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Phototrophic biofilms: diversity, ecology and applications

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Abstract Phototrophic biofilms are complex conglomerations of light-driven microorganisms as autotrophs with heterotrophs embedded in a mucilaginous matrix comprising EPS (extracellular polymeric substances), attached to a solid surface. EPS provide structural and functional integrity and is essential for the physico-chemical and biological properties of the biofilms. These biofilms thrive in simple to extreme environments and comprise cyanobacteria, diatoms, microalgae, fungi, bacteria and protozoa. Formation of flocs/biofilms is an essential facet of bioremediation and wastewater treatment. Biofilm formation is a scourge in medical sciences, but in agriculture, they can be potent candidates for integrated nutrient and disease management or soil structure improvement, as they aid in better and effective colonization in soil and around roots, enabling a network from soil to the plant. The process of biofilm formation is intriguing and presents a challenge for understanding the signals and metabolites involved and the orchestration of multiple biochemical pathways. Metagenomic analysis of biofilms has unveiled complex genomic data and molecular diversity among culturable and non-culturable microbial communities dwelling in such biofilms; however, information on phototrophic biofilms is scanty. Particle-tracking techniques have shown the significance of water channels in mediating water flow, nutrient cycling and exchange of metabolites within the biofilm community. Proteomic analyses and their bioinformatic delineation have illustrated that in these biofilms, the phototrophic partner is involved in intercellular signaling, aggregation, carbohydrate and amino acid metabolism. The present review focuses on phototrophic biofilm formation, their diversity, applications and ecological roles with special emphasis on agriculture and allied sectors.

Keywords Algae · Biofilm · Bioremediation · Cyanobacteria · Nutrients · Soil fertility

Introduction

Phototrophic biofilms are mixed microbial communities comprising phototrophic and heterotrophic microorganisms, stabilized in a mucilaginous matrix of EPS (extracellular polymeric substances) in light-exposed surfaces. Extracellular polymeric substances exported from intercellular space (Flemming and Wingender 2010) form the matrix and act as an adhesive for the biofilm architecture. The phototroph nurtures microbial communities in a phototrophic biofilm (Paerl et al. 2000), while regeneration of nutrients is derived by chemotrophic heterotrophs (Canfield and Des Marais 1993). Phototrophic biofilms have immense applications in basic sciences, environment, pharmaceuticals, bioremediation and energy production, and recently, their role in agriculture as sustainable systems is being much appreciated (Fig. 1).

Diversity and ecology of phototrophic biofilms

A great deal of understanding has been gathered regarding the diversity of phototrophic biofilms, based on their morphological, ultrastructural and molecular aspects. Metagenomic studies have been helpful in deducing the role of non-culturable diversity in biofilms (Krohn-Molt et al. 2013; Sanli et al. 2015). Phototrophic biofilms often form thick mats where light-dependent redox gradients localize different groups of microbes inside the mat (Babauta et al. 2014). The upper light exposed layer is dominated by oxygenic phototrophs comprising cyanobacteria and

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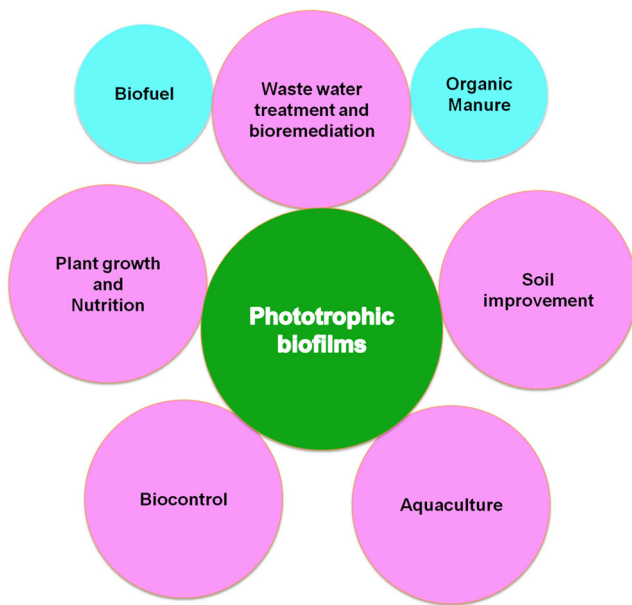
Fig. 1 Functional role of phototrophic biofilms in agriculture and allied sectors

microalgae such as green algae and diatoms, while the interior zone comprises anoxygenic phototrophs along with the heterotrophs, which includes bacteria, protozoans and fungi, forming a complex community (Roeselers et al. 2007). However, there are gaps in information regarding photoautotrophic-heterotrophic interactions, due to lack of suitable pure-culture laboratory techniques.

Organisms associated within phototrophic biofilms occupy distinct ecological niches, because of differences in trophic levels and growth phase, and the participating species adapt to fluctuating environments, particularly those related to nutrients and light. It is difficult to obtain axenic cultures of phototrophs from the biofilm with those they are associated, as some of them form intimate associations with their heterotrophic partners. At present, biofilms (natural or laboratory grown) are also being explored to broaden their scope in agro-based research as novel plant growth promoting, biofertilizing, or biocontrol agents. Such biofilms can be integrated into nutrient and pest management strategies, providing ecofriendly options for agriculture. Metagenomics, proteomics and transcriptomics are being employed as modern tools for investigating the molecular and genetic basis of biofilm formation, community organization, phylogeny and their complex interactions in photic zones and with plants.

Phototrophic biofilms are found in a wide range of illuminated environments (Table 1). Phototrophic biofilms can be micrometres to several centimetres thick layer, often observed as greenish-brown mucoid films (Buhmann et al. 2012), which create colourful mats. Most of the phototrophic biofilms in nature are dominated by cyanobacteria, which are cosmopolitan due to their inherent capacity to withstand various biotic and abiotic stresses

such as a temperature range from hot to freezing point, or salinity, acidity, desiccation, high light intensity and UV radiations. This leads to high net productivity even in such hostile environments. In aquatic systems, factors including light, irradiance, flow velocity and temperature affect development and physiology of phototrophic biofilms (Hill 1996; Stevenson 1996; Staats et al. 2000; Sabater et al. 2002). Intertidal mud flat sediments (estuaries and low coast environments) that are considered as productive areas are stabilized by cohesive silt particles and exudes of EPS, secreted by biofilms/mats of diatoms (Stal and De Brouwer 2003). De Brouwer et al. (2005) showed that the structuring of EPS plays an important role in the biogenic stabilization of intertidal sediments and diatoms such as *Nitzschia* cf. *brevissima* are actively involved in this process. Comparison of endurance and survival of biofilms of two strains of *Chrococcidiopsis* (CCMEE 057 and CCMEE 029) exposed to space and Martian simulations, both as dried biofilms or multilayered planktonic samples, illustrated that the biofilms of strain CCMEE 057 may have better tolerance (Baqué et al. 2013). Recent studies in astrobiology using microalgae revealed that on anoxic planets, UV radiation can be a strong selection pressure on surface-dwelling organisms. *Chroococcidiopopsis*, being a polyextremophile, tolerant of multiple combined stressors including desiccation, ionizing radiation and temperature excursions, was found to be the most tolerant (Cockell et al. 2011).

Extracellular mucilage or EPS

EPS form the backbone of biofilms, acting as a prerequisite for building up extensive biofilms in the biosphere by providing structural and functional integrity, and are essential for the physico-chemical and biological properties of the biofilms. EPS resemble a gel-like, hydrated biofilm matrix, in which microorganisms are embedded (Wingender et al. 1999). EPS are versatile, accounting for 50 to 90% of the total organic carbon and comprise polysaccharides, proteins, glycolipids, uronic acid, extracellular DNA, etc. Inorganic components such as silt, silica and carbonate may also contribute to the EPS of phototrophic biofilms (Sigmon and Cahoon 1997). The matrix interconnects the cells in the biofilm and mediates digestion of dissolved, colloidal and solid biopolymers by extracellular enzymes (Flemming and Wingender 2010). EPS act as light transmitters to provide photons to the organisms located deeper in a phototrophic mat (Flemming and Wingender 2010). The matrix plays a major role in the collective behaviour of microbes in the biofilm and gives them ecological advantages including protection from predators and biocides, mechanical stability, genetic stability, nutrient sequestration from oligotrophic environment and network of intercellular water channels helps in nutrient flow and

Table 1 Diversity of phototrophic biofilms in various niches

Niche	Phototrophs/Heterotrophs in biofilms	Reference
Phyllosphere	*Nostoc, Anabaena, Calothrix, Gloeotrichia*, green algae, diatoms	Venkatachalam et al. (2016)
Biological Crust	*Nostoc* sp., *Microcoleus* sp., *Calothrix* sp	Bates et al. (2010)
	Lichens (*Collema coccophorum, Lecanora muralis, Psora decipiens)*, fungi (*Cryptococcus, Thelebolus, Alternaria, Acremonium*)	Belnap et al. (2001)
	Chroococcidiopsis	Dong et al. (2007)
	Mycoplana dimorpha, Stenotrophomonas, Ralstonia frigida, Synechocystis sp.	Ozturk and Aslim (2010)
Marine water	Cyanobacteria, Bacteriodetes, Alphaproteobacteria	Leary et al. (2014)
	Oscillatoria sp., *Beggiatoa* sp.	Guidi-Rontani et al. (2014)
	Chroococcus sp., *Aphanothece* sp., *Oscillatoria* sp., *Lyngbya* sp., *Phormidium* sp.	Montoya (2009)
	Synedra, Licmophora, Navicula, Leptolyngbya, Lyngbya, Rivularia;	De Philippis et al. (2005)
	Microcoleus sp., *Oscillatoria* sp., *Lyngbya*	Woebken et al. (2012)
	Trichodesmium	Passow et al. (2012)
Buildings/Caves	*Hassallia, Tolypothrix, Scytonema, Lyngbya, Calothrix*	Keshari and Adhikary (2014)
	Aphanocapsa sp., *Calothrix* sp., *Chroococcus* sp., *Gloeocapsa* sp., *Nostoc* sp., *Oscillatoria* sp., *Phormidium* sp., *Chlorella* sp., *Scenedesmus* sp., *Navicula* sp., *Nitzschia* sp., black fungi	Cuzman (2009)
	Geitlerinema deflexum, Leptolyngbya antarctica, Leptolyngbya frigida, Phormidium murrayi, Phormidium priestleyi, Oscillatoria subproboscidea, Calothrix sp.	Taton et al. (2006)
Fresh water	*Microcystis*	Worm and Sondergaard (1998)
	Lyngbya wollei, Scytonema cincinnatum	Seifert et al. (2007)
	Cladophora , Escherichia coli;	Olapade et al. (2006)
	Oscillatoria sp.	Hamill (2001)
Ice Sheet/Glaciers	*Acaryochloris marina, Nostoc* sp., *Oscillatoria* sp.	De Los Rios et al. (2007)
	Nostoc, Oscillatoria, Gloeocapsa, Chroococcidiopsis, Phormidium sp., *Lyngbya, Microcoleus, Calothrix, Synechococcus*	Vincent (2000)
	Nodularia sp., *Anabaena* sp., *Nostoc* sp.	Hitzfeld et al. (2000)
	Phormidium sp., *Chlorella* sp., *Cylindromonas* sp., *Chlamydomonas nivalis*, ciliates (*Monodinium, Strombidium, Halteria*)	Sawstrom et al. (2002)

separation of one microcolony from another (James et al. 1995; O'Toole et al. 2000; De Philippis et al. 2001; Ramanan et al. 2010; Di Pippo et al. 2013; Pereira et al. 2013).

Wide varieties of sugars, from monomers to polysaccharides, were reported in EPS of cyanobacteria belonging to Nostocales, Oscillatoriales, Stigonematales and Chroococcales (De Philippis and Vincenzini 1998). These sugars include glucose, galactose, mannose, ribose, xylose, arabinose, fucose and rhamnose along with acidic hexoses such as glucuronic and galacturonic acid. Sulphated heteropolysaccharides of commercial importance, such as emulcyan by *Phormidium* sp. strain J-1 (Bar-Or and Shilo 1987), are components of EPS.

Prevalence of biofilms in diverse habitats

Aquatic environment

Phototrophic biofilms often predominate the surface of submerged rocks, plants and sediments. In aqueous environment, they are the basic component of food webs, contributing to primary production (Cahoon 1999; Glud et al. 2002). Diatoms are among the most important primary producers and

dominant members of biofilms in littoral zones (Bahulikar and Kroth 2008).

Phototrophic biofilms also invade natural streams in the form of attached microbial communities, where matrix provides refuge for these communities prone to hydraulic shear forces (Lock 1993). A mat of *Phormidium* and *Oscillatoria* spp. and epilithic tufts of a *Klebsormidium* sp predominated in flowing waters, while *Zygnema* was present in slow flowing shallow streams (Hawes and Brazier 1991). Phototrophic biofilms influence the survival of marine invertebrates as reported in didemnid ascidian (*Lissoclinum patella*), harbouring the biofilm of cyanobacterium (*Acaryochloris marina*) and anoxygenic phototrophs in their tunic tissue, benefitting the invertebrate through their photosynthetic metabolism (Behrendt et al. 2012). Romani and Sabater (2000) emphasized the relevance of algal biomass to the heterotrophic component of biofilms in rivers which is intrinsically related to the polymeric carbohydrates available in algal exudates. Battin et al. (2003) highlighted the functional links between algal biomass and the heterotrophic populations in glacial streams.

At the air-sea interface, thin transparent exopolymer particles (TEPs) (Sieburth 1983) form the basis of biofilm formation in aquatic environments (Berman and Passow 2007) and cover 70% of the Earth's surface, leading to significant nutrient and gaseous exchange between atmosphere and ocean. TEPs are the coagulated biogenic polysaccharides produced by phytoplankton, which often act as binders in biofilm formation. Verdugo (2012) reported that EPS are important components of marine DOC (dissolved organic carbon) and play a significant role in self-assembled microgels (SAG). However, in seas and oceans, the submerged portion of ships, submarines and other industrial implants in water bodies are often negatively impacted by proliferation of these biofilms, which cause degradation, generally termed as fouling.

Terrestrial/subterrestrial environment

Phototrophic biofilms on terrestrial and subterrestrial environments include soil environment, phyllosphere, rhizosphere and lithic surfaces (rocks and building structures). The primary colonizers of newly exposed terrestrial surfaces are generally algae and bacteria (including cyanobacteria), as well as micromycetes (Gorbushina and Broughton 2009). Subaerial biofilms (SABs) are found on land surface and lithospheric environment (Gorbushina and Krumbein 2000). In lithic environments, biofilm communities thrive on surface layer, fissures or in interstitial spaces between the lithic layers. Scanning electron microscopy revealed that the dominant population of inhabitants of open pores between mineral particles on building stones was endolithic algal morphotypes (coccoid algae and diatoms), growing as phototrophic biofilms. Phototrophic organisms boost the fungal ability to produce organic acids by their carbon inputs and thus

accelerate the weathering and mineralization of rocky lithosphere in conjugation with other chemotrophic bacteria. Cyanobacterial biofilm-like growth was reported in phyllosphere or on soil-water interface flooded wetlands, including rice. Biofilms comprising cyanobacteria (*Nostoc*, *Anabaena, Calothrix* and *Gloeotrichia*), green algae and diatoms were reported on the leaf sheaths of rice plants (Venkatachalam et al. 2016).

Phototrophic biofilms negatively impact monumental buildings, as they are responsible for their degradation and the colourful growth reduces their aesthetic value (Scheerer et al. 2009). These structures are often dwelled by species of algae (Chlorophyta and Bacillariophyta), and cyanobacteria which represent both coccoid (*Chroococcus* spp., *Gloeocapsa* spp.) and filamentous forms (*Calothrix* spp., *Leptolyngbya* spp., *Nostoc* spp. and *Phormidium* spp.), besides heterotrophs such as black mould (*Alternaria* spp., *Aspergillus* spp. and *Phoma* spp.). SABs in the atmosphere act as bioindicators for changing climate (Gorbushina 2007), as they absorb gas and particulate matter present in atmosphere.

Extreme environments

Cyanobacterial mats exhibit a ubiquitous presence, and their taxonomic composition and physiological activities in streams, ponds, lakes and melt-waters at different places in continental Antarctica are well-documented (Jungblut et al. 2005). Cyanobacteria are known to be the primary colonizers of ice sheets with the genera *Nostoc*, *Oscillatoria*, *Phormidium* and *Leptolyngbya* forming pigmented mats and surviving in fissures and interstitial spaces of Arctic and Antarctic rocks, making these ecosystems productive (Vincent 2000). These phototrophic mats are responsible for primary productivity in ice-covered regions such as polar ice valleys (Antarctica) and ice capped lakes.

In the desert ecosystem, most of the productivity is facilitated through biological soil crust formation mediated by phototrophic biofilm communities, such as cyanobacteria in association with lichens, mosses and other heterotrophic microbes (Pointing and Belnap 2012). Biological soil crusts (BSCs), formed in soil horizons of arid and semi-arid environments, provide most of the nitrogen (Belnap 2002) to the vegetation. Biofilms in soil crusts bring improvement in various soil attributes and are involved in "greening of degraded lands/deserts". These crusts improve soil attributes such as organic matter, aggregation, porosity, structure and rehabilitation of desert ecosystems (Mazor et al. 1996; Zhao et al. 2014). BSCs simulate multifunctional communities, mediating hydrological and nutrient cycling processes and providing erosion resistance, and thereby influence the establishment and performance of vascular plants (Belnap et al. 2001). Coilica et al. (2014) undertook an interesting study on the significance of induced biological soil crusts, which illustrated

the important role of the EPS in these crusts, facilitating not only the trapping and moisture retention, but indirectly reducing water infiltration and soil erosion.

Nostoc commune is among the most investigated stress-tolerant organisms, produces a distinct extracellular sheath, which contains UV-absorbing pigments, osmo-protecting sugars and enzymes such as superoxide dismutase (SOD), and exhibits a mechanical strength associated with high fluidity, resistance to desiccation and ability to absorb and hold water (Potts and Bowman 1985; Potts 1994). The EPS of *N. commune* possess the ability to resist extreme desiccation and to restore metabolic activity upon rehydration leading to stabilization of the cells in the matrix. Phototrophic biofilms are responsible for altering the hydrobiological properties of sand dunes and retaining moisture in the crust in most months of year, where morning dew is the only moisture available (Mazor et al. 1996). Hu et al. (2002) demonstrated the indispensable role of algae in the crust formation and maintaining cohesion of sand in greenhouse experiments, using four filamentous cyanobacteria and one single celled green alga. They demonstrated the critical role of algae in the initial stages of crust formation and observed that fungi, lichens and mosses influenced the soil structural and physico-chemical properties to a greater extent thereafter.

Dryland agriculture, particularly in arid and semi-arid regions, has minimal productivity due to low nutrient status, sodicity, low moisture content, instability of organic matter and low microbial diversity. Phototrophic biofilms, as biological crusts, generate favourable conditions for the growth and proliferation of flora in these ecosystems. These crusts, predominated by cyanobacteria, green and brown algae, mosses, lichens, fungi, bacteria and liverworts, show successional changes in different stages of crust development (Zhang et al. 2009) and provide nutrients and moisture for the rest of the community. The filamentous nature of cyanobacteria, fungal hyphae, rhizines/rhizoids of lichens and mosses in conjugation with other heterotrophic bacteria facilitates binding of soil particles (Belnap 1995) which become encased in the biofilm matrix. Biological crusts benefit desert ecosystems in many ways. Being diazotrophic, cyanobacteria and their biofilms provide basic carbon and nitrogen through phototrophic metabolism and withstand stress conditions due to desiccation, high temperature, salinity and low water availability.

Cyanobacteria confer structural stability and productivity in desert soils (Manchanda and Kaushik 2000; Nisha et al. 2007). Some plants benefited by crust include *Festuca octoflora*, *Mentzelia multiflora* (Belnap 1994; Belnap and Harper 1995), *Linum perenne* and *Sphaeralcea coccinea* (Harper and St Clair 1985). Filamentous cyanobacteria and green algae create surface topography in crusts. Stable aggregates improve resistance to wind and water erosion in desert ecosystems. Crusts being dark coloured increase the soil

temperature (Weber et al. 2014), conducive for germination of seeds. Xu et al. (2013) demonstrated the significance of cyanobacterial polysaccharides in promoting the growth of the shrub *Caragana korshinskii*. Their investigation illustrated that these polysaccharides not only enhanced germination rate but also eliminated reactive oxygen species, thereby stimulating photosynthetic and other metabolic activities of the plants. Desertification and degradation of soil due to the high use of agricultural chemicals reduce arable lands; in this context, such studies on BSCs have immense ecological and economic significance in arid and semi-arid ecosystems to provide fertile niche for greater cropping density and productivity.

Acidic ecosystems are often associated with phototrophic biofilms and their mats, composed of Chlorophyta (*Chlamydomonas*, *Chlorella*) and *Euglena*, besides genera *Klebsormidium* and *Zygnemopsis* (Aguilera et al. 2006). Phototrophic mats of cyanobacteria, *Synechococcus* and anoxygenic phototrophic green non-sulphur bacterium *Chloroflexus* have been well documented in extreme environment of North American hot springs with maximum temperature limit of 72 °C (Papke et al. 2003). In extraterrestrial environments, the survival capacity of cyanobacteria in biofilm state has been analysed, and *Chroococcidiopsis* sp. strain CCMEE 057 tolerated UV polychromatic radiation of 5×10^5 kJ m^{-2} with space vacuum of 780 Pa (Baqué et al. 2013). These experimental clues give further impetus for research in space microbiology and astrobiology for the possibility of enriching oxygen and biomass production.

Phototrophic biofilm formation: signaling and molecular insights

The sequential development of phototrophic biofilm involves cell attachment, colony formation, maturation and finally the dispersal of cells to form new biofilm which are mediated by different signaling mechanisms (Figs. 2 and 3). Although published reports on molecular mechanisms involved in biofilm formation and their dispersal in bacteria are available (Rendueles and Ghigo 2012), information on the genetic basis and the processes involved in cyanobacteria or microalgae is limited (Roeselers et al. 2007; Egan et al. 2008). Some of the reports available on molecular mechanisms and genes involved in growth, functioning and biofilm formation in cyanobacteria are given in Table 2.

Biofilms communicate through signal transduction pathways (quorum sensing) by secreting diffusing molecules such as oligopeptides in gram-positive bacteria and γ butyrolactones in *Streptomyces* species or acyl homoserine lactone in gram-negative bacteria, including cyanobacteria (Cuzman 2009). Cyanobacteria dominated biofilms from prehistoric caves produce AHL autoinducers (Laiz et al. 1999). Based on the data from controlled environment studies,

Fig. 2 Steps in formation of phototrophic biofilms

Step 1
- Substrate recognition and conditioning with organic molecules (Loeb and Neihof, 1975) such as proteins

Step2
- Primary colonisation by microbial species such as bacteria, green algae, diatoms, coccoid cyanobacteria, followed by secondary invasion by filamentous cyanobacteria, fungi and protozoa etc. (Cuzman, 2009)

Step 3
- Formation of microcolony, production of extracellular polysaccharide
- Cell to cell communication through secretion of signal molecules

Step4
- Maturation of biofilm through continous EPS secretion
- Development of three dimensional biofilm architecture(Bryers, 1987; Bagge et al., 2001)

Step5
- Dislodging of cells as a result of predation, enzymatic action, ageing of biofim or by artificial means (e.g. chemical treatment)

Light + CO$_2$ + O$_2$

Roeselers et al. (2007) reported that phototrophic biofilm development involves a series of successional community changes, wherein the growth rate of biofilm and community composition is highly influenced by the light during the initial phase of biofilm growth. Moreover, the development of

Fig. 3 Schematic illustration of phototrophic biofilm formation. Initiation of biofilm formation in presence of light, oxygen and carbon dioxide gradients (*1*). Surface adsorption by heterotrophic bacteria (*2*). Microcolony formation surrounded by polysaccharide matrix (*3*). Maturation and expansion of biofilm with more EPS production (*4*). Dislodging/dispersion of cells towards new substrates (*5*). Cyanobacteria (coccus and filamentous) ; Green algae ; Diatoms ; Bacteria (rod and coccus) ; Fungi ;Protozoa ; Signal molecules ● ●

phototrophic biofilms was faster in surfaces, which were precolonized by heterotrophic bacteria, marking the importance of associated heterotrophic bacteria in the initial establishment and development of phototrophic biofilms (Roeselers et al. 2007). Cyanobacterial biofilms incubated under different light regimes (light and dark) are observed to use altered metabolic functions in relation to the reuse of organic matter. Under photosynthetic conditions, increased excretion of EPS and proteins involved in micronutrient transport were observed, indicating the micronutrient requirements for extracellular organic matter incorporation in light (Stuart et al. 2016). Moreover, cyanobacteria-associated heterotrophic bacteria were reported to upregulate transport proteins during dark conditions, as compared to daylight.

In biofilms, metabolites are transported by diffusion as well as through advection by interconnected channels (Bishop 1997). Algal cells possess organically rich zones called phycosphere (Bell and Mitchell 1972); this attracts bacteria as their food, leading to biofilm formation. Small noncoding RNAs (sRNAs) may play an important role in regulating whether the bacteria remain sessile and form biofilms or exist as planktonic (free-floating) cells (Chambers and Sauer 2013). Cyanobacterial genomes are reported to contain *gro*EL genes (*gro*EL1 and *gro*EL2), which play a role in adaptation to hot environments; in *Thermosynechococcus elongatus*, although both the *gro*EL genes were heat-induced, *gro*EL2 was also cold-induced, as illustrated through primer extension and gel mobility shift analyses (Satoa et al. 2008).

In the recent past, studies have focused on understanding the genetics of EPS biosynthesis in bacteria (Whitfield 2006). The putative genes involved in exopolysaccharide production are mostly clustered and found scattered throughout different

Table 2 Genes involved in modulating growth, function and biofilm formation in cyanobacteria

Cyanobacteria	Genes	Functions	References
Calothrix sp.	*apcC*, *cpcL*, *cpcM*	Synthesis of linker polypeptides	Füglistaller et al. (1984, 1985, 1986); Lomax et al. (1987)
Calothrix sp.	*gvpA1*, *gvpA2*	Structural gas-vesicle protein	De Marsac et al. (1985); Damerval et al. (1987)
Calothrix sp.	*cpcB2*, and *cpcA2*	Phycobilisome (Phycobiliprotein) synthesis and hormogonia differentiation	Conley et al. (1985); Capuano et al. (1988)
Calothrix sp.	*cpeB* and *cpeA*	Phycobilisome (Phycobiliprotein) synthesis and hormogonia differentiation	Mazel et al. (1986)
Nostoc commune	*wspA*	Important for the structure and/or the function of the extracellular matrix and involved in conferring tolerance to adverse environmental conditions	Wright et al. (2005); Morsy et al. (2008)
Synechococcus elongates	pcc7942_1133, pcc7942_1134	Biofilm formation	Schatz et al. (2013)
Synechococcus elongates	*pteB* / *ebfG1-4*	Peptidase transporter essential for biofilm formation / Enable biofilm formation with a GG-motif (ebfG), a mediator in biofilm development	Parnasa et al. (2016)
Synechocystis sp.	*Cph2*	A cyanobacterial phytochrome2 play a physiological role in biofilm formation	Schwarzkopf et al. (2014)
Synechocystis	*gumB*, *gumC*	EPS synthesis and aggregation	Fisher et al. (2013)
Anabaena sp.	*hesF*	Maintenance of heterocyst cell wall structure and facilitation of filament adhesion and culture aggregation	Oliveira et al. (2015)
Several genera	*rfb*	Involved in assembly of cyanobacterial surface polysaccharides (rhamnose)	Pereira et al. (2009)

regions of the genome in multiple copies, as revealed by in silico analysis of the cyanobacterial genomes (Pereira et al. 2009, 2013; Rossi and De Philippis 2015, 2016). Information related to EPS synthesis in cyanobacteria is limited (Yoshimura et al. 2007); however, the biosynthetic pathway for EPS formation has been studied in many gram-positive and gram-negative bacterial species (Wingender et al. 1999; O'Toole et al. 2000; Sutherland 2001), and *rfb* genes are known to be involved in the assembly of cyanobacterial surface polysaccharides (rhamnose sugar), which is biosynthesized by *rml* genes (Reeves et al. 1996). The presence of acidic or neutral monosaccharides in cyanobacterial EPS shows the possibility of even more complex biosynthetic pathways (Sutherland 2001; Li et al. 2002; Pereira et al. 2009). These polysaccharides are also known to show hydroxyl radical/reactive oxygen scavenging activity, and antioxidant activities and structural characterization revealed alkali-extractable heteroglycan (Wang et al. 2008). The sulphated sugars of EPS from several microalgae are involved in cell recognition and cell adhesion, and thereby find use in anti-adhesive therapies for controlling bacterial infections (Guzman-Murillo and Ascencio 2000). The c-di-GMP signaling is suggested to mediate cell aggregation and biofilm formation in cyanobacteria (*Thermosynechococcus*) via activation of a PilZ domain of a cellulose synthase, which produces cellulose or related extracellular polysaccharide (Enomoto et al. 2014). Involvement of extracellular matrix

protein (WspA) has been reported in cyanobacterium, *N. commune*, wherein WspA helps to bind with the UV-absorbing pigment, scytonemin, allowing *N. commune* to survive in adverse environments (Wright et al. 2005). Cyanobacteria code for proteins involved in the ABC-dependent pathway and subsequent EPS synthesis, which are identified as KpsC and KpsS (Pereira et al. 2013). A glycoprotein-mediated cell-cell interaction in *Microcystis aeruginosa* was identified by Zilliges et al. (2008) which provides information regarding cell aggregation in cyanobacteria. Capsular polysaccharides (CPSs) are reported to be a representative of a large portion of the cell dry weight (De Philippis et al. 2001; Rossi and De Philippis 2015, 2016), and most of the reports found no qualitative differences between the composition of CPSs and RPSs (Vincenzini et al. 1990; Freire-Nordi et al. 2006; Di Pippo et al. 2013).

Schatz et al. (2013) reported that the components of a type II protein secretion system (T2S)/type IV pilus assembly system are essential for biofilm formation in *Synechococcus elongatus*. Two genes (pcc7942_1133 and pcc7942_1134) required for biofilm formation in *S. elongatus* were also identified. Similar "community escape response" was reported in the photosynthetic bacterium *Rhodobacter sphaeroides* (Puskas et al. 1997). The gene *hes*F (heterocyst-specific attachment factor) was found to play a crucial role in maintaining the heterocyst cell wall structure (Oliveira et al. 2015).

This interacts with heterocyst-specific polysaccharides and was responsible for filament adhesion and culture aggregation in *Anabaena* sp. Genes (*cpe*B, *cpe*A, *cpc*B2 and *cpc*A2). Involved in phycobilisome (phycobiliprotein) synthesis and hormogonia differentiation (Conley et al. 1985; Mazel et al. 1986; Capuano et al. 1988) are also reported. Reports also illustrated the involvement of linker polypeptides synthesis (*apc*C, *cpc*L, *cpc*M) (Füglistaller et al. 1984, 1985, 1986, Lomax et al. 1987) and genes encoding structural gas-vesicle protein in *Calothrix* 7601(*gvp*A1 and *gvp*A2) (De Marsac et al. 1985, Damerval et al. 1987). Enomoto et al. (2014) identified a Cyanobacteriochrome (CBCR) SesA (sessility-A), which acts as a diguanylate cyclase (via c-di-GMP) and regulates sessile (cell aggregation) or planktonic form transition along with chromatic acclimation and motility in a thermophilic cyanobacterium *Thermosynechococcus* under blue light and low temperature. Cell aggregation is reported to provide an effective mechanism to protect against photoinhibition by self-shading in a thermophilic cyanobacterium *Synechococcus vulcanus* (Hirano et al. 1997). A signal molecule (2*E*, 4*E*/*Z*-decadienal) from a diatom was proposed to be a part of defence mechanism(s) against grazers in biofilms (Ianora et al. 2004).

Phototrophic biofilms and their role in agriculture

Agriculture in the current scenario depends heavily on agrochemicals for crop production and protection, which consumes a large part of resources such as fertilizers, pesticides, herbicides and growth hormones, for enhancing quality and quantity of food basket. A more environment friendly approach involves the use of biofertilizers, which augment natural microflora to promote plant growth and development. In the last few years, a novel concept of development and formulation of plant growth promoting microorganisms, including cyanobacteria as matrices, and developed as phototrophic biofilms has been envisaged.

As root colonizer and plant growth promoting agents

Cyanobacteria are a major component of phototrophic biofilms and are well-known for their root colonization ability (Nilsson et al. 2002) and plant growth promotion under adverse conditions (Zahran 1999). Most cyanobacteria being phototrophs and nitrogen-fixers can meet the carbon and nitrogen requirements through CO_2 and N_2 fixation, respectively (Fay 1992; Gibson and Tabita 1996), thus supplying carbon and nitrogen in fixed and available forms to the plants. Phototrophic biofilms excrete excess of carbon (Ramanan et al. 2016) in nutrient-rich environment, often utilized by other neighbouring microbial species. Cyanobacterial inoculants are reported to enhance crop growth and yield (Mandal

et al. 1999), besides their nitrogen-fixing potential, several genera such as *Anabaena*, *Nostoc*, *Cylindrospermum*, *Calothrix* and *Plectonema* produce phytohormones such as indole acetic acid (Sergeeva et al. 2002; Prasanna et al. 2009) and other bioactive secondary metabolites that induce systemic response in plants to protect them from pests and diseases. Extracellular products from cyanobacterial biofilms stimulate the increased production of phytoregulators in *Lupinus termis* (Haroun and Hussein 2003), involved in rice calli organogenesis and replaced the artificial phytoregulators (De Cano et al. 2003). Extracellular fractions of cyanobacteria are also reported to enhance bulblet production in *Lilium alexandrae* (Zaccaro et al. 2006) and increase oil content in *Mentha piperita* (Shariatmadari et al. 2015). Cyanobacterial biofilms on rock surfaces of mountainous peaks promote vegetation by supplying nitrogen through leaching process (Dojani et al. 2007). Cyanobacterial EPS provide effective protection from widely applied pesticides and herbicides in fields that may be toxic to non-target organisms including plant growth promoting rhizobacteria. *Nostoc muscorum*, which produces extensive EPS, could tolerate and retain nitrogenase activity in the presence of Goltix (50 and 100 ppm) and Sencor at 10, 20, 50 and 100 ppm (Gadkari 1987).

The cyanobacterial mucilage is a nutrient-rich niche for several heterotrophs, and based on this feature, agriculturally important bacteria such as *Azotobacter*, *Rhizobium* and *Pseudomonas*, as also fungi such as *Trichoderma*, were used as partners. Such laboratory-developed biofilms have been evaluated successfully in pot and field experiments for their growth promoting attributes in cereals (rice and wheat) (Prasanna et al. 2015a; Swarnalakshmi et al. 2013a, 2013b), legumes (mungbean, soybean, chickpea) (Prasanna et al. 2014; Bidyarani et al. 2016), vegetables (okra, tomato) (Manjunath et al. 2016; Prasanna et al. 2013) and cash crops (cotton and maize) (Prasanna et al. 2015b, 2015c). Biofilm of *Microcoleus* sp. showed increased nitrogenase activity and growth in young mangrove seedling (Toledo et al. 1995). Application of cyanobacterial biofilmed biofertilizers or wastewater-grown algal biofilms is also reported to improve micronutrient content (Zn, Fe, Cu and Mn) of soil and grains of rice and maize (Adak et al. 2016; Prasanna et al. 2015b; Renuka et al. 2016). These investigations illustrated the promise of cyanobacterial biofilms as effective matrices for beneficial microbes and their utilization as environment-friendly multispecies inoculants in integrated practices in agriculture.

Biocontrol agents

Biofilm formation is an important trait among biocontrol agents, which not only helps in colonizing the roots but also aids in persisting and antagonizing other predators/grazers or pathogens. Besides the biofilm-forming ability, many

cyanobacteria produce cytotoxic, antifungal, antibacterial and antiviral metabolites (Dahms et al. 2006), including hydrolytic enzymes and secondary metabolites, and thus induce or elicit defence responses in plants. Among cyanobacteria, *Nostoc muscorum* and strains of *Anabaena* and *Calothrix* exhibit fungicidal activity against *Pythium*, *Fusarium* and *Rhizoctonia* (Moon et al. 1992; Prasanna et al. 2008; Radhakrishnan et al. 2009; Manjunath et al. 2010). Methanol extracts of *Nostoc linckia* and *Phormidium autumnale* have showed biocontrol properties against *Fusarium* wilt in tomato (Alwathnani and Perveen 2012). *Oscillatoria chlorina* could suppress root knot nematode in tomato under potted field soil in greenhouse (Khan et al. 2007). Co-inoculation of agriculturally important bacteria and fungi such as *Bacillus* spp., *Pseudomonas* spp. and *Trichoderma* spp. led to the development of novel cyanobacterial biofilms, with anti-grazer traits against microfauna/pathogenic fungi. Several reports on the effectiveness of *Anabaena* biofilms in controlling root rot of cotton and diseases in okra are published (Babu et al. 2015; Prasanna et al. 2013, 2015c; Manjunath et al. 2016).

Nutrient accretion and soil structure

Microbes have been utilized for soil improvement programs worldwide, as they sequester nutrient and mobilize them, making it available to plants (Madigan et al. 2003). Phototrophic biofilms represent novel microbial inoculants, which are multitrophic, and their synergistic activities work in coordination to colonize soil particles, which bring about physico-chemical, structural and biological changes in soil.

A large number of filamentous bacteria, cyanobacteria and fungi that form an integral part of phototrophic biofilms can easily associate with soil particles through EPS and enzymes or organic acids. Higher biomass density in biofilms optimizes the conditions such as pH, solute concentrations and redox potential, thereby facilitating the soil mineralization processes (Singh et al. 2006). Therefore, phototrophic biofilms are favoured in technologies to engineer soil physical properties (Mitchell and Santamarina 2005) such as permeability, hydraulic conductivity, shear strength, compressibility, stiffness and texture which in turn improve fertility, structure and better water conductivity. These properties are used commercially to minimize environmental hazards, due to chemicals and mechanization involved in soil amendments.

Microbial mineral precipitation technologies have commercial importance in improving durability of construction materials such as limestone (Achal et al. 2010), bricks (Dhamia et al. 2012) and cementitious materials such as sand consolidation (Gurbuz et al. 2011). The biofilms of *Phormidium-Calothrix-Pleurocapsa* were able to precipitate calcium in the aquatic ecosystems under supersaturated conditions (Arp et al. 2003). Stromatolites (Logan et al. 1964) well known for $CaCO_3$ deposition are linked to cyanobacteria

or cyanobacterial mats (Dupraz and Visscher 2005), as the acidic exopolysaccharide of biofilms alters the factors responsible for calcium precipitation, such as concentration of calcium and dissolved inorganic carbon, pH and availability of nucleation sites (Hammes and Verstraete 2002). Biocementing (Adolphe et al. 1990) by phototrophic biofilm promotes the strength of construction buildings that reduces its long-term maintenance costs. Decrease in hydraulic conductivity is related with groundwater recharge (Gette-Bouvarot et al. 2015) and in situ bioremediation of organic contaminants in the subsurface environment. The biofilms of cyanobacteria (*Oscillatoria*, *Phormidium* and *Aphanocapsa*) mediate calcite precipitation (Arp et al. 2003). The property of calcite formation by species of *Bacillus* and *Micrococcus* has been exploited for improving construction materials (limestone) by decreasing porosity (Tiano et al. 1999).

Aquaculture

Seafood forms an important food component for human consumption due to their nutritional value. The role of microbial biofilms in enhancing fish production through periphyton proliferation on available substrates has been reported (Shankar et al. 1998). The beneficial attributes of phototrophic biofilms in terms of EPS or as nutraceuticals and feed are being exploited in aquaculture. Dissolved organic carbon from seawater ($\sim 10^{-3}$ g L^{-1}) is 100 times more diluted than the carbon from EPS which is nearly 10 g L^{-1} (Verdugo 2012). The larval stages of metazoans directly feed on large EPS aggregates in marine ecosystems (Alldredge et al. 1993). Phototrophic biofilms can be an alternative quality feed material in aquaculture, optimizing the yield efficiency in hatcheries for fish production. However, these biofilms are studied mainly for waste buildup and recirculation of culture through removal of suspended solids. Since these aggregates represent the primary trophic level in marine food webs, further research in elucidating their potential as fish feeds is needed.

Bioremediation

Bioremediation through microbes or their consortia are useful strategies to combat pollutants responsible for contamination of water bodies and aquifers. Bioremediation potential of cyanobacteria and their mats have been reported for hydrocarbon degradation by liberating oxygen, organics and nitrogen to aerobic heterotrophic degraders (El-Bestawy et al. 2007). Microbial assimilation of carbon from oil can be stimulated by the addition of nitrogen supplements (Coffin et al. 1997). Mat surfaces carry out both aerobic and anaerobic degradation by diurnal shift from anaerobic sulphide-rich habitat in the dark to oxic conditions in light (Cohen 2002). Use of microalgal

biomass from wastewater as biofertilizers is reported in wheat (Renuka et al. 2016). This biomass can also be converted to Biochar (a form of charcoal) that acts as slow release of nutrients in the soil, improves its water retention capacity and helps in land reclamation.

Cyanobacterial growth as biofilms has been studied for oxidizing oil components, pesticides and herbicides. *Microcoleus chthonoplastes* and *Phormidium corium* were able to degrade *n*-alkanes (Al-Hasan et al. 1998), *Agmenellum quadruplicatum* oxidized naphthalene to 1-naphthol (Cerniglia et al. 1979) and *Oscillatoria* sp., and strain JCM oxidized biphenyl to 4-hydroxybiphenyl (Cerniglia et al. 1980). Cyanobacterial biofilms are reported to accumulate high concentration of insecticides in aquatic bodies. Methyl parathion has been degraded by *Nostoc linckia* and *Nostoc muscorum* (Megharaj et al. 1994), atrazine by *Selenastrum* sp. (Zablotowicz et al. 1998), Dichlorprop-methyl (2,4-DCPPM) by *Chlorella vulgaris* and *Scenedesmus obliquus* (Li et al. 2008). Heavy metal decontamination is reported by several cyanobacterial species that brings out reduction in metal load by means of intracellular uptake through EPS, surface adsorption or precipitates of sulphides or phosphates mediated by EPS. Mucilaginous sheaths of cyanobacteria, *Microcystis aeruginosa* and *Aphanothece halophytica* have strong affinity for copper, lead and zinc ions (Parker et al. 2000). Immobilized cyanobacteria as *Anabaena doliolum*, secreting mucilage, possess the potential for metal removal through biosorption (Rai and Mallick 1992). Biofilm of *Chlorococcum* sp. and *Phormidium* sp. immobilizes metals, under mixed metal exposure condition (Garcia-Meza et al. 2005). Pollutants such as nitrogenous and phosphorous compounds present in wastewater along with pernicious metal ions can be easily removed using phototrophic biofilms, which proliferate in such waters (Posadas et al. 2013; Boelee et al. 2011).

Wastewater treatment and biofuel generation

Phototrophic biofilms are being utilized in tertiary wastewater treatment units for their ability to form aggregates compared to suspended growth of other microalgae (Sandefur et al. 2014). During treatment, the algal biomass proliferates, by using inorganic substrates such as nitrogenous compounds. The ease of harvesting of aggregative/flocculating biomass make them reliable, energy-saving and economical options for cleaning water and providing value-added products as clean energy fuels (Cho et al. 2011), nutraceuticals (Pyle et al. 2008), fertilizers (Chan et al. 2008), etc. An exhaustive review on the molecular aspects and the use of EPS producing cyanobacteria in the removal of heavy metals from water illustrated the promise and drawbacks, besides complexities involved in their practical applications (De Philippis et al.

2011). They pointed out that though the process is specific to each alga, the costs involved are a major hurdle. Engineering of specific genes related to structural aspects or composition can lead to cyanobacterial strains with greater specificity and higher metal sorption capacity; these can be integrated into industrial processes.

Cyanobacterial and microalgal biofilms are also used in treating water from agricultural effluents (pesticide and chemical fertilizer residues), industrial waste/metal polluted water bodies or improving nutrient mobilization and uptake by plants using the wastewater-grown biomass (Gadd 2009; Abdel-Raouf et al. 2012; Olguin 2012; Renuka et al. 2013, 2016). Recently, microcystin, a toxin from a cyanobacterial bloom, was eliminated by phototrophic biofilms (Babica et al. 2005). Phototrophic biofilms apart from treating wastewater also act as an efficient biological source of carbon sequestration (CO_2 fixation from both atmosphere and water bodies). By-products as biofuels are economical and environment friendly, generated from waste biomass. These biofuels have been utilized in running engines/vehicles, and recently, a hydrogen fuel-based tractor has been developed (New Holland 2009) as an alternative to non-renewable energy source (fossil fuels). More concerted efforts are needed in this niche area.

Future prospects and conclusion

Biofilms represent structured natural communities, omnipresent in air, land and water bodies. Often considered as a nuisance due to their pervasive and persistent nature, recently, biofilms have evolved as promising options in agriculture in the form of multifaceted inoculants in various crop plants, including cereals, vegetables, flowers and medicinal plants. Association and colonization of rhizospheric bacteria with green algae and other cyanobacteria reveal the possibility of their coevolution (Goecke et al. 2013; Ramanan et al. 2015; Cooper and Smith 2015). The biofilm communities have often been found in association with plant growth promoting bacteria, where cyanobacteria provides carbon and fixed nitrogen input and improve soil structure and function through their proliferation. Molecular insights into phototrophic biofilm formation have illustrated the extensive diversity, genes involved, survival mechanisms and interaction among species in biofilms. EPS of biofilms are being looked as fish feed for aquaculture and hatcheries. Phototrophic biofilms can pay back indirectly to farming system, by managing pollutants in wastewater and bioremediation (oil clean-up, desalination and pesticide removal). Additionally, phototrophic biofilms act as carbon sinks and counterbalance methane emission in rice cultivation fields, thereby mitigating greenhouse gas effects through oxygenation and other biochemical activities.

Focussed work on the intricacies of nutrient dynamics in the soil/water and phototrophic biofilms interface and development of protocols for their metabolic and genetic modulation can be interesting areas for future research.

Compliance with ethical standards

Conflict of interest The authors state that they have no conflicts of interest.

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