al. 2012
Protection from toxic compounds	Sulphide-oxidising bacteria inhabiting seagrass roots are able to accelerate the process of sulphide oxidation with consequent relief of sulphite toxic effects on plants	Lee and Dunton 2000 Küsel et al. 2006
Protection from oxidative stress	Seagrass microbiome can produce oxidative enzymes to protect themselves in case of plant ROS production. In case of cellular death with consequent release of intracellular molecules, bacterial oxidative enzymes may protect the plant itself, acting as a sink for extracellular oxidative radicals	Sanchez-Amat, Solano and Lucas-Elío 2010

Table 2. Continued

Process	Process description	References
Protection from pathogens	Seagrass leaf and root epi- and endophytes are able to synthesise antiviral, antiparasitic and antibacterial compounds. These molecules include lactonase, which degrades Gram- QS molecules and an extracellular DNase used to rapidly break up the biofilms of both Gram+ and Gram- competitors	Burja et al. 2001 Nijland, Hall and Burgess 2010 Wu et al. 2012
Protection from biofouling organisms	Bacterial endo and epiphytes, in particular cyanobacteria, have a strong antifouling activity due to their ability of producing a variety of anti-algal compounds, such as fischerellin, aponingalactosyldiacylglycerol and cyanobacterin	Mazard et al. 2016 Ghasemi et al. 2003

attached exclusively to the seagrass tissue in preference to abiotic surfaces and remained viable for the duration of the experiment (60 hours), while the free-living bacteria showed no selectivity of adhesion to either biotic or abiotic surfaces (Kurilenko, Ivanova and Mikhailov 2007). Moreover, the bacteria that settled on seagrass leaves were considered not viable 30 hours after settlement, suggesting that plant defences and/or competition with resident bacteria and/or incapability of using nutrients secreted by seagrass tissues may have affected their viability (Kurilenko, Ivanova and Mikhailov 2007).

NEGATIVE SEAGRASS-BACTERIAL INTERACTIONS

Seagrass defences against pathogens include secondary metabolites and reactive oxygen species (ROS; Fig. 1, Table 2). Plant secondary metabolites can be divided into three chemically distinct groups: terpenes (e.g. terpenoids), phenolics (e.g. flavonoids and phlorotannins) and nitrogen-containing compounds (e.g. alkaloids; Zidorn 2016). Sieburth and Conover (1965) were among the first to show that phenolic compounds from two macroalgae species inhibit fouling bacteria. Following studies have shown that metabolites extracted from seagrasses can inhibit a variety of microorganisms associated with biofilm formation (e.g. Steinberg and De Nys 2002; Engel et al. 2006; Newby et al. 2006), and help plants resist decomposition by saprophytes and pathogens (Zapata and McMillan 1979; Engel et al. 2006; Iyapparajet al. 2014). For example, caffeic acid, a phenolic compound, has demonstrated activity against a species of *Labyrinthula* isolated from diseased eelgrass (Vergeer and Develi 1997).

It is not clear whether seagrasses present an induced or activated chemical defence against bacterial settlers. In general, vascular plants (Vera et al. 2011) and macrophytes (Weinberger 2007) usually have innate immune receptors on the outer cell plasma membrane. These membrane receptors (encoded by resistance R-genes) recognise and bind specific molecules (elicitors) originating from pathogens, and thus 'alert' the plant (e.g. *Thalassia testudinum*) of their presence (Bent 1996; Boller and Felix 2009; Loucks, Waddell and Ross 2013). Subsequently, a process of local defence responses begins with the production of secondary metabolites and ROS at the site of the attempted attack (Fig. 1, Table 2; Bent 1996). Many plant pathogenic bacteria are dependent on quorum sensing (QS) to invoke disease

and, in regards to plant defence, the mechanism of interference with QS is achieved by producing metabolites that degrade QS signal molecules (e.g. N-acyl homoserine lactone – AHL) (Fig. 1; Manefield et al. 2002; Bauer and Mathesius 2004). However, it is unknown whether seagrasses are able to produce AHL-degrading enzymes.

ROS, generated in response to a stressor by NADPH oxidase in the infected area (Torres, Jones and Dangel 2006), include different compounds (such as superoxide anion radical, O_2^- , hydrogen peroxide, H_2O_2 and hydroxyl radicals, $\cdot OH$) that target bacterial macromolecules (e.g. DNA, RNA, proteins and lipids; Cabiscol Català, Tamarit Sumalla and Ros Salvador 2000; Zhao and Drlica 2014). To protect themselves, seagrass-associated bacteria can express a variety of antioxidant enzymes (in particular peroxidase and catalase) that degrade ROS (Sanchez-Amat, Solano and Lucas-Elío 2010). Moreover, it seems that some of the bacteria that successfully settle on seagrass tissue produce oxidising enzymes that may enhance the plant's tolerance of oxidative stress (Štajner et al. 1997; Sanchez-Amat, Solano and Lucas-Elío 2010). Following the production of ROS in response to a pathogenic attack, the seagrass has a need to protect itself from oxidative stress through the additional production of several enzymes that express antioxidant activity. For example, Costa and colleagues (2015) found a higher antioxidant scavenging capacity via higher production of ROS within the leaves of *P. oceanica* covered with epiphytes (both eukaryotes and prokaryotes), when compared to leaves that were not colonised by epiphytes. Among the cultivable microorganisms of *P. oceanica* leaves, the bacterium *Marinomonas mediterranea* MMB-1 has shown to be an excellent source of oxidative enzymes, such as tyrosinase which produces melanin from L-tyrosine (Sanchez-Amat, Solano and Lucas-Elío 2010). Since melanins are known free radical scavengers, they could protect the producer strains from oxidative stress. It would be interesting to investigate whether *M. mediterranea*, in case of cellular death with consequent release of intracellular molecules, may act as a sink for extracellular oxidative radicals, thus alleviating seagrass oxidative stress (Fig. 2; Geng et al. 2008; Sanchez-Amat, Solano and Lucas-Elío 2010).

POSITIVE SEAGRASS-BACTERIAL INTERACTIONS

Bacteria that successfully colonise the seagrass surface must be able to withstand interactions with the plant's defence and competition with other microorganisms (Egan et al. 2013). In turn,

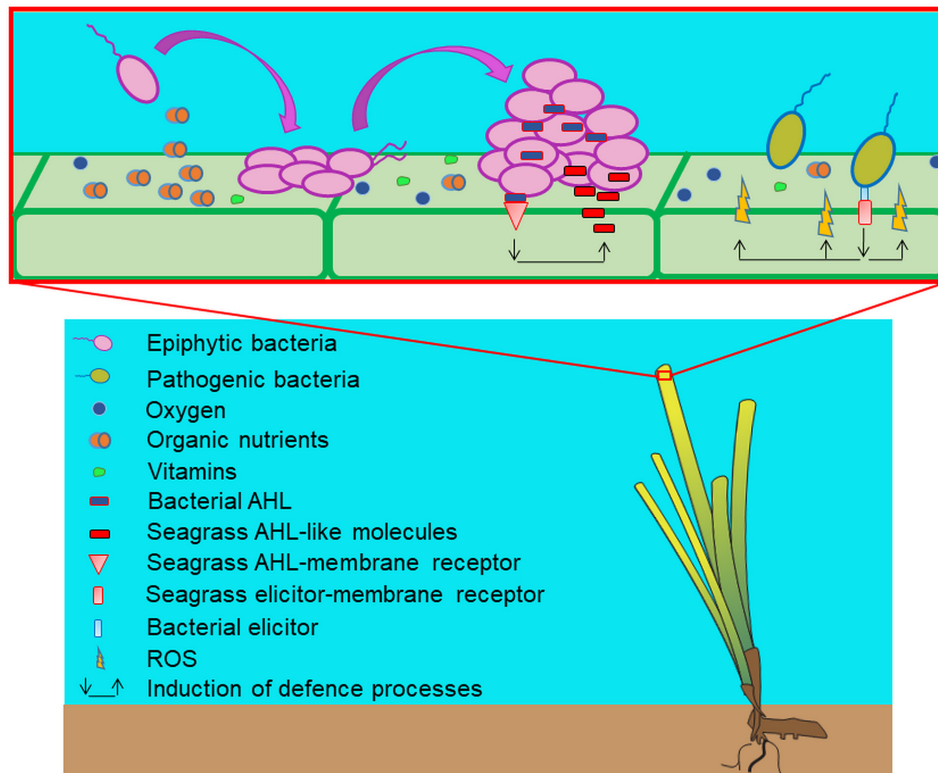


Figure 1. A conceptual diagram of the positive and negative interactions that can take place on leaves and roots of seagrasses as reported in Table 2.

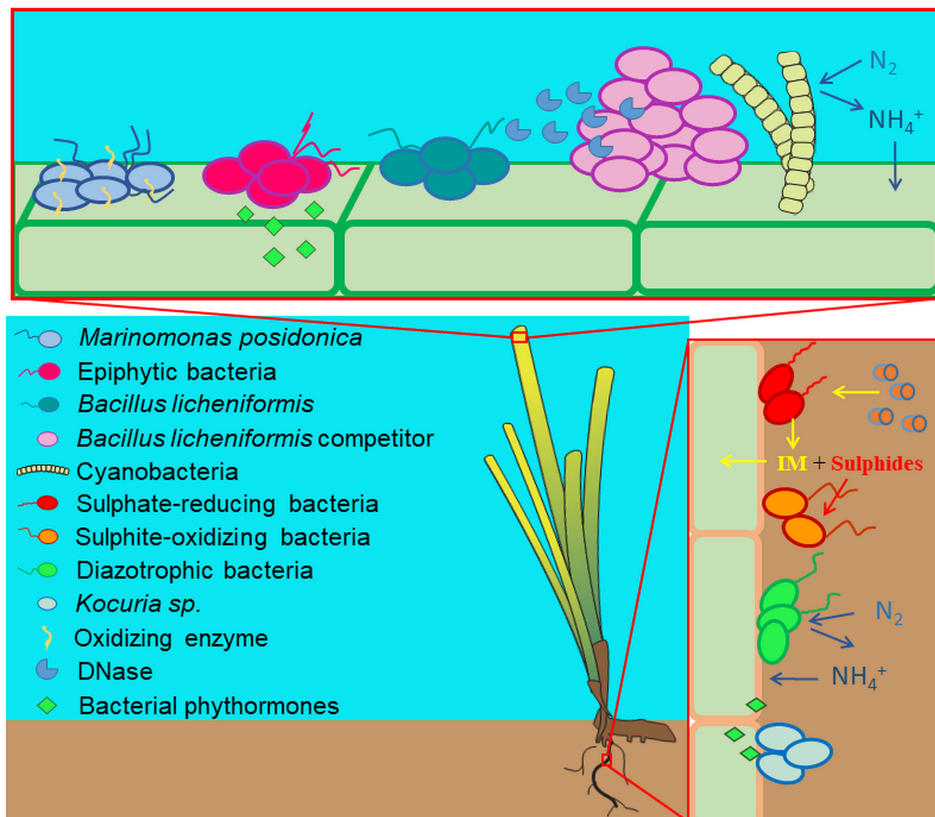


Figure 2. A conceptual diagram of the functions played by bacteria on the leaves and roots of seagrasses in sustaining plant fitness as reported in Table 2.

they benefit from the release of dissolved organic nutrients from plant tissues (Fig. 1; Table 2; McRoy and Goering 1974; Penhale and Thayer 1980; Kirchman et al. 1984; Wang et al. 2014). Bacterial epiphytes of *Z. marina* obtain carbon (C), nitrogen (N) and phosphorus (P) from low molecular weight organic compounds lost through leaching from the leaves (Fig. 1; Brylinsky 1971; Kirchman, 1984). By placing *Z. marina* roots in a solution containing enriched substrates [e.g. $(^{15}\text{NH}_4)_2^{14}\text{CO}_3$], it was found that nutrients were absorbed from the solution by plant roots, transferred to leaves and consumed by leaf-associated epiphytes (Kirchman et al. 1984). Seagrass roots and rhizomes also exude 2%–11% of the organic carbon produced during photosynthesis, which can be used by bacteria to satisfy their C demand (Moriarty, Iverson and Pollard 1986; Pollard and Moriarty 1991; Holmer et al. 2001).

Importantly, seagrasses may also represent a source of vitamins and iron for their microbial community (Donnelly and Herbert 1998; Brodersen et al. 2017). For example, ferric iron represents a key molecule for cell-cell communication of some bacterial species in biofilms, including *Bacillus subtilis* (Vlamakis et al. 2013), a common component of the biofilm of seagrass and terrestrial plants (Nugraheni et al. 2010; Chen et al. 2012). Since *B. subtilis* is responsible for terrestrial plants' defence against pathogens (by inhibiting the growth of plant pathogens such as *Pseudomonas syringae*; Bais, Fall and Vivanco 2004), the exudation of these molecules by its seagrass host may be pivotal to the recruitment of the 'right microorganisms' from the environment (Vlamakis et al. 2013). Seagrass-associated microorganisms are also able to use dimethylsulfoniopropionate (DMSP) excreted by seagrasses (Borges and Champenois 2015) as a source of sulphur, which can then be incorporated into bacterial proteins (Kiene, Linn and Bruton 2000). Genetic evidence indicates that strains of *Roseobacter*, commonly found on macroalgae (Brinkhoff, Giebel and Simon 2008), have the capacity to utilise DMSP produced by the algae (Egan et al. 2013). Since populations of *Roseobacter* are also commonly detected on the leaves of the seagrass *Z. marina*, and the aquatic plants *P. perfoliatus*, and *S. pectinata* (Crump and Koch 2008), these bacteria may also be able to use DMSP produced by seagrasses. Indeed, information from whole genome sequencing of *Marinomonas* sp. MWYL1A, isolated from the roots of the salt marsh *Spartina anglica*, and its relative, *M. posidonica* IVIA-Po-181T, isolated from *P. oceanica*, indicate that these *Marinomonas* strains share the capability to catabolise DMSP (Lucas-Elío et al. 2012).

ROLE OF EPIPHYTIC AND ENDOPHYTIC MICROORGANISMS IN SUSTAINING PLANT FITNESS

Vascular plants support a variety of epi- and endophytic microorganisms, which may profoundly influence plant health and productivity. Bacteria can enhance plant growth through increased nutrient availability, for example, via nitrogen fixation or by mineralising organic compounds (Fig. 1, Table 2; Welsh 2000; Evrard et al. 2005; Cole and McGlathery 2012). They can also produce or modulate plant hormones, thus influencing shoot and root development (Werner and Schmölling 2009; Kurtz et al. 2003), and confer immunity against a variety of plant pathogens by producing antibacterial compounds (Armstrong et al. 2001; Burja et al. 2001; Wu et al. 2012; Vlamakis et al. 2013). Many plant growth-promoting bacteria (PGPB) associated with terrestrial plants have been identified (Bashan and Holguin 1998; Vessey 2003), and the use of PGPB to increase crop yields has

become a common practice in the field of agriculture (Ortiz-Castro et al. 2009). Bacteria with metabolic properties similar to terrestrial PGPB have been identified associated with seagrasses, which implies a potential role of seagrass-associated microorganisms in supporting their host fitness.

MICROORGANISMS PROVIDE NUTRIENTS TO SEAGRASS

Experimental evidence for nutrient limitation of seagrass growth in tropical and temperate regions is provided by a number of studies (Zimmerman, Smith and Alberte 1987; Fourqurean, Zieman and Powell 1992), and marine plants may depend on their associated bacteria for enhanced nutrient availability (Donnelly & Herbert 1998; Hansen et al. 2000; Welsh 2000; Cole and McGlathery 2012). Nitrogen (N) and phosphorous (P) are two essential nutrients that can limit seagrass growth and primary production (Zimmerman, Smith and Alberte 1987; Williams 1990; Touchette and Burkholder 2000). Thus, most studies on bacterial-seagrass interactions have focused on N fixation and mineralisation of organic N and P. A significant portion of the seagrass plant's N requirement may be fulfilled through N fixation on the leaves by cyanobacteria, and on the roots by sulphate-reducing bacteria (SRB) (Fig. 2; Welsh 2000; Nielsen et al. 2001; Pereg-Gerk, Sar and Lipkin 2002; Hamisi et al. 2009; Agawin et al. 2016). In reality, most of the studies conducted on cyanobacteria reached similar conclusions through indirect evidence, and more direct evidence (e.g. by using stable isotopes) are required to show a real exchange of N between seagrasses and leaf cyanobacteria. For example, Uku and colleagues (2001) found that cyanobacterial abundance was higher on seagrasses sampled from oligotrophic waters when compared to the same species from a less oligotrophic site, suggesting that a mutualistic symbiosis may exist between seagrasses and cyanobacteria, and that seagrasses may benefit from the diazotrophic nature of their epiphytic community in terms of N supply. Additionally, considerable nitrogenase activity has been identified in cyanobacterial populations associated with various seagrass species at different locations (Welsh 2000; Hamisi et al. 2009; Cole and McGlathery 2012; Agawin et al. 2016). For SRB, quantification of the contribution of anaerobic nitrogen fixation to seagrass productivity shows that it may represent a substantial input of N, especially for seagrasses located in tropical and subtropical regions, where up to 65% of N requirement could be provided by this process (Hansen et al. 2000). *Z. capricorni* roots incubated with $^{15}\text{N}_2$ showed the appearance of about 50% of the total ^{15}N within seagrass tissue after 6 hours of incubation (O'Donohue, Moriarty and Mac Rae 1991). These results illustrate: (i) the existence of direct exchange of N between the bacteria and the plant itself; or (ii) the possibility that fixed N may become available to the plant once the bacteria die and the cell components are mineralised (O'Donohue, Moriarty and Mac Rae 1991). Recently, Tarquinio and colleagues (2018) visualised for the first time the exchange of organic N between seagrass microorganisms and plant leaf tissue using nanoscale secondary ion mass spectrometry. In fact, mineralisation of organic nutrients by seagrass microorganisms may also increase the availability of N and P for uptake by seagrasses (Smith, Hayasaka and Thayer 1984a,b; Evrard et al. 2005). In field-based experiments, after marine sediment was fertilised with organic matter, inorganic nutrients were provided by microbial mineralisation, and seagrasses (e.g. *Thalassia* sp. and *Halodule* sp.) showed significant growth responses to nutrient additions (Powell, Kenworthy

and Fourqurean 1989). It also seems possible that seagrass leaf epiphytes, such as cyanobacteria *Anabena* sp., *Calothrix braunii*, and *Nostoc* sp. (Uku et al. 2007; Hamisi et al. 2013), may increase P availability for seagrass uptake by being able to solubilise phosphorous compounds to inorganic forms (Sharma et al. 2013).

The internal cells of seagrass roots support a diverse community of bacteria, which may have beneficial effects on the plant by expressing protease activity and being able to solubilise inorganic phosphorus from insoluble compounds (Jose, Sivakala and Jebakumar 2014), thus increasing nutrient availability. Endophytic bacteria (including *Kocuria* sp., *Vibrio* sp., *Saccharomonospora* sp., *Bacillus* sp., *Desulfovibrio zosterae* and *Celerianthimonas diazotrophicus*) isolated from the root tissues of *C. serrulata*, *P. oceanica* and *Z. marina* are also able to fix nitrogen (Nielsen, Liesack and Finster 1999; Ivanova et al. 2004; Garcias-Bonet et al. 2016). Nutrient translocation experiments using labelled N isotopes have shown that nitrogen is not only translocated in the same seagrass shoot from roots to leaves and vice versa, but also between shoots of the clonal plant up to tens of centimetres apart (Marbà et al. 2002). This clonal connectivity suggests that, although endophytic bacteria may be present only in a few shoots of the clone (such as in the case of *P. oceanica* endophytic N fixing bacteria), the whole plant could benefit from their activity (Garcias-Bonet et al. 2016).

MICROORGANISMS PROTECT SEAGRASS FROM TOXIC COMPOUNDS

Seagrasses often grow in suboxic or anoxic sediments (Goodman, Moore and Dennison 1995; Borum et al. 2005). Anaerobic mineralisation of organic matter in seagrass inhabited sediments is mainly carried out by SRB (Jørgensen 1982), which are significantly more abundant in the seagrass rhizosphere compared with non-vegetated sediments (Shiehand Yang 1997), probably due to the increased organic carbon availability surrounding the plant's below-ground tissue (Holmer and Nielsen 1997). An endophytic *Sulfitobacter* and *D. zosterae*, both isolated from *Z. marina* roots, are capable of mineralising organic nutrients by reducing sulphate (Nielsen et al. 2001; Ivanova et al. 2004). The process of mineralisation supplies nutrients for seagrass growth (Holmer et al. 2001), but also results in the accumulation of hydrogen sulphides that are highly toxic to seagrasses (Bagarinao 1992). In fact, sulphide poisoning has been reported as the principal cause of die-back events of seagrasses worldwide (Koch and Erskine 2001; Borum et al. 2005; Holmer, Pedersen and Ikejima 2006). Seagrasses can respond to this potential phytotoxin by translocating photosynthetically produced oxygen from leaves into the roots, with consequent leaching of oxygen into the sediment to enhance sulphide oxidation (Armstrong and Armstrong 2005; Borum et al. 2007). Slow, spontaneous sulphide oxidation can be accelerated by intervention of some of the seagrass epiphytic bacteria that metabolise toxic substances. For example, nitrate-reducing SOB have been found to be associated with *H. wrightii* and *P. oceanica* roots (Küsel et al. 2006; Garcias-Bonet et al. 2012). SOB may be partly responsible for the oxidation of sulphide that has been observed during daytime in seagrass inhabited sediments (Lee and Dunton 2000) as well as the saltmarsh *Spartina alterniflora* roots (Lee, Kraus and Doeller 1999), with consequent relief of sulphide toxic effects on plants (Fig. 2).

MICROORGANISMS ENHANCE SEAGRASS GROWTH

Plant hormones, also known as phytohormones, regulate plant growth and affect seed germination, time of flowering and fruit production (Davies 2010; Miransari and Smith 2014). Five major classes of plant hormones exist: abscisic acid, auxins, cytokinins, ethylene and gibberellins (Gaspar et al. 1996; Kende and Seevaart 1997; Davies 2010). In terrestrial plants, root-associated microorganisms are able to synthesise and release hormones as secondary metabolites, enhancing plant development and root proliferation (Kampert, Strzelczyk and Pokojaska 1975; Ortiz-Castro et al. 2009). It is commonly thought that bacterial production of plant hormones, which do not have the same function in microbial cells, may have evolved in bacteria because of their importance for the bacterium-plant relationship (Bacon and Hinton 2011). Of these growth-regulating substances, indole-3-acetic acid (IAA) represents the primary active auxin in most plants, and both IAA and cytokinins affect cell division and stimulate growth of plant roots and shoots (Woodward and Bartel 2005). Bacteria with plant growth-promoting traits have been found associated with a number of seagrasses. For example, *Kocuria* sp. and *Vibrio* sp. isolated from *C. serrulata* internal root cells are both involved in the production of IAA (Werner and Schmülling 2009). Epiphytic *Methylophilus* sp., associated with *H. stipulacea* leaves and *V. americana* internal root tissue (Kurtz et al. 2003) can produce cytokinins with similar growth-promoting activity to that found in terrestrial plants (Fig. 2; Ryu et al. 2006). A Proteobacterium isolated from *H. stipulacea* leaves is closely related to *Alteromonas macleodii*, which has also been found to produce plant growth-promoting oligosaccharides which originate from alginate, a polymer commonly found in algal cells (Natsume et al. 1994; Ferrier, Martin and Rooney-Varga 2002). PGPB belonging to *Marinomonas* sp. have already been shown to assist the differentiation and growth of macroalgae from the genus *Ulva* (Singh et al. 2011; Wichard 2015), while *M. posidonica*, a member of the endophytic microbial community of *P. oceanica* leaves (Lucas-Elío et al. 2011, 2012; Celdrán et al. 2012; Goecke and Imhoff 2016), is suspected to play a similar role in the development of seagrass shoots (Celdrán et al. 2012). Celdrán and colleagues (2012) grew *P. oceanica* shoots from sterilised seeds and performed experiments by inoculating germinated seeds with and without *M. posidonica*. The low growth rates of 2-week-old *P. oceanica* shoots cultured in sterilised media confirmed that inoculation with *M. posidonica* significantly enhanced shoot growth and development, suggesting that this bacterium may have profound implications for the development of *P. oceanica* during its early life-history stages (Celdrán et al. 2012).

MICROORGANISMS PROTECT SEAGRASS FROM PATHOGENS AND FOULING ORGANISMS

Bacteria associated with above- and below-ground tissue of seagrasses represent a rich source of bioactive metabolites, and some microorganisms may play a protective role, releasing chemicals that protect their host from pathogens and biofouling by other organisms (Fig. 2, Table 2; Armstrong et al. 2001). The epiphytic bacterium *M. mediterranea* MMB-1 on *P. oceanica* synthesises an antibacterial agent, marinocine, with activity against both Gram+ and Gram- bacteria, such as *E. coli* and *P. aeruginosa* (Lucas-Elío et al. 2005, 2006). Endophytic bacteria

such as *Actinobacteria*, which are commonly associated with the internal root tissue of seagrasses (e.g. *Z. marina*, *T. hemprichii*; (Jensen, Kühl and Priemé 2007), are also able to synthesise a broad spectrum of antiviral, antiparasitic and antibacterial compounds, which are active against several pathogens (e.g. *Vibrio* sp., *Aeromonas hydrophyla* and *Aeromonas sobria*; Ravikumar et al. 2012; Wu et al. 2012). In reality, very little is known about the potential role played by endophytic and epiphytic bacteria in defending marine plants from pathogens and our knowledge derived from indirect evidences (e.g. extraction of bacterial secondary metabolites). More attention should be focused on this topic including the role on cyanobacteria. In fact, epiphytic cyanobacteria on seagrasses are able to produce antimicrobial and antifungal molecules, such as majusculamide A-D, malynolide, laxaphycin A-B and diterpenoids (Burja et al. 2001). Representatives of the genus *Bacillus* are usually found in high abundance in leaf epi- and endophytes of the seagrasses *E. acoroides* and *T. hemprichii*, and show extremely high activity against biofilm-forming bacteria (Marhaeni et al. 2011). Interestingly, Nijland, Hall and Burgess (2010) found that *Bacillus licheniformis* can use an extracellular DNase, in addition to AHL-degrading enzymes, to rapidly break up the biofilms of both Gram+ and Gram- bacteria (Fig. 2). *B. licheniformis* has recently been isolated from the seagrass *T. hemprichii* (Nugraheni et al. 2010), and it would be interesting to see if this bacterium uses a similar strategy against its bacterial competitors, thus providing its eukaryotic host with a powerful tool to control bacterial biofouling (Fig. 2).

The presence of specific epiphytic bacteria also seems to influence the structure of epiphytic algal assemblages of marine plants (Celdrán et al. 2012). The ability of seagrass-associated microorganisms to influence algal fouling depends upon the production of a variety of compounds with antifouling activity (Dahms, Ying and Pfeiffer 2006). In the case of *P. oceanica*, algal epiphytes can be present in high abundance (up to 30% of the seagrass biomass; Mazzella and Ott 1984), supporting a substantial community of grazers (Orth and Van Montfrans 1984), and displaying high species diversity (Mazzella, Scipione and Buia 1989; Jacquemart and Demoulin 2008). Although antifouling molecules produced by *M. posidonica* have not been characterised yet, Celdrán and colleagues (2012) showed that this endophytic bacterium plays an important role in regulating algal settlement. Patterns in the epiphytic algal community were driven mainly by changes in the abundances of red crustose, filamentous and red corticated algae, which were higher on *P. oceanica* leaves where the bacterium *M. posidonica* was present, in comparison to leaves that did not contain the bacterium (Celdrán et al. 2012). Among seagrass epiphytes, cyanobacteria show a strong antifouling activity by producing a variety of anti-algal compounds, such as fischerellin, aponin and galactosyldiacylglycerol, with the most studied compound being cyanobacterin (Gleason and Paulson 1984; Papke, Gross and Francke 1997; Jaki, Orjala and Sticher 1999; Ghasemi et al. 2003), which inhibits the growth of the common fouling diatom *Nitzschia pusilla* (Gleason and Paulson 1984; Dahms, Ying and Pfeiffer 2006; Bhadury and Wright 2004; Mazard et al. 2016). Bioactivity against green algae was also detected in cyanobacterial species commonly associated with seagrass leaves (e.g. *Fischerella*, *Nostoc*, *Calothrix* and *Oscillatoria*; Bagchi, Palod and Chauhan 1990; Schlegel et al. 1998; Mazard et al. 2016). However, while we are aware of the broad spectrum of antifouling molecules produced by cyanobacteria, further studies are needed to understand their potential role in protecting seagrass tissues from fouling organisms.

NEGATIVE IMPACT OF PATHOGENS ON SEAGRASS HEALTH

Seagrasses are declining worldwide, particularly in response to growing anthropogenic pressures and vulnerability to pathogens (Waycott et al. 2009; Trevathan-Tackett et al. 2018). A significant example of pathogenic effects on seagrasses relates to wasting disease, which was first observed in the 1930 s, when *Labyrinthula* spp. killed up to 90% of *Z. marina* in the Northern Hemisphere (Jakobsson-Thor et al. 2018). *Labyrinthula* are protists, phylogenetically basal to oomycetes. The current hypothesis implies that *Labyrinthula zosterae*, an endemic seagrass saprophyte, becomes pathogenic under high environmental levels of N (Van Katwijk et al. 1997; Hauxwell, Cebrián and Valiela 2003), causing necrotic lesions of its host leaf tissues (Muehlstein, Porter and Short 1988; Ralph and Short 2002; Bockelmann, Beining and Reusch 2012; Hughes et al. 2017). Although the exact mechanism of infection is uncertain, the disease starts with enzymatic degradation of eelgrass leaf cell walls by single *Labyrinthula* individuals. After infection, *Labyrinthula* destroys the host cell cytoplasmic contents, comprising chloroplasts, and progressively moves to neighbouring cells. This creates lesions and, as the pathogen moves fast through leaf tissues, sometimes entire leaves are killed through interruption of photosynthesis (Ralph and Short 2002; Schwelm et al. 2018).

As previously described, phenolics (rich in carbon but lacking N) are used by seagrasses to defend themselves from pathogenic attacks, herbivores and saprophytes (Martínez-Crego et al. 2015; Steele and Valentine 2015); however, leaf N and phenolic acid concentrations are inversely related (Steele et al. 2005; Hughes et al. 2017). N enrichment of coastal waters is mainly due to intensive agricultural use of fertilizers (Nedwell et al. 1999), particularly nitrate (Hughes et al. 2017). Coastal N enrichment leads to a reduction of the seagrass C:N ratio and consequently lowers the production of phenolic acids, increasing seagrass vulnerability to the wasting disease (Buchsbaum, Short and Cheney 1990; Vergeer, Aarts and De Groot 1995; Vergeer and Develin 1997). Already in 1990, Buchsbaum and colleagues found that phenolic acid concentrations were four times higher in seagrass leaves exposed to low nitrogen sites than plants located in high nitrogen sites, and those plants presented a higher resistance to wasting disease (Hughes et al. 2017). This would be particularly dramatic in seagrasses, such as *Z. marina*, that already present a reduced number of genes involved in biosynthesis of carbohydrate-based flavonoids compared to terrestrial plants (only 52 in *zosteraceae* against the 237 found in *Oryza*; Olsen et al. 2016).

It has also been predicted that other factors, such as climate warming and eutrophication, may increase seagrass stress with consequent raise in the frequency of disease outbreaks (Sullivan et al. 2018). In terrestrial ecosystems, specific bacteria are provided to plants not only to enhance their growth (e.g. PGPB) but also to increase plant resilience against abiotic stressors, such as salinity and draught (O'Callaghan 2016). Seagrass restoration programs are used to mitigate against these impacts, including wasting disease (Paling et al. 2009), yet traditional seagrass restoration efforts may fail due to the persistence of external pressures, which decrease seagrass health and increase their susceptibility to diseases. However, these restoration projects could possibly be improved through manipulation of seagrass-associated microorganisms, as the presence of specific bacteria could help seagrasses withstand environmental stressors. Therefore, we need to better understand the diversity and metabolic properties of bacteria associated with seagrass tissues.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES FOR SEAGRASS-BACTERIA INTERACTIONS IN SEAGRASS MANAGEMENT

Seagrasses and their epiphytic bacterial communities comprise both generalist and specialist microorganisms (Crump and Koch 2008; Lucas-Elío et al. 2011). Some bacteria are well adapted to live in association with plants and are common epiphytes of several seagrass species, whereas others (e.g. *Marinomonas* spp.) appear to be associated with specific seagrasses (*Posidonia* spp.). While seagrasses defend themselves from pathogenic bacteria through mechanisms such as secondary metabolite production, some bacteria clearly play a positive role for seagrass through the production of bio-available nutrients (Hansen et al. 2000); a process that would be particularly important in oligotrophic waters. In addition, bacteria and their secondary metabolites can provide important cues for the morphological development of their host such as seed germination, highlighting a key role for bacteria in the early life stages of seagrass (Celdrán et al. 2012). The close and important interactions between seagrasses and their microbial communities support the existence of a seagrass holobiont, which plays a critical role in seagrass fitness and sustainability. It is therefore important to consider a micro-scale perspective of seagrass ecosystems when assessing and understanding ecosystem processes that support these systems and the wider seascape in which they interact (Hyndes et al. 2014). However, despite the pivotal role played by the seagrass-specific microorganisms, there still remain questions in regard, for example, to the mechanisms of recruitment of microorganisms from the environment. Also, most studies have investigated only bacteria-seagrass associations, overlooking the diversity and role that archaea and other microorganisms may play in maintaining plant fitness.

Regarding future perspectives for seagrass management, following the example of the terrestrial environment, we propose manipulation of the seagrass microbial community and inoculations with specific bacteria as a novel way to enhance seagrass resilience to environmental stressors and successfully restore seagrass habitats. In terrestrial ecosystems, there has been an increasing interest in the use of beneficial microorganisms, not only to increase crop yields, but as alternatives to chemical pesticides and synthetic fertilizers in agricultural production (O'Callaghan 2016). By inoculating terrestrial plant seeds with beneficial bacteria, great results have been achieved in overcoming diseases caused by pathogenic bacteria as well as invertebrate pests, including insects and parasitic nematodes (Kabaluk and Ericsson 2007; O'Callaghan 2016). Similar to terrestrial plants, marine plant bacteria can enhance plant fitness through protection from pathogens and environmental stressors (Santos et al. 2011). However, despite the long history of terrestrial seed inoculations, this represents a completely unexplored field for marine plants. More attention should be focused on this new exciting field of research as it can offer a new way to improve seagrass health, resilience to abiotic stress and increase restoration success.

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