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Effects of rhamnolipids on microorganism characteristics and applications in composting: A review

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ABSTRACT

Biosurfactant rhmnolipids have been applied in many fields, especially in environmental bioremediation. According to previous researches, many research groups have studied the influence of rhamnolipids on microorganism characteristics and/or its application in composting. In this review, the effects of rhamnolipids on the cell surface properties of microorganisms was discussed firstly, such as cell surface hydrophobicity (CSH), electrical, surface compounds, etc. Moreover, the deeper mechanisms were also discussed, such as the effects of rhamnolipids on the structural characteristics and functional characteristics of the cell membrane, and the effects of rhamnolipids on the related enzymes and genes. Additionally, the application of rhamnolipids in composting was discussed, which is an important way for pollutant biodegradation and resource reutilization. It is believed that rhamnolipids will play more and more important role in composting.

1. Introduction

With the development of the society, many kinds of industrial materials and products, such as petroleum (Ron and Rosenberg, 2014), pesticides (Zeng et al., 2013), medical waste (Duan et al., 2008), have caused a great pollution to water, soil and air. They seriously threaten the sustainable functioning of ecosystems and the human health (Liu et al., 2013). Hence, many efforts in development of environmental and eco-friendly chemicals and/or techniques should be carried out to strengthen pollution prevention and treatment.

Compared to harsh chemical and physical treatments, bioremediation has the potential to eliminate contaminants through biochemical mineralization in a permanently and cost-effectively way (Huang et al., 2008; Kumar et al., 2011). Additionally, bioremediation holds a variety of advantages over chemical and physical remediation, e.g., low cost, few or no by-products, reusability, eco-friendliness (Sun et al., 2016), and is widely applied in the pollution remediation. However, some pollutants (e.g., Polycyclic aromatic hydrocarbons (PAHs), Phenols, Petroleum hydrocarbons, Heavy metal (Liu et al., 2010; Liu et al., 2016)) possess high toxicity and low bioavailability to microorganisms, resulting in low efficiency and even failure of bioremediation (Zhong et al., 2016a). Therefore, some additives such as surfactants have been used to improve the remediation efficiency in the application of practical bioremediation. These surfactants enhance the removal of contaminants may through increasing the apparent solubility and bioavailability of contaminants (Tang et al., 2014; Liu et al., 2017), changing the microbial surface properties more hydrophilic or hydrophobic and strengthening the interaction between pollutants and microorganisms (Liu et al., 2014b). Meanwhile, these surfactants also can increase the activity and/or quantity of related enzymes and genes in microorganisms (Liang et al., 2010) and reduce the toxicity of pollutants to microorganisms (Liu et al., 2010), which is also in favor of bioremediation of pollutants.

Commonly used surfactants are divided into synthetic surfactants and biosurfactants. They are amphiphilic molecules containing polar and non-polar groups and possess surface active properties (Banat et al., 2010), such as emulsification, dispersion, foaming, detergency, wetting and stabilization etc. (Gudiña et al., 2015; dos Santos et al., 2016; Zhong et al., 2016b). Biosurfactants are usually produced by microorganisms and have several advantages compared to synthetic surfactants, e.g., biodegradability, high environmental compatibility, strong surface activity and lower toxicity (Zhou et al., 2011b; Yu et al., 2015). Rhamnolipids are the most extensively studied biosurfactants for bioremediation of pollutants (An et al., 2011), especially for the

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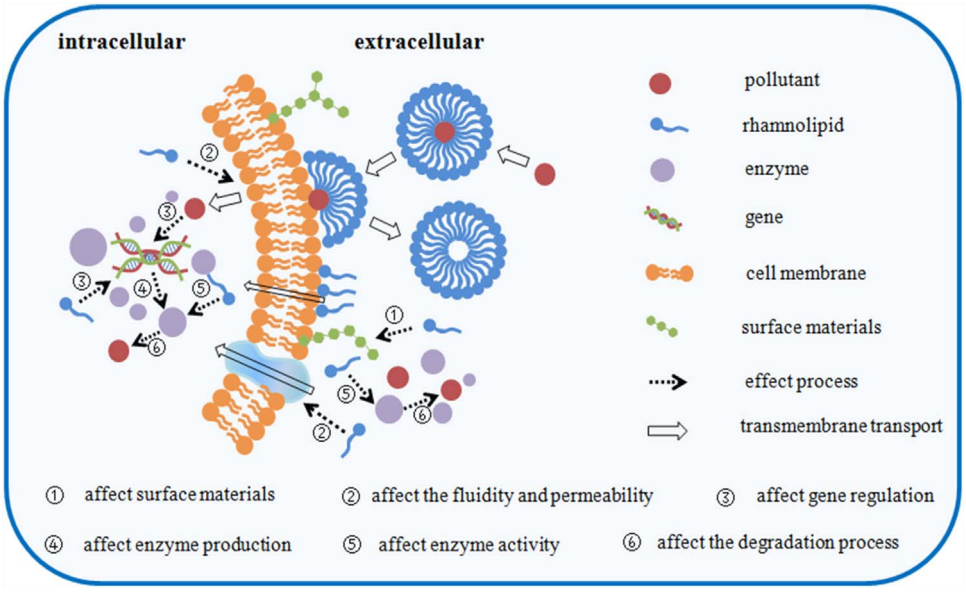

Fig. 1. The process of rhamnolipids effects on microorganism characteristics and the degradation of pollutants.

hydrophobic organic pollutants (Trellu et al., 2016).

It is well-known that the elimination of pollutants by microorganism is a systemic bioprocess and can be separated as two phases: a rapid removal process by adsorption and a following degradation process (Sun et al., 2016; Zhong et al., 2016c). The adsorption process is not only influenced by the types and physicochemical properties of pollutants, but is related closely to surface properties and cell membrane structure of microorganism (Luo et al., 2003). The degradation process is related to internal activities of microbes, and is catalyzed by degrading enzymes which is controlled by related genes. The bioremoval process including adsorption and degradation processes may experience alteration in the presence of rhamnolipids which exert impacts on the cell surface properties (e.g., CSH, cell surface charge, surface compounds, surface free energy (Fig. 1 ①) and membrane structure (Fig. 1 ②)) (Kaczorek et al., 2008; Zeng et al., 2011) and the internal activities (e.g., degrading enzymes (Fig. 1 ③-⑤)) of microorganism (Zeng et al., 2006).

This review mainly focuses on the impacts of rhamnolipids on the cell surface properties and the internal activities of microorganism. Studying the effects of rhamnolipids on the metabolic process may be an important way to illustrate the influence of rhanmolipids on bioremediation process, such as the metabolic pathways, intermediate product, metabolic dynamics, degrading enzyme activity and gene expression, etc. However, there are few studies about the effects of rhamnolipids on microbial metabolism, and there is less research about the effects of rhamnolipids on microbial degradation of pollutants on the genetic level. Meanwhile, the application of rhamnolipids in composting (an effective bioremediation technology) has also been discussed. The compost medium contains a variety of pollutants, and they can be effectively removed by microbial degradation (Kästner and Miltner, 2016). Studying the effects of rhamnolipids on microorganism characteristics is important to illustrate the mechanism of composting in the presence of rhamnolipids, and benefit to develop more effective bioremediation technology. The process of rhamnolipids effecting on microorganism characteristics and the degradation of pollutants is shown in Fig. 1.

2. Production and characteristic of rhamnolipids

Most of biosurfactants are produced by microorganisms. Based on their biochemical nature, biosurfactants can be classified into low-molecular and large-molecular compounds (Lovaglio et al., 2015). The low-molecular biosurfactants, such as lipopeptides (e.g. surfactin and fengycins) (de França et al., 2015), glycolipids (e.g. rhamnolipids and sophorolipids) (Smyth et al., 2010) and phospholipids (e.g. phosphatidylethanolamine) (Janek et al., 2013), can efficiently lower surface and interfacial tension. The large-molecular biosurfactants, such as lipoproteins, lipopolysaccharide (LPS), proteins, polysaccharides and biopolymer complexes (e.g. emulsan and alasan) are more effective as emulsion stabilizing agents (Abdel-Mawgoud et al., 2010; Lovaglio et al., 2015).

Rhamnolipids are the most widely studied glycolipids biosurfactants. The discovery of them can be traced back to 1946 (Rikalovic et al., 2015). They are produced by a variety of species of microorganisms (e.g. bacteria, fungi, yeast), and the main producing species is the gram-negative strains of *Pseudomonas aeruginosa* isolated from various habitats (water, soil or even plants) (dos Santos et al., 2016) (Table 1). Other species, e.g., *Nocardiopsis* spp. (Roy et al., 2014), *Acinetobacter calcoaceticus.* (Rooney et al., 2009), *Enterobacter* spp. (Hoskova et al., 2013) and *Burkholderia* spp. (Hošková et al., 2015), also have good productions of rhamnolipids under the suitable conditions.

The production cost of rhamnolipids is high since the expensive raw materials used in bacterial fermentation and the complex purification process, that limits the application of rhamnolipids in industrial scale (Henkel et al., 2012). Therefore, many efforts have been carried out in order to reduce the costs and increase yield in the former studies, such as using cheap substrates (Moya Ramirez et al., 2015), optimizing the production conditions (Borges et al., 2015), using different production process (Nalini and Parthasarathi, 2014), screening new natural producing strains (Roy et al., 2014), using genetic engineering strategy (Lovaglio et al., 2015), researching more efficient methods for separation and purification of rhamnolipids homologue (Zhang et al., 2016a) (Fig. 2). A lot of researches have evaluated low-cost substrates, developed efficient fermentation processes and screened new strains to increase the yields of rhamnolipids. However, little studies have been described in the genetic handling of strains to increase production efficiency (Lovaglio et al., 2015). Several important gene regulation process and key genes are involved in the complexity genetic network in the rhamnolipids production by *Pseudomonas aeruginosa* (Dobler et al., 2016). The biosynthesis of rhamnolipids includes three major steps, some key genes and quorum sensing signals: The synthesis of two important precursors during the first two steps, namely β-hydroxyalkanoyl-β-hydroxyalkanoyl-ACP (HAA-ACP) and dTDP-L-rhamnose. Then, two special rhamnosyltransferases sequentially catalyze the condensation of the precursors to mono-rhamnolipids (mono-RL) and di-rham-

Table 1
The production of rhamnolipids in recent researches.

Substrates	Strain	Methods	Maximum yield	Refs.
Glycerol	*P. aeruginosa* SQ6	Anaerobic fermentation	1.61 g/L	Zhao et al. (2015)
	P. aeruginosa UFPEDA 614	Submerged culture	15.9 g/L	de Santana-Filho et al. (2015)
	P. aeruginosa A11	Aerobic fermentation	4.4 g/L	Singh and Cameotra (2013)
	Pseudomonas sp. 2B	Shake flask fermentation	4.97 g/L	Aparna et al. (2012)
Glucose	*P. aeruginosa* ATCC 9027	Under phosphate limitation fermentation	4.261 g/L	Clarke et al. (2010)
	P. nitroreducens	Shake flask fermentation	5.46 g/L	Onwosi and Odibo (2012)
	P. aeruginosa TMN	Liquid fermentation	0.3 g/L	Moussa et al. (2014)
Waste frying oil	*P. aeruginosa* MTCC 2297	Submerged batch Fermentation	7.6 g/L	Venkatesh and Vedaraman (2012)
	P. aeruginosa ATCC 9027	Fed-batch fermentation	6.6 g/L	Luo et al. (2013)
Plant oils	*P. aeruginosa* MTCC 7815	Shake flask fermentation	6.9 g/L	Singh et al. (2013)
	P. aeruginosa ATCC 10145	Shake flask fermentation	13.3 g/L	Colak and Kahraman (2013)
	P. aeruginosa KVD-HR42	Stilling culture	5.9 g/L	Deepika et al. (2016)
	P. aeruginosa TIB-R02	Fermentation-defoaming tandem system	60 g/L	Gong et al. (2015)
	P. aeruginosa E03-40	Aerobic fermentation	55 g/L	Sodagari and Ju (2014)
	Pseudomonas sp. 2B	Shake flask fermentation	4.97 g/L	Aparna et al. (2012)
Others low-cost raw materials	*P. aeruginosa* ATCC 10145	Batch bioreactor	5.37 g/L,	Borges et al. (2015)
	P. aeruginosa #112	Shake flask fermentation	3.2 g/L	Gudiña et al. (2015)
	P. aeruginosa S15	Shake flask fermentation	6.9 g/L	Rebello et al. (2013)
	P. aeruginosa UFPEDA 614	Solid-state cultivation	46 g/L	Camilios-Neto et al. (2011)

nolipids (di-RL) (Dobler et al., 2016). The key genes include *rhlR, rhlA, rhlB* and quorum sensing signals responsible for the regulation of biosynthesis (Juhas et al., 2005). Although there are more and more researches about gene regulation, there is still a long way to completely understand the complexity regulation network and control the process of rhamnolipids production. Understanding the biosynthesis and genetic regulation systems will contribute to the development of non-pathogenic, high-producing strains and increase the yields of rhamnolipids in a more affordable way.

Rhamnolipids have a diverse and typical molecular structure consisted of one rhamnose (Rha) (mono-RL) or two rhamnose (di-RL) moieties and one or more saturated/unsaturated 3-hydroxy fatty with 8–14 carbon atoms (Hošková et al., 2015). According to previous studies, di-RL has greater polarity compared to mono-RL due to the more Rha, but mono-RL with higher ionization efficiency. Additionally, the mono-RL was oily, while the two rhamnolipid was solid (Gai and Song, 2010; Liu et al., 2014a). Furthermore, there are approximately 60 types of congeners and homologs produced by different strains (Abdel-Mawgoud et al., 2010). For example, four common rhamnolipids produced by *Pseudomonas aeruginosa* are the 3-[3-(α-L-Rhamnopyrano-

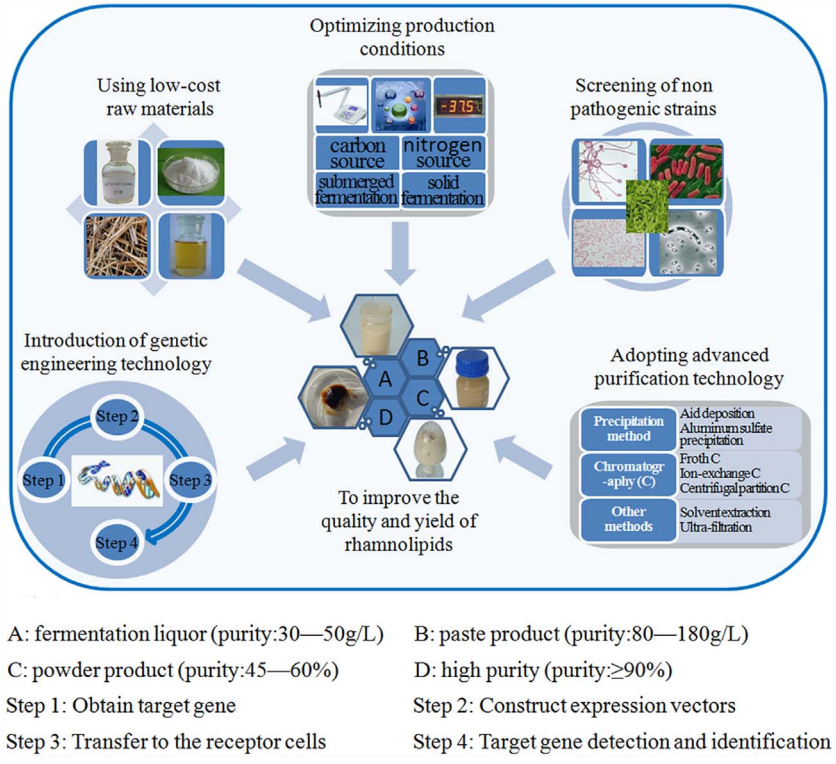

Fig. 2. The frequent strategy to improve the quality and yield of rhamnolipids.

syloxy)decanoyloxy]decanoic acid (Rha-C_{10}-C_{10}), 3-[3-(2-*O*-α-L-*R*hamnopyranosyl-α-L-rhamnopyranosyloxy)decanoyloxy]decanoic acid (Rha_2-C_{10}-C_{10}), 3-[(2-*O*-α-L-*R*hamnopyranosyl-α-L-rhamnopyranosyl) oxy] decanoic acid (Rha_2-C_{10}) and 3-[(6-Deoxy-α-L-mannopyranosyl) oxy]decanoic acid (Rha-C_{10}) (Hošková et al., 2015). The ratio of rhamnolipids homologues depend on many factors: the specie of microorganisms, medium composition and cultivation conditions. Many previous researches have shown that the ratio of homologues determines the properties of rhamnolipids, and even small differences in the mixture composition will cause a significant impact on its physiochemical properties (Guo et al., 2009).

Several physiochemical properties are the key factors to evaluate the applicability of biosurfactants, such as surface tension, interfacial tension, critical micelle concentration (CMC), particle size and emulsification capacity (Mendes et al., 2015). Rhamnolipids have very low surface tension values (28–30mN/m), high emulsifying activity (emulsifying indexes up to 60–70%) and low CMC (10–200 mg/L) (Gudiña et al., 2015). Therefore, rhamnolipids can effectively reduce the surface tension of air-liquid interfaces or liquid–liquid interfaces even at a low concentration. These characteristics of rhamnolipids will contribute to the application in the environmental remediation (Mao et al., 2015), washing or cleaning industry, and cosmetic industry (Lourith and Kanlayavattanakul, 2009). In addition, the anti-microbial, anti-adhesive and anti-biofilm activity properties are also important characteristics of rhamnolipids. For example, rhamnolipids can effectively inhibit the growth and activity of microorganism like fungi (Abalos et al., 2001), and are widely used in food industry (Nitschke and Costa, 2007), pharmaceutical (Stipcevic et al., 2006) and agriculture etc. (da Silva et al., 2015). The dramaticlly tensioactive, emulsifying properties and expanding application make rhamnolipids have attracted more and more attentions (Deepika et al., 2016).

3. Effects of rhamnolipids on cell surface properties

The cell surface properties are important characteristics of microorganism, which directly affect the interactions between microorganism and the external environment, and further affect the material transport, growth and metabolism of microorganism. These properties, including CSH, cell surface charge, cell surface compounds and cell surface morphological structure etc. (Hamadi et al., 2009), they are influenced by each other and different according to various environmental conditions. For example, many studies showed that the cell surface compounds closely affect others properties, such as cell surface charge and CSH (Kaczorek et al., 2010; Kim et al., 2015). That because the surface compounds consist of charged groups and hydrophilic-hydrophobic composition, such as extracellular polymeric substances (EPS), which includes several charged groups (carboxyl, phosphoric, sulfhydryl, phenolic, and hydroxyl groups) and polar groups (aromatics and aliphatics in proteins, and hydrophobic regions in carbohydrates) (Li and Zhu, 2012; Nguyen et al., 2012). According to previous studies, the surfactants have different effects on the cell surface properties when applied in bioremediation (Fig. 3). Firstly, surfactants can affect the cell surface properties due to the alteration of the cell surface compounds when surfactants adsorb on cell surface. For example, Liu et al. (Liu et al., 2012b) observed that rhamnolipids can modify the CSH and the surface charge of *Penicillium simplicissimum* due to the change of the cell surface functional groups (increased the hydrophobic functional group) and element concentrations (decreased the concentrations of C, P, S, K, but increased the concentrations of O and Cl) when rhamnolipids adsorb on cell surface. Meanwhile, surfactants adsorb on cell surface may also cause the change of membrane structure and character, which will alter the major membrane functions (such as matter transport, energy generation and membrane permeability), and cell surface properties (Sotirova et al., 2008; Banat et al., 2010). For example, it was observed that rhamnolipids increased the membrane permeability of *Bacillus subtilis and Pseudomonas aeruginosa*, resulting in metabolite leakage, that because the rhamnolipids covered on the cell surface and resulted in the change of cell surface properties (Sotirova et al., 2009). It was also reported that surfactants can induce the increase of membrane lipids and led to the decrease of membrane fluidity of *Arthrobacter* sp. Strain Sphe3 (Kallimanis et al., 2007). The effects of rhamnolipids on cell surface properties depend on the concentration and types of rhamnolipids, the species of microorganism, and environmental conditions etc. (Yuan et al., 2007). In this section, the mainly effects of rhamnolipids on cell surface properties are discussed.

3.1. The CSH

CSH is a key factor and affects the efficiency of various bioprocesses, such as cell-to-cell interaction and the uptake of nutrients etc. (Liu et al., 2014b). CSH is dependent on the ratio of hydrophobic and hydrophilic regions on the cell envelope (Zhong et al., 2007). Many studies have shown that rhamnolipids have some effects of on the CSH. For example, Zhang and Miller (Zhang and Miller, 1994) observed that rhamnolipids increased the CSH of the slow degraders (*Pseudomonas aeruginosa* ATCC 9027 and NRRL 3198) but had no effects on the CSH of the fast degraders (*Pseudomonas aeruginosa* ATCC 15442 and ATCC 27853) on degradation of Octadecane in presence of rhamnolipids. Kaczorek et al. (Kaczorek et al., 2008) observed that the rhamnolipids have no effects on the hydrophobicity of yeast (*Candida maltosa* and *Yarrowia lipolytica*) when the concentration of rhamnolipids is below 75 mg/L, but the hydrophobicity will decrease rapidly when higher rhamnolipid concentration was applied. Owsianiak et al. (Owsianiak et al., 2009) showed that rhamnolipids increased hydrophobicity of microbial consortia with low CSH and decreased CSH of those with high hydrophobicity on biodegradation of diesel fuel. Zhong et al. (Zhong et al., 2008) reported that bacterial (*Pseudomonas aeruginosa*) CSH more likely to be higher in the presence of di-RL compared with mono-RL.

There are two general mechanisms responsible for the increase of CSH by rhamnolipids. The first one is the adsorption of rhamnolipids onto cell surface (Zhong et al., 2007). The driving force of the adsorption include the diffusion force, electrostatic attraction or repulsion, Van der Waals interaction, hydrogen bonding, dipolar force, as well as the hydrophobic interaction (Yuan et al., 2007). It is the monomer adsorption mode when the rhamnolipids adsorb on the cell surfaces at low biosurfactant concentration and the micelle adsorption mode at high biosurfactants concentration. The adsorption causes the rapid increase of CSH at low rhamnolipids concentrations and the stabilization or decrease of CSH at high rhamnolipids concentration. Additionally, the effects of monomer adsorption is more significant than the micelle adsorption generally (Zhong et al., 2007). The second mechanism is that rhamnolipids can change the compounds of cell surface (Al-Tahhan et al., 2000; Owsianiak et al., 2009). It was reported that LPS plays an important role on CSH, and the LPS lease from the cell surface resulted in the increase of CSH (Al-Tahhan et al., 2000). The concentration of surface compounds, such as proteins, polysaccharides, etc., will be changed when rhamnolipids interaction with cell surface functional groups (Mohanty and Mukherji, 2013), which leads the change of the CSH. According to the present studies, the change of CSH on microorganism by rhamnolipids at low concentration is a hotspot (Liu et al., 2014b), that will contribute to the efficient use of rhamnolipids in bioremediation.

3.2. Zeta potential

The zeta potential is another important property of the microbial cell surface which reflects the charge of cell surface (Mohanty et al., 2013). Generally, it is negatively charged on microbial cell surface due to the presence of anionic groups, such as carboxyl and phosphate, on cell surface (Yuan et al., 2007). Previous studies have shown that the rhamnolipids can significantly change the zeta potential of microorganism (Zeng et al., 2011; Liu et al., 2012b). For example, Liu et al. (Liu

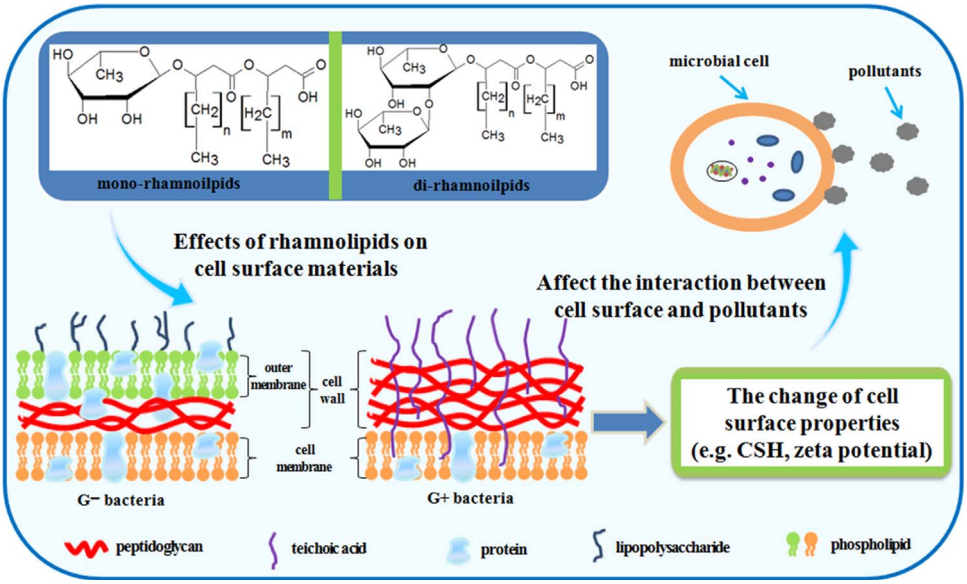

Fig. 3. Effects of rhamnolipids on cell surface properties.

et al., 2012b) observed that the zeta potential of *Penicillium simplicissimum* increased in the presence of rhamnolipids. Hua et al. (Hua et al., 2003) reported that the presence of mono-RL increased the zeta potential of *Candida antarctica* in the fermentation system and such increase was related closely to the rhamnolipids concentrations (below or above the CMC). However, Ishigami et al. (Ishigami et al., 1987) showed that mono-RL decreased the zeta potential of *Pseudomonas aeruginosa*. That because the adsorption of rhamnolipids as an anionic biosurfactants could bring some negative charge to cell surfaces. Al-Tahhan et al. (Al-Tahhan et al., 2000) reported that rhamnolipids can induce the release of cell surface compounds (e.g., surface proteins and LPS) from the cell membrane of *Pseudomonas aeruginosa*. That will decrease the zeta potential since these components confer a considerable negative charge upon the cell surface and favor electrostatic interactions with cations, removal of these components may reduce the negativity of the cell surface charge. The mechanisms of rhamnolipids modifying the cell surface charges may be as follows. Firstly, rhamnolipids can be adsorbed on the cellular envelope (Liu et al., 2011) which can neutralize or enhance the original surface charge of the cells. In addition, the rhamnolipids may have an interaction with functional groups (e.g., hydroxyl, carboxyl, phosphate and amines groups) on cell surface when adsorbed on it, and changing the cell surface charge (Liu et al., 2012b; Mohanty and Mukherji, 2013). Secondly, rhamnolipids can increase the permeability of biomembrane (Liu et al., 2011) and lead to the release of some components (e.g., proteins, polysaccharides, glycoproteins, and LPS) from the intracellular and remain on cell surface, which may influence the cell surface charge (Guibaud et al., 2008). Thirdly, rhamnolipids may cause the release of chemical components (e.g., proteins and LPS) from the cell surface and modify cell surface charge (Liu et al., 2011). Kim et al. (Kim et al., 2015) observed that the increase of the surface charge of *Pseudomonas aeruginosa* due to the removal of negatively charged, such as humic-like, protein-like, and fulvic acid-like substances, from the cell surface in the presence of rhamnolipids. Surface charge of microorganisms can play an important role in adsorption. The studies about the effects of rhamnolipids on the surface charge will contribute to its use in bioremediation.

3.3. Cell membrane permeability and fluidity

The cell membrane of microbes is a layer of soft and elastic semipermeable membrane, which is attached to the inside of the cell wall. And it is a kind of phospholipid bilayer structure, which is mainly composed of protein, lipid and polysaccharide. The cell membrane mainly has two important characteristics: permeability and fluidity. The permeability and fluidity of the membrane have an important effects on the uptake and intracellular degradation of pollutants (Weber and de Bont, 1996). According to research, the permeability is related closely to the ion concentrations between intracellular and extracellular, however, the fluidity is related closely to the content of unsaturated fatty acid in membrane, and they can be altered in the presence of rhamnolipids (Li et al., 2002).

Rhamnolipids may have an effect on the structure and components of cell membrane, and cause the increase of membrane permeability and even membrane disruption, which may lead to metabolite leakage and cellular lysis (Van Hamme et al., 2006) (Fig. 4). For example, Yuan et al. (Yuan et al., 2012) observed an increase of cell membrane permeability of *Penicillium simplicissimum* pretreated by rhamnolipids, that resulting in an accumulation of negative charges on the cell wall surface and decreasing in cell zeta potential. Sotirova et al. (Sotirova et al., 2009) showed that the content of outer membrane proteins was decreased for gram negative bacteria (*Pseudomonas aeruginosa*) in the presence of rhamnolipids at the concentration below CMC. Bharalia et al. (Bharali et al., 2013) reported that the rhamnolipids significantly damage the cell membrane of *Staphylococcus aureus* (MTCC 3160), which enhancing the membrane permeability and even leading to cell lysis. The reason for the increase of the membrane permeability in the presence of rhamnolipids may because rhamnolipid-induced the release of protein, and the fusion of rhamnolipids to cell membrane, which results in the formation of transmembrane pores on cell membranes (Sotirova et al., 2008; Sotirova et al., 2009).

The fluidity of cell membrane was mainly governed by protein content and membrane lipid structure, e.g., the ratio of saturated fatty acid to unsaturated fatty acid in lipid, the composition and average chain length of fatty acid (Kallimanis et al., 2007). It was reported that the rhamnolipids can change the fluidity of cell membrane by changing the content and composition of fatty acid and protein. For example, Sotirova et al. (Sotirova et al., 2008) observed that the high concentration (higher than CMC) of rhamnolipids caused an increase in membrane-lipid composition (include fatty acid and glycerol) and decreased the membrane fluidity of *Bacillus subtilis*. However, it was also reported that rhamnolipids can stabilize the cellular membranes. For example, it was reported that the decrease of membrane fluidity of *Staphylococcus haemolyticus* in response to the increased diphosphatidylglycerol level

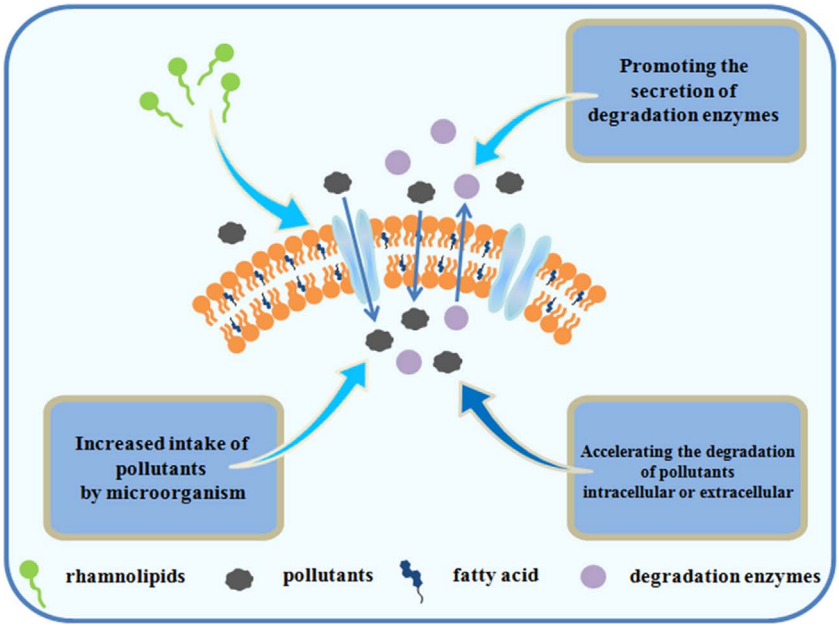

Fig. 4. Effects of rhamnolipids on cell membrane fluidity and permeability.

was stopped and the membrane became stable in the presence of rhamnolipids (Nielsen et al., 2005).

4. Influences of rhamnolipids on enzyme and genes

Enzyme is a kind of biological macromolecules with biocatalytic function. Gene is the fragment of DNA with genetic information. All life phenomena of organisms are related to enzymes and genes (Lorenz et al., 2002). Various of enzymes will be produced by microorganism under the genes regulation in bioremediation. It is established that the degradation of pollutants occurs under the catalysis of the enzyme inside the cell, on the cell membrane of microorganism, or in the environmental solutions (Zeng et al., 2006). Previous studies have reported that surfactants can enhance the activity of enzymes so as to enhance the efficiency of pollutants-degradation (Noordman and Janssen, 2002). Meanwhile, the surfactants can also affect the pollutants-degradation by affecting the expression of related genes due to the enzymes are encoded by related genes (Marlowe et al., 2002). It is possible for surfactants as a means of controlling the gene regulation, so as to improve pollutants-degradation efficiency in the practical application of bioremediation. The clear mechanisms for such effects, however, are still not clear. Therefore, exploration in the effects of surfactants on biodegradation of pollutants in genetic level is important for bioremediation of contaminated soils and groundwater. In this section, the related effects of surfactants on the enzymes and genes are discussed.

4.1. The impacts on enzyme

The enzyme is synthesized and secreted by microorganism, and involved in the degradation of various pollutions in bioremediation. It has been reported that the rhamnolipids can affect the enzyme activity, enzyme production and the enzyme structure etc. (Liang et al., 2010; Zhou et al., 2011a) (Fig. 5). For example, the effects of rhamnolipids on relative enzymes (xylanase, CMCase, amylase and protease) during the composting were studied, and it was found that rhamnolipids could increase the activity and production of enzymes depending on the types of enzymes and the composting conditions (Shi et al., 2006; Zeng et al., 2006). Liu et al. (Liu et al., 2012a) found that di-RL increased the activity of laccase and the removal of phenol with the increase of di-RL concentrations. Meanwhile, the same results were also reported by the research of Liu et al. (Liu et al., 2008) and Zhou et al. (Zhou et al., 2011a), where the activity of enzymes (laccase, CMCase, xylanase and lignin peroxidase) was strengthened by rhamnolipids. According to previous research, the common reason for rhamnolipids increased the production of enzyme is that rhamnolipids increased the permeability of the cell membrane, that increasing the secretion of enzymes out of cells (Rama et al., 1999). However, the enzymatic activity was changed may due to the alteration of enzymatic structure under the effects of surfactants. The alteration of enzymatic structure due to some interactions between surfactant and enzyme, such as the electrostatic interactions between the surfactant head group and the charged amino acid residues of the enzyme, and the hydrophobic interactions between the alkyl chains of the surfactant and the hydrophobic amino acid residues of the enzyme (Karbassi et al., 2003).

Meanwhile, the main component of the enzyme is protein. A lot of researches have reported that surfactants can alter the enzymatic structure by protein-surfactant interactions (Vishvakarma et al., 2015). Vishvakarma et al. (Vishvakarma et al., 2015) reported that gemini surfactants (bis-N-alkyl nicotinate dianion) are useful in the bovine serum albumin (BSA, a protein) stabilization due to the strong electrostatic and hydrophobic interactions between the surfactants and protein. Wu et al. (Wu et al., 2007) reported that cationic gemini surfactant (1,2-ethane bis(dimethyldodecylammonium bromide)) interact with gelatin and BSA through electrostatic and hydrophobic forces. These interactions are determined by many factors, such as the charge of the head groups, hydrophobic content and protein structure (Lima et al., 1997). Moreover, the combination of the surfactants and protein can affect the secondary structure of the protein functional properties (Parker and Song, 1992). Surfactants may either stabilize or destabilize the protein structure and/or it may either support or oppose protein aggregation depending on the characteristics of surfactants and surfactant concentrations (Jung et al., 2008). For example, Ishtikhar et al. (Ishtikhar et al., 2015) observed that the secondary structure of human serum albumin (HAS) was decreased, while the loss of α-helical structure was accompanied by the gain in the random structure of the protein as there was no major change inβ-sheet structure of the protein in the presence of rosin surfactants. That's because of their large side chains which probably cause steric hindrance while interacting with the active sites of serum albumin. Akram et al. (Akram et al., 2016) reported that gemini surfactant (ethane-1, 2-diyl bis(*N*, *N*-dimethyl- *N*-dodecylammoniumacetoxy) dichloride) could disrupt the secondary structure of xanthine oxidase by binding to xanthine oxidase, which

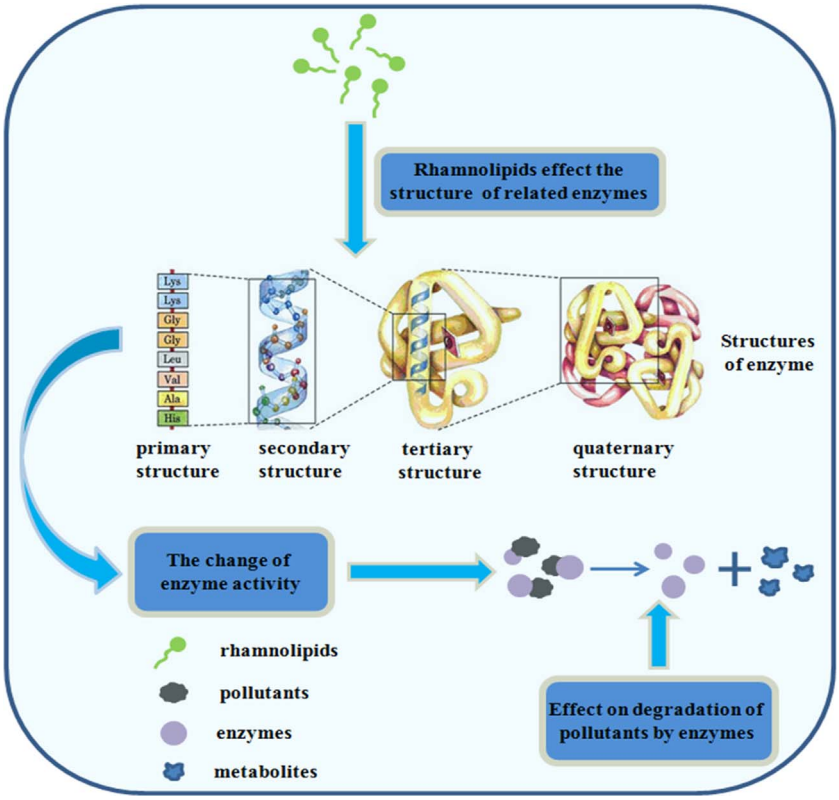

Fig. 5. Effects of rhamnolipids on related enzymes structure and pollutant degradation.

might directly twist the activity of protein/enzyme. Eriksson et al. (Eriksson et al., 2002) observed that rhamnolipids did not affect the tertiary or secondary structure of three different commercially used enzymes (cellulose Carezyme (CT), phospholipase Lecitase Ultra (LT) and aamylase Stainzyme (SZ)) at room temperature compared to Sodium dodecyl sulfate (SDS)). However, the study on the effects of surfactants on proteins or enzymes concentrates more on the medical field, and majors in chemical surfactants, there is few the research about biosurfactants in the field of environmental (Vishvakarma et al., 2015). Moreover, the structure of the enzyme has important influence on the enzyme performance. The enzyme has primary structure, secondary structure, tertiary structure, quaternary structure which have important influence on the activity of enzymes. For example, Vertegel et al. (Vertegel et al., 2004) reported that the activity of lysozyme retention more nativelike when less significant perturbation of lysozyme's secondary structure. However, the studies about the effects of surfactants on the structure of the protein or enzyme are mostly about primary structure and secondary structure, and the effects of surfactants on the tertiary structure and quaternary structure are still unclear. Loo et al. (Loo et al., 1994) observed that various surfactants (SDS, Taurocholate sodium, Cholate sodium, Cetyl trimethyl ammonium bromide, Lauryl dimethyl amine oxide, 3-((3-Cholamidopropyl) dimethylammonium)-1-propanesulfonate, Tween 20, Thesit, Triton X-100, Nonylphenyl-polyethylene glycol, *n*-Octyl sucrose, *n*-Dodecyl sucrose, *n*-Dodecyl maltoside, Octyl glucoside, Octyl thioglucoside, *n*-Hexyl glucoside, *n*-Dodecyl glucoside) can affect both the tertiary and quaternary structures of myoglobin. Additionally, the enzymes include intracellular and extracellular enzymes, however, most previous studies are concerned on the effects of surfactants on extracellular enzymes, while ignoring the influence on intracellular enzyme, (Liu et al., 2006; Zhou et al., 2011a). Generally, intracellular enzymes work together with extracellular enzymes in bioremediation system. Hence, it is important to study the effects of surfactants on intracellular enzyme. Although the growing body of research on the effects of surfactants on enzymes, the mechanism is not very clear, especially about the effects of biosurfactant on enzymes. Therefore, the more attention should be paid to the study on the molecular level for understanding the mechanisms.

4.2. The regulation and expression of relative gene

Gene regulation plays an important role in bioremediation (in particular, membrane fluidity and enzyme activity) (Li et al., 2015), there are many studies on the key genes in the process of pollutant degradation. For example, Sabirova et al. (Sabirova et al., 2011) observed that the gene *blc* plays an important role in alkane uptake by *A. borkumens*is Sk2. Hearn et al. (Hearn et al., 2009) observed that for *P. putida*, *alkL* the *alk* operon plays an important role in alkane transporting into the cell. Waigi et al. (Waigi et al., 2015) reported that the genes *bphA2cA1c*, $bphA1_{[a-e]}A2_{[a-e]}$ (which both require *bphA3b-phA4*) and *bphC* are key genes on the degradation of phenanthrene by *sphingomonads*. Successful bioremediation requires high microbial activity, meanwhile, the biodegradation of pollutants involves multiple genes, which include structure gene (encoding proteins/enzymes) and regulation gene (encoding a protein that inhibiting or activating structure gene transcription).

It is possible that surfactants can regulate the gene expression and then affect microbial activity (enzyme activity, cell membrane fluidity and permeability) (Marlowe et al., 2002). For example, Li et al. (Li et al., 2015) investigated the expression levels of three genes (Δ9 fatty acid desaturase gene, ring-hydroxylating dioxygenase gene and 1-hydroxyl-2-naphthoate dioxygenase gene) of *Arthrobacter* sp. SA02 in the biodegradation of phenanthrene as a typical hydrophobic organic contaminants (HOCs) at different concentrations of sodium dodecyl benzenesulfonate (SDBS). The results showed that these three genes were upregulated in the presence of SDBS, and then enhanced the biodegradation of phenanthrene. Li et al. (Li et al., 2015) proposed that the upregulation of the expression level of the Δ9 fatty acid desaturase gene increased the membrane fluidity and the transmembrane transport of phenanthrene. Meanwhile, the increase of the expression level of the

ring-hydroxylating dioxygenase gene and 1-hydroxyl-2-naphthoate dioxygenase gene (which play a key role in decomposing doubly hydroxylated aromatic compounds) enhanced the intracellular biodegradation of phenanthrene. Marlowe et al. (Marlowe et al., 2002) observed that biosurfactants (rhamnolipids and hydroxypropyl-β-cyclodextrin (HPCD)) have different influence on the two important genes (*nahAc*, a naphthalene dioxygenase gene, and *rpoD*, a housekeeping gene) in biodegradation of PAHs. Results indicated that the lag period preceding *nahAc* gene induction decreased from 312 to 48 h in the presence of biosurfactants. Cessation of induction could have resulted from the upregulation of alternate pathways or the accumulation of toxic intermediates. In contrast, the expression of the *rpoD* gene was maintained throughout the duration of each experiment.

Surfactants may form complexes with genetic material, which may affect the gene regulation. That just likes pulmonary surfactant affect some genes expression in clinically. For example, Ishii et al. (Ishii et al., 2014) found that *Staphylococcus aureus* (a clinically important opportunistic pathogen) membrane stress caused by free fatty acids present in the pulmonary surfactant through the regulation of virulence gene expression, which contributes to its pathogenesis within the lungs of the host animal. The mechanisms of the effects of surfactants on microorganisms in the genetic level are important for their application in bioremediation. However, there is still lack of investigations.

5. The application of rhamnolipids in composting

Composting has been widely applied in many countries and regions. It is not only a bioremediation process but also is an effective measure of recycling utilization of waste resources. The main purpose of composting is to obtain high quality compost products (an organic fertilizer). Many studies have shown that high quality compost is a good soil conditioner, and it plays an important role in soil remediation (Hargreaves et al., 2008). It is generally recognized that the composting process occurs in a very thin layer of liquid on the surfaces of waste particles (Fig. 6). It can degrade organic matter and form stable humus under the action of a variety of microorganisms (including bacteria, actinomyces, fungi and protozoa, etc.) in a certain temperature, humidity, carbon and nitrogen ratio and ventilation conditions (Augenstein et al., 1996). The metabolism of microorganisms is the essence of composting (Shi et al., 2006). However, only a small part of small molecules can be directly used by microorganisms. Most of the organic matter is polymer, and need to be decomposed into soluble organics by the various microbial extracellular enzymes, then penetrating into the microbial cell for metabolism in composting (Zhu et al., 2004), which leading to the traditional composting time is long and the quality is low. In order to shorten the composting time, and improve the efficiency and quality of composting, many researchers try to add some rhamnolipids to promote the composting (Gabhane et al., 2012; Zhang and Sun, 2014) (Table 2). The promoting mechanisms may be as follows: Firstly, rhamnolipids can improve the physical-chemical conditions of composting micro-environment, such as temperature, humidity, oxygen, porosity, pH, etc. (Fu et al., 2007; Zhang and Sun, 2014), which improving the growth conditions of microorganisms (Fig. 6I) Meanwhile, more microorganisms will secrete more extracellular enzymes, which are benefit for composting. Zhang and Sun (Zhang and Sun, 2014) reported that rhamnolipids enhance aeration and water permeability, resulting in a favorable particle-size distribution and pH, decease the C/N ratio, which enhancing the numbers of microorganisms and the yield and activity of enzymes on the two-stage composting of green waste. Shi et al. (Shi et al., 2006) observed that rhamnolipids had slight stimulatory effects on the microbial populations of bacteria, actinomycetes and fungi, at the same time, the activity of extracellular enzymes of microorganisms were also improved in composting of waste rich in cellulose. Secondly, rhamnolipids has an important influence on the organic matter and heavy metals in composting. For example, the rhamnolipids can improve the desorption of organic matters from the surface of garbage particles, and increase their bioavailability (Fig. 6II). Meanwhile, rhamnolipids can promote the interaction between compost organic matter and microorganisms, which accelerating the biodegradation of organic matter (Fig. 6IV). Gabhane et al. (Gabhane et al., 2012) observed that adding rhamnolipids to an organic waste composting, the hydrophobic group of rhamnolipids binded to the surface of the organic matter while the hydrophilic group dissolved in the water, which accelerates the biodegradation of organic matter. Fu et al. (Fu et al., 2007) reported that rhamnolipids can strengthen the dispersion of organic matter into the substrate water phase in kitchen waste composting, that accelerating the uptake of organic matter by microorganisms. Additionally, rhamnolipids can promote the transformation of heavy metals from unstable to stable form, then reduce their bioavailability and biotoxicity (Gabhane et al., 2012; Zhang et al., 2016b) (Fig. 6III). Zhang et al. (Zhang et al., 2016b) reported that rhamnolipids reduce the concentrations of bio-available Cu and Zn during chicken manure composting, that improving the activity of microorganisms and the quality of compost. Thirdly, rhamnolipids have many important influences on microorganisms characteristics. Therefore, adding rhamnolipids in composting may be an effective measure to strengthen the activity of microorganisms and the extracellular enzymes and significantly improve the efficiency and quality of composting. The mechanisms may be as follows: (1) Rhamnolipids can change the surface properties of microorganisms and will promote the interaction between microorganisms and organic matters (Fig. 6IV). Al-Tahhan et al. (Al-Tahhan et al., 2000) reported that rhamnolipids can change the cell surface properties of *Pseudomonas aeruginosa* and strengthen the interaction with hydrophobic substrates, that improving the degradation of hydrophobic substrates. (2) The change of cell surface properties will promote the migration of microorganisms in compost medium, which is beneficial to the widely distribution of microorganisms in the compost medium and increasing the contact of organic matter and microorganisms (Sotirova et al., 2009; Zhong et al., 2016c) (Fig. 6V). For example, Zhong et al. (Zhong et al., 2016c) reported that low-concentration rhamnolipids can promote the transport of *Pseudomonas aeruginosa* ATCC 9027 in an ideal porous medium by changing CSH. That can be used to simulate the migration of microorganisms in compost medium due to the similarity of the medium. (3) The functions of cell membrane (fluidity, permeability etc.) also will be changed in the presence of rhamnolipids (Sotirova et al., 2008; Parthasarathi and Sivakumaar, 2010), that promoting the secretion of microbial extracellular enzymes and the uptake of soluble organics by microorganisms (Fig. 6VI). Parthasarathi and Sivakumaar (Parthasarathi and Sivakumaar, 2010) found that rhamnolipids can improve the cell permeability of *Pseudomonas aeruginosa* MTCC 2297 and *Pseudomonas fluorescens*, which increasing the secretion extracellular enzymes in sugar cane bagasse composting. Liu et al. (Liu et al., 2006) found that rhamnolipids alter the cell membranes to facilitate the production and release of extracellular enzymes (cellulase and xylanase) by *Trichoderma viride* in solid substrate fermentation. The release of extracellular enzymes will be conducive to the decomposition of macromolecular organic matter (Fig. 6VII). (4) Rhamnolipids may affect the expression of genes involve in composting, which helping the synthesis of enzymes or eliminating the adverse genes. Li et al. (Li et al., 2015) found that rhamnolipids affect the expression of the Delta9 fatty acid desaturase gene, the ring-hydroxylating dioxygenase and the 1-hydroxyl-2-naphthoate dioxygenase genes in the biodegradation of phenanthrene by *Arthrobacter* sp. SA02, that affecting the synthesis of related enzymes and the biodegradation of phenanthrene. The degradation of this kind of material also can be found in composting. Zhang et al. (Zhang et al., 2016b) reported that rhamnolipids can decreasing the relative abundances of antibiotic resistance genes and integron gene in chicken manure composting, which reduces the amount of harmful genes in compost and improves the quality of compost. (5) Rhamnolipids promote the desorption of microbial extracellular enzymes from compost medium surface, and enhance the stability of the enzymes, so

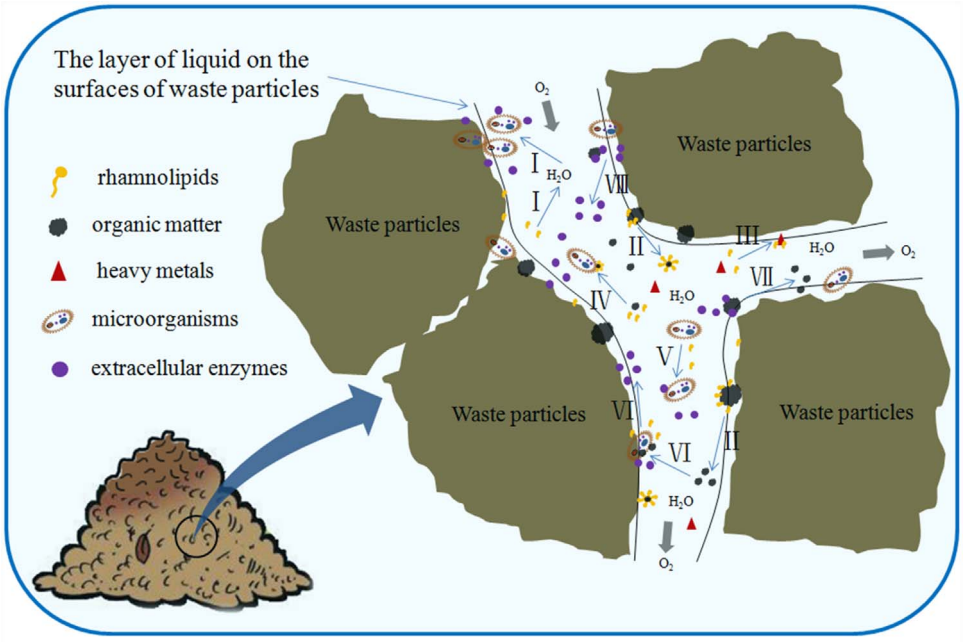

Fig. 6. Effects of rhamnolipids in composting.

Table 2
The application of rhamnolipids in composting in recent researches.

Substances	Influences of rhamnolipids	Refs.
Kitchen waste	Preventing water evaporation, changing the distribution of microorganisms, improving the control of odor. Increase the enzyme activities of amylase, CMCase and xylanase. Decreasing the adsorption of the bacteria on the substrate, slowing down water evaporation, strengthening the dispersion of organic matter into the substrate water phase, promoting the growth of microorganism.	Du et al. (2015) Zeng et al. (2006) Fu et al. (2007)
Municipal waste	Rhamnolipids could be degraded during composting, but not preferentially utilized. Accumulating the uptake rate and consumption of oxygen, the accumulation of H_2S in outlet gas was reduce, the microenvironment be enhanced effectively. Promoting the adsorption of Pb^{2+} by humus at low concentrations, but weakened at sufficiently high concentration.	Zeng et al. (2007) Huang and Zhang (2005) Fu et al. (2015)
Livestock manure	Decreasing the relative abundances of antibiotic resistance genes and integron gene, reducing the concentrations of bio-available Cu and Zn.	Zhang et al. (2016b)
Rice straw and bran	Rhamnolipids had slight stimulatory effects on the microbial populations, increasing the peak xylanase activity, increasing the contents of water-soluble carbon.	Shi et al. (2006)
Fallen leaves and branch cuttings	Enhancing aeration and water permeability, resulting in a favorable particle-size distribution and pH, decreasing the C/N ratio, enhancing microbial numbers and enzyme activities.	Zhang and Sun (2014)
Coal ash and organic matter	Enhancing the of reservation and permeation water.	Ma et al. (2012)
Sugar cane bagasse	Improving the permeability of the cell membrane and led to the secretion extracellular enzymes, improving the cellulase stability and preventing the denaturation during the hydrolysis of cellulose, facilitativing the desorption of enzymes from cellulose matrix.	Parthasarathi and Sivakumaar, (2010)

as to improve the activity of enzymes (Fig. 6VIII). For example, Parthasarathi and Sivakumaar (Parthasarathi and Sivakumaar, 2010) also found that rhamnolipids facilitative the desorption of enzymes from cellulose matrix, and prevent the denaturation of cellulase and improve the stability during the hydrolysis of cellulose in sugar cane bagasse composting. Zeng et al. (Zeng et al., 2006) reported that rhamnolipids increase the enzyme activities of amylase, CMCase and xylanase of *Penicillium simplicissimum* in kitchen waste and agricultural waste composting. Helle et al. (Helle et al., 1993) revealed that rhamnolipids might improve the enzyme stability and prevent denaturation of enzymes during heterogeneous enzymatic hydrolysis of cellulose. Additionally, there are many harmful pathogens during composting. However, rhamnolipids play a role in removing pathogenic bacteria in composting due to the antibacterial and antiviral. Haba et al. (Haba et al., 2003) reported that rhamnolipids can inhibit the growth of phytopathogenic fungal species when the concentration reach to 64ug/ml due to the antimicrobial activity. These effects of rhamnolipids on microorganisms and their extracellular enzymes will not only contribute to microbial degradation of organic matter and increase the efficiency of composting but also promote the quality of composting products.

Although there are so many advantages of rhamnolipids when used in composting, the application of rhamnolipids in composting is an area with limited studies, so more experiments need to be done for the better application. It is believed that rhamnolipids will play more and more important role in composting. The mechanism was shown in Fig. 6 as well.

6. Concluding remarks and future perspective

This review demonstrated that rhamnolipids are a promising biosurfactant, whose excellent properties make them be potentially useful in composting. That is because rhamnolipids have directly or indirectly important effects on microorganisms and microbial extracellular enzymes in composting, and improving the quality of compost products. Meanwhile, the metabolism of microorganism is the essence of composting, so it is very important to understand the mechanism of the effects of rhamnolipids on microorganism. The mainly effects are reflected as follows: (1) rhamnolipids can affect the uptake of pollutants by affecting the surface properties of microorganisms; meanwhile, (2) rhamnolipids can affect enzymes production by changing the regulatory pathways of related genes, or affect enzymatic activity by affecting enzyme structure. A variety of enzymes involved in the metabolic process. The change of enzyme is bound to affect the efficiency of metabolism. However, the studies mainly focus on the uptake of pollutants by microbial in presence of rhamnolipids, and few researches are done about the effects of rhamnolipids on the metabolic process, especially about the effect on genes. In the future, related researches can be strengthened in the following aspects: Firstly, to further study the effects of rhamnolipids on the physicochemical properties of microbial cells, and the relationship between various physical and chemical properties, and the influence of these properties on pollutants uptake; Secondly, studying the impacts of rhamnolipids on the enzymes/proteins involved in the degradation process, and the related mechanisms; Thirdly, studying the effects of rhamnolipids on the related genes and the regulatory pathways involved in the process of microbial degradation of pollutants. Exploring the role of rhamnolipids in bioremediation at the molecular level lies in the theoretical foundation for rhamnolipids practical engineering. Additionally, the high cost of production has limited the application of rhamnolipids widely. Thus, it is important to find a cheap method to produce a good performance rhamnolipids to expand their use. Although the excellent properties of rhamnolipids make them have great application potential, the adverse effects also can't be ignored when applied in practical. Therefore, the relevant toxicology researches about this biosurfactants also need to be done.

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