Review

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Plant-bacteria partnership: phytoremediation of hydrocarbons contaminated soil and expression of catabolic genes

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Abstract

Petroleum hydrocarbons are harmful to living organisms when they are exposed in natural environment. Once they come in contact, it is not an easy to remove them because many of their constituents are persistent in nature. To achieve this target, different approaches have been exploited by using plants, bacteria, and plant-bacteria together. Among them, combined use of plants and bacteria has gained tremendous attention as bacteria possess set of catabolic genes which produce catabolic enzymes to decontaminate hydrocarbons. In return, plant ooze out root exudates containing nutrients and necessary metabolites which facilitate the microbial colonization in plant rhizosphere. This results into high gene abundance and gene expression in the rhizosphere and, thus, leads to enhanced degradation. Moreover, high proportions of beneficial bacteria helps plant to gain more biomass due to their plant growth promoting activities and production of phytohromones. This review focuses functioning and mechanisms of catabolic genes responsible for degradation of straight chain and aromatic hydrocarbons with their potential of degradation in bioremediation. With the understanding of expression mechanisms, rate of degradation can be enhanced by adjusting environmental factors and acclimatizing plant associated bacteria in plant rhizosphere.

Keywords: Phytoremediation; catabolic genes; plant-bacteria interactions; expression.

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Introduction

Petroleum hydrocarbons (PHCs) in soil and water are one of the major causes of environmental deterioration. PHCs contain hazardous and persistent organics which can pose serious threat to the health of plants, animals and humans if they come into environment from point sources like leakages from pipelines and underground storage tanks (UST), or non-point sources like natural seepages and landfill leaching (Yadav and Reddy 1993; Bamforth and Singleton 2005). These organic pollutants include simple aliphatic as well as complex aromatic compounds such as benzene, toluene, naphthalene, methylbenzene, polychlorinated biphenyls, polycyclic aromatic compounds, nitroaromatics, or straight chain halogenated hydrocarbons. These compounds may enter the animal and human system via inhalation, ingestion and skin contact lead to hepatic, renal, respiratory and neurological risks which are inevitable. At molecular level, these hydrocarbons are toxic, mutagenic, and carcinogenic (Maertens et al., 2008).

Diesel, a dominant fuel source of modern industrial society, is derived from crude oil through cracking during oil refining and it is complex mixture of aromatic and saturated hydrocarbons (Eriksson et al., 2001; Zanaroli et al., 2010). It is medium-weighted petroleum product whose boiling point ranges 175°C to 355°C (Brady, 2001). Generally, diesel contains over 200 hydrocarbon compounds which are distributed as 30% aliphatic hydrocarbons, 45% cyclic hydrocarbons and, approximately, 24% polycyclic aromatic hydrocarbons (PAHs) like naphthalene (Riffaldi et al., 2006; Zytner et al., 2001). Low molecular weight compounds in diesel are, generally, more toxic than long chain hydrocarbons. It is because long chain hydrocarbons are less soluble and not easily available for reaction purpose (Dorn and Salanitro, 2000). On the other hand, it is easy to degrade low molecular weight (LMW) hydrocarbons as compared to high molecular weight hydrocarbons (HMW) because of their availability in biochemical reaction (Mrozik and Labuzek, 2002).

Diesel spillage takes place, usually, during refining processes, storage and transportation. Such spillages can create acute problems of pollution, if not scavenged, from the environment on time. They may pose serious threat to living organisms and to ecosystem because of accumulation of contaminants with the passage of time. Hence, diesel hydrocarbons need to be remediated on time if there is any possibility of contamination in soil/water (Shah, 2013).

Bioremediation: use of living organisms toward degradation

Bioremediation and phytoremediation are most commonly used traditional methods for remediation of soil/water polluted with petroleum hydrocarbons. Bioremediation, the use of microorganisms for decontamination of pollutants, is economical and effective treatment used in past (Riser-Roberts, 1998). Bioremediation is a triangular interaction among microorganism, nutrients and contaminants (Fig. 1). So, the methodology works efficiently when all these things can interact and with each other.

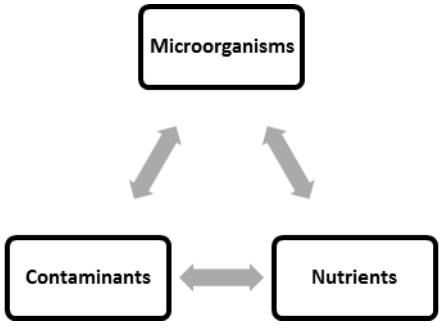


Figure 1: Bioremediation Triangle: Degradation mechanism.

Microbial use for remediation of hazardous compounds and their transformation into less toxic compounds is not a new approach. In 600 B.C, Romans used this technology for cleaning of their wastewaters (Khoei et al., 2013). Same methodology is used for treatment of soil/water and has been commercialized since few decades. First commercial application of bioremediation of hydrocarbons was made in 1972 for cleaning of Sun-Oil Ltd. pipeline spillage in Amber, Pennsylvania (National Academy Press; Washington, D.C. 1993). An important thing to consider is to decide whether particular microorganisms are suitable for biodegradation of on site contaminants. Although, indigenous microbial communities also play their role in degradation of on site contaminants but the process of bioremediation can be enhanced by biostimulation and bioaugmentation. In biostimulation, degradative potential of microbial communities can be enhanced by addition of extra energy sources (Andreoni and Gianfreda, 2007) while bioaugmentation introduces the bacterial strains capable of degrading pollutant in contaminated zone. Bioaugmentation is used to enhance degradation and transformation of pollutants by inoculation of particular microbes having pollutants degradation abilities. Such degradation abilities are due to presence of contaminants degrading genes which can mineralize the pollutants i.e. chlorinated aliphatics, long chain alkanes, simple aromatics, polycyclic aromatic hydrocarbons, and nitroaromatics (Cao et al., 2009; CE, 1997 ; Grosser et al., 1991). The complete breakdown and mineralization of PHCs (C_yH_x) is based on respiration rate of inoculum and is represented by following equation (Baker et al., 2000).

$$C_yH_x + (y + 0.25x)\ O_2 \rightarrow yCO_2 + 0.5x\ H_2O$$

where y is used for the representation of carbon atoms while x denotes the number of hydrogen atoms in petroleum hydrocarbon compounds. Above equation also represents the molar ratio of oxygen:carbon-dioxide which is necessary to complete aerobic biodegradation by bacterial strain (Van De Steene and Verplancke, 2007).

Microbial degradation of straight chain hydrocarbons is far easier as compared to polycyclic aromatic hydrocarbons (PAHs). PAHs are composed of more than two benzene rings fused in either linear, angular, and/or cluster arrangement. However, biodegradation of polycyclic aromatic hydrocarbons having more than three benzene rings is less ubiquitous and has not been done successfully by the application of microorganisms (Nawaz et al., 1993). Hence, low molecular weight PAHs (two or three fused aromatic rings) are relatively easy to degrade as compared to high molecular weight PAHs (four or more aromatic rings). Moreover, high molecular weight PAHs are hydrophobic and persistence in nature. They are more resistant and less available to microbial degradation compared to low molecular weight PAHs (Mrozik and Labuzek, 2002).

Phytoremediation: use of plants to decontaminate pollutants

Another approach, phytoremediation, is carried out by growing plants having ability to survive and utilize the pollutants in contaminated zone. Plants are used to extract, sequester, or detoxify pollutants. Hence, these plants are used to remove, transform, or utilize toxic contaminants present in soil, sediments, groundwater, surface water, and even from the atmosphere (Gerhardt et al., 2009; Susarla et al., 2002). The concept of phytoremediation which was firstly given in 1904 was came from the ideology that plants are natural cleaner of polluted environments and they decontaminate the pollutants by the action of secondary metabolites (Hartmann et al., 2008; Smith and Boyko, 2007). However, it was firstly taken in consideration by US Environmental Protection Agency (USEPA) in 1991 and was first time used in literature in 1993 by Cunningham and Berti (Cunningham and Berti, 1993). This methodology was a sudden breakthrough for uptakes and degradation of inorganic and organic compounds. There are several strategies that come under this concept of phytoremediation and are described below.

Phytodegradation or phytotransformation: It is the method in which plants uptake contaminants from the soil and degrades them.

Phytoextraction or phytoaccumulation: In this method, plant took contaminants/pollutants from soil and store in their leaves and shoots.

Phytostabilization (PS): Pollutants are adsorbed and accumulated by the roots and prevented their leaching and spreading in the environment.

Rhizodegradation (RD) / Phytostimulation: Plant roots produce root exudates and degradation enzymes which enhance microbial proliferation and metabolic activity in the plant rhizosphere beneficial for degradation.

Phytovolatilization (PV): Pollutants are adsorbed from soil and released into atmosphere through transpiration. Plants with high transpiration rate are engineered genetically for enhanced phytovolatilization.

All these approaches mentioned above are in practice since 1990s with little modifications for remediation of heavy metals. Since 2002, phytoremediation has been used for removal of hydrocarbons and other organic pollutants. In simple words, plants transform organic pollutants from more toxic to less toxic form and then sequester in their tissues. However, bacteria degrade the organic pollutants into very simpler products CO_2 and H_2O. Individually, both plant and bacteria play effective role in degradation which is shown in Fig 2.

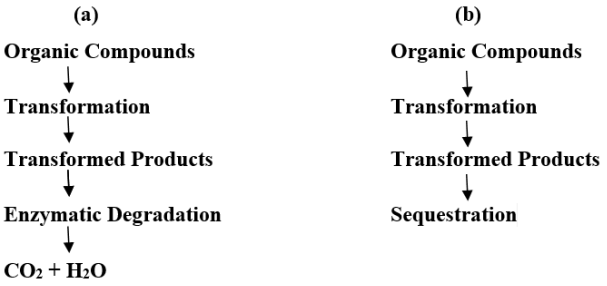


Figure 2: Pathways adopted for degradation of organic compounds in soil by plants.

Pollutants which can be cleaned by phytoremediation are categorized into elemental and organic pollutants. First concept of phytoremediation was developed for uptake of heavy metals from soil directly but later studies have shown that the same methodology can be used for removal, degradation and sequestration of organic compounds such as petroleum hydrocarbons with little modifications (Salt et al., 1998). There are very few remediation methods for removal of elemental pollutants from soil as compared to organic pollutants (Clemens et al., 2002; Cobbett and Goldsbrough, 2002). It is reported that elemental contaminants like heavy metals cannot be destroyed biologically because "degradation" refers to change in nuclear structure which is not possible with phytotechnologies. Hence, they can be transformed only from one oxidation state to another oxidation state (Alkorta and Garbisu, 2001; Ghosh and Singh, 2005). Phytoextraction and phytostabilization of heavy metals are major principles for cleaning of metal contaminated soil (Ali et al., 2013; Chaney et al., 1997). This is done by extraction of pollutants, translocation to aboveground storage tissues, sequestration of elements in the root system which prevent spreading into soil/groundwater, and, finally, converting them into less toxic chemicals (Meagher, 2000).

In contrast to the phytoremediation of heavy metals, second group of pollutants, organic pollutants, can be remediated by using plants. Degradation of low molecular weight (LMW) petroleum hydrocarbons can be performed easily by using many plants while the compounds with high molecular weight (HMW) are restricted to few varieties (Chaudhry et al., 2005; Huang et al., 2004). In order to degrade these complex compounds, a new approach has been used which is through co-metabolic processes involving plants and bacteria (Afzal et al., 2013; Khan et al., 2013; Weyens et al., 2009).

Role of plant innate immunity in phytoremediation

Plant innate immunity or natural defense system helps plant to survive in harsh conditions not only by removing inorganic contaminants from soil but also through enzymatic degradation of organic pollutants. This, usually, done by producing secondary metabolites from primary metabolites which trigger the natural defense system of plant to become activate when plant is grown in stressed environment. These secondary metabolites are further divided into three categories according to their functions in different environmental conditions i.e. phenolics, terpenes, and nitrogen /sulfur containing compounds (Harborne 1997).

Phenolics are supposed to be involved in resisting wide range of toxins produced by fungi including some nematodes while terpenes play vital role in resisting and killing of plant feeding insects (Wuyts et al., 2006). Among nitrogen containing secondary metabolites, alkaloids are responsible for defending plant against bacterial infections, herbivoral attacks, and stresses due to variety of organic compounds (Hegnauer, 1988). These secondary metabolites have nothing to do with plant biomass and are solely responsible for defense and produced when they are needed only (Makkar et al., 2007; Rosenthal, 1991). In addition to these secondary metabolites, plants also produce pollutant degrading enzymes against different allelochemicals (Singer and Stireman, 2003).

Rhizo-microbial-remediation: beneficial plant bacteria interactions

Rhizo-microbial-remediation can be considered as plant-microbe interaction which is synergistic relationship among plants and plant-associated bacterial communities. Importance of this relationship has been exploited as enhanced degradation mechanism in plant rhizosphere studies (Afzal et al., 2013; Arslan et al., 2015; Ho et al., 2007; Kidd et al., 2008). Plant rhizosphere plays vital role in mineralization, degradation, stabilization, and sequestration of organic pollutants especially hydrocarbons. During absorption of water and nutrients from contaminated soils, plants normally absorb toxic pollutants for which they have developed detoxification mechanisms (Eapen et al., 2007). Furthermore, roots of plants oozes out liquid in small drops known as root exudates which are organic in nature and can increase the microbial activity and abundance of pollutant degrading rhizobacteria in plant rhizosphere (Afzal et al., 2011; Anderson, 1993). Sometimes, plant growth promoting hormones are also produced by rhizobacteria which help plant to gain more biomass and, thus, allow more colonization and high density of rhizobacteria in rhizoplane (Weyens et al., 2009). Hence, combined use of bacteria with plant roots offers high of remediation compared to their alone usage (Glick, 2010). This combined and stimulatory approach of phytoremediation was initially described by Hiltner et al., (1904) such as "plant rhizosphere is a zone in which roots of plants influence growth activity of microorganisms" (Hartmann et al., 2008; Hiltner, 1904). Syner-

gistic mechanism of plant-bacteria interaction for the remediation of diesel hydrocarbons is shown in Figure 3.

Selection of microorganisms in plant rhizosphere for hydrocarbons degradation is very important for bioaugmentation (Kuiper et al., 2002). It is better to select and inoculate only those rhizosphere-competent rhizobacteria that have potential of efficient degradation in all the conditions (Normander and Hendriksen, 2002).

Degradation mechanisms of organic compounds during plant-bacteria interactions

Plants themselves can detoxify the pollutants by oozing enzymes and phytoharmones but the process of degradation can be enhanced by natural attenuation of indigenous species of bacteria possessing catabolic genes (Anderson, 1993; Gerhardt et al., 2009; Yateem, 2013). Even though, detoxification of pollutants through phytoremediation (using plants only) is an economically more appealing technique (Olson et al., 2008; Pilon-Smits, 2005), but these phytotechnologies do not support degradation for wide range of plant species, especially, when they are grown in hydrocarbons contaminated soil (Chaudhry et al., 2005; Huang et al., 2004; Kaimi et al., 2007). Moreover, many plants can not grow well and, hence, do not support degradation even they are tolerable and resistant to hydrocarbons (Germaine et al., 2009). To prevail over these problems, synergistic approach of using plants and pollutant degrading bacteria together has been proposed to enhance the process of phytoremediation (Tara et al., 2013). Furthermore, remediation rate can be enhanced if pollutant degrading bacteria possess PGPR activities in addition (Glick, 2010; Weyens et al., 2009). During these interactions, plant-roots produce root exudates containing nutrients and necessary metabolites which support the microbial proliferation and colonization of rhizobacteria in plant rhizosphere. These metabolites can be organic acids such as amino acids, and sugars (Hirsch et al., 2013; Shi et al., 2013; Vancura and Hovadik, 1965). Therefore, successful colonization of plant growth promoting rhizobacteria can enhance not only the plant biomass but also helps in hydrocarbons degradation even in harsh conditions. In response, several phytohormones such as auxin, gibberellins, and cytokinin etc. are synthesized by PGPR whose presence affects plant biomass and growth in greater extent (Ashraf et al., 2013; Tahir and Sarwar, 2013). Usually, functioning of PGPR can be illustrated in three different ways which are as follows

- they PGPR synthesize plant growth promoting hormones having ACC-deaminase activity and acts as a regulator by consuming aminocyclopropane 1-carboxylate as precursor of plant growth suppressor.
- PGPR facilitate nutrients uptake in hydrophobic conditions due to the presence of hydrocarbons as a selective pressure
- Lastly, PGPR help plants to defend against infection or foreign invagination of pathogens through bio-control mechanism.

In the first mechanism, aminocyclopropane 1-carboxylate is immediate precursor of ethylene and, naturally, produces in stress environment. PGPR reduce the ethylene production by consuming aminocyclopropane 1-carboxylate due to its ACC-deaminase activity. Hence, the presence of PGPR act as a regulator of plant growth mechanism in hydrocarbons contaminated soil. . The whole mechanism of plant growth and suppression system is shown in Figure 4. In addition to this, PGPR also play vital role in fixation of atmospheric nitrogen which help plant to grow well in contaminated environment (Afzal et al., 2011; Zhuang et al., 2007).

In the second mechanism, PGPR facilitates nutrients availability by synthesizing high-affinity metal chelating compounds (mostly iron) known as siderophores. This allows sequestration of metals (iron) from the soil and makes it available for plants as a mineral. Plants take up these nutrients in the form of bacterial-siderophores-iron complex and utilize them in its own growth and development. This is why, PGPR have been exploited in the field of agriculture to facilitate nutrients uptake in plants since longer times (Zhuang et al., 2007).

In addition to plant growth-promoting activities, bacterial pathways for the degradation of hydrocarbons contaminants suggest several important physiological events as key factors that lead to the efficient catabolism of pollutants, i.e. bioavailability, chemo-

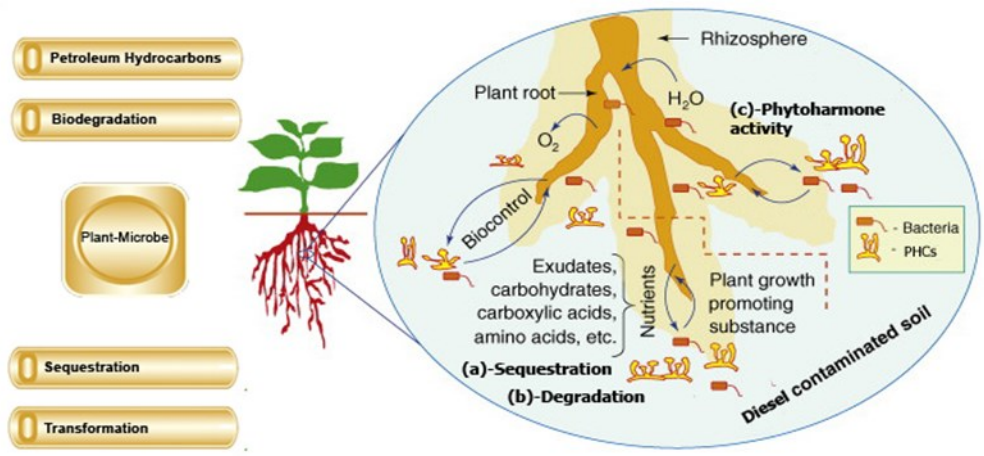


Figure 3: Plant-bacteria partnerships for the remediation of hydrocarbons contaminated soil.

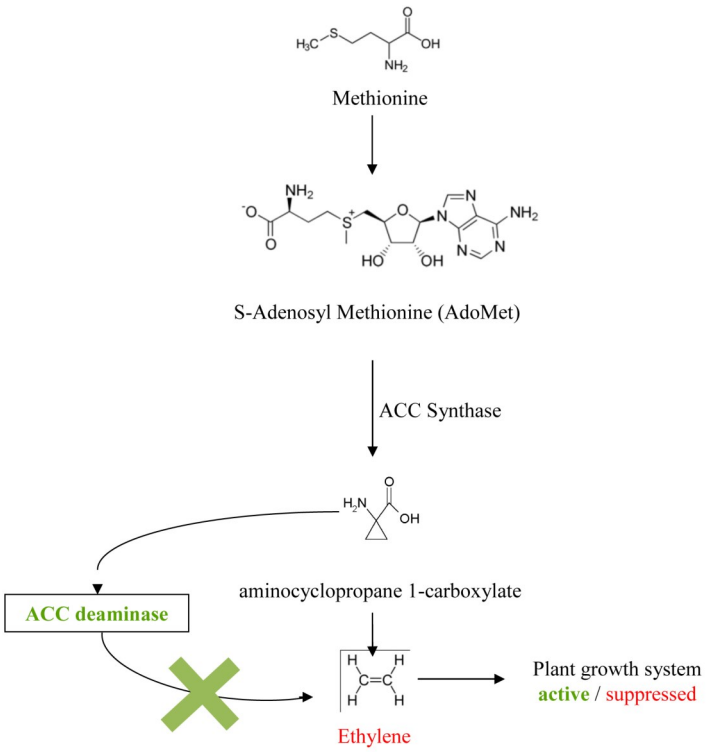


Figure 4: Mechanism of ethylene production and its effect on plant growth (Arslan et al., 2014).

taxis, organism itself moves toward contaminants and perform degradation activities (Segura et al., 2009). Degradation of hydrocarbons by bacteria takes place through complex sequence of oxidation-reduction mechanisms, which are catalyzed by set of enzymes. Aliphatic hydrocarbons are oxidized by several alkane hydroxylase enzyme systems including cytochrome P450 enzyme systems, an integral membrane mono or di-iron alkane hydroxylase (i.e. alkane monooxygenase), and soluble di-iron methane monooxygenase (sMMO) (van Beilen and Funhoff, 2007; van Beilen et al., 2006). For the reaction to take place, the compound must pass through the bacteria's cell membrane so the organism's electron transport system can be used for energy storage. Many hydrocarbons degrading bacteria such as *Pseudomonas, Micrococcus, Arthrobacter, Alcaligenes, Achromobacter, Flavobacterium, Corynebacterium Mycobacterium, Nocardia,* and *Pantoea* have been reported very efficient in degradation among all other genera (Frick et al., 1999).

Genes involved in the biodegradation of petroleum hydrocarbons

Genes involved in the degradation of contaminants are known as catabolic genes. Such genes require set of other genes for their expression and functioning such as transport genes and/or regulatory genes. It is presumed that transport genes are involved in the uptake of pollutants by microorganisms while regulatory genes play fundamental role in the expression of transport as well as catabolic genes (Díaz and Prieto, 2000). Furthermore, it has been reported that activities of catabolic genes are not because of microbial abundance having potential of pollutant degradation but due to horizontal gene transformation to soil microflora which results into high copy number of catabolic genes (Siciliano et al., 2003). Such activities, normally, depend upon different parameters like bacterial species/genera (Siciliano and Germida, 1998), adaptations of microorganisms allowing horizontal transformation of more genetic elements (Van Elsas et al., 2003), and expression of catabolic genes in the presence of contaminant which creates selective pressure for microbes (Romantschuk et al., 2000). Genes involved in degradation of PAHs are distantly related to genes of straight chain hydrocarbons in sequence homology and gene organization. Such genes are arranged in complex and scattered form through several clusters (Pinyakong et al., 2003). Availability of molecular oxygen (O_2) defines the fate of reaction that it will go either aerobic degradation pathway or anaerobic degradation pathway.

Microbial genes and enzymes involved in aerobic degradation

Expression of catabolic genes for the degradation of PHCs has been observed in aerobic as well as anaerobic conditions (Van Hamme et al., 2003). Under aerobic conditions, free molecular oxygen is available and, hence, it is incorporated into reaction by oxygenases enzyme. Monooxygenase introduce one oxygen atom while dioxygenases introduce two oxygen atoms. Aerobic catabolism of PHCs is easier and faster as compared to anaerobic catabolism because of availability of O_2 as an electron acceptor in the reaction (Cao et al., 2009).

Further degradation is followed by peripheral pathways and they convert hydrocarbons into Acetyl CoA. As we know that, Acetyl CoA is the precursor of TCA (citric acid) cycle, so this intermediate product of biodegradation enters into TCA cycle for complete breakdown. Finally, CO_2 and H_2O came out from the reaction with some inorganic minerals/elements after the result of complete aerobic biodegradation.

Oxygenases are also known as hydroxylases because of hydroxylation of one of the main substrate in the first step. This is why both terms, hydroxylase and oxygenase, are commonly used interchangeably. However, oxygenases belong to the class of oxidoreductases that catalyze the incorporation of oxygen to the substrate. For the better understanding of their functions, oxygenases are classified into two different types i.e. monooxygenases and dioxygenases. Monooxygenases are categorized into alkane monooxygenases and aromatic monooxygenases (Luz et al., 2004). Furthermore, alkane monooxygenases are classified into three different types according to the length of hydrocarbons being degraded by the action of catabolic enzymes and their source (Malkawi et al., 2009). Different types of monooxygenases genes are:

I. *alk*B monooxygenases isolated from *Pseudomonas putida* which possess ability to degrade hydrocarbons ranges between C_5 to C_{12}.

II. *alk*B1 and *alk*B2 types of monooxygenases which were isolated from *Rhodococcus* and have potential to degrade hydrocarbons ranging between C_{12} to C_{16}.

III. *alk*M monooxygenase isolated from *Acinetobacter* sp. of strain ADP-1 which can degrade hydrocarbons between C_{10} to C_{20}.

In addition to this, alkane monooxygenases can also be classified in three types depending upon their length and enzyme systems (van Beilen et al., 2007).

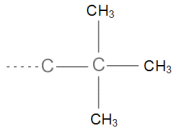
I. Methane monooxygenase like enzymes which are responsible for oxidation of methane to butane (C_1-C_4) hydrocarbons.

II. Cytochrome P450 enzyme system or integral membrane non-heme iron enzymes having potential to oxidize pentane to hexadecane (C_5-C_{16}) hydrocarbons.

III. Unknown enzyme systems which are responsible for oxidation of C_{17} or longer alkanes.

Degradation reactions take place by terminal or sub-terminal addition of oxygen by any of these enzymes system. Degradation of straight chain hydrocarbons, usually, takes place through β-oxidation. . In the first step of β-oxidation, terminal $–CH_3$ is transformed into 1-alkanol which is further converted to aldehyde or carboxylic acid. This lead to release of one $–CH_2$ ($2CO_2$ and H_2O) group and allow complete mineralization of straight chain hydrocarbons (Manahan, 2005; Watkinson and Morgan, 1991).

It is important to notify that β-oxidation of branched chain hydrocarbons is not possible because of unavailability of attacking site. Hence, they are resistant to degradation compared to straight chain hydrocarbons as illustrated in above reactions. Branching hinders the β-oxidation at the site of branch which, ultimately, doesn't facilitate the incorporation of oxygen. Presence of quaternary carbon structure as shown below always inhibits the degradation of branched hydrocarbons by β-oxidation (Manahan, 2005).



Aromatic hydrocarbons are usually degraded by dioxygenases in which dioxygenases insert both atoms of oxygen molecule (O_2) into substrate. Usually, dihydroxylation of aromatic ring is prerequisite prior to the action of dioxygenases (Dagley, 1978). Dioxygenases responsible for dihydroxylation belongs to large family of compounds known as aromatic-ring-hydroxylating dioxygenases (Butler and Mason, 1996). Monooxygenases, unlike dioxygenases, do not require dihydroxylation of aromatics as a prerequisite. By the action of dioxygenases, degradation of aromatic hydrocarbons takes place in three steps. During the first step, aromatic ring is hydroxylated and converted into hydroxylated-aromatic structures like 1, 2-dihydroxybenzene (catechol), 3,4-dihydroxybenzoic acid (Protocatechuic acid), or 2,5-dihydroxybenzoic acid (gentisic acid). The reaction takes place in aerobic microbial system which produces dihydrodiol as early byproduct of first step (Peng et al., 2008).

In the second step, hydroxylated-aromatic ring provides site of attack to dioxygenase enzymes in order to cleave the ring either by *ortho*-cleavage or *meta*-cleavage pathway and yield straight chain unsaturated aliphatic acids and aldehydes. Ring cleavage due *ortho* or *meta*-cleavage pathway is either intradiol or extradiol depending upon the catabolic genes functioning and their location on chromosomes and plasmids, respectively. In nature, catechol and protocatechuic acid are cleaved by *ortho* and *meta* cleavage pathway. However, gentisic acid is cleaved by *para*- cleavage pathway. Enzymes require Fe^{2+} as a prosthetic group. Hence, products of second step are further converted into TCA cycle intermediates and lead to biomass production (Cerniglia, 1993; Peng et al., 2008).

Cytochrome P450 alkane hydroxylase enzyme family (CYP153)

Straight chain hydrocarbons degradation is facilitated by important enzyme system known as cytochrome P450 alkane hydroxylase enzyme family (Van Beilen et al., 2006). In bacteria these enzyme are encoded by CYP153 genes (encoding class I P450s), in eukaryotic yeast and fungi they are encoded by CYP52 genes, in mammals are CYP2E and CYP4B (encoding class II P450s); substrate range for bacteria C_4-C_{16} (e.g. *Sphingomonas* sp., *Mycobacterium* sp., *Acinetobacter* sp.), substrate range for eukaryote C_{10}-C_{16} (e.g. *Candida maltose*, *Yarrowia lipolytica*), substrate range for mammals C_6–C_{10} (humans and rabbits) (van Beilen and Funhoff, 2007).

Cytochrome P450 alkane hydroxylase are very catabolic in nature when their host colonizes the plant rhizosphere. More than 4000 different enzymes are transcribed by cytochrome P450 alkane hydroxylase enzyme system of which major are reported in prokar-

yotes (10-15%). So far only few P450s enzymes have been identified and characterized.

The cytochrome P450 enzyme families are divided into two classes. Class I P450 enzymes are soluble enzymes located in the cytoplasm, and consist of 3 component systems comprising cytochrome P450, ferredoxin and ferredoxin reductase subunits. These enzymes need heme (conjugated protein) as well as iron sulfur as cofactor during catalysis. This enzyme system is found among bacteria that oxidize straight chain alkanes, alicyclic compounds and limonene, encoded by CYP153 gene family (Van Beilen and Funhoff, 2005, 2007) and is commonly found in alkane degrading bacteria that lack the integral membrane alkane hydroxylase (van Beilen et al., 2006). Class II P450s enzymes are contained in the microsome, consist of two-component systems comprising a membrane bound cytochrome P450 and a reductase, and need heme as cofactor. Enzymes encoded by genes belonging to the CYP52 family have been observed in multiple copies of many yeast strains. CYP2E1 gene, in mammals, is presumed to be involved in metabolism of xenobiotics and seems to be a key enzyme of ethanol oxidation in the microsomal pathway.

Enzyme systems work on the principle of monooxygenases and also have ability to catalyze the hydroxylation of C-H bonds, epoxidation of unsaturated bonds, oxidation of aromatic compounds, and so on. Cytochrom P450 consists of large family of cysteinatoheme enzymes with protoporphyrin-IX Iron-III as a prosthetic group which is covalently linked with sulfur atom of cysteine (Meunier, De Visser et al. 2004). Reaction takes place by addition of one atom of molecular oxygen (O_2) to substrate and other atom being reduced to water by utilizing two electrons provided by NAD(P)H. Reaction can be summarized as,

$$\text{Substrate} + O_2 + 2e^- + 2H^+ \longrightarrow \text{Oxidized Substrate} + H_2O$$

Van Beilen et al., (2007) have also proposed that these hydroxylases seems to be located over whole genome like plasmids, transposons, and chromosomes.

Microbial Genes and Enzymes Involved in Anaerobic Degradation

Although, aerobic reactions are faster than anaerobic but, still, anaerobic reactions have their own importance in environments where free oxygen is not easily available. Hence, in anaerobic condition, reaction is carried out by terminal electron acceptors (TEA). Such conditions develop in mangroves, aquifers, and sludge treatment plants (Santos et al., 2011). In the absence of oxygen, either hydrocarbons themselves act as a terminal electron acceptors or the reaction is carried out by exogenous species of electron acceptors. Benzoyl CoA is formed instead of acetyl CoA (Gibson and S. Harwood, 2002) which is attacked by benzoate CoA ligase on carboxy group and activate benzoate metabolism. Further attack of hydratase enzyme breaks ring and convert it into Acetyl CoA which enters in the TCA cycle for further degradation into CO_2, H_2O and simple inorganic compounds or elements (Schink et al., 2000).

Reductive potential of oxygen is more than exogenous terminal electron acceptors or aromatic hydrocarbons itself acting as terminal electron acceptors. Hence, the reactiondoes not take place efficiently but has its own significance in nature. Depending onthe physiochemical conditions, different electron acceptors can be used like nitrates, sulfates, iron (III) etc. in anaerobic environments (Cao et al., 2009).

Abundance and expression of catabolic genes during remediation of hydrocarbons

Survival and metabolic activities of bacteria can be illustrated in terms of gene abundance and expression in which oxidative enzymes are produced due to contaminated environment. These oxidative enzymes are actually responsible in degradation of contaminated soils (Panicker et al., 2010). Hence, degradation rate can be explained by quantifying the metagenomic RNA and DNA from soil samples respectively. Furthermore, quantification of catabolic genes has been improved by the advent of realtime PCR, metatranscriptomics, and functional gene arrays analysis (Jørgensen, 2008).

Expression of catabolic which leads to enzymatic degradation can be achieved by either aerobic or anaerobic pathway (discussed earlier). Aerobic pathways have advantage over anaerobic pathways because reaction starts with the action of oxygenases by reducing elemental oxygen and activating the rest of compound. However, in anaerobic pathways, oxygen is incorporated to the compound by other means such as organic acids are added onto hydrocarbons by the action of synthsases (Sinha et al., 2011). Expression of particular genes having degradation abilities; their maintenance; and abundance in rhizosphere are of prime importance to be considered for effective degradation purposes. Required expression of protein, the central dogma of life, for particular contaminant degrading gene is possible only when environment support the microbial colonies with their all basic needs of life. Colonies of microorganisms in contaminated soil cannot, necessarily, be there in numbers required for high rate of bioremediation. Their growth, expression, and activities must be better enough and it is only possible if rhizosphere support their survival. Studies indicate that microbes having genes for degrading abilities but with poor survival in plant rhizosphere can't give better results (Gilbertson et al., 2007; Gunderson et al., 2007). Composition, ecology, and diversity of microbial population in the rhizosphere depend on root exudates and plant species, root type, plant age, soil type, and history of soil (Afzal et al., 2011; Kaimi et al., 2007). Among all these physiochemical properties, soil type has also major effect on microbial colonization, gene expression, and petroleum hydrocarbons (PHCs) degradation (Afzal et al., 2011). Loamy soils allow more bacterial colonization as compared to sandy or loamy sand soil. It is because hydrocarbons can bind strongly with the clay minerals, hence, bioavailability for their degradation is high (Richnow et al., 1995). Also, the water holding capacity of clay minerals is high which in turn lead to high action mechanism of microbes. In contrast to this, sandy soils allow hydrocarbons degradation by adsorbing them on the surface (Löser et

et al., 1999). Finally, soil properties are important in expression of hydrcarbon degrading catabolic genes and quantification of these catabolic genes by using tools of biotechnology helps to build a clear relationship between their abundance and degradation rate (Piskonen et al., 2005). Validation of correlation with observed degradation rate in field activities is a major challenge during quantification of expressed gene (Jørgensen, 2008).

Nutrients availability, electrical conductivity, organic matter, pH, soil texture, and particle size are also important parameters affecting the survival and activity of microorganisms. Nutrients are basic building blocks of new cells and, also, allow them to produce necessary enzymes to transform and degrade contaminants. Presence of nutrients can affect the degradation rate of petroleum hydrocarbons significantly especially, nitrogen, phosphorus, potassium and sometimes iron. Nutrients act as limiting factors in degradation process (Cooney et al., 1985).

Diesel contamination increases the level of carbon; hence, nitrogen and phosphorus become limiting factors. For effective biodegradation purposes, addition of extra nutrients like nitrogen, phosphorus and potassium plays a vital role in improving the efficiency of degradation. On the other hand, higher nutrients level can also inhibit or lower the biodegradation rate as shown in (Choi et al., 2002; Kim et al., 2005). Negative effects of higher NPK level have been reported (Chaîneau, 2005; Oudot et al., 1998) especially on aromatic hydrocarbons (Carmichael and Pfaender, 1997).

Nutrients also play an important role in enhancing the cation exchange capacity of soil. Cation exchange capacity of soil not only affects the plant growth and metabolism of microbes but also improve the degradation rate of organic contaminants (Haritash and Kaushik, 2009; Jangid et al., 2008; Kaakinen et al., 2007). Nutrients have significant influence on development of microbial communities, soil colonization, subsequent survival, gene expression, and gene abundance (Kaimi et al., 2007). Role of carbon in framework of life is of building block; hence, it is required in greater amount for generation of new cell mass. Optimum ratio of carbon to nitrogen should be 10:1 and carbon to phosphorus is 30:1 (V.Sridevi, 2012).

Temperature has also significant effect on solubility of PHCs during bioremediation as it directly affects the reactivity/chemistry of pollutants and, also, diversity of microbial flora (Atlas and Bartha, 1972; Foght and Westlake, 1996). Biodegradation of PHCs is highest between 30-40 $^{\circ}$C in soil, 20-30 $^{\circ}$C in freshwater bodies, and 15-20 $^{\circ}$C in marine environments (Bossert, 1984; Cooney et al., 1985).

Besides environmental factors such as oxygen, temperature, soil physical and chemical conditions, bioavailability of the contaminant and available nutrients (Romantschuk et al., 2000), the capability to degrade hydrocarbons in soil is also influenced by other factors such as

- bacterial species dependent capability; that makes every species differ in their capability to metabolize hydrocarbons (Siciliano and Germida 1998).
- the bacterial ability to quickly distribute genetic information within a population and thereby to adapt to environmental changes (Van Elsas, Turner et al. 2003) .
- the presence of the contaminant as selective pressure to maintain their degrading capability.
- catabolic genes encoding degradation enzymes (Romantschuk, Sarand et al. 2000).

Conclusions

Exploiting plant–bacteria interactions can enhance the rate of degradation during phytoremediation of hydrocarbons contaminated soils. This can be achieved by ensuring successful colonization of hydrocarbons degrading rhizobacteria in plant-rhizosphere. Plants roots ooze out exudates which facilitate microbial survival and their metabolic activity which increases degradation rate significantly. Gene abundance and expression in plant rhizosphere reflects survival and metabolic activities of rhizobacteria, respectively. Furthermore, selection of particular species of native plants and indigenous microflora possessing catabolic genes for effective degradation is of prime importance. Hence, combined approach of using plants and their associated bacterial species seems to be a more promising towards the remediation of hydrocarbons contaminated zones compared to simple bioaugmentation (use of microorganisms) and phytoremediation (use of plants alone).

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