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MINI-REVIEW

Assessment of the horizontal transfer of functional genes as a suitable approach for evaluation of the bioremediation potential of petroleum-contaminated sites: a mini-review

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Abstract Petroleum sludge contains recalcitrant residuals. These compounds because of being toxic to humans and other organism are of the major concerns. Therefore, petroleum sludge should be safely disposed. Physicochemical methods which are used by this sector are mostly expensive and need complex devices. Bioremediation methods because of being eco-friendly and cost-effective overcome most of the limitations of physicochemical treatments. Microbial strains capable to degrade petroleum hydrocarbons are practically present in all soils and sediments and their population density increases in contact with contaminants. Bacterial strains cannot degrade alone all kinds of petroleum hydrocarbons, rather microbial consortium should collaborate with each other for degradation of petroleum hydrocarbon mixtures. Horizontal transfer of functional genes between bacteria plays an important role in increasing the metabolic potential of the microbial community. Therefore, selecting a suitable degrading gene and tracking its horizontal transfer would be a useful approach to evaluate the bioremediation process and to assess the bioremediation potential of contaminated sites.

Keywords Petroleum hydrocarbons · Petroleum sludge · Bioremediation · Microbial community · Functional genes · Horizontal gene transfer

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Introduction

Typically, petroleum waste is recalcitrant residuals characterized as a stable water-in-oil emulsion of water, petroleum hydrocarbons, solids, and metals (Mazlova and Meshcheryakov 1999). Chemical composition of oil sludge is different regarding the origin of crude oil, petroleum refinery processing methods, and utilized reagents and equipment in refining process (Hu et la., 2013). Petroleum sludge because of being toxic to humans and other organism are of the major concerns (Wickliffe et al. 2014). Therefore, safe disposal of produced sludge in the environment is one of the major problems faced by petroleum sector. For solving this problem, the petroleum industry applied some methods for disposal of produced sludge. Oxidative treatments, such as ultrasonication, ferrosonication, Fenton's oxidation, ozonation, and wet air oxidation which are used for degradation of organic compounds, have been used for treatment of oil sludge (Rivas 2006; Ferrarese et al. 2008).

The common drawback in most of the physicochemical treatments is that they are mostly expensive and need expensive devices (Couto et al. 2010; Das and Chandran 2011). Bioremediation techniques as environment friendly and cost-effective methods can overcome most of limitations of physicochemical treatments (Megharaj et al. 2011). This technique is the process of employing microorganisms to degrade contaminants. Bioremediation is a simple to operate, economic, and effective method which has been used widely in treatment of oily sludge and petroleum-contaminated soil (Battikhi 2014). The bioremediation residuals are mostly safe products such as carbon dioxide, water, and different fatty acids (Das and Chandran 2011; Ubani et al. 2013; Dindar et al. 2013). In recent years, bioremediation had a rapid growth and various microorganisms have been successfully used for treatment of different kinds of contaminants. The biodegradation of

petroleum hydrocarbons is a complicated process and the determining the type of bioremediation approach and operational conditions depends on the amount and types of hydrocarbon compounds in the contaminated site and sludge (Jain et al. 2011). Bioremediation is capable of degrading completely all petroleum wastes apart from heavy polyaromatic's presence in the asphaltenes and resins (Liu et al. 2010). Land farming, biopiles, and bioreactor methods are common and the most studied bioremediation approaches for treatment of petroleum sludge (Powell et al. 2007).

Degradation by microorganisms is an important process of petroleum hydrocarbon attenuation in the soil and sediments (Fathepure 2014). Its rates depend on the types of petroleum hydrocarbons, microbial population diversity, and ecological conditions of the contaminated region (Das and Chandran 2011). Microbial strains which are capable to degrade petroleum hydrocarbons are almost present in all soil and sediments and their population density increases in touch with contaminant. Microbial population uses the petroleum hydrocarbons as carbon source (Martins and Peixoto 2012; Dindar et al. 2013). They used different electron acceptors regarding the ecological and geochemical conditions of the region (Nie et al., 2014). Bacteria capable of biodegrading petroleum hydrocarbons are usually classified based on the final electron acceptor which they use. Aerobic bacteria which use oxygen as final electron acceptor, nitrate reducing, iron reducing, manganese reducing, sulfur reducing, and methanogenic bacteria are bacterial groups which can degrade petroleum hydrocarbons (Maloney et al. 2004). In petroleum-contaminated sites such as oil-polluted groundwater plumes, different biodegradation zones based on the prevalent electron acceptor can be detected. These zones can be determined using obtained data from geochemical and microbial analysis (Tiehm and Schulze 2003). Biodegradation zones also provide useful information about degradation rates. Aliphatic, cycloalkane, and aromatic hydrocarbons with low to moderate molecular weight show high biodegradation rate in optimum conditions, whereas hydrocarbons with high molecular weight have low biodegradation rates (Das and Chandran 2011). Asphaltenes are among the most recalcitrant compounds for biodegradation (Liao et al. 2009; Singh et al. 2009). Refinery sludge because of containing a large amount of asphaltenes and resins is difficult to degrade by bioremediation process on its own (Hu et al. 2013; Ubani et al. 2013). Some studies, however, have reported large amount of organic conversion in this kind of sludge using bioremediation approach.

In bioremediation process, parameters such as types of microorganisms, remediation duration, nutrient amounts, and hydrocarbon concentrations in oily sludge are important factors which affect the biodegradation rates (Jordening and Winter 2004). Many bacteria and fungi can degrade petroleum hydrocarbons but any single strain can afford biodegradation of all compounds found in petroleum sludge (Fan and Krishnamurthy 1995). Biodegradation of petroleum hydrocarbons is realized by sequential reactions where bacteria in a microbial consortium collaborate with each other for degradation of oily sludge (Hu et al. 2013). Horizontal transfer of functional genes between bacteria is an important contributor to bacterial genetic diversity and increases the metabolic potential of the microbial community (Wong et al. 2012). This phenomenon is an important process for a successful bioremediation (Boopathy, 2000; Singh et al., 2006). This review tries to give evidence of successful experiences in studying the horizontal transfer of functional genes in the hydrocarbon-contaminated sites and whether horizontal gene transfer (HGT) can be used for assessment of the bioremediation potential of petroleum-contaminated site and as a monitoring approach for having a successful bioremediation process.

Horizontal transfer of functional genes between Gram-bacteria in the petroleum-contaminated sites

In the bioremediation of petroleum-polluted sites, bioavailability is one of the most important factors. Functional genes have also been used in the evaluation of the bioavailability of the petroleum hydrocarbons in contaminated sites. The evaluation of hydrocarbon-degrading functional gene gives valuable information about the degradation capability of the polluted sites. *Alk* gene as a functional gene in alkane-degrading bacteria is present in the genomes of different Gram-negative and Gram-positive bacteria. Many strains which can utilize alkane as carbon and energy source contain one or more *alk* genes. *Alk* genes are generally chromosomal. Regarding the PAH-degrading functional genes, Foght and Westlake (1991) and Sayler and Layton (1990) were detected naphthalene degraders in aquatic and terrestrial regions using gene probes which have been prepared for NDO and NAH7 plasmids. Sanseverino et al. (1993) showed that the nah degrading system or the NAH plasmid may mediate the catabolism of more PAHs than previously thought. They concluded that conserving and monitoring of catabolic capacity of one bacterial population may be enough for degradation of a major part of PAHs Ahn et al. (1999) reported the ability of *nahA*-derived probe to detect a large proportion of the naphthalene- and phenanthrene-degrading strains. Using *phnAc* gene, Widada et al. (2002) could detect 19 strains of PAH-degrading bacteria from various environments. Hamann et al. (1999) using *ndoB* gene of the NDO plasmid from *Pseudomonas putida* NCIB 9816 could detect successfully a wide range of PAH-degrading bacterial strain from quit different genera. Bacterial strains carrying *pah* genotype are more numerous in the contaminated soils than those carrying *nah* genes (Laurie and Lloyd-Jones, 2000).

HGT plays an important role in the successful adaptation of bacteria to the contaminated environment (Boronin and Kosheleva 2014). In this process in which genetic material moves between bacterial strains plasmids play the main role (Fig. 1). Through HGT, microbial community adapts to the contaminated site and can degrade the contaminants via spreading of the catabolic pathways. Furthermore, catabolic pathways can be evolved too due to HGT. HGT in microbial community in the environment have been previously demonstrated (Top and Springael 2003). The presence of highly conserved *nahAC* gene in naphthalene catabolic plasmids (pDTG1-like) in diverse bacteria from different geographical

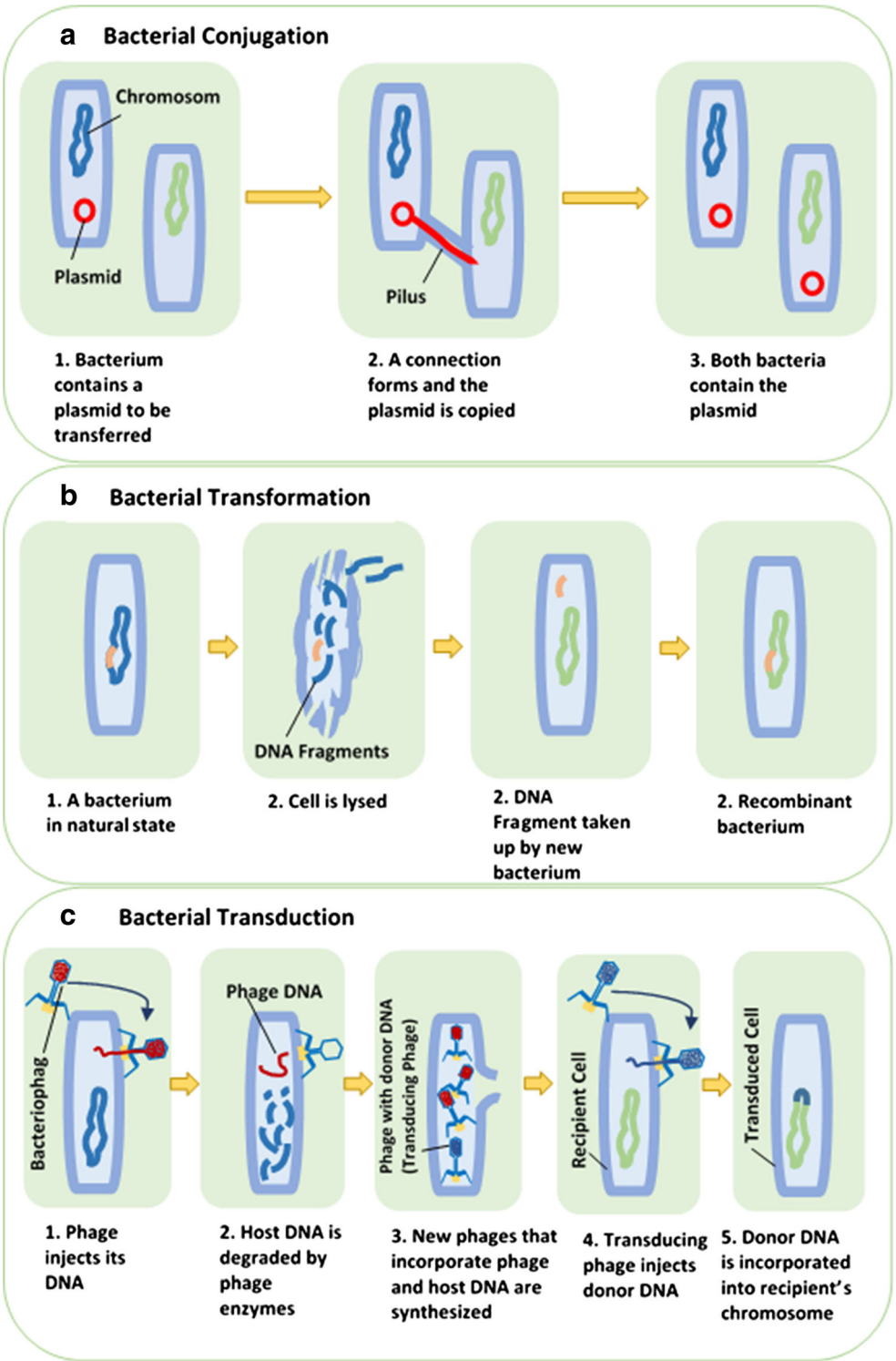

Fig. 1 Horizontal gene transfer between bacteria. **a** Bacterial conjugation occurs by cell-to-cell contact between bacteria and plasmid is exchanged through pilus between bacteria. **b** Bacterial transformation occurs when naked DNA is released with lysis of one bacterium and taken up by another bacterium. **c** Bacterial transduction occurs when DNA fragments are transferred from one bacterium to another one by bacteriophages

regions (Herrick et al. 1997) and *dhaA* gene in three different organisms *Rhodococcus rhodochrous* NCIMB13064, *Pseudomonas pavonaceae* 170, and *Mycobacterium* sp. strain GP1 are two examples. Horizontal transfer of genes involved in naphthalene catabolic pathway in soil system has been also demonstrated due to experiments using labeled conjugative plasmids (Akhmetov, et al. 2008; Boronin and Kosheleva 2014). Horizontal transfer of naphthalene biodegradation genes between soil bacteria leads to the enhancement of the biodegradation rate of petroleum hydrocarbons due to the appearance of more effective degrader strains (Shahi et al., 2016). By development of an effective degrading microbial population, HGT can increase the biodegradation potential of contaminated soils. Therefore, determination of suitable degrading genes on mobile genetic elements which can promote the HGT will be a useful approach for ensuring successful bioremediation process. Based on numerous related studies, *alkB* gene which encodes alkane monooxygenase enzyme and *phnAc* and nah genes are ideal markers for the evaluation of the petroleum hydrocarbon degradation potential in the contaminated sites (Shahi et al. 2015). Targeting and quantitative analysis of these genes have been surveyed successfully for characterizing the abundance and diversity of petroleum-degrading bacterial community. Table 1 summarizes some aerobic aliphatic and aromatic hydrocarbon-degrading genes in literature which are found on plasmids in bacteria.

A strong relationship between the presence of functional genes and HGT has been reported through various works. Wilson et al. (2003) have reported the horizontal transfer of *phnAc* gene by naphthalene-degrading bacteria isolated from petroleum-polluted soil. Yousaf et al. (2010) have demonstrated the transporting of *alkB* gene through horizontal gene transfer between Gram-negative and Gram-positive bacteria in petroleum-contaminated soil. Nie et al. (2014) have supported these findings and showed the horizontal transfer of *alkB* in oil-polluted environment. By extraction the plasmid DNA from collected soil samples and using quantitative PCR, Shahi et al. (2015) evaluated the horizontal transfer of *alkB*, nah, and *phnAc* gene through a biostimulation practice of petroleum-contaminated soil and showed the transfer of *alkB* and *phnAc* genes under high nutrient concentrations. They have found a positive correlation between nutrient content and HGT. Increasing of the carbon per nitrogen relation from 100:5 to 100:15 was simultaneous with an increase in HGT rates in their study.

Horizontal gene transfer as a bioremediation monitoring approach

Bioremediation as an effective approach is used for treatment of petroleum-contaminated soil. When naturally existing bacteria are exposed to organic pollutants, they start to develop, adapt, and increase their ability to degrade the contaminant. Many groups of microorganisms can degrade the hydrocarbons including petroleum hydrocarbons. However, not all the contaminated sites have the potential for natural attenuation and the capability of such region for a successful bioremediation should be enhanced due adding of necessary nutrient, electron acceptors, or some effective microorganisms. For an effective bioremediation practice, the natural potential of the native microorganisms should be evaluated and the best alternative for bioremediation then can be chosen. After selecting of a suitable approach, the bioremediation procedure should be observed during the process. Therefore, for a successful bioremediation practice, an acquisitive monitoring before and during the bioremediation process is needed. Different monitoring approaches have been tested by researchers. Physicochemical methods have been used widely by different researchers. Geophysical analysis using electrical induced polarization (IP) measurement and finding correlation between changes in groundwater geochemistry accompanying stimulated iron and sulfate reduction and sulfide mineral precipitation when acetate injection to groundwater (Williams et al. 2009), employing of electrode-based approach with installing of borehole graphite anodes from a region of acetate injection for stimulation of bioreduction of U(VI) and reporting of a correlation between levels and availability of acetate and the removal of uranium from groundwater (Williams et al. 2010), using successfully remote sensing technique for the monitoring of benzene level throughout the pipeline (Noomen et al. 2015) and benefiting from the different level of deformation in microfossils under different concentrations of petroleum contamination for monitoring of bioremediation process in a crude oil-polluted costal region (Sabean et al. 2009) are some examples from researches which have done for finding a suitable physical monitoring approach. Using stable isotope ratio of contaminant residuals is the other chemical method which has been used for assessment of bioremediation practice (Stehmeier et al. 1999). Stable isotope fractionation analysis (SIFA) has been used by Meckenstock et al. (2004) for a qualitative or even a quantitative monitoring and evaluation of biodegradation in the environment. Almost all these methods rely on the monitoring of contaminant and detecting any diminishing in the contaminant concentration in the contaminated site during bioremediation process. However, they cannot give detailed information about the fate of the contaminant and cannot separate the biotic and abiotic removals. Monitoring approaches which are based on the microbial analysis give closer information about the biologic degradation of pollutants. Microbial community as the main players of bioremediations process gives us the exact information about what happened in the contaminated site. Shahi et al. (2015, 2016) employed successfully the evaluation of microbial population and functional genes as monitoring approaches for analysis of the efficiency of bioremediation system. They tested successfully the horizontal transfer of functional gene as an effective monitoring approach for evaluation of the

Table 1 Some aerobic aliphatic and aromatic hydrocarbon-degrading genes which are found on plasmids in bacteria and their substrate specificities

Substrate	Gene	Function of the encoded enzyme	Plasmid	Host bacterium	Reference
n-Alkanes (C10-C16)	*alkB*	Alkane monooxygenase	OCT plasmid	*Rhodococcus erythropolis* SK121	Nie et al. (2014)
n-Alkanes (C9–C18)	*CYP153*	Alkane hydroxylase	Plasmid	*Alcanivorax borkumensis* SK2	Nie et al. (2014)
n-Alkanes (C15–C36)	*ladA*	Long-chain alkane monooxygenase	pLW1071	*Geobacillus thermodenitrificans* NG80–2	Feng et al. (2007)
Long-chain *n*-alkanes	*alkM*	Terminal alkane-1-monooxygenase	pCom7M	*Acinetobacter* sp. ADP1	Smits et al. (2002)
n-Alkanes	*alkL*	Outer membrane protein increasing oxygenation activities	*pBT10*	*Pseudomonas putida* GPo1	Julsing et al. (2012)
Alkane	*alkF*	Rubredoxin-1	OCT plasmid	*Pseudomonas oleovorans*	Kok et al. (1989)
Akane	*alkG*	Rubredoxin-2	OCT plasmid	*Pseudomonas oleovorans*	Kok et al. (1989)
Large variety of alkyl	*alkBGT*	NADH-dependent ω-hydroxylation	pBT10	*Pseudomonas putida* GPo1	Julsing et al. (2012)
Aldehyde	*alkH*	Aldehyde dehydrogenase	OCT plasmid	*Pseudomonas oleovorans*	Kok et al. (1989)
Dibenzothiophene sulfone (DBTO2)	*dszA*	DBTO2 monooxygenase	pSOX	*Mycobacterium goodii*	Pylro et al. (2012)
Dibenzothiophene (DBT)	*dszC*	DBT monooxygenase	pSOX	*Mycobacterium* sp. G3	Pylro et al. (2012)
Naphthalene	*nahAc*	α subunit of naphthalene dioxygenase	pNAH7	*Pseudomonas putida*	Gomes et al. (2010)
Naphthalene	*ndo*	Naphthalene-1,2-dioxygenase	Plasmid	*Pseudomonas* sp.	Ma et al. (2006)
Naphthalene	*nahAd*	β subunit of naphthalene 1,2-dioxygenase	pDTG149	*Pseudomonas* sp. NCIB 9816–4	Parales et al. (1998)
Naphthalene	*nagAc*	α subunit naphthalene 1,2-dioxygenase	pWWU2	*Pseudomonas* sp. U2	Fuenmayor et al. (1998)
Naphthalene	nagAd	β subunit naphthalene 1,2-dioxygenase	pWWU2	*Pseudomonas* sp. U2	Fuenmayor et al. (1998)
Naphthalene	*nagB*	Naphthalene *cis*-dihydrodiol dehydrogenase	Plasmid	*Pseudomonas* sp. U2	Fuenmayor et al. (1998)
Naphthalene	*nagF*	Salicylaldehyde dehydrogenase	pWWU2	*Pseudomonas* sp. U2	Fuenmayor et al. (1998)
Chloroaromatics	*nahI*	2-Hydroxymuconic semialdehyde dehydrogenase	pKW1	*Pseudomonas stutzeri* OM1	Kunze et al. (2009)
Chloroaromatics	*nahN*	2-Hydroxymuconic semialdehyde hydrolase	pKW1	*Pseudomonas stutzeri* AN10	Kunze et al. (2009)
Chloroaromatics	*nahL*	2-Hydroxypent-2,4-dienoate hydratase	pKW1	*Pseudomonas putida* MT53	Kunze et al. (2009)
Chloroaromatics	*nahK*	4-Oxalocrotonate decarboxylase	pKW1	*Pseudomonas stutzeri* AN10	Kunze et al. (2009)
Chloroaromatics	*cbzE*	Catechol 2,3-dioxygenase	pKW1	*Pseudomonas fluorescens* SK1	Kunze et al. (2009)
Chloroaromatics	*cbzG*	2-Hydroxymuconic semialdehyde dehydrogenase	pKW1	*Pseudomonas fluorescens* SK1	Kunze et al. (2009)
Chloroaromatics	*cbzJ*	2-Hydroxypent-2,4-dienoate hydratase	pKW1	*Acidovorax* sp. JS42	Kunze et al. (2009)
2,3-Dihydroxyphenylpropionate	*mhpF*	Acetaldehyde dehydrogenase	pKW1	*Pseudomonas putida* PaW630	Kunze et al. (2009)
2,3-Dihydroxyphenylpropionate	*mhpD*	2-Hydroxypent-2,4-dienoate hydratase	pKW1	*Pseudomonas putida* W619	Kunze et al. (2009)
2,3-Dihydroxyphenylpropionate	*mhpC*	2-HMS hydrolase	pKW1	*Pseudomonas putida* W619	Kunze et al. (2009)
2,3-Dihydroxyphenylpropionate	*mhpB*	2,3-Dihydroxyphenylpropionate 1,2-dioxygenase	pKW1	*Pseudomonas putida* ML2	Kunze et al. (2009)
Catechol	*xylE*	Catechol 2,3-oxygenase	TOL Plasmid	*Pseudomonas putida*	Burlage et al. (1989)
Xylene	*xylA*	Xylene monooxygenase	TOL pWW0	*Pseudomonas putida*	Burlage et al. (1989)
Xylene	*xylD*	Xylonate dehydratase	TOL Plasmid	*Pseudomonas putida*	Burlage et al. (1989)
Toluene	*todC1*	α subunit of toluene dioxygenase	pKK223–3	*Pseudomonas putida* F1	Zylstra and Gibson (1991)

Table 1 (continued)

Substrate	Gene	Function of the encoded enzyme	Plasmid	Host bacterium	Reference
Toluene	*todC2*	β subunit of toluene dioxygenase	pKK223–3	*Pseudomonas putida* F1	Parales et al. (1998)
Dinitrotoluene	*ntdAc*	α subunit of 2-nitrotoluene dioxygenase	pUC13	*Pseudomonas* sp. JS42	Parales et al. (1998)
Dinitrotoluene	*ntdAd*	β subunit of 2-nitrotoluene dioxygenase	pUC13	*Pseudomonas* sp. JS42	Parales et al. (1998)
Dinitrotoluene	*dntAc*	α subunit of 2,4-dinitrotoluene dioxygenase	pDTG953	*Burkholderia* sp. DNT	Parales et al. (1998)
Dinitrotoluene	*dntAd*	β subunit of 2,4-dinitrotoluene dioxygenase	pDTG951	*Burkholderia* sp. DNT	Parales et al. (1998)

bioremediation process in their project in petroleum-contaminated soil. They also showed that the assessment of horizontal transfer of functional genes is not only a method for checking out the bioremediation manner but also can be used for assessment of the biodegradation potential of contaminated site (Shahi et al., 2015).

Conclusion

Horizontal gene transfer plays a crucial role in petroleum hydrocarbon biodegradation and influences active microbial community. Successful bioremediation of the petroleum-contaminated soil is dependent on the successful transferring of the functional genes between microbial community members. This phenomenon, which takes place in different microbial types regardless of the genus and Gram strain, enables the bacterial consortium to degrade major parts of hydrocarbon compounds found in the petroleum sludge. Since the abiotic factors such as macronutrient availability affect the happening of horizontal gene transfer in contaminated sites, the biodegradation capacity differs from one contaminated site to another. Therefore, the assessment of functional genes and mobile elements promoting the HGT could be an efficient method for the investigation the biodegradation potential of contaminated site. Furthermore, since the occurrence of HGT in a contaminated site represents the acquisition of biodegradation skills by microbial consortia, evaluation of HGT in contaminated site can be used as bioremediation monitoring approach for assessment of a successful biodegradation process.

qPCR as a highly sensitive tool for analyzing the quantity of given functional genes found in different bacterial genera is considered for assessment of the quantity of horizontally transferred genes in the contaminated sites. The frequency of horizontal gene transfer is affected by abiotic factors and ecological interactions among co-occurring bacterial species. However, to which degree these factors affect natural HGT are still not known and need to be studied more. Further studies are also necessary to reveal the relations between HGT and functional genes by nucleotide sequence analysis.

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Compliance with ethical standards

Conflict of interest Aiyoub Shahi declares that he has no conflict of interest. Bahar Ince declares that she has no conflict of interest. Sevcan Aydin declares that she has no conflict of interest. Orhan Ince declares that he has no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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