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MINI-REVIEW

Substrate properties as controlling parameters in attached algal cultivation

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Abstract

There is growing interest in attached algae cultivation systems because they could provide a more cost- and energy-efficient alternative to planktonic (suspended algae) cultivation systems for many applications. However, attached growth systems have been far less studied than planktonic systems and have largely emphasized algae strains of most interest for biofuels. New algal biorefinery pathways have assessed the commercial potentials of algal biomass beyond biofuel production and placed more emphasis on value-added products from that biomass. Therefore, algal strain selection criteria and biomass cultivation methods need to be updated to include additional strains for improved efficiency. One possible way of improving attached cultivation systems is through engineering substrate surface characteristics to boost algal adhesion and enable strain selective algal colonization and growth. This review explores the effect of substrate chemical and topographical characteristics on the cultivation of attached algae. It also highlights the importance of considering algal community structure and attachment mechanisms in investigating attached algae systems using the example of filamentous algae found in algal turf scrubber (ATS™) systems.

Key points

- *Attached algal cultivation is a promising alternative to planktonic cultivation.*
- *Performance increase results from tuning surface qualities of attachment substrates.*
- *Attachment adaptation of periphytic algae has innate potential for cultivation.*

Keywords Attached algae · Algal biofilm · Attachment adaptation · Filamentous algae · ATS · Periphyton

Introduction

Algae are a polyphyletic group of mostly photosynthetic organisms with substantial ecological significance and numerous application potentials in the human economy. High growth rate, high bio-compound concentration, ability to use wastewater as a nutrient source, and lower land area requirements for cultivation compared to conventional crops are among the characteristics which make algae compelling for commercial applications (Mata et al. 2010; Schnurr et al. 2013). Rich in high-value bio-compounds including carbohydrates, lipids, proteins and pigments, algal biomass is a promising feedstock in many industries including biofuels, pharmaceuticals, cosmetics, animal feed, human food, fertilizer, industrial enzymes, bioplastics, and composites (Barry et al. 2016; Budzianowski 2017; Khoo et al. 2019). In addition, algal cultivation has been considered for environmental and bioremediation (i.e., phycoremediation) applications,

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including nutrient recovery, heavy metals adsorption, and carbon dioxide sequestration (Craggs et al. 1996; Hoffmann 1998; Liu et al. 2019; Zeraatkar et al. 2016). The focus of this review is on literature related to planktonic and periphytic algae and cyanobacteria and excludes the research on seaweeds (marine macroalgae).

Since the early 1950s, various systems and cultivation methods have been developed and investigated with the goal of using algae for different applications (Wang et al. 2017). Much of the research on algal cultivation systems was spurred by the goals of the Aquatic Species Program (ASP), which was funded by the US Department of Energy between 1978 and 1996 (Sheehan et al. 1998). The main focus of ASP was to develop renewable transportation fuels/biofuels from algae. Initially, many different photosynthetic aquatic species including microalgae, macroalgae, and emergent aquatic plants were investigated for their potential as a source of natural oils, but then the focus of the program shifted to producing biodiesel from high-lipid planktonic microalgae (Barry et al. 2016; Sheehan et al. 1998). Therefore, most of the algal cultivation systems and methods developed in conjunction with ASP, including raceway ponds and photobioreactors (PBRs), were explicitly designed for a few species of microalgae, most of which are high in lipid content and naturally prefer growing in suspension (Brennan and Owende 2010). This approach omitted a variety of algae of different morphologies and ecologies, and thus other cultivation methods with potential applications beyond biofuel production.

Development of novel algal biorefinery pathways that aim for the simultaneous production of high-value or value-added products alongside biofuel is frequently suggested as a strategy for improving the economic viability of algae-based products and processes (Dong et al. 2016; Khoo et al. 2019; Roux et al. 2017; Witarsa et al. 2020; Xu et al. 2020). This requires innovation in the cultivation methods and moving beyond current understanding of how to best cultivate high-lipid planktonic algae. Assessing algal strains based on their prospective performance in a multifunctional system targeting a range of applications including, for example, bioremediation, carbon dioxide (CO_2) sequestration, biofuels, and biochemical compound production may require reevaluating the conventional cultivation methods and criteria for strain selection.

To date, major challenges for the commercialization of many algae-based products and processes include the cost associated with harvesting and dewatering the algal biomass and low reliability and yield consistency of the cultivation systems (Schnurr and Allen 2015; Uduman et al. 2010). It is estimated that up to 30% of the production costs of algae cultivated in suspension (planktonic algae) is due to the harvesting and dewatering process (Schnurr and Allen 2015). One potential way of reducing the harvesting and dewatering cost is through attached cultivation, which consistently produces harvested biomass with a solids content higher by roughly an order of magnitude. In attached algae cultivation systems, algae grow attached to a physical substrate and are harvested by mechanical scraping, typically resulting in solid biomass content of 10–20% of the wet harvest (Gross and Wen 2014; Wang et al. 2017). This solids content is comparable to that obtained from planktonic (suspended) cultivation systems after multiple steps of concentration processing, including sedimentation, flocculation/flotation, and centrifugation (Davis et al. 2011; Uduman et al. 2010). In addition to the potential for easier harvesting processes and energy efficiency, attached algal cultivation systems can be advantageous because of smaller space requirements, higher productivity rates, lower water consumption, enhanced water treatment performance, and flexible lipid accumulation strategy (i.e., easier process of nutrition depletion for targeting higher lipid accumulation) (Adey et al. 2011; Calahan et al. 2018; Yu et al. 2020; Zhuang et al. 2018).

There has been an increase in attention towards designing and studying attached algal cultivation systems. Attached algal systems vary based on several operational parameters, including the substrate material, algal species present, water flow regime, and chemical composition of the growth medium (Gross et al. 2015; Wang et al. 2018). In these systems, the attachment substrate could be stationary or moving. Based on the orientation of the substrate (configuration), attached systems can be classified into four categories: horizontal, vertical, radial, and rotating (Wang et al. 2018). The green microalgae, *Scenedesmus* and *Chlorella*, are the most common taxa chosen for cultivation in attached systems (Gross et al. 2015; Schnurr and Allen 2015; Zhuang et al. 2018). The popularity of these species might be due to the residual influences of ASP on the field in encouraging the use of high lipid producing microalgae and despite their natural preference for unattached planktonic growth. There are also a small number of studies that try to evaluate attached algal biomass (biofilm based and periphytic cultivation) in biorefinery frameworks (Choudhary et al. 2020; Moreno-Garcia et al. 2017; Witarsa et al. 2020; Zhuang et al. 2020).

Substrate selection is a critical component of attached cultivation systems. Substrate characteristics influence initial algal cell adhesion, adhesion strength, growth dynamics, and algal community composition in non-axenic and mixed culture conditions (Adey et al. 2013; Blersch et al. 2017; Calahan et al. 2018; Gross et al. 2015; Ozkan 2012; Wang et al. 2018; Zeriouh et al. 2019b). Both the intrinsic chemical properties of the substrate material and its topography have a significant effect on attachment (Cui et al. 2013; Kardel et al. 2018; Khoshkhoo et al. 2019; Schumacher et al. 2007; Stevenson et al. 1996; Tuchman and Stevenson 1980), and these parameters have been the subject of many different studies involving a range of materials and application of textured substrate surfaces. However, there is limited fundamental understanding and synthesis of the effects of physical, chemical, and topographical properties of the substrate on selection for colonizing species of algae, and this remains a significant challenge in engineering substrates optimized for accelerated and selective algae cultivation. Moreover, current knowledge on the effect of substrate characteristics on algal attachment is spread across different fields and disciplines which muddles the process of acquiring a comprehensive outlook on the subject. This will be discussed in more detail throughout the review. In addition, there is limited understanding of the effect of substrate properties on the various stages of algal attachment and growth. Advances in these areas of understanding may enable improved economic feasibility of the algal cultivation processes through the ability to design systems selective for specialized periphytic algae, which are often currently less studied.

While many of the attached algal cultivation systems developed and studied to date have been either at the lab scale or pilot scale, a notable exception is algal turf scrubbers (ATS) (Adey 1982; Wang et al. 2018) (note that algal turf scrubber and ATS are trademarks of HydroMentia Technologies LLC, Ocala, Florida). ATS systems and other similar periphyton-based systems such as filamentous algae nutrient scrubbers (FANS) and periphyton nutrient removal systems (PNRS) (Sutherland et al. 2020; Sutherland and Craggs 2017) are engineered mini-ecosystems that can be used for managing water quality through cultivation of three dimensional mats of attached algae (algal turfs) in a shallow flow environment (Adey et al. 1993). As the most widely recognized variation of the mentioned periphyton-based systems, algal turf scrubbers have been built at scale for use in removal of excess nutrients from agriculture and municipal wastewaters, and recovery of non-point source waste nutrients from natural waters (Adey et al. 2011; Craggs et al. 1996). Algal communities in ATS systems typically have complex ecological structure, affording a unique ability to be competitive under low and variable environmental nutrient conditions (Adey and Loveland 2011). A combination of their effectiveness in uptake of excess pollutant nutrients such as phosphorus and nitrogen from water (Adey et al. 1993; Adey et al. 1996; Liu et al. 2016; Mulbry and Wilkie 2001; Sutherland and Craggs 2017) and three-dimensional multi-story periphytic community structure makes ATS a good candidate for further investigation in attached growth systems. The lack of knowledge regarding the interaction between the algal community in the ATS and the substrate surface, however, makes understanding the colonizing dynamics of algae and performance of the system in many applications challenging.

This review paper summarizes the current knowledge on the effect of physicochemical and topographic characteristics of the substrate on attached algae cultivation systems. The goal is to assess the potential of these parameters to control and optimize attached algal systems through algal colonization and attachment and community structural assembly. In addition, the example of filamentous algal species with specialized attachment adaptations that are often found in ATS systems is used to highlight the importance of understanding the dynamics of biofilm formation and structure in controlling attached algal cultivation systems, especially in the case of algae with complex life cycle and morphology. Moreover, efforts have been made to clarify ambiguities in the terminology that are common to attached algal systems because of the multidisciplinary nature of the field.

Algal attachment (from biofilms to periphytic algae in ATS)

Attached algal systems rely on growth of algae immobilized on surfaces (substrates). Depending on the cultivation conditions, including the algal species and/or strains present and the substrate characteristics, the structure and life cycle of the attached algal biomass can vary significantly, impacting the algae from the initial attachment stage all the way to maturation/harvesting (Genin et al. 2014; Mieszkin et al. 2013). Algal biofilm, attached algae and periphytic algal community are among the terms which have been used in the literature for referring to microbial assemblages dominated by algae attached to a substrate. Despite the similarities between the three, these terms cannot necessarily be used interchangeably and can often refer to different entities. While understanding algal-substrate interactions offers promise for improving attached cultivation systems, the challenge arises from the provincial nature of relevant fundamental knowledge about algal colonization and growth derived from in situ phycological studies on a limited number of species discordant from application-based needs of cultivation systems. The next section is devoted to defining algal biofilms and periphyton community in the context of attached algal and cyanobacterial systems and to discussing the knowledge gaps in understanding the interaction of attached algae with the attachment substrate.

In nature, biofilms are oftentimes mixed communities consisting of microbial organisms including algae and bacteria living within a matrix of extracellular polymeric substance (EPS) while attached to a surface (Genin et al. 2014; Mieszkin et al. 2013). The focus of this paper is on oxygenic aquatic phototrophic biofilms—otherwise stated, biofilms that are colonized mainly by chlorophyll-bearing algae and cyanobacteria, or more succinctly, algal biofilms. In algal biofilms, photosynthesis by algae and cyanobacteria produces organic compounds (by carbon dioxide reduction) and molecular oxygen which contributes to the metabolic processes of the entire community, including the heterotrophs (mainly bacteria and protists) (Evans 2003; Roeselers et al. 2006). Green algae, cyanobacteria, and diatoms are often the major primary producers in algal biofilm communities (Zancarini et al. 2017).

Algal biofilm formation and development is a dynamic process consisting of several steps including cell attachment, colony formation, maturation, and sloughing (Bharti et al. 2017). Each microbial species present in the biofilm has a specific response to the environmental limitations and opportunities which can also change throughout the course of biofilm development, but there are general principles which guide the succession within the biofilm community (Brislawn et al. 2019). It is believed that in non-axenic/mixed communities, bacteria are the pioneering species that attach to and condition the surface initially by secreting EPS, although pre-conditioning of the surface happens when organic and inorganic molecules are brought to the solid-liquid interface from the bulk flow (Palmer et al. 2007). Therefore, in the early stages of algal biofilm development, there is a high proportion of EPS and bacteria attached to the surface relative to algae and cyanobacteria (Schnurr and Allen 2015). Several studies have shown that the bacterial conditioning in the early stages promotes algal cell adhesion (Bharti et al. 2017; Roeselers et al. 2007; Wang et al. 2017). The early stages are followed by colonization of algae and cyanobacteria in the biofilm (Fig. 1).

Attachment, growth, and reproduction of algae and cyanobacteria can majorly influence the structure of the biofilm (Lowman et al. 2013). Depending on the characteristics of the species of cyanobacteria and algae present in the algal biofilm including lifecycle, morphology, and attachment adaptations, many biofilm characteristics such as thickness, interaction with the flow, interaction with the substrate (attachment strength), nutrient transport, and light penetration can potentially change. These changes have not been comprehensively studied before and there are significant knowledge gaps, particularly with respect to ATS systems.

Although the early stages of algae colonization in ATS systems are similar to other algal biofilms, the mature community includes turf-like three-dimensional structures, often formed by filamentous algae that grow as a canopy outside the EPS matrix (Fig. 2). In freshwater systems, periphyton is a more accurate term for referring to attached algae found in ATS. By definition, periphytic communities are the aquatic biota including photosynthetic organisms attached to a submerged substrate. Similar in concept to the algal biofilm, periphyton typically includes sessile organisms attached to the substrate and mobile forms that live associated to the attached community (Azim et al. 2005)).

Periphytic algal communities in the ATS can have high growth rates in low nutrient environments (~5–50 g m^{-2} day^{-1} dry weight) (Adey et al. 2013; Adey and Loveland 2011). High surface area-to-volume ratio to the overlying flow created by a web of mostly filamentous algae growing outward from the substrate might be the factor that allows periphytic algal communities to overcome nutrient transport limitations typically experienced by more prostrate biofilm structures. Studies on freshwater periphytic communities suggest that the attachment strength and dominant algal species are influenced by substrate type (Azim et al. 2005; Cattaneo and Amireault 1992). However, not much is known about the effect of the interactions between the substrate and periphytic algae on the performance of the ATS systems. While various substrate materials, including nylon, polypropylene mesh, rock, and concrete, have been used in ATS systems (Adey and Loveland 2011; Liu et al. 2017), materials

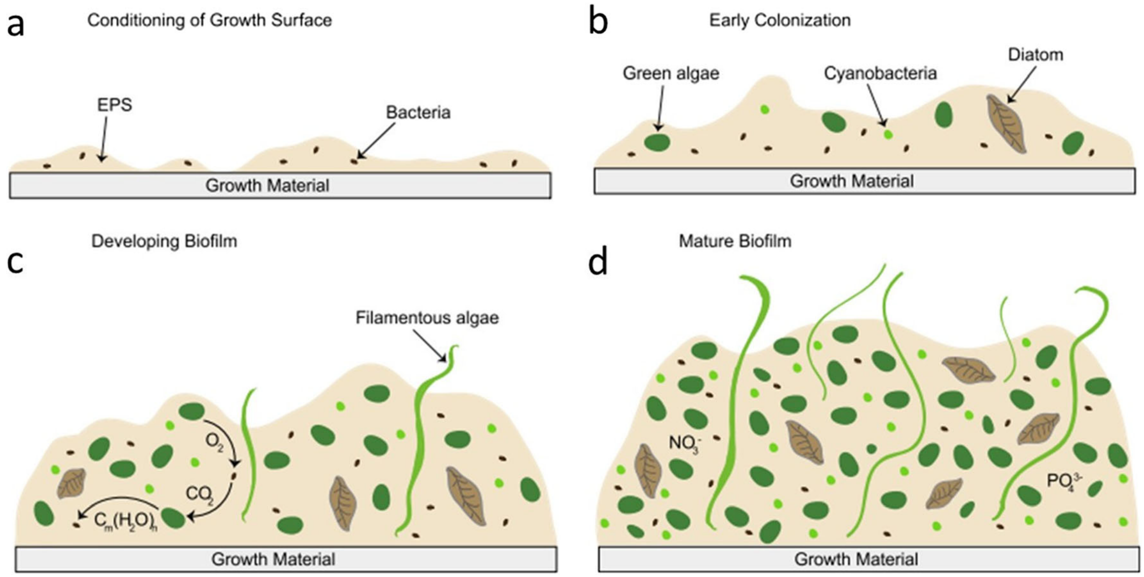

Fig. 1 Development sequence of a mixed community algal biofilm on a substrate: **a** bacterial conditioning of the substrate through EPS exudation; **b** early colonization of the EPS matrix by various species of algae from the overlying medium; **c** growth and reproduction of algal cells and formation of a algal-bacteria symbioses in the EPS matrix; **d** mature biofilm matrix, densely populated with algal cells, that retains nutrients in the EPS matrix. Figure reprinted from (Schnurr and Allen 2015) with permission from Elsevier

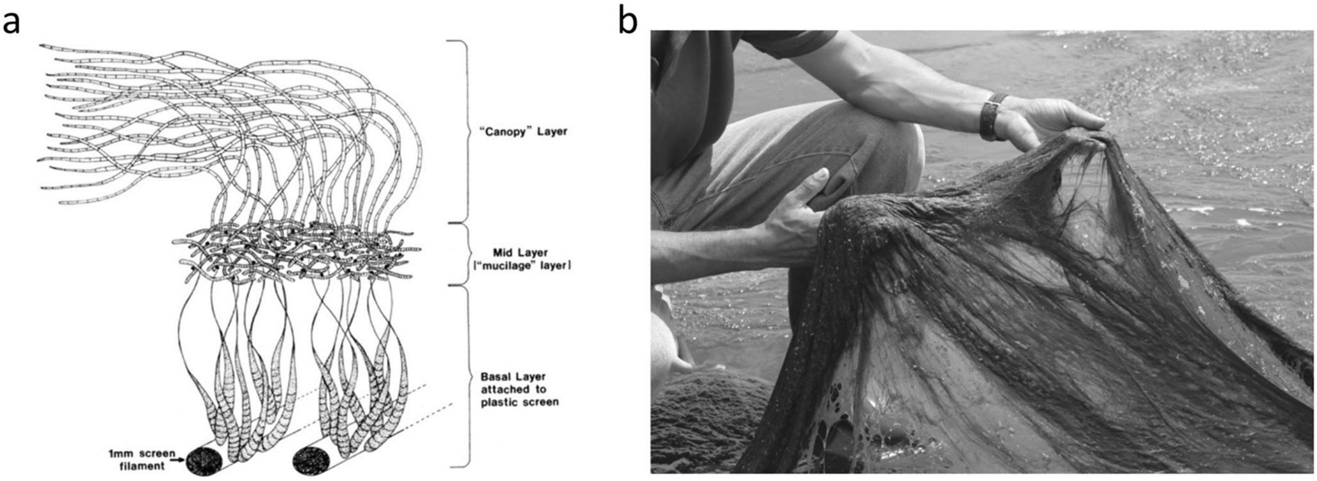

Fig. 2 **a** Concept of a multi-layered algal community on a freshwater algal turf scrubber screen; **b** mat of filamentous algae from an algal turf scrubber. Figures reprinted from (Adey and Loveland 2011) with permission from Elsevier

effects on algal community structure and function in ATS systems are poorly understood. A study by Kangas et al. (2017) found that the periphyton communities cultivated in an ATS system can be highly diverse in both algal species and attachment adaptations, with attached filamentous species dominating the total biomass. The diverse set of attachment adaptations found within periphytic algal communities includes mucilage, mucilage pads, holdfasts and rhizoids (Azim et al. 2005; Hoagland et al. 1982; Kangas et al. 2017), and each of these is expected to have different interaction characteristics with any given substrate material (Lowe and LaLiberte 2017). The set of adaptations for attachment within the algal community is often an overlooked subject of study for designing systems for cultivation of attached algae. This is despite its potential importance in understanding the algae-substrate interactions and inter-specific competition within the community.

There is generally a lack of understanding of colonization dynamics for many algal species present in ATS attached communities, which often have complex morphologies and life cycles. For example, the filamentous green algal genera *Oedogonium* and *Stigeoclonium* have been reported to be present in several ATS systems (Kebede-westhead et al. 2003; Liu et al. 2016; Mulbry and Wilkie 2001), and each of these taxa has been individually studied for potential applications in wastewater treatment and as biomass feedstock (Liu et al. 2019; Zhang et al. 2016; Zhuang et al. 2018). *Oedogonium* is an unbranched filamentous green alga known to attach to substrates via mucilage basal pads and *Stigeoclonium* is a branched filamentous green alga that attaches via basal rhizoids (Fritsch 1949; Godward 1942; Pickett-Heaps 1972; Romaní et al. 2013; Skinner and Entwisle 2006). Based on current understanding, it is challenging to describe the potential impacts of these specific attachment adaptations, or even morphological features of the mentioned algae, on the performance or operation of an ATS system or any other system targeting attached cultivation of these species. Attachment adaptations are an often-neglected aspect of interaction of algae with a substrate. The differences in the attachment strategy between the two suggests different colonization dynamics for any given substrate material. Knowledge about colonization dynamics differences between the two might be useful in designing species-specific substrate materials; however, the effects of substrate chemistry and texture to these, and most other periphytic filamentous algae are generally unknown. Attachment adaptations and complex responses to surface are not exclusive to periphytic filamentous algae and can be found in different groups of algae including green microalgae that have been widely studied in biofilm-based attached systems. Therefore, consideration of attachment adaptations in studying the algae-substrate interaction needs to be further explored.

Substrate effects on algal attachment

The main component that separates attached algal cultivation systems from other algal biomass cultivation systems is the presence of an attachment surface that allows for immobilization of algal cells and their growth. Therefore, investigating the initial contact and growth interactions of algae with the attachment substrate is a key factor in better understanding attached systems. Since the early 1900s, glass slides and other artificial substrates have been used for sampling and studying periphyton communities in freshwater inland water systems (Cattaneo and Amireault 1992). This led to observations that the taxonomic composition of the attached assemblages can be affected by substrate (Yang and Flower 2012). Certain species were oftentimes under or overrepresented depending on the characteristics of the substrate used for sampling, environmental factors (e.g., temperature and flow regime), and colonization period (Aloi 1990; Barbiero 2000; Cattaneo and Amireault 1992). Therefore, a better understanding of the effect of substrate characteristics on attached algal growth can lay the foundations for designing strain selective substrates. This is important since difficulties of downstream processing of mixed algal biomass are among the obstacles to yield consistent algae products and fulfilling the potential of attached systems in providing a more cost- and energy-efficient alternative over planktonic cultivation systems (Fabris et al. 2020; Gross et al. 2015; Ozkan et al. 2012; Witarsa et al. 2020). While there have been a number of studies on the role of the substrate in algal growth, the majority of these studies have focused on microalgae which can generate a biofilm, and there are only a few studies that include filamentous algae which have evolved attachment adaptations and are able to form long three dimensional networks (Cao et al. 2009; Cui et al. 2010; Huang et al. 2018; Kardel et al. 2015; Ozkan and Berberoglu 2013b). Despite the need for more in-depth understanding, it is generally accepted that two factors that have a significant impact on attachment are the substrate's intrinsic chemical properties and topography.

Effects of intrinsic chemical properties

The attachment of algae to a solid surface is a complicated process involving the living cell, the substrate, and the surrounding liquid (Cui et al. 2013). Studies on the effect of material chemistry on algal attachment and growth fall into three general categories: those that do not quantify surface properties of the substrate and only test for adhesion on different material; those that quantify and relate chemical surface properties to the attachment/adhesion behavior; and those that quantify the physicochemical properties of both algae and substrate to explain the attachment and adhesion (Schnurr and Allen 2015). Artificial substrates made from many different materials, including glass, ceramics, cotton, cellulose acetate, stainless steel, brass, aluminum, polycarbonate, polystyrene, polyethylene, polytetrafluorethylene, and nylon have been used for investigating the effect of substrate material on algal attachment (Gangadhara and Keshavanath 2008; Gross et al. 2015; Tuchman and Stevenson 1980; Wang et al. 2017). The effect of material physicochemical surface properties on cell-substrate adhesion and attachment has been described using a range of explanations; the effect of surface hydrophobicity/hydrophilicity and surface energy on the attachment (Faria et al. 2020; Fattom and Shilo 1984; Genin et al. 2014; Gross et al. 2016; Zheng et al. 2016), measuring the work of adhesion (Cui and Yuan 2013), and more detailed measurements of interaction energy between a single algal cell and the substrate using thermodynamic theories such as extended Derjaguin-Landau-Verwey-Overbeek (xDLVO) theory (Barros et al. 2019; Ozkan and Berberoglu 2013b; Yuan et al. 2019; Zeriouh et al. 2017).

The xDLVO thermodynamic modeling approach measures the favorability of bio-adhesion by treating the algae and the substrate as colloidal entities and ultimately measuring the total interaction energy between an algal cell and the substrate as a function of distance. The total interaction energy G^{TOT} (Eq. 1) is the linear sum of three interaction energies that are functions of distance (Fig. 3), comprising the following: Lifshitz-van der Waals (LW) interactions (G^{LW}), which originate from instantaneous asymmetrical distribution of electrons in molecules; electric double layer/electrostatic (EL) interactions (G^{EL}) from the electrostatic interactions between the cell and the substrate; and acid-base (AB) interactions (G^{AB}), which originate from polar interactions in the aqueous media (van Oss 2008). Negative G^{TOT} values indicate attraction, while positive values indicate repulsion between the cell and the substrate.

$$G^{TOT}(d) = G^{LW}(d) + G^{EL}(d) + G^{AB}(d). \quad (1)$$

Ozkan and Berberoglu (2013b) found that acid-base interactions were the dominant component in cell-substrate interaction for several microalgae species including *Tetradesmus (=Scenedesmus) dimorphus* (Turpin) M.J.Wynne and *Chlorella vulgaris* Beyerinck. A later study by Yuan et al. (2019) on several microbial adhesion data obtained via experimentation and literature for microalgae, bacteria, and fungi showed that either acid-base or electrostatic interaction can be dominant in the microbial adhesion to an abiotic substrate. In electrostatic-interaction dominated systems, the increase or decrease in the adhesion strength can be predicted using the surface zeta potential of algae and substrate, whereas in acid-base interaction dominated systems, the electron donor

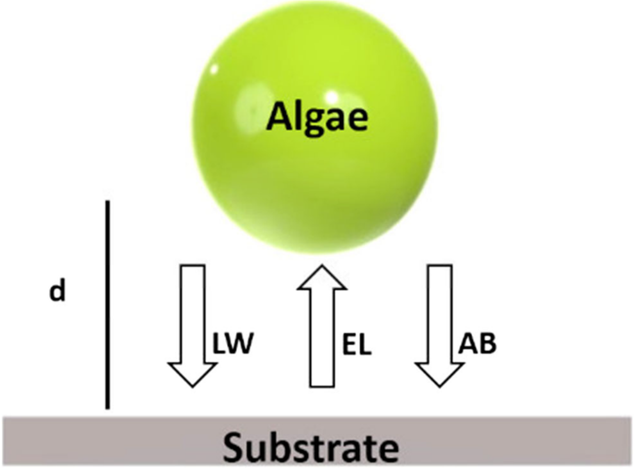

Fig. 3 Algae-substrate interactions, where Lifshitz-van der Waals (LW) interactions are usually attractive, electric double layer/electrostatic (EL) interactions are usually repulsive due to the negative charges of both the surface and algae, and acid-base (AB) interactions are usually attractive. All are defined as a function of the distance (d) between the substrate and the algae cell (Ozkan and Berberoglu 2013a)

surface characteristics of both the algae and substrate are better indicators of the adhesion behavior (Yuan et al. 2019). A key limitation of most studies is that they do not consider the dynamic nature of the algal attachment. Physicochemical properties of the algal cell and the substrate can change throughout the colonization process as a result of environmental conditions, ultimately influencing the number of algal cells attached and the strength of attachment. A study by Zeriouh et al. (2017) on biofouling of marine microalgae showed that the surface energy (described by contact angle measurements) and zeta potential of algae and the attachment substrate surface change over time and with biofilm development. Therefore, the xDLVO measurements based on initial algae and substrate physicochemical properties are inaccurate in describing the long-term adhesion behavior (Zeriouh et al. 2019a; Zeriouh et al. 2017).

Despite the overall convenience of xDLVO theory in describing the early stage attachment behavior of mostly monocultures of algae, its applications have only been explored for a limited number of algal species neglecting morphological complexities. Lack of species diversity and not considering specialized features of algae is not exclusive to studies that have used xDLVO and is a major limitation of most studies trying to explain the effect of chemical surface properties on attachment. To the authors' knowledge, there are no studies available which thermodynamically model and explain the adhesion behavior and cell-substrate interaction of freshwater algae with attachment adaptations such as rhizoids (root-like structures common in some filamentous algae) and mucilage pads (common in many algae including diatoms and cyanobacteria) or address the possible effects of morphological changes that several algal species undergo from the initial to mature phases of growth on algae-substrate interactions. Thermodynamic models and explanations generally neglect the possible effects of other microbial components present in the system, such as bacteria, on adhesion and attachment. Bacteria are believed to be the early colonizers of the algal biofilm and periphyton communities (Azim et al. 2005; Schnurr and Allen 2015); consequently, the presence of bacteria and EPS exudation on the substrate prior to algal attachment can shift the physicochemical properties of the substrate. This introduces possible errors into modeling and/or quantification of algae-substrate interactions that rely on measuring the substrate properties at pristine conditions. In most modeling efforts, changes in the properties of both algae and substrate during different stages of colonization and biofilm formation are neglected and interaction measurements are limited to a single algal cell and the substrate.

It has been speculated that, like many other microorganisms, attachment of microalgal cells is preceded by the transport of cells to the proximity of the substrate surface and within the range of interaction forces. The attachment process starts with an instantaneous reversible phase of attachment, followed by an irreversible molecular and cellular phase, which is time-dependent (Cui et al. 2010). Substrate properties can affect all the mentioned stages of the attachment process, but the magnitude of the effect of substrate chemical properties on each stage is not well understood. When it comes to physicochemical properties of the substrate material and their effects on the interaction energy, it is not clear whether the number of attached cells or strength of the attachment would be affected the most. Therefore, more effort on designing experiments with the goal of identifying and investigating the effect of physicochemical substrate properties on the adhesion and attached growth is warranted. Additionally, any material intended to be used in algal attachment systems should be able to withstand the environmental and harvesting conditions (Gross et al. 2015). Properties such as mechanical strength and degradability of the substrate are also important to assess.

Effect of substrate topography

Alongside the physicochemical properties, topography of a substrate is another crucial factor that influences algal attachment and growth. Substrate topography impacts the flow characteristics including at the surface boundary layer, which can ultimately affect algal attachment and growth (Blersch et al. 2017; Gross et al. 2016; Zhang et al. 2020). Many of the studies on the effects of substrate texture on algal attachment have been conducted in the field of marine biofouling with the goal of understanding the fouling behavior of marine microorganisms such as bacteria and algae (Carve et al. 2019; Erramilli and Genzer 2019). These studies suggest that in addition to substrate material properties and environmental factors, cell attachment is influenced by the scale of surface micro-texture (feature size), size of cells and, settlement behavior of the cells (Cui et al. 2013; Fletcher and Callow 1992; Scardino et al. 2006; Whitehead and Verran 2006). Biofouling is a broad field of study which includes algal biofouling in both marine and freshwater environments. Chlorophytes and diatoms are among the most intensively studied microorganisms for determining the effect of surface texture and interrelated properties on marine biofouling. The attachment point theory is a common explanation in the marine biofouling literature for describing the effect of texture features on algal adhesion, associating more contact points between the algae and substrate surface with increased chance of successful attachment (Carve et al. 2019). Despite the relationship between the fields of biofouling and attached algal cultivation, there seems to be an academic disconnection between these two areas of knowledge. Surface modification methods, modeling approaches, and the available knowledge from algal biofouling literature have rarely been used for promoting substrate adhesion properties in the design of systems for the cultivation of attached algae.

While studying the microalgal species *T. dimorphus* and *Nannochloropsis oculate* (Droop) D.J.Hibberd, Cui et al. (2013) reported that rates of attachment are greatest on surfaces with feature sizes close to the algal cell diameter, compared to larger or smaller sizes. In that study and others, surface wettability was used to explain the effect of substrate texture on algal attachment (Cui et al. 2013; Ferrari and Benedetti 2015; Gross et al. 2016; Sekar et al. 2004). Although wettability is not solely a function of texture, and material properties of a substrate can vastly affect it, it can be used for comparing the effects of texture across surfaces made of the same material, or it can be considered as summative for both material properties and texture. The effect of topography on surface wetting can be explained using Wenzel or Cassie-Baxter models (Cassie and Baxter 1944; Wenzel 1936). Although algal adhesion is a complex process to predict, it is speculated that textured substrate surfaces falling into Wenzel wetting behavior are more favorable for attachment since cells can theoretically fully penetrate into the texture (Fig. 4) (Cui et al. 2013). A study by Gross et al. (2016) investigated the co-effect of substrate physicochemical properties and texture on initial colonization and long term growth of microalgal biofilms. Results from this study suggested that co-effect of these parameters on cell attachment could be quantitatively described using a second order polynomial regression. A recent study on the adhesion of *C. vulgaris* to different rough natural surfaces (i.e., rice husk and pine sawdust) with root mean square roughness (S_q) values between 13.0 and 45.2 μm found increased algal cell retainment and adhesion rates on rougher substrates at early stages followed by long term effects on the cultivation (Zhang et al. 2020).

In recent years, additive manufacturing has provided researchers the ability to easily create substrates with controlled surface topographical features for algal attachment (Blersch et al. 2017; Huang et al. 2018; Kardel et al. 2015; Khoshkhoo et al. 2019). There have been several recent studies on the effects of topographies produced by additive manufacturing on attached filamentous algae. In one of these studies, 3D-printed acrylic surfaces with feature sizes ranging from 100 to 2000 μm were exposed to a natural freshwater stream for 33 days. Results showed that surface feature size influenced the overall species diversity of the periphyton community grown on the substrates, indicating the preference of some species for specific feature sizes (Blersch et al. 2017). Khoshkhoo et al. (2019) showed that by mimicking the surface characteristics found on periphyton-covered natural rocks, early colonization of filamentous algae on substrata can be enhanced through control of three interrelated descriptor parameters describing the microscale topography. Surface texture can also impact the local hydrodynamic conditions which are important in determining whether or not the algal cell would be able to settle on a substrate and stay attached in flow environments (Gross et al. 2016). It has been reported that v-shaped grooves are more favorable than u-shaped grooves for attachment of *Tetradesmus* (=*Scenedesmus*) *obliquus* (Turpin) M.J.Wynne (Huang et al. 2018). Zhang et al. (2020) used computational fluid dynamics (CFD) and particle tracing simulation for demonstrating the effect of surface roughness on adhesion behavior of *C. vulgaris* finding v-shaped grooves important for algal cell retention in the flow environment. This study indicated the formation of low shear regions and particle accumulation in the v-grooves.

A small number of studies have explored the possible benefits of employing three- dimensional substrates (woven fabrics with rather large feature sizes) in ATS systems and cultivation of periphytic filamentous algae as an alternative for highly common plastic screens (Adey et al. 2013; Ekong et al. 2019). In one study, flat high density polyethylene (HDPE) screens (mesh size 3 × 5 mm) were compared to three dimensional screens which had 1–2 cm thick and loose braided fibers in ATS floways (Adey et al. 2013). The study concluded that utilizing three-dimensional screens as substrates significantly increased the overall algal biomass production from the system. Ekong et al. (2019) also reported the advantage of

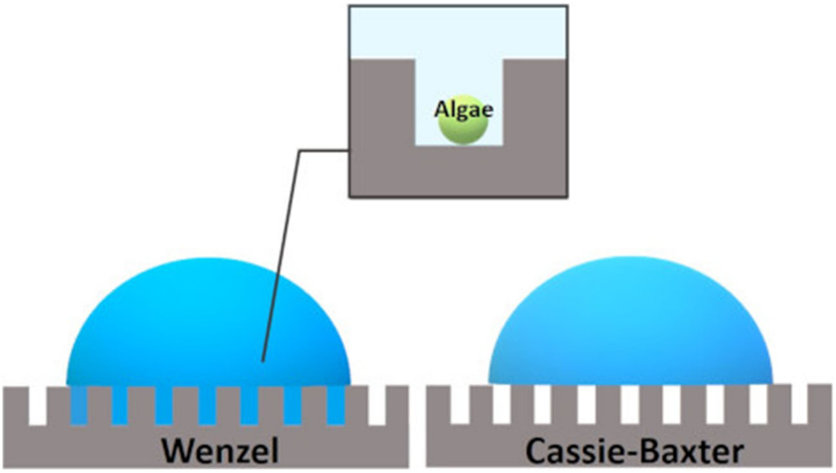

Fig. 4 Wenzel and Cassie-Baxter wetting modes. In the Wenzel mode, the liquid can fully penetrate the rough surface, theoretically enabling algae with cell sizes smaller than the roughness features to reside between the surface features. In contrast, the Cassie-Baxter mode prevents full penetration of liquid into the features

three-dimensional woven fabrics over the commonly used nylon mesh in attached cultivation of a periphytic algal community dominated by filamentous algae *Microspora floccosa* (Vaucher) Thuret and *Mougeotia scalaris* Hassall. Topographical features can impact the liquid flow pattern around the substrate and create low or high shear stress zones. The consequences of the creation of such zones and changes in the hydrodynamics of the systems can have different implications for different algae and at different stages of periphytic algal community/biofilm formation (Sandefur et al. 2014; Sutherland et al. 2020). Low shear zones can promote a sheltered space for algal cell accumulation but might also induce limitation in nutrient advection from the bulk flow. One may consider the example of periphytic algae mats found in the ATS systems, where there are often species in the community that have specialized adaptations for attachment (Azim et al. 2005; Kangas et al. 2017). With the exception of some algae found in ATS systems such as species of *Ulothrix* and *Ulva* (Fletcher and Callow 1992; Long et al. 2010; Tarakhovskaya 2014), the details of interaction of these adaptation features (such as rhizoids) with the substrate topographical features are not generally well understood. In addition, because mature ATS mats have macroscale web structures, a combination of micro- and macro-scale topographical features can be assessed for efficiency optimization. More experiments and studies (especially simulations and modeling work) are required for understanding the optimized feature size for long-term promotion of algal biomass production. In addition, substrate texture (depending on feature size, shape, and other parameters) can promote or demote bacterial attachment (Carve et al. 2019; Velic et al. 2019). Since bacteria are often the species preconditioning the substrate for the attachment, the effects of the substrate topographical features on the pioneer bacteria might be a worthwhile topic to investigate. From a practical aspect, topographical substrate features intended for use in attached algal cultivations systems should not introduce complications to the harvesting process and need to be assessed for their performance over several cycles of growth and harvest.

Conclusions and recommendations for future research

Many of the research efforts in designing and optimizing attached algal systems build upon the knowledge available on planktonic (suspended cultivation) systems and target a limited number of algae species and/or strains that often have high lipid content. With the recent efforts in utilizing algae for applications beyond biofuel and in a biorefinery context, optimization and understanding of the attached systems will require a thorough understanding of substrate-algae interaction that is inclusive of different lifecycles and morphologies. Substrate chemical and topographical characteristics have been shown to have an important effect on the favorability of algal attachment, especially during the early stages of development. Therefore, there is potential for designing substrates to target attached algae cultivation through altering the surface topographical features (texture) and chemical properties such as surface energy and zeta potential. But there are limitations to the application of the conclusions obtained about the effect of topography and chemistry of the substrate on the attached algal cultivation systems due to the following reasons:

a) Most of the conclusions are drawn based on studies undertaken on only a few algal species (mostly green microalgae), resulting in a lack of knowledge about algae with specialized mechanisms for attachment.
b) The effect of other microbial components present in the system, including bacteria, is often neglected despite evidence of their interaction with the substrate. For example, in the case of the application of xDLVO theory for predicting algal attachment favorability, surface conditioning by bacteria can vastly change the properties of the substrate that are used for measuring the total interaction energy.
c) The effect of biofilm/periphyton architecture and size (thickness) on the algae-substrate interaction is not well explored. Depending on the size and properties of the algal community, the short- and long-term interactions with the substrate may be affected.
d) There is a disconnection between the fundamental phycological knowledge of attached algal communities and what is known about attachment adaptations, and how these communities are described in studies involving engineered attached systems. Attached algal systems are part of a broad interdisciplinary field that relies on information from several fields of study, including phycology, ecology, engineering, and chemistry. Therefore, the terminology for referring to attached algal communities and the associated phenomena and processes is different across fields, creating difficulty in finding available background information. Literature available on algal biofilms, periphyton communities attached to the artificial substrates for water quality assessment and monitoring and, marine and freshwater biofouling can be good sources for acquiring fundamental knowledge about algae-substrate interactions that can help in improving attached cultivation systems.
e) Only a limited number of algal species and/or strains have been studied in attached cultivation systems under very specific environmental conditions, but results obtained from these studies are overgeneralized to all attached cultivation systems. However, differences in the morphology, lifecycle, and environmental preferences of different algae and cyanobacteria are substantial.

f) Many of the algal species targeted for cultivation in attached systems are found mostly in planktonic habitats in nature. One might argue that these species are less compatible with attached cultivation in comparison to benthic algae that are often found attached to substrates. As a result, there is a need for assessing the potentials of species that naturally thrive while growing attached.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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