Brazilian Journal of Microbiology (2020) 51:1317–1326
https://doi.org/10.1007/s42770-020-00295-0

FUNGAL AND BACTERIAL PHYSIOLOGY - RESEARCH PAPER

Effect of rhamnolipid on the physicochemical properties and interaction of bacteria and fungi

Nurhidayah Hamzah[1] · Norhafezah Kasmuri[1] · Wei Tao[2] · Naresh Singhal[3] · Lokesh Padhye[3] · Simon Swift[4]

Received: 25 August 2019 / Accepted: 7 May 2020 / Published online: 13 May 2020

Abstract

Bacterial adhesion on surfaces is an essential initial step in promoting bacterial mobilization for soil bioremediation process. Modification of the cell surface is required to improve the adhesion of bacteria. The modification of physicochemical properties by rhamnolipid to *Pseudomonas putida* KT2442, *Rhodococcus erythropolis* 3586 and *Aspergillus brasiliensis* ATCC 16404 strains was analysed using contact angle measurements. The surface energy and total free energy of adhesion were calculated to predict the adhesion of both bacteria strains on *the A. brasiliensis* surface. The study of bacterial adhesion was carried out to evaluate experimental value with the theoretical results. Bacteria and fungi physicochemical properties were modified significantly when treated with rhamnolipid. The adhesion rate of *P. putida* improved by 16% with the addition of rhamnolipid (below 1 CMC), while the increase of rhamnolipid concentration beyond 1 CMC did not further enhance the bacterial adhesion. The addition of rhamnolipid did not affect the adhesion of *R. erythropolis*. A good relationship has been obtained in which water contact angle and surface energy of fungal surfaces are the major factors contributing to the bacterial adhesion. The adhesion is mainly driven by acid-base interaction. This finding provides insight to the role of physicochemical properties in controlling the bacterial adhesion on the fungal surface to enhance bacteria transport in soil bioremediation.

Keywords Acid-base interactions · Biological adhesion · Physicochemical properties · Rhamnolipid · Water contact angle

Introduction

Soil bioremediation strategy is limited to the physical access of bacteria in targeting pollutants. Bacteria mobilization is restricted to access porous soil as it contains less water present and has higher air-water interface, which would influence bacteria accumulation [1]. Many studies were conducted to improve bacteria migration, including electrophoresis [2], environmental control [3–5], polymers [6] and bio-accessor (earthworm, chemotactic bacteria and fungi) [7]. Since fungi and bacteria share the same place in soil and are found to be abundant in contaminated site, it is important to make use of their interaction. As part of its growth properties, fungi are able to penetrate soil and provide continuous thin water film for bacteria to glide on the fungal surface [8]. Bacteria and fungi interaction is known to increase the degradation rate of hydrocarbon due to their potential to release some enzymes and tolerate high toxicity of hydrocarbons [9, 10], including polycyclic aromatic hydrocarbons (PAHs). PAHs are compounds that consist of more than two rings, which often generated during incomplete combustion of organic materials and have a strong correlation with human health [11]. The US Environmental Protection Agency (USEPA) has classified 16 groups of PAHs due to their mutagenic and carcinogenic properties [12].

Bacteria and fungi interactions have been widely discussed in root zone as bacteria transport via fungal hyphae for nutrient uptake by plant tissue [13–16]. The initial step before the mobilization is bacteria biofilm need to form on fungal

Responsible Editor: Rosane Freitas Schwan.

✉ Norhafezah Kasmuri
norhafezahkasmuri@uitm.edu.my

[1] Department of Water Resources and Environmental Systems, Faculty of Civil Engineering, Universiti Teknologi MARA, 40450 Shah Alam, Selangor, Malaysia

[2] School of Chemistry and Environmental Engineering, Sichuan University of Science and Engineering, Zigong 643000, People's Republic of China

[3] Department of Environmental Engineering, Faculty of Civil and Environmental Engineering, University of Auckland, Auckland, New Zealand

[4] Department of Molecular Medicine and Pathology, University of Auckland, Auckland, New Zealand

surfaces for symbiotic interaction. Hydrophobic interaction is known to be important for bacteria and fungi to adhere to the host plant. The mechanism for bacteria colonization in fungal hyphae is presumable by bacterial chemotaxis towards fungal metabolites [17]. In some cases, bacterial cells attach to the fungal hyphae. *Bacillus subtilis* interacts with fungus when grown with *Aspergillus niger* by attaching and growing on the hyphae [18], in sand column, *Mortierella* sp. LEJ702 facilitates the translocation of *Aminobacter* sp. MSH1 [19], and *Pseudomonas putida* PpG7 (NAH7) mobilized along a mycelium of *Pythium ultimum* [20].

Surfactants as the surface-active agent were found to modify the surface hydrophobicity of bacteria and fungi, thereby affecting the degradation activity [21–25]. For example, rhamnolipid and tergitol could alter the hydrophobicity of *R. erythropolis* 3586 and hydrophilicity of *P. putida* 852 to different extents [26]. Rhamnolipid could remove the lipopolysaccharide from the surface of *P. putida* 852 [26] and *P. aeruginosa* [27], hence lowering the values of surface tension parameters and causing the hydrophilic head of tergitol to interact with hydrophilic *P. putida* 852. In the treatment of *R. erythropolis* 3586 with surfactant solution, the hydrophobic tail of the surfactant is likely to interact with hydrophobic bacteria [26].

To our knowledge, fewer studies have been done on the effect of surfactants on bacteria and fungi physicochemical properties which is found to contribute to the adhesion activity of studies related to the study of hydrocarbon biodegradation. The objective of this study is to examine the effect of rhamnolipid on physicochemical properties of hydrophobic filamentous fungus, *Aspergillus brasiliensis* ATCC 16404; hydrophilic bacteria, *Pseudomonas putida* KT2442; and hydrophobic bacteria, *Rhodococcus erythropolis* 3586. Specifically, the focus is to evaluate the relationship between water contact angle, surface energy, total adhesion free energy (thermodynamic principals) and bacterial adhesion on fungal hyphae in the presence of surfactant. Further study should focus on bacterial adhesion using surface energy, and free energy of adhesion based on the physicochemical properties is due to the requirement to evaluate beyond water contact angle data [28]. In this study, we provide the strategy to modify bacteria and fungi physicochemical properties by treating them with surfactant. This would assimilate the adhesion of bacteria on the fungal surface which can be altered using different concentrations of surfactants despite the bacteria's surface hydrophobicity.

Materials and methods

Bacteria preparation

Two pure strains of bacteria were used: hydrophilic Gram-negative *Pseudomonas putida* ATCC 47054 (KT2440) was obtained from ATCC via Cryosite (Australia), and a spontaneous rifampicin-resistant mutation was selected to recreate KT2442 for counter selection (*P. putida* KT2442). The strain was labelled with Gfp using a mini-Tn7 transposon system as suggested by Lambertsen et al. [29] (*P. putida* KT2442-Gfp); and hydrophobic Gram-positive *Rhodococcus erythropolis* (New Zealand Reference Culture Collection, ESR, Porirua, New Zealand) were transformed with plasmid DNA expressing the red fluorescent protein tdTomato (pTEC27, a mycobacterial plasmid containing the red fluorescent protein tdTomato, resistant to hygromycin) (*R. erythropolis*-pTEC27), using the electroporation protocol introduced by Goude and Parish [30]. They were chosen on the basis of their potential to degrade PAHs and abundance in PAHs contaminated sites [31, 32].

For the bacteria preparation, this study follows the method of Feng et al. [26]. *P. putida* KT2442 was pre-cultivated in Difco tryptic soy broth (TSB; Fort Richard Laboratories) in a capped flask for 12 h at 28 °C. The flask was shaken at 200 rpm until the stationary phase was reached. For hydrophobic strain of *R. erythropolis* 3586, single colony of the strain was streak plated on Difco tryptic soy agar plates (TSA; Fort Richard Laboratories) with hygromycin B solution (50 μg.ml^{-1}) (Thermo Fisher Scientific, New Zealand) and incubated for 48 h at 28 °C. *P. putida* KT2442 and *R. erythropolis* 3586 were inoculated to obtain sufficient quantity of cells for bacterial number absorbance. Both cells were harvested by transferring to a centrifuge tube and washed twice with sterilized saline solution using a centrifuge (10,000×*g*, 10 min) (Sorval RC6 Centrifuge, F14S-6 × 250y rotor). A bacterial pellet was formed at the bottom of the centrifuge tube after the centrifugation process. The pellet of the bacteria was re-suspended with saline solution. Then, the bacterial suspension was adjusted to an absorbance of 0.3 at 600 nm (1 cm path length, Novaspec II visible spectrophotometer, Biochrom Ltd., Cambridge, UK), giving the final bacterial concentration of approximately 6×10^7 and 5.4×10^7 cfu.ml^{-1} for *P. putida* KT2442 and *R. erythropolis* 3586, respectively.

A homogeneous bacterial lawn was prepared for contact angle measurement (CAM) following the method of Feng et al. [26]. An amount of 40 ml of the bacterial suspension with OD_{600} of 0.3 for both bacteria was filtered after mixing with surfactant solution at different concentrations for 2 h using CA membrane filter with a diameter of 47 mm and pore size of 0.22 μm (Millipore, Merck) under Büchner funnel vacuum filtration.

Fungi preparation

Aspergillus brasiliensis ATCC 16404 (Cryosite, Australia) was used in this study due to the mostly found strain in the contaminated site and able to degrade a wide range of organic

pollutants, including PAHs. An amount of 10 ml aliquot of saline solution was poured over an *A. brasiliensis* plate, and an L-shaped spreader was used to lift-off the spores. For re-growth of the mould, 1 ml of the fungal spore suspension was spread evenly on the Difco Potato Dextrose Agar (PDA; Fort Richard Laboratories) plate and incubated at 28 °C for 3 days for mycelium growth and more than 3 days for sporulation. For experimental purposes, 1 ml of the fungal spore suspension was transferred to 1 ml of saline solution. The suspension was adjusted to an absorbance of between 0.9 and 1.0 at 600 nm, to give between 5×10^7–1×10^8 spore.ml^{-1}.

For fungi CAM experiments, the method from Smits et al. [33] was adapted with modification as explained by Hamzah et al. [24]. Briefly, the PDA was freshly prepared in plastic petri dishes and allowed to solidify, followed by placing the 8 μm pore size and 47 mm diameter of MCE membrane filter (Millipore, Merck) on top of the agar. Then, 5 μl of the spore suspension was grown in the middle of the membrane filter agar and incubated at 28 °C for 3 days. The filter paper, which overgrown with mycelium, was aseptically removed from the agar using sterile forceps. The mycelium filter paper was washed with potassium buffer saline (PBS) solution three times before fully immersed in 15 ml of different concentrations of surfactant solution for 2 h. Subsequently, the mycelium filter paper was filtered under vacuum (Büchner funnel) and cut into halves before being placed on a glass slide using double-sided tape to ensure a smooth surface for contact angle measurement. For adhesion assay, a mycelial pellet was used. Hence, to grow the mycelial pellet, 200 μl of the spore suspension was inoculated in 40 ml glass bottle containing 20 ml of Difco Potato Dextrose Broth (PDB; Fort Richard Laboratories) and was incubated in incubator shaker (28 °C, 150 rpm) for 3 days.

Rhamnolipid preparation

Rhamnolipid *JBR 210* (Jeneil Biosurfactant Company) was selected because it is readily biodegradable and environmentally friendly which shows that it has low toxicity to contaminant-degrading bacteria [34, 35]. Stock solution of the surfactant was prepared by pouring the surfactant in sterilized filtered water, and the sterilized mixture was then filtered through 0.22 μm RC filters for further experiments. The critical micelle concentration (CMC) of the surfactant is 40 mg.l^{-1} in aqueous phase [26]. At below concentration of 40 mg.l^{-1}, the surfactant molecules tend to adsorb on the surface. Above this value, the intense competition of the molecules is occurring between the interface and in bulk [36] and, thus, influences the adsorption and wetting properties of the surfactant on the surface [37]. From the stock solution, the surfactant was diluted in sterilized PDB at different concentrations (0.5, 1.0, 12.5, 20 and 25 x CMC) without any modification [26].

Inhibition test

As for inhibition test, this study follows the protocol suggested by Wick et al. [38]. First, a 5 μl of *A. brasiliensis* spore suspension was inoculated in the middle of a PDA plate petri dish. Next, 10 μl of bacteria suspension was inoculated at four different points around the fungal inoculum at a distance of 1 cm. Then the plate was incubated at 28 °C, and the mutual growth inhibition was analysed by visually comparing the growth pattern of individual colony plate daily for 5 days.

Contact angle measurements

Fungi and bacteria surface thermodynamic properties were determined by means of contact angle measurement (CAM) (KSV Instrument CAM 101 with an accuracy of ± 0.1°) after being treated with rhamnolipid as described by Renfro et al. [39]. One apolar liquid, 1-Bromonaphthalene (Sigma), and two polar liquids, formamide (Merck) and water, were used as diagnostic liquids. The contact angle was measured by dropping 1 μl of diagnostic liquid at total of 6 different points on a full mycelium filter paper and bacterial lawn using a gas-tight syringe (Hamilton GAS TIGHT) on a goniometer. All samples were repeated with analytical and biological triplicates to get the standard deviation of the contact angle measurement. The fungus is defined as hydrophobic when the water contact angle, θ, is ≥ 90° and hydrophilic when θ ≤ 90° [40, 41], while for bacteria, the water contact angle that is more than 40° is considered hydrophobic and less than 40° is hydrophilic [42].

The cell surface hydrophobicity is originated from the acid-base interaction exerted from cell surfaces. This interaction (γ) can be easily observed by the surface tensions of the fungi which consist of surface free energy components, γ^{LW} (Lifshitz-van der Waals) and γ^{AB} (acid-base):

$$\gamma = \gamma^{LW} + \gamma^{AB} \quad (1)$$

$$\gamma^{AB} = 2\sqrt{\gamma^{+}\gamma^{-}} \quad (2)$$

where γ^{-} is electron donor and γ^{+} is electron acceptor.

After the contact angle of each liquid on treated fungi and bacteria was estimated, the surface tension of fungi and bacteria based on acid-base components, electron donor, γ^{-}, and electron acceptor, γ^{+}, and Lifshitz-van der Waals component, γ^{LW}, can be easily determined according to Van Oss et al. [43]:

$$(1 + \cos\theta)\gamma_l = 2\left(\sqrt{\gamma_f^{LW}\gamma_l^{LW}} + \sqrt{\gamma_f^{+}\gamma_l^{-}} + \sqrt{\gamma_f^{-}\gamma_l^{+}}\right) \quad (3)$$

where θ is mean contact angle value (°) and subscript l represents known surface tension components of liquid diagnostic solutions and f for fungi surface. The subscript f can be

changed to *b* to determine the surface tension components for bacteria. All surface tension value is in the unit ($mJ.m^{-2}$).

Total free energy of adhesion calculations

In this study, the interaction (ΔG_{adh}) between fungi (*f*) and bacteria that are immersed can be expressed as follows [42, 44, 45]:

$$\Delta G_{adh} = \Delta G_{fwb}^{LW} + \Delta G_{fwb}^{AB} \quad (4)$$

$$\Delta G_{fwb}^{LW} = 2\left(\sqrt{\gamma_f^{LW}} - \sqrt{\gamma_w^{LW}}\right)\left(\sqrt{\gamma_w^{LW}} - \sqrt{\gamma_b^{LW}}\right) \quad (5)$$

$$\Delta G_{fwb}^{AB} = 2\left(\sqrt{\gamma_f^+\gamma_w^-} + \sqrt{\gamma_b^+\gamma_w^-} + \sqrt{\gamma_f^-\gamma_w^+} + \sqrt{\gamma_b^-\gamma_w^+} - 2\sqrt{\gamma_w^+\gamma_w^-} - \sqrt{\gamma_f^+\gamma_b^-} - \sqrt{\gamma_f^-\gamma_b^+}\right) \quad (6)$$

The subscripts *w* and *b* are surface tension components of water and bacteria, respectively. Thermodynamically, the adhesion of bacteria on fungi surface is considered favourable when the $\Delta G_{adh} < 0$ and unfavourable when $\Delta G_{adh} > 0$.

Bacterial adhesion assay

Fungal mycelial pellet and bacterial suspension (initial concentration of the bacteria is 10^7 $cfu.ml^{-1}$) were inoculated in 40 ml amber glass bottle, which contained 20 ml of surfactant solution at different surfactant concentrations. The bottle was tightly closed with the bottle cap before shaken at 150 rpm for 2 h at a temperature of 28 °C in the incubator. The rapid duration of incubation was selected mainly to analyse the initial bacterial adhesion and to inhibit the biofilm formation [46]. According to Renfro et al. [39], less than 2% of rhamnolipids are biodegraded within 4 h of incubation time, which indicates that the growth of bacteria can be neglected. Subsequently, 200 μl of the sample was pipetted to 96-well plate to measure the absorbance intensity of the bacteria in the sample. For this purpose, the fluorescence intensity multiwell plate reader count (EnSpire® 2300 Multimode Plate reader, PerkinElmer) with Wallace Envision Manager software program was used. Their fluorescence signal detects the bacteria intensity. Hence, the multiple plate reader was installed with two sets of commercial filters: excitation/wavelength of 473/535 nm for *P. putida* and at 554/581 nm for *R. erythropolis*. The adhesion assay was run triplicate with the sample without surfactant and the sample without fungus as control.

Since the absorbance intensity of bacteria was linearly correlated with the bacteria colony-forming unit per millilitre ($cfu.ml^{-1}$) (data not shown), therefore the absorbance intensity data was used to calculate the percentage of bacterial adhesion on fungus surface by the following formula:

$$I_{adh} = \frac{I_i - I_f}{I_i} x100\% \quad (7)$$

where I_{adh} describes the percentage of bacterial adhesion on fungus surfaces, I_i and I_f indicate absorbance intensity of initial bacteria in suspension (without fungus) and absorbance intensity of remaining bacteria in suspension with fungus, respectively.

Statistical analysis

The statistical evaluations were performed using two-way ANOVA test. A significant difference was assumed for analyses with $P < 0.05$. The surface energy component and the total adhesion free energy data were the mean value of CAM from 18 data samples.

Results and discussions

Rhamnolipid modified the physicochemical properties of *A. brasiliensis*, *P. putida* and *R. erythropolis*

The inhibition test shows that the fungus and the bacteria have synergistic interaction and do not inhibit each growth. To gain a better understanding of the effect of rhamnolipid, the surface physicochemical properties of *A. brasiliensis*, *P. putida* and *R. erythropolis* are summarized in Table 1. Principally, *P. putida* has hydrophilic surface due to the water contact angle, $\theta°$ value (34.7° < 40°). It also has a higher value of the electron-donating component, γ^- compared with *A. brasiliensis* and *R. erythropolis*. The initial water contact angle of *A. brasiliensis* was 118° indicating that the hydrophobic surfaces were (> 90°). This is consistent with the value of electron donor (γ^-) (0.97 $mJ.m^{-2}$) and an electron acceptor (γ^+) (3.48 $mJ.m^{-2}$). Similar results were found for *R. erythropolis*, which has a hydrophobic surface (95.7° > 40°) with lower γ^- and γ^+ value (0.56 $mJ.m^{-2}$ and 0.13 $mJ.m^{-2}$). This result shared a similar trend for hydrophobic surface and hydrophilic surface from previous studies [26, 47].

The addition of rhamnolipid significantly changed the electron donor component and slightly improved the electron acceptor component of *A. brasiliensis* and *P. putida*, hence causing the γ^{AB} to increase. Rhamnolipid has less influence on the acid-base (AB) and Lifshitz-van der Waals (LW) components of *R. erythropolis*. The cohesive free energy (ΔG^{TOTAL})

Table 1 Water contact angle values, surface energy and their components of bacterial and fungal surfaces with rhamnolipid of different concentrations

Substratum	Rhamnolipid conc. (CMC)	Contact angle ($\theta_w°$)[b]	Surface energy components[a]				ΔG^{LW}	ΔG^{AB}	ΔG^{TOTAL}
			γ^{LW}	γ^-	γ^+	γ^{AB}			
A. brasiliensis ATCC 16404	*0*	118 ± 6	23.75	0.97	3.13	3.48	− 0.08	− 53.37	− 53.45
	0.5	92.3 ± 3	13.20	34.92	5.54	27.82	0.42	− 16.28	− 15.86
	1	77.3 ± 4	24.47	64.24	14.44	60.91	− 0.11	9.30	9.18
	12.5	59.8 ± 3	11.30	75.00	5.10	39.12	0.53	0.99	1.53
	20	55.3 ± 4	15.40	87.99	4.75	40.87	0.30	5.07	5.37
	25	47 ± 3	25.50	111.31	9.57	65.28	− 0.16	20.19	20.04
P. putida KT2442	*0*	34.7 ± 1	28.83	39.88	0.29	6.80	− 0.98	22.83	21.85
	0.5	50.3 ± 2	28.66	34.66	0.28	6.19	− 0.96	19.01	18.05
	1	45.8 ± 7	27.5	43.70	0.54	9.72	− 0.81	25.00	24.20
	12.5	31.2 ± 0.3	28.3	62.02	0.35	9.27	− 0.90	36.78	35.88
	20	32.3 ± 1	28.83	62.30	0.35	9.36	− 0.98	36.94	35.96
	25	32.0 ± 1	28.68	61.45	0.44	10.35	− 0.96	36.28	35.32
R. erythropolis 3586	*0*	95.7 ± 1	33.9	0.56	0.13	0.54	− 2.66	− 80.68	− 83.34
	0.5	117.6 ± 0.2	30.52	0.05	2.11	0.63	− 1.97	− 76.25	− 78.23
	1	116.1 ± 1	30.93	0.29	2.72	1.79	− 2.06	− 71.53	− 73.59
	12.5	109.3 ± 0.5	34.62	0.03	0.18	0.15	− 2.80	− 85.43	− 88.23
	20	107.5 ± 0.4	35.27	0.02	0.10	0.08	− 2.93	− 86.86	− 89.79
	25	107.2 ± 0.4	35.40	0.02	0.07	0.08	− 2.95	− 87.03	− 89.99

[a] Units of surface energy components, surface energy, ΔG^{LW}, ΔG^{AB}, and ΔG^{TOTAL} are in $mJ.m^{-2}$

[b] Mean value of 18 data samples

Can be considered as these are the values for the concentration of Rhamnolipid

denotes the interaction energy between *A. brasiliensis* and rhamnolipid, *P. putida* and rhamnolipid or *R. erythropolis* and rhamnolipid. The negative value of ΔG^{TOTAL} indicates that the surface hydrophobicity of fungi or bacteria is hydrophobic or vice versa. The LW component representing the energy between the surface and rhamnolipid was positive and did not change as the concentration of the applied rhamnolipid was varied. The positive sign of the LW components reveals that the electrostatic force is not the dominant force for the adhesion of both bacteria on the fungi surface.

The effect of rhamnolipid on the surface energy and total adhesion free energy of *P. putida* and *R. erythropolis* to the *A. brasiliensis*

Surface energy (γ) is a significant parameter describing the solid surface and its interaction with other materials, which not only related to surface hydrophobicity but also adhesion properties [48]. Table 2 shows that the untreated surface energies for *A. brasiliensis*, *P. putida* and *R. erythropolis* are 27.2 $mJ.m^{-2}$, 35.6 $mJ.m^{-2}$ and 34.4 $mJ.m^{-2}$, respectively, indicating that fungi surface is less energetic than bacteria surface. The surface energy of *A. brasiliensis* was altered dramatically, but the surface energy for both bacteria was slightly modified. The surface energy for both bacteria was within the range of 34 $mJ.m^{-2}$ to 39 $mJ.m^{-2}$ as the surfactant concentration increased.

The two-way ANOVA test suggested that rhamnolipid significantly influenced bacteria and fungi surface energy ($P < 0.05$) and increased the adsorption capacity to the fungi rather than to the bacteria. Higher surface energy indicates higher adsorption capacity [48]. It is in agreement with the previous research that *A. brasiliensis* adsorbed surfactant linearly as the surfactant concentration increased [24]. Moreover, Khan et al. [28] found that bacteria firmly adhered to the higher surface energy of self-assembled monolayers (SAMs) surface. The theoretical surface energy result (Table 2) shows that modification of fungal surface is more important to promote the bacterial adhesion and treating with rhamnolipid is anticipated to increase the adhesion of *P. putida* and *R. erythropolis* on *A. brasiliensis* surface.

The total adhesion free energy, ΔG_{adh}, is calculated to further predict the adhesion and understand the mechanism involved in the interaction. Since the adhesion process involves bacteria and fungus physicochemical properties, the correlation between the properties and the total adhesion free energy, ΔG_{adh}, is required. Therefore, the main factors contribute to the process can be determined. The total adhesion free energy, ΔG_{adh}, as listed in Table 3 predicts bacteria adhesion to untreated and treated *A. brasiliensis* with respect to different concentrations

Table 2 Surface energy of fungi and bacteria as a response to rhamnolipid at different concentration

Rhamnolipids conc. (CMC)	Surface energy (γ) mJ.m^{-2}		
	A. brasiliensis 2ATCC 16404	*P. putida* KT2442	*R. erythropolis* 3586
0	27.23	35.63	34.44
0.5	41.02	34.85	31.15
1	85.38	37.22	32.72
12.5	50.42	37.57	34.77
20	56.27	38.19	35.35
25	90.78	39.03	35.48

This value refers to the concentration of Rhamnolipid

of rhamnolipid. From the table, forces that drive in the theoretical adhesion on fungal surfaces were obtained.

The total adhesion free energy of untreated *P. putida* and *R. erythropolis* is less than 0 (− 28.37 mJ.m^{-2} and − 66.83 mJ.m^{-2}, respectively), indicating favourable adhesion. It is similar to the finding for *P. aeruginosa Olin*, which adheres to dolomite (a hydrophobic surface) at − 25.66 mJ.m^{-2} [49]. After 0.5 CMC of rhamnolipid was introduced in the systems, the total adhesion free energy, ΔG_{adh}, of *P. putida* increased to be positive (13.71 mJ.m^{-2}), and the total adhesion free energy, ΔG_{adh}, for *R. erythropolis* also increased but remained to be negative (− 18.10 mJ.m^{-2}). As the surfactant concentration rose beyond 1 CMC, the total adhesion free energy, ΔG_{adh}, of both bacteria on fungus surfaces increased accordingly and became positive. Therefore, the thermodynamic approach predicts that the adhesion of *P. putida* and *R. erythropolis* on *the A. brasiliensis* surface in addition of rhamnolipid will be less favourable at below 1 CMC and not favourable at beyond 1 CMC. In addition, the ΔG^{AB} component was higher than the ΔG^{LW} component, indicating that the theoretical adhesion of hydrophilic *P. putida* and hydrophobic *R. erythropolis* on hydrophobic *A. brasiliensis* should be driven mainly by the short-range force (acid-base interaction).

The comparison of bacterial and fungal water contact angle and electron donor component with the total adhesion free energy was conducted to identify the impact factor. In the case of treated fungi and bacteria, rhamnolipid was predicted to affect the adhesion of *P. putida* on *A. brasiliensis* compared to *R. erythropolis*. Higher ΔG_{adh} value was obtained for *P. putida* and *R. erythropolis*, which shows less favourable adherence at below 1 CMC for both variables. Hence, the adhesion of *P. putida* is theoretically predicted to be lesser than *R. erythropolis*. A good correlation (which is shown as regression value) was found between the total adhesion free energy (ΔG_{adh}) and bacteria and fungi water contact angle (θ_w) and electron donor property (γ^-), as shown in Table 4. Similar results were observed in Sadiki et al. [35] who found that the total adhesion free energy of *Thielavia hyalocapa* was correlated to cedarwood physicochemical properties.

A higher regression value was found for linear regression of *A. brasiliensis* compared with the polynomial regression for *P. putida* and *R. erythropolis.* This indicates that the fungus water contact angle (θ_w) and electron donor component (γ^-) might strongly affect the bacterial adhesion. However, the bacterial adhesion is more likely facilitated by the bacteria water contact angle, especially for *P. putida*. The correlation was weak for *R. erythropolis* which explains that the bacteria water contact angle (θ_w) ($r^2 = 0.8253$) and electron donor component (γ^-) ($r^2 = 0.7328$) have less impact on the adhesion. This result suggests that the water contact angle and electron donor of the surface are the important factors to control bacterial adhesion. Faten et al. [50] also reported that the adhesion of *Lactobacillus plantarum* on modified surface of olive increased as the electron donor of the olive surface increased.

Rhamnolipid influenced the adhesion of bacteria on the A. brasiliensis surface in batch experiment

Since the objective of this study is to investigate the response of bacterial adhesion to physicochemical properties

Table 3 The free energy of adhesion (ΔG_{adh}) between treated *P. putida* and *R. erythropolis* on treated *A. brasiliensis* surface

A. brasiliensis ATC 16404

Bacteria	Concentration of surfactant (CMC)	ΔG^{LW}_{adh} (mJ.m^{-2})	ΔG^{AB}_{adh} (mJ.m^{-2})	ΔG_{adh} (mJ.m^{-2})	Bacteria	ΔG^{LW}_{adh} (mJ.m^{-2})	ΔG^{AB}_{adh} (mJ.m^{-2})	ΔG_{adh} (mJ.m^{-2})
P. putida KT2442	*0*	− 0.29	− 28.38	− 28.67	*R. erythropolis* 3586	− 0.47	− 66.36	− 66.83
	0.5	1.42	12.29	13.71		1.77	− 19.87	− 18.10
	1	− 0.32	29.49	29.17		− 0.50	8.90	8.40
	12.5	1.69	47.99	49.67		3.18	6.21	9.39
	20	1.04	54.93	55.97		1.89	12.83	14.72
	25	− 0.52	59.21	58.68		− 0.98	33.44	32.46

Untreated bacteria and untreated fungi data are shown at zero (0) concentration of rhamnolipid

As this value of concentration referred to Rhamnolipid

Table 4 Regression of water contact angle, θ_w, and electron donor component, γ^-, with respect to the total adhesion free energy, ΔG_{adh}, in the presence of rhamnolipid

Water contact angle, θ_w (°)	*P. putida* KT2442	*R. erythropolis* 3586	Electron donor component, γ^- ($mJ.m^{-2}$)	*P. putida* KT2442	*R. erythropolis* 3586
Fungus	0.9824	0.9289	*Fungus*	0.9364	0.9426
Bacteria	0.9005[a]	0.8253[b]	*Bacteria*	0.9436[a]	0.7328[b]

[a] Regression value for the *P. putida* water contact angle/electron donor component

[b] Regression value for *R. erythropolis* water contact angle/electron donor component

modification, the experimental assay was conducted looking at the treated bacteria and fungus before compared to the untreated sample.

The comparison between the experimental and theoretical prediction of bacterial adhesion on *A. brasiliensis* in the presence of rhamnolipid has not yet been reported. Consequently, a dynamic adhesion of *P. putida* and *R. erythropolis* on *A. brasiliensis* surfaces was observed in experimental test. The adhesion capacity of *P. putida* and *R. erythropolis* varied according to the rhamnolipid concentrations. The phenomenon may be associated with the modification of both bacteria and fungus physicochemical characteristics which has altered their surface hydrophobicity and become more electron donor rather than electron acceptor in nature, thereby weakening the interaction.

These tendencies were true for water contact angle of the rhamnolipid-treated bacteria, while the surface hydrophobicity of fungi decreased with the increase of surfactant concentration. These observations indicate that the adhesion tendency for both bacteria is more likely mediated by the water contact angle of bacteria than the fungus surface hydrophobicity (Fig. 1).

At below 1 CMC, *P. putida* adhesion has the tendency to follow the bacteria water contact angle, which increases towards 1 CMC. The adhesion decreases after the bacteria become hydrophilic ($P < 0.05$). *P. putida* becomes hydrophobic at below 1 CMC, which is more likely to adhere on the fungal surface, as shown in Fig. 1. However, rhamnolipid did not influence the water contact angle of *P. putida* at above 1 CMC. Therefore, no changes in bacterial adhesion were observed. The adhesion beyond 1 CMC could facilitate by *P. putida* surface energy, *A. brasiliensis* water contact angle and surface energy.

As the Gram-negative bacteria, the outer membrane of *P. putida* plays a significant role in adhesion. Most of the Gram-negative bacteria have exopolymeric substances (EPS) and proteinous cell appendages for adhesion purposes and act as adhesin between the cell body [51]. Therefore, *P. putida* adhesion to *A. brasiliensis* increases when the surface is hydrophobic and still manages to adhere to the hydrophilic state as long as the fungal surfaces serve higher surface energy. This is in agreement with a study done by Zhang et al. [52] which the lower the difference between bacteria surface energy and solid surface energy, the higher the bacterial adhesion would be. To obtain lower value of the surface energy difference, higher surface free energy is required on the solid surface. In our study, the negative value of surface energy

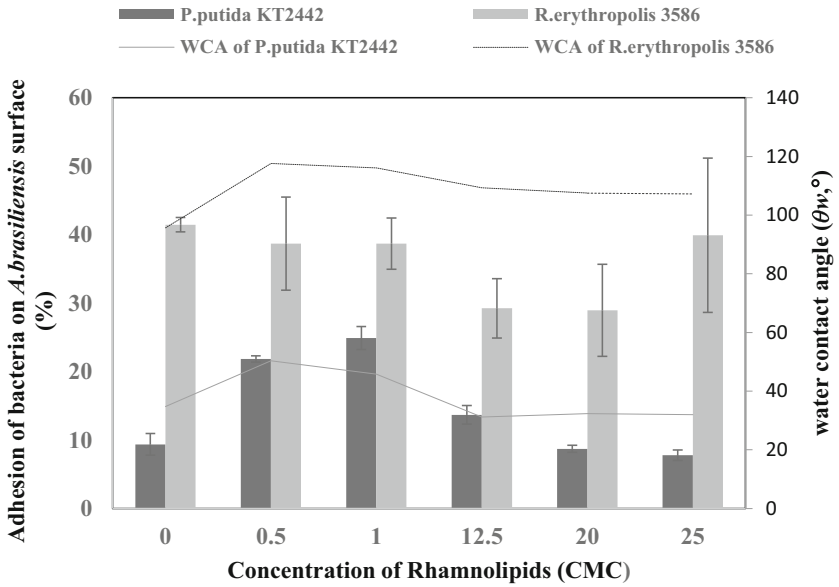

Fig. 1 There is a significant difference between *P. putida* and *R. erythropolis* adhesion on *A. brasiliensis* surfaces for bacterial water contact angle ($P < 0.05$). The error bars indicate standard deviation of triplicate measurements

difference was observed to indicate favourable adherence of both bacteria on fungal surfaces in the presence of rhamnolipid.

The adhesion result shows that only the water contact angle of *R. erythropolis* is significantly contributed to the adhesion on *A. brasiliensis* ($P < 0.05$). There is no significant difference with the water contact angle of *A. brasiliensis* and the surface energy of the bacteria and the fungi ($P > 0.05$). The adhesion of *R. erythropolis* at below 1CMC was strongly mediated by the bacteria water contact angle through acid-base (hydrophobic-hydrophobic) interaction force and fungal surface energy. However, the adhesion of *R. erythropolis* at above 1 CMC was still unclear whether the bacteria are adhering on the fungal surface or become bigger colony. This might be due to hydrophobic interaction between the cells, hence leaving the tiny colony in liquid medium. At above 1 CMC of rhamnolipid, the *A. brasiliensis* surface is in hydrophilic nature, but the adhesion result shows strong *R. erythropolis* adhesion on the fungal surfaces. In many studies, a linear relationship was found between microbial surface hydrophobicity and their adhesion to hydrophobic solid surfaces. The results of this study are in agreement with previous studies saying that hydrophobic bacteria have stronger adhesion on hydrophobic surface than hydrophilic surface [28, 52–54]. Moreover, our findings are also in line with Schreiberová et al. [53] and Feng et al. [26], which found that surface hydrophobicity of *R. erythropolis* increased when treated with rhamnolipid and form strong biofilm on hydrophobic surfaces.

Conclusion

The rhamnolipid modified the cell surface hydrophobicity of bacteria and fungus and increased their electron donor properties. The addition of rhamnolipid not only alters the bacteria and fungus physicochemical properties but also varies the adhesion surface activity. At below 1 CMC, the adhesion of *P. putida* improved by 16% and no improvement at above 1 CMC. Meanwhile, the *R. erythropolis* adhesion on *A. brasiliensis* was less influenced by the addition of rhamnolipid. Clearly, the physicochemical properties of fungus are quantitatively significant and responsible for the adhesion of bacteria on fungi. The adhesion driving force for the bacterial adhesion is mainly driven by acid-base interaction. The thermodynamic principals (surface energy and total free energy of adhesion) successfully predict the adhesion of bacteria on fungal surfaces. Overall, these findings suggest that the adhesion of hydrophilic bacteria on hydrophobic fungal surfaces can be optimized by modifying the bacteria and fungi physicochemical properties using rhamnolipid. In the future, the mechanism of bacteria and fungi interaction in the presence of surfactants should consider the changes in physiological state of both fungus and bacteria that could be altered during treatment.

Funding information The author would like to thank Universiti Teknologi MARA for the LESTARI (grant 600-IRMI/MyRA 5/3/LESTARI (013/2017)), Fundamental Research Grant Scheme (FRGS) (600-IRMI/FRGS 5/3 (334/2019)) and also the Ministry of High Education Malaysia (MoHE) for supporting this study.

Compliance with ethical standards

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

References

1. Schafer A, Ustohal P, Harms H, Stauffer F, Dracos T, Zehnder AJB (1998) Transport of bacteria in unsaturated porous media. J Contam Hydrol 33:149–169. https://doi.org/10.1016/s0169-7722(98)00069-2
2. Wick LY, Mattle PA, Wattiau P, Harms H (2004) Electrokinetic transport of PAH-degrading bacteria in model aquifers and soil. Environ Sci Technol 38:4596–4602. https://doi.org/10.1021/es0354420
3. Jimenez-Sanchez C, Wick LY, Cantos M, Ortega-Calvo JJ (2015) Impact of dissolved organic matter on bacterial tactic motility, attachment, and transport. Environ Sci Technol 49:4498–4505. https://doi.org/10.1021/es5056484
4. Logan AJ, Stevik TK, Siegrist RL, Rønn RM (2001) Transport and fate of Cryptosporidium parvum oocysts in intermittent sand filters. Water Res 35:4359–4369. https://doi.org/10.1016/s0043-1354(01)00181-6
5. Mohd Kamil NAF, Hamzah N, Abdul Talib S, Hussain N (2016) Improving mathematical model in biodegradation of PAHs contaminated soil using gram-positive Bacteria. Soil Sediment Contam 25:443–458. https://doi.org/10.1080/15320383.2016.1168356
6. Zhong H, Liu G, Jiang Y, Yang J, Liu Y, Yang X (2017) Transport of bacteria in porous media and its enhancement by surfactants for bioaugmentation : a review. Biotechnol Adv 35:490–504. https://doi.org/10.1016/j.biotechadv.2017.03.009
7. Harms H, Centre H (2011) Bioavailability and bioaccessibility as key factors in bioremediation. Compr Biotechnol 1:83–94. https://doi.org/10.1016/B978-0-08-088504-9.00367-6
8. Furuno S, Päzolt K, Rabe C, Neu TR, Harms H, Wick LY (2010) Fungal mycelia allow chemotactic dispersal of polycyclic aromatic hydrocarbon-degrading bacteria in water-unsaturated systems. Environ Microbiol 12:1391–1398. https://doi.org/10.1111/j.1462-2920.2009.02022.x
9. Liu S-H, Zeng G-M, Niu Q-Y, Liu Y, Zhou L, Jiang L-H, Tan X, Xu P, Zhang C, Cheng M (2016) Bioremediation mechanisms of combined pollution of PAHs and heavy metals by bacteria and fungi: a mini review. Bioresour Technol 224:25–33. https://doi.org/10.1016/j.biortech.2016.11.095
10. Wei Z, Hessler CM, Sorial G, Seo Y (2016) Influence of nonionic surfactants on fungal and bacterial degradation of hexane. CLEAN - Soil, Air, Water 44:1–8. https://doi.org/10.1002/clen.201500347
11. Zhu Y, Duan X, Qin N, Lv J, Wu G, Wei F (2019) Health risk from dietary exposure to polycyclic aromatic hydrocarbons (PAHs) in a typical high cancer incidence area in southwest China. Sci Total Environ 649:731–738. https://doi.org/10.1016/j.scitotenv.2018.08.157

12. USEPA (2017) Toxicological Review of Benzo [a] pyrene [CASRN 50–32-8],Integrated Risk Information System, National Center for Environmental,Assessment, Office of Research and Development, U.S. Environmental Protection Agency, Washington, DC
13. Nazir R, Warmink JA, Boersma H, van Elsas JD (2010) Mechanisms that promote bacterial fitness in fungal-affected soil microhabitats. FEMS Microbiol Ecol 71:169–185. https://doi.org/10.1111/j.1574-6941.2009.00807.x
14. Toljander JF, Lindahl BD, Paul LR, Elfstrand M, Finlay RD (2007) Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. FEMS Microbiol Ecol 61:295–304. https://doi.org/10.1111/j.1574-6941.2007.00337.x
15. Warmink JA, Nazir R, Corten B, Van Elsas JD (2011) Soil Biology & Biochemistry Hitchhikers on the fungal highway : the helper effect for bacterial migration via fungal hyphae. Soil Biol Biochem 43:760–765. https://doi.org/10.1016/j.soilbio.2010.12.009
16. Van Overbeek LS, Saikkonen K (2016) Impact of bacterial – fungal interactions on the colonization of the Endosphere. Trends Plant Sci 21:230–242. https://doi.org/10.1016/j.tplants.2016.01.003
17. Deveau A, Brulé C, Palin B, Champmartin D, Rubini P, Garbaye J, Sarniguet A, Frey-Klett P (2010) Role of fungal trehalose and bacterial thiamine in the improved survival and growth of the ectomycorrhizal fungus Laccaria bicolor S238N and the helper bacterium Pseudomonas fluorescens BBc6R8. Environ Microbiol Rep 2:560–568. https://doi.org/10.1111/j.1758-2229.2010.00145.x
18. Benoit I, van den Esker MH, Patyshakuliyeva A, Mattern DJ, Blei F, Zhou M, Dijksterhuis J, Brakhage AA, Kuipers OP, de Vries RP, Kovács ÁT (2015) *B acillus subtilis* attachment to *A spergillus niger* hyphae results in mutually altered metabolism. Environ Microbiol 17:2099–2113. https://doi.org/10.1111/1462-2920.12564
19. Knudsen BE, Ellegaard-Jensen L, Albers CN, Rosendahl S, Aamand J (2013) Fungal hyphae stimulate bacterial degradation of 2,6-dichlorobenzamide (BAM). Environ Pollut 181:122–127. https://doi.org/10.1016/j.envpol.2013.06.013
20. Furuno S, Päzolt K, Rabe C, Neu TR, Harms H, Wick LY (2010) Fungal mycelia allow chemotactic dispersal of polycyclic aromatic hydrocarbon-degrading bacteria in water-unsaturated systems. Environ Microbiol 12:1391–1398. https://doi.org/10.1111/j.1462-2920.2009.02022.x
21. Tang S, Yin H, Chen S, Peng H, Chang J, Liu Z, Dang Z (2016) Aerobic degradation of BDE-209 by Enterococcus casseliflavus: isolation, identification and cell changes during degradation process. J Hazard Mater 308:335–342. https://doi.org/10.1016/j.jhazmat.2016.01.062
22. Ghosh I, Mukherji S (2016) International Biodeterioration & Biodegradation Diverse effect of surfactants on pyrene biodegradation by a Pseudomonas strain utilizing pyrene by cell surface hydrophobicity induction. Int Biodeterior Biodegradation 108:67–75. https://doi.org/10.1016/j.ibiod.2015.12.010
23. Smulek W, Zdarta A, Milewska M, Kaczorek E (2015) Alkyl polyglucosides as cell surface modification factors: influence of the alkyl chain length. Toxicol Environ Chem 98:13–25. https://doi.org/10.1080/02772248.2015.1101113
24. Hamzah N, Singhal N, Padhye L, Swift S (2018) Journal of Environmental Chemical Engineering E ff ect of surfactants on Aspergillus brasiliensis ATCC 16404 physicochemical properties. J Environ Chem Eng 6:3392–3398. https://doi.org/10.1016/j.jece.2018.04.068
25. Tao W, Mei C, Hamzah N (2020) The application of surfactant colloidal gas aphrons to remediate contaminated soil: a review. J Contam Hydrol 231:103620. https://doi.org/10.1016/j.jconhyd.2020.103620
26. Feng W, Swift S, Singhal N (2013) Colloids and surfaces B : biointerfaces effects of surfactants on cell surface tension parameters and hydrophobicity of Pseudomonas putida 852 and Rhodococcus erythropolis 3586. Colloids Surfaces B Biointerfaces 105:43–50. https://doi.org/10.1016/j.colsurfb.2012.12.034
27. Al-tahhan RA, Sandrin TR, Bodour AA, Maier RM (2000) Rhamnolipid-induced removal of lipopolysaccharide from Pseudomonas aeruginosa : effect on cell surface properties and interaction with hydrophobic substrates. Appl Environ Microbiol 66:3262–3268
28. Khan MMT, Ista LK, Lopez GP, Schuler AJ (2011) Experimental and theoretical examination of surface energy and adhesion of nitrifying and heterotrophic bacteria using self-assembled monolayers. Environ Sci Technol 45:1055–1060. https://doi.org/10.1021/es101389u
29. Lambertsen L, Sternberg C, Molin S (2004) Mini-Tn 7 transposons for site-specific tagging of bacteria with fluorescent proteins. Environ Microbiol 6:726–732. https://doi.org/10.1111/j.1462-2920.2004.00605.x
30. Goude R, Parish T (2009) Electroporation of mycobacteria. In: Parish T, Brown AC (eds) Mycobacteria protocols, Second edn. Humana Press, Totowa, pp 203–215
31. Seo Y, Bishop PL (2007) Influence of nonionic surfactant on attached biofilm formation and phenanthrene bioavailability during simulated surfactant enhanced bioremediation. Environ Sci Technol 41:7107–7113
32. Li Y, Wang H, Hua F, Su M, Zhao Y (2014) Trans-membrane transport of fluoranthene by Rhodococcus sp. BAP-1 and optimization of uptake process. Bioresour Technol 155:213–219. https://doi.org/10.1016/j.biortech.2013.12.117
33. Smits THM, Wick LY, Harms H, Keel C (2003) Characterization of the surface hydrophobicity of filamentous fungi. Environ Microbiol 5:85–91. https://doi.org/10.1046/j.1462-2920.2003.00389.x
34. Kim LH, Jung Y, Yu H-W, Chae K-J, Kim IS (2015) Physicochemical interactions between rhamnolipids and Pseudomonas aeruginosa biofilm layer. Environ Sci Technol 49:3718–3726. https://doi.org/10.1021/es505803c
35. Wang L, Li F, Zhan Y, Zhu L (2016) Shifts in microbial community structure during in situ surfactant-enhanced bioremediation of polycyclic aromatic hydrocarbon-contaminated soil. Environ Sci Pollut Res 23:14451–14462. https://doi.org/10.1007/s11356-016-6630-4
36. Chu KC, Hu SW, Tsao HK, Sheng YJ (2019) Strong competition between adsorption and aggregation of surfactant in nanoscale systems. J Colloid Interface Sci 553:674–681. https://doi.org/10.1016/j.jcis.2019.06.075
37. Rekiel E, Zdziennicka A, Jańczuk B (2020) Adsorption properties of rhamnolipid and ethanol at water/ethanol solution-air interface. J Mol Liq 308:113080. https://doi.org/10.1016/j.molliq.2020.113080
38. Wick LY, Remer R, Würz B, Reichenbach J, Braun S, Schäfer F, Harms H (2007) Effect of fungal hyphae on the access of bacteria to phenanthrene in soil. Environ Sci Technol 41:500–505. https://doi.org/10.1021/es061407s
39. Renfro TD, Xie W, Yang G, Chen G (2014) Rhamnolipid surface thermodynamic properties and transport in agricultural soil. Colloids Surfaces B Biointerfaces 115:317–322. https://doi.org/10.1016/j.colsurfb.2013.12.021
40. Chau HW, Si BC, Goh YK, Vujanovic V (2009) A novel method for identifying hydrophobicity on fungal surfaces. Mycol Res 113:1046–1052. https://doi.org/10.1016/j.mycres.2009.06.007
41. Kim SH, Vujanovic V (2018) Changes in mycoparasite-Fusarium hosts interfaces in response to hostile environment as revealed by water contact angle and atomic force microscopy. Biol Control 121:247–255. https://doi.org/10.1016/j.biocontrol.2018.03.013

42. Gu H, Chen Y, Liu X, Wang H, Shen-tu J, Wu L, Zeng L, Xu J (2017) The effective migration of Massilia sp . WF1 by Phanerochaete chrysosporium and its phenanthrene biodegradation in soil. Sci Total Environ 593–594:695–703. https://doi.org/10.1016/j.scitotenv.2017.03.205
43. Van Oss CJ, Chaudhury MK, Good RJ (1989) The mechanism of phase separation of polymers in organic media—apolar and polar systems. Sep Sci Technol 24:15–30. https://doi.org/10.1080/01496398908049748
44. Sharma PK, Hanumantha Rao K (2003) Adhesion of Paenibacillus polymyxa on chalcopyrite and pyrite: surface thermodynamics and extended DLVO theory. Colloids Surfaces B Biointerfaces 29:21–38. https://doi.org/10.1016/S0927-7765(02)00180-7
45. Bos R, Van Der Mei HC, Busscher HJ (1999) Physico-chemistry of initial microbial adhesive interactions - its mechanisms and methods for study. FEMS Microbiol Rev 23:179–229. https://doi.org/10.1016/S0168-6445(99)00004-2
46. Nguyen V, Karunakaran E, Collins G, Biggs CA (2016) Colloids and surfaces B : biointerfaces physicochemical analysis of initial adhesion and biofilm formation of Methanosarcina barkeri on polymer support material. Colloids Surfaces B Biointerfaces 143:518–525. https://doi.org/10.1016/j.colsurfb.2016.03.042
47. Sadiki M, Elabed S, Barkai H, Balouiri M, Nasri A, Koraichi SI (2017) The modification of cedar wood surface properties for the prevention of fungal adhesion. Int J Adhes Adhes 75:40–46. https://doi.org/10.1016/j.ijadhadh.2017.01.007
48. Kozbial A, Li Z, Conaway C, Mcginley R, Dhingra S, Vahdat V, Zhou F, Urso BD, Liu H, Li L (2014) Study on the surface energy of Graphene by contact angle measurements. Langmuir 30:8598–8606. https://doi.org/10.1021/la5018328
49. Grasso D, Smets BF, Strevett KA, Machinist BD, Van Oss CJ, Giese RF, Wu W (1996) Impact of physiological state on surface thermodynamics and adhesion of Pseudomonas aeruginosa. Environ Sci Technol 30:3604–3608. https://doi.org/10.1021/es960332x
50. Faten K, Hamida K, Soumya EA, Saad ISK, Hasna M, Hassan L, Moktar H (2016) Lactobacillus plantarum: effect of a protective biofilm on the surface of olives during storage. Brazilian J Microbiol 47:202–209. https://doi.org/10.1016/j.bjm.2015.11.028
51. Hori K, Matsumoto S (2010) Bacterial adhesion: from mechanism to control. Biochem Eng J 48:424–434. https://doi.org/10.1016/j.bej.2009.11.014
52. Zhang X, Zhang Q, Yan T, Jiang Z, Zhang X, Zuo YY (2015) Quantitatively predicting bacterial adhesion using surface free energy determined with a spectrophotometric method. Environ Sci Technol 49:6164–6171. https://doi.org/10.1021/es5050425
53. Schreiberová O, Hedbávná P, Cejková A, Jirků V, Masák J (2012) Effect of surfactants on the biofilm of Rhodococcus erythropolis, a potent degrader of aromatic pollutants. New Biotechnol 30:62–68. https://doi.org/10.1016/j.nbt.2012.04.005
54. Whitehead KA, Olivier S, Benson PS, Arneborg N, Verran J, Kelly P (2015) The effect of surface properties of polycrystalline, single phase metal coatings on bacterial retention. Int J Food Microbiol 197:92–97. https://doi.org/10.1016/j.ijfoodmicro.2014.12.030