

# Chapter 10

## Plant-Microbiome Interactions in Hydrocarbon-Contaminated Soils



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**Abstract** The use of green remediation technologies (i.e., phytoremediation, bioremediation, mycoremediation) for the restoration of hydrocarbon-contaminated sites is one of the keys for sustainable development. These technologies rely on the joint action of biotic components of the ecosystem, namely, plants, bacteria, and fungi. Despite the fact that previous studies showed that the clean-up of hydrocarbons could be achieved individually by plants or microorganisms, present investigations suggest that the interaction of plants with their surrounding microbiome determines the outcomes of green remediation technologies. This book chapter reviews the state of the art to explain the two-way relationship established between plants and their associated microbiome in hydrocarbon-polluted soils. Special focus is put on stressing the results obtained in recent studies that employ omics approaches.

### 10.1 Introduction

Petroleum hydrocarbons (HCs) are a large family of heterogeneous organic compounds that are found in crude oil, its derived materials (e.g., diesel, gasoline, kerosene), and waste by-products, which have in common C and H atoms as their main chemical constituents. As a function of the chemical structure, four HC fractions can be separated from crude oil: saturates, aromatics, resins, and asphaltenes (SARA)

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(Aske et al. 2001). Saturated HCs are aliphatics that contain C and H joined together in saturated straight (i.e., n-alkanes), branched (i.e., paraffins), or cyclic (i.e., cycloalkanes) chains. Aromatic HCs are formed by one or more benzene rings: when two or more rings are fused, they originate polycyclic aromatic hydrocarbons (PAHs) (Abdel-Shafy and Mansour 2016). On the other hand, the fractions of resins (i.e., pyridines, quinolines, carbazoles, sulfoxides, and amides) and asphaltenes (i.e., phenols, fatty acids, ketones, esters, and porphyrins) do not have a definite structure like saturates and aromatics but a very complex constitution with the addition of heteroatoms like N, S, and O (Mullins 2008). Due to the extensive worldwide use of petroleum products, contamination with HCs is not uncommon either during the exploration, as a consequence of the generation of refinery waste by-products, or as a result of accidental spills throughout transportation and storage processes (Krahfors and Healey 2017). Indeed, petroleum-HC contamination is of great concern as it poses severe toxic effects for the whole ecosystem affecting both environmental compartments (e.g., soil, air, water bodies) and human health (Ahmed and Fakhruddin 2018; Tormoehlen et al. 2014).

Considering that environmental protection is one of the pillars of sustainable development, improving green remediation technologies appears to be a suitable approach for the restoration of HC-contaminated sites (USEPA 2008). In this sense, technologies such as bioremediation and phytoremediation are passive energy remediation systems driven by little or no external energy, which maximize remediation sustainability. Bioremediation takes advantage of heterotrophic microorganisms, which obtain the energy by the oxidation of electron donors in their environment (Abatenh et al. 2017; Singh et al. 2017). This feature can be exploited to achieve the complete mineralization of xenobiotics to non-toxic end products such as CO<sub>2</sub> and H<sub>2</sub>O (Das and Chandran 2011; Varjani 2017). Indeed, bioremediation is not limited to bacteria but extended to fungi, which contribute to pollutant removal through specific mechanisms in a distinct type of bioremediation, i.e., mycoremediation (Morelli et al. 2013; Prasad 2017, 2018). On the contrary, as phototrophic organisms, green plants use the energy from light to convert CO<sub>2</sub> and H<sub>2</sub>O into carbohydrates, and thus do not rely on HC catabolism as a source of carbon and energy to sustain their metabolic functions. Still, plants may play an important role for the remediation of HCs through phytodegradation, which can take place both inside the plant and/or within the rhizosphere zone (Newman and Reynolds 2004). Plants can either take an active part (i.e., adsorption, accumulation, degradation, and/or volatilization) in cleaning-up organic pollutants or play a secondary role sustaining rhizosphere microbial communities responsible for pollutant removal throughout rhizoremediation (Correa-García et al. 2018).

The current trend toward developing reliable and predictable green remediation technologies focuses on the application of integrative omics tools to explore and harness the microbiome of polluted soils (Bell et al. 2014b; Quiza et al. 2015). Indeed, sustaining soil microbiome diversity certainly plays a major role in HC biodegradation. For instance, Bell et al. (2014a) demonstrated that the highly diverse initial soil microbiome of a polluted soil degraded more crude oil than a more specialized but less diverse bacterial assemblage selected on crude oil media. Furthermore, the diversity of the soil microbiome is subject to the selective pressure

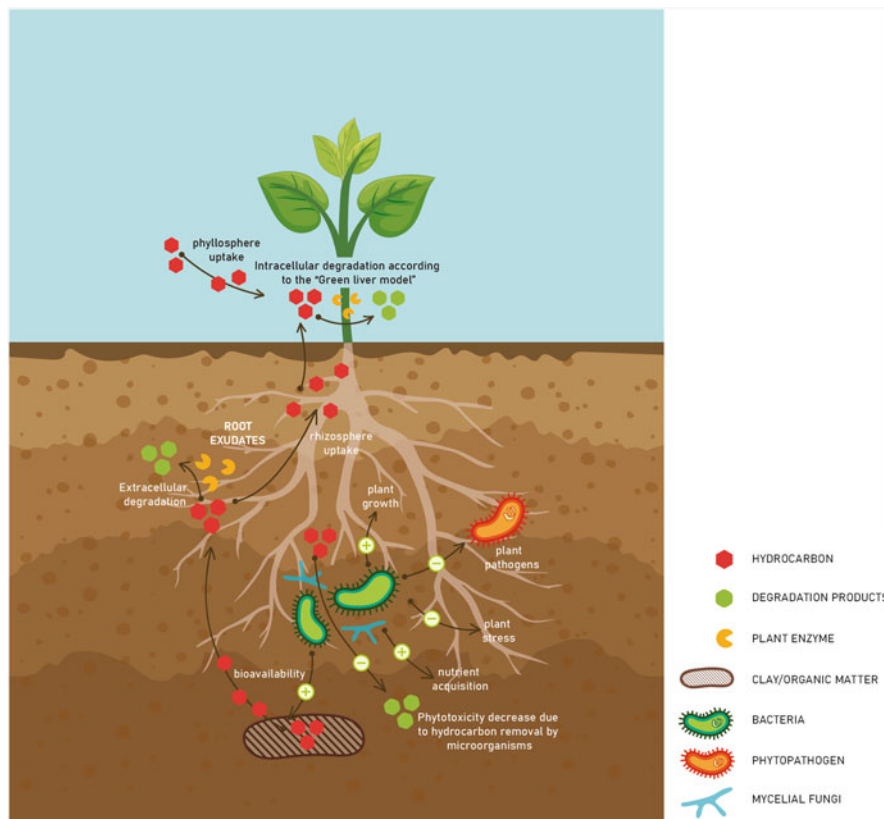
that exerts the coexistence of HCs and plants. For example, Tardif et al. (2016) observed that increasing contamination levels of petroleum HCs were related to large shifts in the microbiome composition of bulk soil, favoring HC degraders and microorganisms associated with plant health. Besides, these shifts were moderated in the plant surroundings (i.e., rhizosphere, root, and stem tissues), probably because of a more controlled and protected environment provided by plants. Although less studied than bacteria, fungi are also crucial constituents of the microbiome whose diversity is also shaped by plants and HCs. Bell et al. (2014a) observed that fungal communities were even more sensitive than bacteria to HCs and that the introduction of willows (*Salix* spp.) promoted more diverse fungal communities, which diverged based on plant phylogeny.

Plant-microbiome interactions taking place in the endosphere and rhizosphere appear to enable much of the outcomes in polluted environments in terms of plant growth and HC degradation. Therefore, this book chapter examines the interactions between plants and their associated microbiomes in HC-contaminated soils. Recent studies are gathered together to shed light on how plants contribute to HC removal and by what means they are assisted by microorganisms and, the other way round, how microorganisms (i.e., bacteria and fungi) metabolize HCs and in what way they are supported by plants to do so.

## **10.2 The Active Role of Plants in the Metabolism of Hydrocarbons and How They Are Assisted by Microorganisms**

### ***10.2.1 Uptake and Degradation of Hydrocarbons by Plants***

Although plants do not rely on an external supply of HCs for their metabolism, the uptake of these compounds can occur, taking place both in the phyllosphere and rhizosphere. HCs can volatilize (from the soil surface) to the leaf surface and be adsorbed and/or uptaken by plant leaves in the phyllosphere. Likewise, in the rhizosphere the process involves the desorption of HCs from soil followed by adsorption and/or uptake by plant roots from soil solution (Collins et al. 2006) (Fig. 10.1). Chemical properties of HCs definitely limit both plant foliar and root uptake. As the octanol-water partition coefficient ( $K_{ow}$ ) and molecular weight of HCs increase, water solubility decreases hindering the transfer of HCs across biological membranes. In addition, soil properties (e.g., clay, soil organic matter content) govern the sorption of HCs to soil. Several studies report a successfully active role of plants to uptake, translocate, and/or degrade a wide variety of HCs. For instance, *Schefflera arboricola* and *Spathiphyllum wallisii*, two ornamental plants, were able to remove benzene from indoor air (Parseh et al. 2018). Similarly, *Scirpus grossus* showed the potential to withstand diesel in contaminated water with the ability to uptake and translocate the HC series C8–C32 (Al-Baldawi et al. 2015). Finally, ornamental *Tagetes patula* and *Mirabilis jalapa* demonstrated to have good



**Fig. 10.1** Metabolism of hydrocarbons by plants and the role of microorganisms to assist them

ability to tolerate and accumulate benzo[a]pyrene from polluted soils (Sun and Zhou 2016), and PAHs were detected in alfalfa (*Medicago sativa* L.) tissues by fluorescence microscopy as well (Alves et al. 2017).

After being taken up by plants, HCs can be catabolized to non-toxic intermediates. The most accepted model that describes the metabolism of xenobiotics by plants considers plants as a 'green liver' due to the resemblance with the detoxification function of the mammalian liver. According to this model, the metabolism of xenobiotics by plants involves three steps: (1) chemical transformation through oxidation, reduction, or hydrolysis reactions, (2) conjugation to endogenous molecules (e.g., malonate, UDP-glucose, glutathione), and (3) internal compartmentalization and storage in the vacuole, incorporation into the cell wall, or excretion to the extracellular space (Sandermann 1992). For instance, *Clitoria ternatea* exhibited a high potential for airborne HC remediation. Ethylbenzene was not only taken up but also metabolized by the plant: 1-phenylethanol, acetophenone, and benzaldehyde were identified as metabolites from ethylbenzene degradation (Daudzai et al. 2018). Besides intracellular metabolism of HCs, plants may also have an active role in HC degradation via the root exudation of enzymes, which catalyze the oxidation of HCs

and degrade them into intermediate products. In support of this, Barone et al. (2016) demonstrated that water-soluble protein extracts derived from maize (*Zea mays* L.) were able to degrade PAHs as a result of peroxidase, polyphenol oxidase, and catalase activities.

### 10.2.2 Phytotoxicity of Hydrocarbons

The balance between the uptake and the degradation of HCs by plants in the pathways explained above is the key of plant tolerance/sensitivity to HCs. The phytotoxicity of HCs can be manifested as a number of symptoms such as inhibition of germination, stunting of plant development, reduced plant growth, and tissue damage (Al-Baldawi et al. 2015; Chaîneau et al. 1997; Siddiqui et al. 2001). Mechanisms underlying HC phytotoxicity may be related both to direct effects on plant physiology (e.g., cell membrane disruption, damage of photosynthetic apparatus) or, indirectly, altering the physical and chemical properties of the soil where plants are growing. Moreover, the chemical structure of HCs, its concentration and bioavailability in soil, and the plant species are among the key factors that determine the severity of phytotoxicity (Efroymson et al. 2004). A typical example of phytotoxicity was surveyed by Somtrakoon and Chouychai (2013) who observed that germination of maize and rice (*Oryza sativa* L.) seeds was retarded by single or mixed PAHs. Similarly, the study carried out by Chaîneau et al. (1997) showed that growth of maize, wheat (*Triticum aestivum* L.), and bean (*Phaseolus vulgaris* L.) was reduced by the presence of fuel oil. Interestingly, growth inhibition increased with HC concentration but was not linearly proportional to the loading rates. Another remarkable example of phytotoxicity is described by Al-Baldawi et al. (2015) who observed that direct exposure to diesel-contaminated water caused severe damage to the root and stem structures, as demonstrated by SEM micrographs of *S. grossus* epidermis and cross-sections. Besides, it is important to highlight that biotransformation of HCs can lead to additional phytotoxic metabolites. This is exemplified in the recent work undertaken by Dubrovskaya et al. (2016) who found that some of the metabolites produced as a result of microbial degradation of phenanthrene (i.e., 9,10-phenanthrenequinone, 1-hydroxy-2-naphthoic and benzoic acids) are more toxic for plants than starting PAH molecules.

Because of the toxic effects of HCs on plants, performing a phytotoxicity assessment is an initial and essential step in phytoremediation trials. Phytotoxicity tests allow finding potential candidate species able to germinate and establish in HC-contaminated sites. In this context, several species of legumes, grasses, and crops have been tested for their ability to withstand the presence of HCs (Kirk et al. 2002; Muratova et al. 2008). The outcome of these screenings showed that the species that most frequently demonstrated a good performance to tolerate HCs, in terms of high germination and growth rates, were alfalfa and ryegrass (*Lolium perenne*). As a result, these species were used later on as candidates in phytoremediation trials with promising applications for the remediation of HC-contaminated soils (Bourceret et al. 2015).

### 10.2.3 *The Role of Bacteria to Assist Plants in Hydrocarbon-Contaminated Soils*

The term plant growth-promoting bacteria (PGPB) refers to a group of bacteria that are beneficial for plant development and can be found in close association with different plant tissues (e.g., roots, shoots, leaves, or even fruits and seeds). Therefore, the habitat of PGPB might be not only the rhizosphere but also internal tissues of plants colonized by endophytes with plant growth-promoting ability (Santoyo et al. 2016; Prasad et al. 2015). PGPB act both through (1) direct mechanisms: like the synthesis of phytohormones that enhance plant growth and the release of compounds that facilitate resource acquisition and (2) indirect mechanisms such as the competition with pathogens and the modulation of plant stress (Olanrewaju et al. 2017). A significant aspect of PGPB is that they act not only under normal conditions but also under environmental stress. PGPB can assist in overcoming the detrimental phytotoxic effects caused by organic pollutants promoting the establishment of plants in HC-contaminated soils by improving plant health and growth performance. The enhancement of a prolific root system by PGPB may benefit the uptake of water and nutrients, promote the rhizosphere effect, and increase the depth of the treatment zone, which often limits the success of phytoremediation. Moreover, bacteria may help plants to cope with pollutants regulating the stress induced by HCs (Fig. 10.1). This is exemplified in the work undertaken by Singha et al. (2018) who observed that rice stress response under the influence of pyrene was modulated by PGPB. Inoculation of rice with PGPB promoted not only the growth of rice (i.e., shoot and root length) but also improved rice antioxidant activity enhancing the levels of glutathione, glutathione-S-transferase, and superoxide dismutase activities. Likewise, PGPB have also demonstrated to influence phytodegradation of pollutants. For example, the inoculation of *C. ternatea* with plant growth-promoting endophytic bacteria *Bacillus cereus* modulated the expression of plant ethylbenzene degradation genes and increased ethylbenzene removal efficiency (Daudzai et al. 2018).

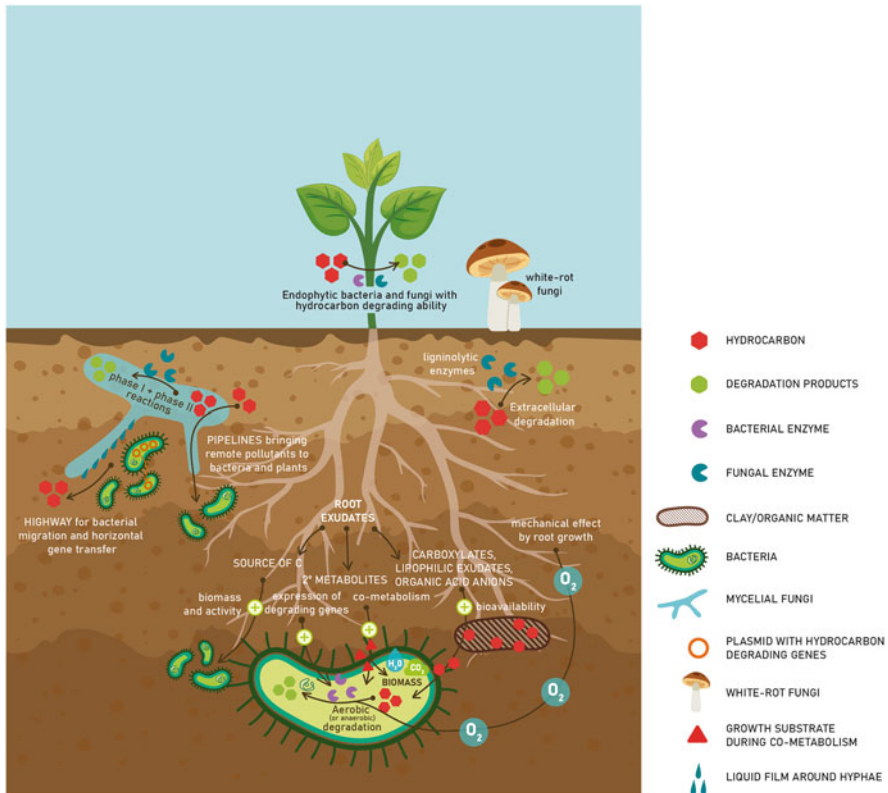
Besides the straight actions that PGPB have on plants, they can also have effects on soil pollutants. A distinct mechanism by which soil microorganisms may influence pollutant removal is the increase of HC bioavailability in the rhizosphere and plant uptake as a result. In support of this, Chen et al. (2017) observed that the inoculation of *Scirpus triqueter* with PGPB increased the amount of pyrene uptaken by the plant. Microorganisms may enhance desorption of HCs from soil by producing surface-active biomolecules termed biosurfactants. As a result of biosurfactant emulsifying action, HCs could be readily available not only for microorganisms but also for plants. In this sense, the degradation of HCs by PGPB may be a supplementary beneficial trait for plants. Bacteria being able to metabolize HCs (refer to Sect. 10.3.1) can reduce soil phytotoxicity via the effective removal of contaminants, which constitutes an additional gain for plants growing in polluted soils. In this sense, Baoune et al. (2018) isolated endophytic bacteria (*Streptomyces* genus) from roots of plants grown naturally in sandy contaminated soil that exhibited plant growth-promoting features and also could use petroleum as sole carbon and energy.

In view of the joint actions that PGPB may exhibit, Pacwa-Płociniczak et al. (2016) performed a broad screening to isolate bacteria strains that combine plant growth-promoting traits, HC-degrading ability, and biosurfactant/bioemulsifier production. Although from 42 HC-degrading isolates they could not identify a unique strain with a high performance for all the above-mentioned characteristics, they propose the application of a consortium composed of biosurfactant-producing strains together with plant growth-promoting strains as promising agents in microbe-assisted phytoremediation.

Extensive research has been conducted over the past years to develop bacteria-assisted phytoremediation as an efficient remedial strategy for petroleum HCs (Fatima et al. 2017). The key to enhance phytoremediation in this way is finding the suitable plant-bacteria partnerships, which can be accomplished through different approaches: native plant growth-promoting rhizobacteria (PGPR) (Gerhardt et al. 2015), colonizing endophytes (Syranidou et al. 2016), bioaugmentation with indigenous (Franchi et al. 2016) or allochthonous (Agnello et al. 2016) bacteria, biostimulation (Agarry et al. 2014), etc.

#### ***10.2.4 The Role of Fungi to Assist Plants in Hydrocarbon-Contaminated Soils***

The interior of plants is an important habitat where colonizing fungi reside. Plants can live in symbiosis with non-pathogenic endophytic fungi like arbuscular mycorrhizae (AM) and ectomycorrhizae. To date, a number of plant-fungal interactions have been reported in contaminated soils, which may favor plants and, in turn, its phytoremediation potential. The main mechanisms by which fungal endophytes can assist plants in HC-contaminated soils are (1) improving plant growth, (2) modulating plant stress levels, (3) enhancing the adsorption and bioaccumulation of HCs by plants, and (4) reducing phytotoxicity by the removal of HCs provided that they possess the suitable degradation pathways (refer to Sect. 10.3.1) (Deng and Cao 2017; Rajtor and Piotrowska-Seget 2016). For example, it has been observed that AM inoculation alleviated diesel toxicity on *Melilotus albus*: plants had a better growth response and higher content of microelements than non-inoculated plants. Moreover, roots of inoculated plants had higher total antioxidant and nitrate reductase activities, indicating an improved physiological response (Hernández-Ortega et al. 2012). In what concerns the influence of fungi on HC bioavailability, it has been demonstrated that AM may facilitate the mobilization of HCs in soil enabling the adsorption and/or uptake by plants (Fig. 10.2). For instance, alkane bioaccumulation in roots of wheat was more important in AM-inoculated plants than in non-inoculated plants although this process accounted for only a small portion of the total HC removal, which was mainly due to biodegradation by bacteria and fungi (Lenoir et al. 2016). The authors hypothesized that the increased HC accumulation was related to a higher lipid content and volume of the root adsorption area in the



**Fig. 10.2** Metabolism of hydrocarbons by microorganisms and the role of plants to assist them

presence of AM. In addition, the uptake of organic contaminants from soil by plants can be mediated by AM hyphae through a distinct mechanism. In a remarkable experiment using a compartmentalized cultivation system, Gao et al. (2010) observed that ryegrass (*Lolium multiflorum* Lam.) roots, which were grown in un-spiked clean soil, accumulated high concentrations of PAHs in the roots because abundant mycorrhizal hyphae extended from PAH-spiked soil, took PAHs and transported them to plants. Interestingly, AM acted as a pipeline dynamically linking soil pollutants, fungi, and plant roots. Furthermore, AM have been reported to synthesize compounds that alter HC bioavailability. This is supported by a recent study in which glomalin-related soil protein (GRSP), a *N*-linked glycoprotein produced by AM hyphae (Schindler et al. 2007), induced changes in roots that favored PAH adsorption and accumulation by ryegrass (Chen et al. 2018). Likewise, Gao et al. (2017) observed that inoculation with AM increased GRSP content and pyrene removal in soils planted with alfalfa.

The synergistic effect of plants and fungi has been used for the removal of organic contaminants in the context of microbe-assisted phytoremediation. For instance,



García-Sánchez et al. (2018) demonstrated that the combination of plants and white rot fungi (i.e., maize-*Crucibulum laeve* association) was more efficient than the individual use of plants or fungi for the treatment of aged PAH-polluted soils. Likewise, Asemoloye et al. (2017) reported that a synergistic approach that combined the joint action of guinea grass (*Megathyrsus maximus*) and rhizospheric fungi (i.e., *Aspergillus flavu*, *Aspergillus niger*, *Talaromyces purpurogenus*, and *Trichoderma harzianum*) isolated from a crude oil polluted site improved the soil nutrient content and sped up PAHs degradation rates. Finally, it is important to highlight that sole inoculation with AM may not be enough to achieve the presumed goals. Indeed, it will require the joint action of fungi and bacteria. For instance, Boldt-Burisch et al. (2018) demonstrated that mycorrhizal inoculation alone did not improve the growth of the legume *Lotus corniculatus* L. and the grass *Elymus trachycaulus* growing in oily substrates. By contrast, the inoculation with mycorrhizae plus bacteria led to a significantly positive response of both plant species.

### **10.3 The Active Role of Microorganisms in the Metabolism of Hydrocarbons and How They Are Assisted by Plants**

#### ***10.3.1 Uptake and Degradation of Hydrocarbons by Bacteria***

The metabolism of HCs by bacteria involves three fundamental steps: (1) access to the target HCs, (2) trans-membrane transport, and (3) enzymatic degradation.

Bacteria can gain access to the target HCs if they are dissolved in the aqueous phase or if small HC droplets are pseudo-solubilized (emulsified). Apart from water-soluble aromatics and short-chain HCs, most HCs are poorly soluble in water. As a result, the most common process to access them is the solubilization of little HC droplets. This can be achieved through the formation of micelles structured in the presence of biosurfactants. In contrast, large HC drops require the attachment of bacteria through direct surface contact, but this mechanism has been reported less frequently and the subsequent uptake mechanism remains poorly understood (Hua and Wang 2014). Indeed, *Sphingomonas paucimobilis* demonstrated to make phenanthrene bioavailable combining both mechanisms, i.e., the production of biosurfactants and the direct contact of cells adhering to phenanthrene crystals developing a biofilm over time (Coppotelli et al. 2010). Moreover, fungi have been suspected to facilitate bacterial access to hydrophobic substrates through direct bacterial-fungal interactions. Mycelial networks can act both as ‘highways’ that accelerate bacterial migration in the hydrophilic film around fungal hyphae as well as ‘pipelines’, which bring remote pollutants to bacteria by taking up and translocating them through their hyphae (Banitz et al. 2013; Harms and Wick 2006).

The transport of HCs across the membrane of bacteria can occur through passive diffusion and/or energy-dependent active transport, depending on HC type and

concentration (Hua and Wang 2014). While most studies are devoted to low-molecular-weight HCs, the trans-membrane transport of high-molecular-weight HCs is rarely reported. Furthermore, it has been described from Gram-negative bacteria a system of outer membrane proteins with pore-like structure and a hydrophobic channel, which facilitate the passive diffusion of small HCs from the extracellular environment to the periplasm (Hearn et al. 2008). Once internalized, there are some reports that show the formation of lipid inclusion bodies inside the cell where HCs (e.g., octadecane) are deposited before being oxidized (Hua and Wang 2012).

The most documented pathways for intracellular HC degradation by bacteria occur under aerobic conditions, where molecular oxygen is critical to initiate the enzymatic attack (Fig. 10.2). The catabolism of aliphatic HCs involves a number of oxidation steps. The first key step consists in the hydroxylation of a terminal carbon, which is catalyzed by monooxygenases (e.g., alkane 1-monooxygenase, CYP153 alkane hydroxylase). Afterwards, the hydroxylated alkane is further oxidized to the corresponding aldehyde and carboxylic acid, which in turn enter in the  $\beta$ -oxidation route of fatty acids. The final product is acetyl-CoA, which is catabolized in the Krebs cycle, and fully oxidized to CO<sub>2</sub>. The degradation of aromatic HCs requires, not only the initial hydroxylation of the aromatic ring, but also the opening of the hydroxylated aromatic ring (i.e., catechol or structurally related compounds) by aromatic-ring cleavage dioxygenases (e.g., intradiol or extradiol dioxygenases) following the ortho- or meta-cleavage of the ring. The resulting di- or trihydroxylated aromatic compounds can be introduced into the Krebs cycle and fully degraded to CO<sub>2</sub> (Das and Chandran 2011). Examples of aerobic bacteria such as *Pseudomonas*, *Alcaligenes*, *Sphingomonas*, *Rhodococcus*, and *Mycobacterium* have often been reported to degrade HCs. Indeed, biodegradation of HCs generally involves a number of different bacterial species within a consortium of microbes with broad enzymatic capacities rather than individual organisms (Santisi et al. 2015; Zafra et al. 2017). Recent studies demonstrate that functional bacterial communities co-acclimate to a changing environment of HC stress and are able to conduct biodegradation of HCs in a cooperative way creating interactive networks with each other (Wanapaisan et al. 2018; Wang et al. 2016).

Although the fastest and most complete degradation of HCs is performed in the presence of O<sub>2</sub>, degradation of HCs is also possible under anaerobic conditions, but these pathways are less studied. Examples of such anaerobic reactions are the addition of toluene or *n*-alkanes to fumarate, the O<sub>2</sub>-independent hydroxylation of ethylbenzene, and the reductive dearomatization of benzoyl-CoA (Rabus et al. 2016). In anaerobic and methanogenic environments, where HCs are biodegraded to methane, mutually beneficial interactions between syntrophic microorganisms play a key role. This implies that a cooperative action of mixed microbial populations is required for the ultimate removal of HCs (Gieg et al. 2014). Considering that O<sub>2</sub> is replenished in the rhizosphere by O<sub>2</sub> diffusion as a function of water/air-filled porosity, the anaerobic pathway is supposed to be less relevant than the aerobic route in the rhizosphere (Uteau et al. 2015).

Some key genes involved in HC degradation can be located on mobile elements. Moreover, the homology of DNA sequences and organization of degrading genes carried by conjugative plasmids may be indicators that horizontal gene transfers can occur between HC-degrading bacteria during microbial adaptation to xenobiotics (Abbasian et al. 2016). This is supported by *in silico* analysis, which demonstrated that HC-degrading genes *alkB* and *catA* can be subjected to horizontal transfer events among bacterial communities spreading the potential to degrade HCs (Rodrigues et al. 2018). In an interesting study, Taghavi et al. (2005) reported for the first time in planta horizontal gene transfer among plant-associated endophytic bacteria. They inoculated poplars with the endophyte *Burkholderia cepacia*, which contained a plasmid coding for toluene degradation. They observed that although the inoculated endophyte could not establish in the endophytic community, there was horizontal gene transfer of toluene degrading ability to different members of the endogenous endophytic community. Moreover, bacterial horizontal gene transfer can be facilitated by the network structures of mycelia. As described above, liquid films around hyphae constitute a continuous highway in which bacterial migration and contacts are favored (Berthold et al. 2016).

### 10.3.2 Degradation of Hydrocarbons by Fungi

Fungi are able to degrade HC both in an assimilative way to obtain energy and in a non-assimilative way through detoxification and co-metabolism pathways (Morelli et al. 2013). Fungi can be classified into ligninolytic and non-ligninolytic according to their ability to metabolize lignin in wood, and both types of fungi have a part in the degradation of PAHs (Aydin et al. 2017) (Fig. 10.2).

Major constituents of ligninolytic fungi are the white-rot fungi (WRF), i.e., wood-decaying basidiomycetes. Ligninolytic fungi are characterized for their ability to produce extracellular enzymes, which are responsible for the complete degradation of lignin. Ligninolytic enzymes encompass a vast array of enzymes such as peroxidases (e.g., lignin, manganese, and versatile peroxidases), laccases, and accessory enzymes ( $H_2O_2$ -generating enzymes and glyoxal oxidase). A key characteristic of the complex ligninolytic enzymatic system is low substrate specificity. As a result, this feature can be exploited to extend the degrading ability of ligninolytic enzymes to break down other complex compounds (Kadri et al. 2017). This is exemplified in the work undertaken by Pozdnyakova et al. (2018) who studied the degradation of three-ringed PAHs by the white-rot fungus *Pleurotus ostreatus* and the litter-decomposing fungi *Agaricus bisporus*, demonstrating that the extracellular enzyme system of ligninolytic fungi plays a key role in the initial attack of PAH molecules yielding quinone metabolites. The degrading ability of ligninolytic fungi clearly represents a promising option for the bioremediation of HCs in soil. This is supported by a recent study performed by Košnář et al. (2018) that compared the removal of PAHs in soil after different bioremediation approaches in relation to extracellular enzyme

activities. They observed that mycoremediation treatment with *P. ostreatus* outperformed natural attenuation and phytoremediation in terms of PAHs removal from soil.

The main weakness of WRF application for bioremediation is that they only grow under specific environmental conditions (e.g., on compact wood rich in lignocellulosic substrates, at acidic pH), which renders them inefficient to compete with non-ligninolytic fungi in soil and limits their contribution in the decomposition of HCs under natural conditions. In this sense, previous studies have demonstrated that it is possible to isolate non-ligninolytic fungi (mainly belonging to the *Ascomycota* and *Zygomycota* phylum) from contaminated sites (Reyes-César et al. 2014). Likewise, highly diverse AM communities demonstrated to be able to colonize plants growing in weathered oil ponds indicating that AM are able to adapt to these harsh conditions (Garcés-Ruiz et al. 2017). This is particularly interesting because this kind of fungi exhibit tolerance to environmental pollutants as well as potential for their enzymatic transformation. The enzymatic transformation of HCs by non-ligninolytic fungi is typically slower than for ligninolytic fungi, and although is not fully understood, it is believed to use phase I (e.g., P450s and epoxide hydrolases) and phase II (e.g., glutathione S-transferases, NAD(P)H: quinone oxidoreductases and UDP-glucuronosyl transferases) intracellular enzymes (Marco-Urrea et al. 2015). These degradative pathways catalyze xenobiotic biotransformation and detoxification in most eukaryotes, thus being extensive to ligninolytic fungi too. Intracellular fungal degradation is exemplified in the study undertaken by Aranda et al. (2017) in which the *Ascomycota* fungi *Penicillium oxalicum* was found to exhibit a high and fast PAH degradation capability. *P. oxalicum* degradation of both anthracene and dibenzothiophene was mediated at the intracellular level by cytochrome P450 enzymes (CYPs). Indeed, the use of  $^{13}\text{C}$ -anthracene enabled the identification of oxidized and hydroxylated derivatives, which are known as Phase I metabolites produced through CYP transformation. Additionally, this work highlighted that the presence of glucose was required to proceed with anthracene degradation, suggesting that fungi may not be able to use PAHs as a sole C and energy supply and may require additional C sources to co-metabolize xenobiotic compounds.

### 10.3.3 *The Role of Plants in Assisting Hydrocarbon Uptake/Degradation by Microorganisms*

Plants have a secondary supportive role in HC removal, both in the rhizosphere and endosphere, improving HC uptake/degradation by microorganisms through different mechanisms (Fig. 10.2).

The degradation of HCs by soil microorganisms is noteworthy under the root influence because of the *rhizosphere effect* to which the root surrounding microbiome is subject to. The rhizosphere effect is used to depict that, in comparison with bulk soil, the biomass and activity of microorganisms in the rhizosphere are enhanced (Warembourg 1997). This is the result of various processes driven by

plants, but the most significant is probably root exudation (Rohrbacher and St-Arnaud 2016). Root exudates consist of a vast array of metabolites (e.g., organic, amino, and fatty acids, sugars, vitamins, nucleotides, flavonoids, phytohormones, etc.) released by plant roots to the surrounding media, many of which can be used as substrates for microbial metabolism leading to increased microbial biomass and/or activity. Moreover, the root architecture also shapes the rhizosphere microbiome by physical processes. The mechanical effect of growing roots comes with soil aeration, which influences the distribution of rhizosphere microorganisms, the concentration of O<sub>2</sub>, and thus aerobic metabolism of HCs (van Dam and Bouwmeester 2016). Rhizodegradation takes advantage of the rhizosphere effect to achieve the removal of HCs in the rhizosphere by stimulating HC-degrader populations. This is evidenced in the study of Bourceret et al. (2018) that, using culture-independent methods, demonstrated that Gram-negative PAH-dioxygenase genes and transcripts were higher in the planted (alfalfa) than unplanted soil and were positively correlated to PAH degradation. Along with the enhancement of microbial biomass and/or activity of HC-degrading bacteria, root exudates can also promote HC biodegradation as a result of increasing HC bioavailability. Root-induced chemical changes in the rhizosphere by the release of organic anions (e.g., citrate, oxalate) contributes to HC desorption from the soil (e.g., organic matter and clay particles), improving the accessibility of degrading bacteria to HCs (Martin et al. 2014). This can be illustrated by a batch experiment showing that low-molecular-weight organic acids in aqueous solution could disrupt soil organic matter (SOM)-metal cation-mineral linkages in soils, resulting in the release of SOM from soil and simultaneous increase of dissolved organic carbon (DOC) in solution. The loss of SOM from soil and increase of DOC in solution were responsible for the enhanced PAH desorption from soil (Ling et al. 2015).

The so-called ‘secondary compound hypothesis’ states that plant secondary metabolites released into the rhizosphere can trigger the biodegradation of environmental pollutants. This may be explained by the fact that plant secondary metabolites can induce the expression of degradative genes or serve as primary substrates during the co-metabolism of HCs (Musilova et al. 2016). In support of the first mechanism, Yergeau et al. (2014) and Pagé et al. (2015) demonstrated through a metatranscriptomic approach an induced expression of several aliphatic- and aromatic-degrading genes in the rhizosphere of willows (*Salix purpurea*) growing in HC-contaminated soils as compared to bulk soils. The authors hypothesize that the secondary metabolite salicylate released by willows could mediate this process, as it has been reported to induce the transcription of PAH-degrading genes. Regarding the second mechanism, Rentz et al. (2005) corroborated that benzo[a]pyrene was removed from solution by *Sphingomonas yanoikuyae* while growing on root products as a primary carbon and energy source. This confirms the hypothesis that co-metabolism of xenobiotics, i.e., the transformation of a non-growth substrate (i.e., benzo[a]pyrene) in the obligate presence of a growth substrate (i.e., root extracts), can take place in the rhizosphere (Crowley et al. 2001; Dalton and Stirling 1982).

In addition to the processes taking place in the rhizosphere, it is important to take into consideration the endosphere as well. The endosphere is the interior of the plant

that functions as a microbial habitat of endophytes where plants provide shelter and protection. Endophytic bacteria like those associated with *L. corniculatus* L. and *Oenothera biennis* L. collected in a long-term petroleum HC-polluted site have been shown to possess HC-degrading genes such as P450 gene, which encodes for cytochrome P450-type alkane hydroxylase (Pawlik et al. 2017). This confirms the importance of plants as the residence of endophytic bacteria with HC-degrading ability and thus with a high potential to improve phytoremediation of petroleum HCs. Moreover, plants can host fungi as well. In this sense, Fu et al. (2018) were able to demonstrate the biodegradation of phenanthrene by endophytic fungus *Phomopsis liquidambari* not only in vitro in liquid culture but also in vivo using rice seedlings.

## 10.4 The Construction of the Holobiont Concept Through Omics Approaches

The current trend toward developing reliable and predictable green remediation technologies puts the focus on the application of integrative omics tools to explore and harness the microbiome of polluted soils in order to fill in present knowledge gaps (Bell et al. 2014b; Quiza et al. 2015). In this sense, omics approaches are definitely enabling a deeper understanding of the complex relationships in the microbial network under the plant influence and subjected to HC stress (Table 10.1). For instance, metagenomics enables the prediction of the HC-degrading potential of rhizosphere microbial communities, metatranscriptomics can reveal the actual expression of HC-degrading genes under the plant influence, and metaproteomics/metabolomics makes possible the identification of the complete metabolic intermediates during HC degradation as well as the myriad of compounds released by root exudates. As a consequence, the use of such innovative technology platforms allows proposing new degradative pathways beyond the individual plant, bacterial, or fungal levels. Indeed, present research intends to understand not only how plants influence degrading microbial communities in the rhizosphere but also how they interplay as a metaorganism or holobiont (i.e., host and microbiome together) to degrade complex pollutants (El Amrani et al. 2015). Based on the latest evidence from the metagenomics level, Thijs et al. (2016) have recently proposed a competition-driven model to explain the establishment of a catabolic rhizosphere microbiome in contaminated soil. Furthermore, Yergeau et al. (2018) highlight the importance of considering plants and their associated microbiota as an ‘interactome’. Performing simultaneous analysis of root and rhizosphere metatranscriptomes they found that plants and their associated microorganisms undergo a complete overhaul under HC stress modulating transcript abundances. Indeed, Gonzalez et al. (2018) conducted a complex metatranscriptomic study taking into consideration the entire microbiome and concluded that trees, fungi, and bacteria establish a tripartite mutualism in HC-polluted soils. They observed that while root and fungal expression patterns

**Table 10.1** Summary of 'multi-omics'-based approaches to understand the role of the microbiome in hydrocarbon-contaminated (rhizosphere) soils

Type of omic-based approach	Technique	Brief description	Application	Example reference
Metagenomics	Amplicon sequencing	Next-generation sequencing of marker genes (typically the 16S rRNA gene and the ITS region), which are amplified from metagenomic DNA	Identify the composition and diversity of HC-contaminated soil's microbial community	Cecotti et al. (2018)
	Functional metagenomics	Large DNA fragments are inserted in vectors (e.g., cosmids, fosmids) and expressed in hosts (e.g., <i>Escherichia coli</i> ) which are then screened for a particular function. Clones showing the desired activity are sequenced	Identify genes coding for specific functions (e.g., HC degrading genes such as alkB, nahAc, etc.) in the microbial community and link the function with the taxa responsible for it	Duarte et al. (2017)
	Shotgun metagenomics	Metagenomic DNA is sheared and sequenced. Both functions and taxonomy are derived from homology search in databases	Identify the microbial community composition, diversity, and functions in HC-contaminated soils (e.g., bioprospection of HC-degrading genes)	Vigneron et al. (2017)
	DNA or RNA SIP	A labeled substrate is used to feed a microbial community. Labeled (heavy) DNA or RNA is retrieved through centrifugation of nucleic acids in a density gradient. The labeled DNA or RNA is then sequenced directly or amplified to sequence marker genes	In combination with 16S rRNA gene amplicon sequencing it is possible to link taxonomic group identity to the metabolism of the substrate. This is particularly useful to study degradation of C-13 labeled HCs (e.g., C13-naphthalene)	Jiang et al. (2015)
Metatranscriptomics	Amplicon sequencing	Next-generation sequencing of marker genes (typically the 16S rRNA gene and the ITS region), which are amplified from cDNA retro-transcribed from total extracted RNA	Identify the composition and diversity of functionally active fraction of microflora in HC-contaminated soils	Bourceret et al. (2018)
	RNA-seq or whole-transcriptome shotgun sequencing	Sequencing of RNA: Not only mRNA transcripts but also miRNA, tRNA and rRNA	Microbial expression analysis of functionally active fraction of microflora in HC-contaminated soils. This represents accurately the activity and can provide a clue to the taxonomic groups that actively contribute to biodegradation and metabolism of HCs	Yergeau et al. (2018)

(continued)

Table 10.1 (continued)

Type of omic-based approach	Technique	Brief description	Application	Example reference
Metaproteomics	Electrophoresis and/or chromatography combined with chemical or metabolic labelling and MS	Gel-based (e.g., 2D-PAGE) or gel-free (e.g., nano-LC) approaches for protein separation coupled to protein identification by MS techniques (e.g., MALDI-TOF)	Identification of differential expression of proteins/enzymes involved in HC metabolism (alkB, nahAc, etc)	Festa et al. (2017)
Metabolomics	LC-MS GC-MS GC/LC-TOF-MS <sup>1</sup> H-NMR	Identification of different metabolites. Depending on their chemical properties (e.g., volatility, polarity, etc.) different types of metabolomics platforms are used	Study metabolic pathways of HC biodegradation: The presence of microbial metabolites can be considered as the ‘ultimate proof’ that a biochemical reaction has occurred. Analysis of metabolites in root exudates and changes in the root exudation patterns triggered by HCs in soils	Tian et al. (2018)

Abbreviations: *HC* hydrocarbons, *SIP* stable-isotope probing, *MS* mass spectrometry, *2D-PAGE* two-dimensional polyacrylamide gel electrophoresis, *LC* liquid chromatography, *GC* gas chromatography, *TOF* time-of-flight, <sup>1</sup>*H-NMR* nuclear magnetic resonance, *MALDI* matrix-assisted laser desorption/ionization nahAc gene coding for naphthalene 1,2-dioxygenase subunit alpha. alkB gene coding for alkane 1-monoxygenase enzyme



responded to HC stress altering pathways associated to microbiome interactions, the apparatus necessary for the direct reduction of contamination stress came from bacteria. These results highlight how crucial it is to investigate the expression of the entire microbiome to have a full picture of the metaorganism responding to soil contamination.

## 10.5 Conclusion and Future Prospects

The evidence reviewed here supports the concept of a conjoint action of plants, bacteria, and fungi building an inseparable and highly dependent relationship. The particular approach of analyzing the contribution of plants to soil HC degradation with the assistance of soil microorganisms and, conversely, how the soil microorganisms could improve their degrading ability with the support of plants revealed a broad perspective of the multiple and diverse interactions that take place between plants and their associated microbiome. Moreover, it becomes manifest how the limitations of one actor could be overwhelmed by the abilities of the other. This leads to the accomplishment of a robust establishment in polluted soils and an effective HC degradation by the metaorganism or holobiont. In this sense, the current state of the art by means of a diffuse application of mixed omics approaches strengthens the idea that an integrated understanding of the relationships between plants, bacteria, and fungi determines the success of green remediation technologies. Furthermore, it is insinuated that green remediation is facing an auspicious transition moving from individual bio-, myco-, phyto-remediation toward the development of an integrative meta/holo-remediation notion.

**Acknowledgments** This review was supported by grant PICT-2016-0947. The authors would like to thank Dr. Sabrina Festa for proofreading the chapter. In addition, the authors are very grateful to industrial designer Carla Di Benedetto, who provided the expertise to create the illustrations presented in Figs. 10.1 and 10.2.

## Glossary

**Endophyte** Microorganism residing within plant tissues (the endosphere). They may establish different types of interactions (e.g, mutualistic, pathogenic) with their plant hosts. For instance, they may improve the plant's ability to tolerate hydrocarbon stress

**Endosphere** Interior of the plant as a microbial habitat of endophytes. The term may refer to either the aerial (i.e., stems, leaves) and/or root components of a plant

**Metaorganism/Holobiont** Plant and its associated microorganisms

**Microbiome** Totality of microorganisms inhabiting a particular environment. For example, the rhizosphere microbiome refers to all microorganisms inhabiting the rhizosphere of a particular plant. The microbiome is a dynamic ecosystem driven by environmental changes (e.g., plant species, soil type, presence of pollutants, etc.)

**Multi-omics Approach** Combination of methods that use innovative technology platforms such as genomics, transcriptomics, proteomics, and metabolomics. Omics approaches typically generate large datasets to provide insight of genes, transcripts, proteins, and metabolites of a biological system. The prefix ‘meta’ is used when performed on all members of a mixed-species community as opposed to a single organism

**Mycoremediation** The use of fungi for soil remediation applications

**Phyllosphere** Surface area of the aerial portions of plants

**Phytodegradation** Breakdown of organic contaminants by plants through metabolic processes that occur within the plant; or through the effect of compounds, such as enzymes, produced by the plant

**Rhizoremediation** Degradation of pollutants by soil microorganisms, which are under the rhizosphere effect

**Rhizosphere** Zone in the soil under the direct influence of plant roots. This includes not only the surface of the roots (rhizoplane) but also any external region that is affected by root exudates

**Rhizosphere Effect** Phenomenon describing that in comparison with bulk soil, the biomass and activity of microorganisms in the rhizosphere are enhanced as a result of different mechanisms driven by plants (mainly root exudation)

**Root Exudates** Set of compounds (e.g., flavonoids, fatty acids, organic acids, aminoacids) produced by plants and secreted by roots into the soil or any other medium surrounding the roots. These molecules can be actively or passively released by plant roots. Root exudation patterns change under the influence of the plant (e.g., cultivar, plant species, developmental stage), environmental factors (e.g., soil type, pH, temperature, nutrient availability), and the presence of microorganisms.

## References

- Abatenh E, Gizaw B, Tsegaye Z, Wassie M (2017) The role of microorganisms in bioremediation: a review. *Open J Environ Biol* 2:38–46. <https://doi.org/10.17352/ojeb.000007>
- Abbasian F, Lockington R, Megharaj M, Naidu R (2016) A review on the genetics of aliphatic and aromatic hydrocarbon degradation. *Appl Biochem Biotechnol* 178:224–250. <https://doi.org/10.1007/s12010-015-1881-y>
- Abdel-Shafy HI, Mansour MSM (2016) A review on polycyclic aromatic hydrocarbons: source, environmental impact, effect on human health and remediation. *Egypt J Pet* 25:107–123. <https://doi.org/10.1016/j.ejpe.2015.03.011>

- Agarry SE, Aremu MO, Aworanti OA (2014) Biostimulation and phytoremediation treatment strategies of gasoline-nickel co-contaminated soil. *Soil Sediment Contam* 23:227–244. <https://doi.org/10.1080/15320383.2014.812612>
- Agnello AC, Bagard M, van Hullebusch ED, Esposito G, Huguenot D (2016) Comparative bioremediation of heavy metals and petroleum hydrocarbons co-contaminated soil by natural attenuation, phytoremediation, bioaugmentation and bioaugmentation-assisted phytoremediation. *Sci Total Environ* 563–564:693–703. <https://doi.org/10.1016/j.scitotenv.2015.10.061>
- Ahmed F, Fakhruddin ANM (2018) A review on environmental contamination of petroleum hydrocarbons and its biodegradation. *Int J Environ Sci Nat Resour* 11:1–7. <https://doi.org/10.19080/IJESNR.2018.11.555811>
- Al-Baldawi IA, Abdullah SRS, Anuar N, Suja F, Mushrifah I (2015) Phytodegradation of total petroleum hydrocarbon (TPH) in diesel-contaminated water using *Scirpus grossus*. *Ecol Eng* 74:463–473. <https://doi.org/10.1016/j.ecoleng.2014.11.007>
- Alves WS, Manoel EA, Santos NS, Nunes RO, Domiciano GC, Soares MR (2017) Detection of polycyclic aromatic hydrocarbons (PAHs) in *Medicago sativa* L. by fluorescence microscopy. *Micron* 95:23–30. <https://doi.org/10.1016/j.micron.2017.01.004>
- Aranda E, Godoy P, Reina R, Badia-Fabregat M, Rosell M, Marco-Urrea E, García-Romera I (2017) Isolation of *Ascomycota* fungi with capability to transform PAHs: insights into the biodegradation mechanisms of *Penicillium oxalicum*. *Int Biodeterior Biodegrad* 122:141–150. <https://doi.org/10.1016/j.ibiod.2017.05.015>
- Asemoloye MD, Ahmad R, Jonathan SG (2017) Synergistic action of rhizospheric fungi with *Megathyrus maximus* root speeds up hydrocarbon degradation kinetics in oil polluted soil. *Chemosphere* 187:1–10. <https://doi.org/10.1016/j.chemosphere.2017.07.158>
- Aske N, Kallevik H, Sjöblom J (2001) Determination of saturate, aromatic, resin, and asphaltenic (SARA) components in crude oils by means of infrared and near-infrared spectroscopy. *Energy Fuels* 15:1304–1312. <https://doi.org/10.1021/ef010088h>
- Aydin S, Karaçay HA, Shahi A, Gökçe S, Ince B, Ince O (2017) Aerobic and anaerobic fungal metabolism and Omics insights for increasing polycyclic aromatic hydrocarbons biodegradation. *Fungal Biol Rev* 31:61–72. <https://doi.org/10.1016/j.fbr.2016.12.001>
- Banitz T, Johst K, Wick LY, Schamfuß S, Harms H, Frank K (2013) Highways versus pipelines: contributions of two fungal transport mechanisms to efficient bioremediation. *Environ Microbiol Rep* 5:211–218. <https://doi.org/10.1111/1758-2229.12002>
- Baoune H, Ould El Hadj-Khelil A, Pucci G, Sineli P, Loucif L, Polti MA (2018) Petroleum degradation by endophytic *Streptomyces* spp. isolated from plants grown in contaminated soil of southern Algeria. *Ecotoxicol Environ Saf* 147:602–609. <https://doi.org/10.1016/j.ecoenv.2017.09.013>
- Barone R, de Biasi MG, Piccialli V, de Napoli L, Oliviero G, Borbone N, Piccialli G (2016) Degradation of some representative polycyclic aromatic hydrocarbons by the water-soluble protein extracts from *Zea mays* L. cv PR32-B10. *Chemosphere* 160:258–265. <https://doi.org/10.1016/j.chemosphere.2016.06.069>
- Bell TH, El-Din Hassan S, Lauron-Moreau A, Al-Otaibi F, Hijri M, Yergeau E, St-Arnaud M (2014a) Linkage between bacterial and fungal rhizosphere communities in hydrocarbon-contaminated soils is related to plant phylogeny. *ISME J* 8:331–343. <https://doi.org/10.1038/ismej.2013.149>
- Bell TH, Joly S, Pitre FE, Yergeau E (2014b) Increasing phytoremediation efficiency and reliability using novel omics approaches. *Trends Biotechnol* 32:271–280. <https://doi.org/10.1016/j.tibtech.2014.02.008>
- Berthold T, Centler F, Hübschmann T, Remer R, Thullner M, Harms H, Wick LY (2016) Mycelia as a focal point for horizontal gene transfer among soil bacteria. *Sci Rep* 6:1–8. <https://doi.org/10.1038/srep36390>
- Boldt-Burisch K, Naeth MA, Schneider U, Schneider B, Hüttl RF (2018) Plant growth and arbuscular mycorrhizae development in oil sands processing by-products. *Sci Total Environ* 621:30–39. <https://doi.org/10.1016/j.scitotenv.2017.11.188>

- Bourceret A, Leyval C, de Fouquet C, Cébron A (2015) Mapping the centimeter-scale spatial variability of PAHs and microbial populations in the Rhizosphere of two plants. *PLoS One* 10: e0142851. <https://doi.org/10.1371/journal.pone.0142851>
- Bourceret A, Leyval C, Faure P, Lorgeoux C, Cébron A (2018) High PAH degradation and activity of degrading bacteria during alfalfa growth where a contrasted active community developed in comparison to unplanted soil. *Environ Sci Pollut Res* 25(29):29556–29571. <https://doi.org/10.1007/s11356-018-2744-1>
- Cecotti M, Coppotelli BM, Mora VC, Viera M, Morelli IS (2018) Efficiency of surfactant-enhanced bioremediation of aged polycyclic aromatic hydrocarbon-contaminated soil: link with bioavailability and the dynamics of the bacterial community. *Sci Total Environ* 634:224–234. <https://doi.org/10.1016/j.scitotenv.2018.03.303>
- Chaîneau CH, Morel JL, Oudot J (1997) Phytotoxicity and plant uptake of fuel oil hydrocarbons. *J Environ Qual* 26:1478–1483. <https://doi.org/10.2134/jeq1997.00472425002600060005x>
- Chen X, Liu X, Zhang X, Cao L, Hu X (2017) Phytoremediation effect of *Scirpus triquetter* inoculated plant-growth-promoting bacteria (PGPB) on different fractions of pyrene and Ni in co-contaminated soils. *J Hazard Mater* 325:319–326. <https://doi.org/10.1016/j.jhazmat.2016.12.009>
- Chen S, Wang J, Waigi MG, Gao Y (2018) Glomalin-related soil protein influences the accumulation of polycyclic aromatic hydrocarbons by plant roots. *Sci Total Environ* 644:465–473. <https://doi.org/10.1016/j.scitotenv.2018.06.370>
- Collins CD, Martin I, Fryer M (2006) Evaluation of models for predicting plant uptake of chemicals from soil. Science Report – SC050021/SR 1, Environment Agency
- Coppotelli BM, Ibarrolaza A, Dias RL, Del Panno MT, Berthe-Corti L, Morelli IS (2010) Study of the degradation activity and the strategies to promote the bioavailability of phenanthrene by *Sphingomonas paucimobilis* strain 20006FA. *Microb Ecol* 59:266–276. <https://doi.org/10.1007/s00248-009-9563-3>
- Correa-García S, Pande P, Séguin A, St-Arnaud M, Yergeau E (2018) Rhizoremediation of petroleum hydrocarbons: a model system for plant microbiome manipulation. *Microb Biotechnol* 11:819–832. <https://doi.org/10.1111/1751-7915.13303>
- Crowley DE, Luepromechai E, Singer AC (2001) Metabolism of Xenobiotics in the Rhizosphere. In: Hall JC, Hoagland RE, Zablutowicz RM (eds) *Pesticide biotransformation in plants and microorganisms: similarities and divergences*, ACS symposium series, vol 777. American Chemical Society, Washington, DC, pp 333–352. <https://doi.org/10.1021/bk-2001-0777.ch018>
- Dalton H, Stirling DI (1982) Co-metabolism. *Philos Trans R Soc Lond Ser B Biol Sci* 297:481–496. <https://doi.org/10.1098/rstb.1982.0056>
- Das N, Chandran P (2011) Microbial degradation of petroleum hydrocarbon contaminants : an overview. *Biotechnol Res Int* 2011:1–13. <https://doi.org/10.4061/2011/941810>
- Daudzai Z, Thiravetyan P, Treesubstorn C (2018) Inoculated *Clitoria ternatea* with *Bacillus cereus* ERBP for enhancing gaseous ethylbenzene phytoremediation: plant metabolites and expression of ethylbenzene degradation genes. *Ecotoxicol Environ Saf* 164:50–60. <https://doi.org/10.1016/j.ecoenv.2018.07.121>
- Deng Z, Cao L (2017) Fungal endophytes and their interactions with plants in phytoremediation: a review. *Chemosphere* 168:1100–1106. <https://doi.org/10.1016/j.chemosphere.2016.10.097>
- Duarte M, Nielsen A, Camarinha-Silva A, Vilchez-Vargas R, Bruls T, Wos-Oxley ML, Jauregui R, Pieper DH (2017) Functional soil metagenomics: elucidation of polycyclic aromatic hydrocarbon degradation potential following 12 years of in situ bioremediation. *Environ Microbiol* 19:2992–3011. <https://doi.org/10.1111/1462-2920.13756>
- Dubrovskaya EV, Pozdnyakova NN, Muratova AY, Turkovskaya OV (2016) Changes in phytotoxicity of polycyclic aromatic hydrocarbons in the course of microbial degradation. *Russ J Plant Physiol* 63:172–179. <https://doi.org/10.1134/S1021443716010052>
- Efroymsen RA, Sample BE, Peterson MJ (2004) Ecotoxicity test data for total petroleum hydrocarbons in soil: plants and soil-dwelling invertebrates. *Hum Ecol Risk Assess* 10:207–231. <https://doi.org/10.1080/10807030490438175>

- El Amrani A, Dumas AS, Wick LY, Yergeau E, Berthomé R (2015) 'Omics' insights into PAH degradation toward improved green remediation biotechnologies. *Environ Sci Technol* 49:11281–11291. <https://doi.org/10.1021/acs.est.5b01740>
- Fatima K, Imran A, Naveed M, Afzal M (2017) Plant-bacteria synergism: an innovative approach for the remediation of crude oil-contaminated soils. *Soil Environ* 36:93–113. <https://doi.org/10.25252/SE/17/51346>
- Festa S, Coppotelli BM, Madueño L, Loviso CL, Macchi M, Neme Tauli RM, Valacco MP, Morelli IS (2017) Assigning ecological roles to the populations belonging to a phenanthrene-degrading bacterial consortium using omic approaches. *PLoS One* 12:1–21. <https://doi.org/10.1371/journal.pone.0184505>
- Franchi E, Agazzi G, Rolli E, Borin S, Marasco R, Chiaberge S, Conte A, Filtri P, Pedron F, Rosellini I, Barbaferi M, Petruzzelli G (2016) Exploiting hydrocarbon-degrading indigenous Bacteria for bioremediation and phytoremediation of a multicontaminated soil. *Chem Eng Technol* 39:1676–1684. <https://doi.org/10.1002/ceat.201500573>
- Fu W, Xu M, Sun K, Hu L, Cao W, Dai C, Jia Y (2018) Biodegradation of phenanthrene by endophytic fungus *Phomopsis liquidambari* in vitro and in vivo. *Chemosphere* 203:160–169. <https://doi.org/10.1016/j.chemosphere.2018.03.164>
- Gao Y, Cheng Z, Ling W, Huang J (2010) Arbuscular mycorrhizal fungal hyphae contribute to the uptake of polycyclic aromatic hydrocarbons by plant roots. *Bioresour Technol* 101:6895–6901. <https://doi.org/10.1016/j.biortech.2010.03.122>
- Gao Y, Zong J, Que H, Zhou Z, Xiao M, Chen S (2017) Inoculation with arbuscular mycorrhizal fungi increases glomalin-related soil protein content and PAH removal in soils planted with *Medicago sativa* L. *Soil Biol Biochem* 115:148–151. <https://doi.org/10.1016/j.soilbio.2017.08.023>
- Garcés-Ruiz M, Senés-Guerrero C, Declerck S, Cranenbrouck S (2017) Arbuscular mycorrhizal fungal community composition in *Carludovica palmata*, *Costus scaber* and *Euterpe precatoria* from weathered oil ponds in the Ecuadorian Amazon. *Front Microbiol* 8:1–13. <https://doi.org/10.3389/fmicb.2017.02134>
- García-Sánchez M, Košnář Z, Mercl F, Aranda E, Tlustoš P (2018) A comparative study to evaluate natural attenuation, mycoaugmentation, phytoremediation, and microbial-assisted phytoremediation strategies for the bioremediation of an aged PAH-polluted soil. *Ecotoxicol Environ Saf* 147:165–174. <https://doi.org/10.1016/j.ecoenv.2017.08.012>
- Gerhardt KE, Gerwing PD, Huang XD, Greenberg BM (2015) Microbe-assisted phytoremediation of petroleum impacted soil: a scientifically proven green technology. In: Fingas M (ed) *Handbook of oil spill science technology*. Wiley, Hoboken, pp 407–427. <https://doi.org/10.1002/9781118989982.ch16>
- Gieg LM, Fowler SJ, Berdugo-Clavijo C (2014) Syntrophic biodegradation of hydrocarbon contaminants. *Curr Opin Biotechnol* 27:21–29. <https://doi.org/10.1016/j.copbio.2013.09.002>
- Gonzalez E, Pitre FE, Pagé AP, Marleau J, Nissim WG, St-Arnaud M, Labrecque M, Joly S, Yergeau E, Brereton NJB (2018) Trees, fungi and bacteria: tripartite metatranscriptomics of a root microbiome responding to soil contamination. *Microbiome* 6:53. <https://doi.org/10.1186/s40168-018-0432-5>
- Harms H, Wick LY (2006) Dispersing pollutant-degrading bacteria in contaminated soil without touching it. *Eng Life Sci* 6:252–260. <https://doi.org/10.1002/elsc.200620122>
- Hearn EM, Patel DR, van den Berg B (2008) Outer-membrane transport of aromatic hydrocarbons as a first step in biodegradation. *Proc Natl Acad Sci* 105:8601–8606. <https://doi.org/10.1073/pnas.0801264105>
- Hernández-Ortega HA, Alarcón A, Ferrera-Cerrato R, Zavaleta-Mancera HA, López-Delgado HA, Mendoza-López MR (2012) Arbuscular mycorrhizal fungi on growth, nutrient status, and total antioxidant activity of *Melilotus albus* during phytoremediation of a diesel-contaminated substrate. *J Environ Manag* 95:S319–S324. <https://doi.org/10.1016/j.jenvman.2011.02.015>
- Hua F, Wang H (2012) Uptake modes of octadecane by *Pseudomonas* sp. DG17 and synthesis of biosurfactant. *J Appl Microbiol* 112:25–37. <https://doi.org/10.1111/j.1365-2672.2011.05178.x>

- Hua F, Wang HQ (2014) Uptake and trans-membrane transport of petroleum hydrocarbons by microorganisms. *Biotechnol Biotechnol Equip* 28:165–175. <https://doi.org/10.1080/13102818.2014.906136>
- Jiang L, Song M, Luo C, Zhang D, Zhang G (2015) Novel phenanthrene-degrading bacteria identified by DNA-stable isotope probing. *PLoS One* 10:1–14. <https://doi.org/10.1371/journal.pone.0130846>
- Kadri T, Rouissi T, Kaur Brar S, Cledon M, Sarma S, Verma M (2017) Biodegradation of polycyclic aromatic hydrocarbons (PAHs) by fungal enzymes: a review. *J Environ Sci (China)* 51:52–74. <https://doi.org/10.1016/j.jes.2016.08.023>
- Kirk JL, Klirnomos JN, Lee H, Trevors JT (2002) Phytotoxicity assay to assess plant species for phytoremediation of petroleum-contaminated soil. *Biorem J* 6:57–63. <https://doi.org/10.1080/1088986029077477>
- Košnář Z, Částková T, Wiesnerová L, Praus L, Jablonský I, Koudela M, Tlustoš P (2018) Comparing the removal of polycyclic aromatic hydrocarbons in soil after different bioremediation approaches in relation to the extracellular enzyme activities. *J Environ Sci* 76:249. <https://doi.org/10.1016/j.jes.2018.05.007>
- Krahforst K, Healey TE (2017) Unraveling the complexities of upland spilled fuels: selected case studies. In: Stout SA, Wang Z (eds) *Oil spill environmental forensics case studies*. Elsevier, Saint Louis, pp 201–238. <https://doi.org/10.1016/B978-0-12-804434-6.00010-0>
- Lenoir I, Anissa L-HS, Laruelle F, Dalpé Y, Fontaine J (2016) Arbuscular mycorrhizal wheat inoculation promotes alkane and polycyclic aromatic hydrocarbon biodegradation: microcosm experiment on aged-contaminated soil. *Environ Pollut* 213:549–560. <https://doi.org/10.1016/j.envpol.2016.02.056>
- Ling W, Sun R, Gao X, Xu R, Li H (2015) Low-molecular-weight organic acids enhance desorption of polycyclic aromatic hydrocarbons from soil. *Eur J Soil Sci* 66:339–347. <https://doi.org/10.1111/ejss.12227>
- Marco-Urrea E, García-Romera I, Aranda E (2015) Potential of non-ligninolytic fungi in bioremediation of chlorinated and polycyclic aromatic hydrocarbons. *New Biotechnol* 32:620–628. <https://doi.org/10.1016/j.nbt.2015.01.005>
- Martin BC, George SJ, Price CA, Ryan MH, Tibbett M (2014) The role of root exuded low molecular weight organic anions in facilitating petroleum hydrocarbon degradation: current knowledge and future directions. *Sci Total Environ* 472:642–653. <https://doi.org/10.1016/j.scitotenv.2013.11.050>
- Morelli IS, Saparrat MCN, Del Panno MT, Coppotelli BM, Arrambari A (2013) Bioremediation of PAH-contaminated soil by fungi. In: Goltapeh EM, Danesh YR, Varma A (eds) *Fungi as bioremediators*. Springer, Heidelberg, pp 159–179. <https://doi.org/10.1007/978-3-642-33811-3>
- Mullins OC (2008) Review of the molecular structure and aggregation of asphaltenes and petroleomics. *SPE J* 13:48–57. <https://doi.org/10.2118/95801-PA>
- Muratova AY, Dmitrieva T, Panchenko LV, Turkovskaya OV (2008) Phytoremediation of oil-sludge – contaminated soil. *Int J Phytoremediation* 10:486–502. <https://doi.org/10.1080/15226510802114920>
- Musilova L, Ridl J, Polivkova M, Macek T, Uhlík O (2016) Effects of secondary plant metabolites on microbial populations: changes in community structure and metabolic activity in contaminated environments. *Int J Mol Sci* 17:1–31. <https://doi.org/10.3390/ijms17081205>
- Newman LA, Reynolds CM (2004) Phytodegradation of organic compounds. *Curr Opin Biotechnol* 15:225–230. <https://doi.org/10.1016/j.copbio.2004.04.006>
- Olanrewaju OS, Glick BR, Babalola OO (2017) Mechanisms of action of plant growth promoting bacteria. *World J Microbiol Biotechnol* 33:1–16. <https://doi.org/10.1007/s11274-017-2364-9>
- Pacwa-Plociniczak M, Plociniczak T, Iwan J, Zarska M, Chorazewski M, Dzida M, Piotrowska-Seget Z (2016) Isolation of hydrocarbon-degrading and biosurfactant-producing bacteria and assessment their plant growth-promoting traits. *J Environ Manag* 168:175–184. <https://doi.org/10.1016/j.jenvman.2015.11.058>

- Pagé AP, Yergeau É, Greer CW (2015) *Salix purpurea* stimulates the expression of specific bacterial xenobiotic degradation genes in a soil contaminated with hydrocarbons. *PLoS One* 10:1–16. <https://doi.org/10.1371/journal.pone.0132062>
- Parseh I, Teiri H, Hajizadeh Y, Ebrahimpour K (2018) Phytoremediation of benzene vapors from indoor air by *Schefflera arboricola* and *Spathiphyllum wallisii* plants. *Atmos Pollut Res* 9:1083. <https://doi.org/10.1016/j.apr.2018.04.005>
- Pawlik M, Cania B, Thijs S, Vangronsveld J, Piotrowska-Seget Z (2017) Hydrocarbon degradation potential and plant growth-promoting activity of culturable endophytic bacteria of *Lotus corniculatus* and *Oenothera biennis* from a long-term polluted site. *Environ Sci Pollut Res* 24:19640–19652. <https://doi.org/10.1007/s11356-017-9496-1>
- Pozdnyakova N, Dubrovskaya E, Chernyshova M, Makarov O, Golubev S, Balandina S, Turkovskaya O (2018) The degradation of three-ringed polycyclic aromatic hydrocarbons by wood-inhabiting fungus *Pleurotus ostreatus* and soil-inhabiting fungus *Agaricus bisporus*. *Fungal Biol* 122:363–372. <https://doi.org/10.1016/j.funbio.2018.02.007>
- Prasad R (2017) *Mycoremediation and environmental sustainability*, vol 1. Springer, Cham. ISBN 978-3-319-68957-9. <https://link.springer.com/book/10.1007/978-3-319-68957-9>
- Prasad R (2018) *Mycoremediation and environmental sustainability*, vol 2. Springer, Cham. ISBN 978-3-319-77386-5. <https://www.springer.com/us/book/9783319773865>
- Prasad R, Kumar M, Varma A (2015) Role of PGPR in soil fertility and plant health. In: Egamberdieva D, Shrivastava S, Varma A (eds) *Plant Growth-Promoting Rhizobacteria (PGPR) and medicinal plants*. Springer, Cham, pp 247–260
- Quiza L, St-Arnaud M, Yergeau E (2015) Harnessing phytomicrobiome signaling for rhizosphere microbiome engineering. *Front Plant Sci* 6:1–11. <https://doi.org/10.3389/fpls.2015.00507>
- Rabus R, Boll M, Heider J, Meckenstock RU, Buckel W, Einsle O, Ermler U, Golding BT, Gunsalus RP, Kroneck PMH, Krüger M, Lueders T, Martins BM, Musat F, Richnow HH, Schink B, Seifert J, Szalaniec M, Treude T, Ullmann GM, Vogt C, Von Bergen M, Wilkes H (2016) Anaerobic microbial degradation of hydrocarbons: from enzymatic reactions to the environment. *J Mol Microbiol Biotechnol* 26:5–28. <https://doi.org/10.1159/000443997>
- Rajtor M, Piotrowska-Seget Z (2016) Prospects for arbuscular mycorrhizal fungi (AMF) to assist in phytoremediation of soil hydrocarbon contaminants. *Chemosphere* 162:105–116. <https://doi.org/10.1016/j.chemosphere.2016.07.071>
- Rentz JA, Alvarez PJJ, Schnoor JL (2005) Benzo[a]pyrene co-metabolism in the presence of plant root extracts and exudates: implications for phytoremediation. *Environ Pollut* 136:477–484. <https://doi.org/10.1016/j.envpol.2004.12.034>
- Reyes-César A, Absalón ÁE, Fernández FJ, González JM, Cortés-Espinosa DV (2014) Biodegradation of a mixture of PAHs by non-ligninolytic fungal strains isolated from crude oil-contaminated soil. *World J Microbiol Biotechnol* 30:999–1009. <https://doi.org/10.1007/s11274-013-1518-7>
- Rodrigues EM, Freitas F d S, Siqueira T d P (2018) Detection of horizontal transfer of housekeeping and hydrocarbons catabolism genes in bacterial genus with potential to application in bioremediation process. *OALib* 05:1–10. <https://doi.org/10.4236/oalib.1104454>
- Rohrbacher F, St-Arnaud M (2016) Root exudation: the ecological driver of hydrocarbon Rhizoremediation. *Agronomy* 6:1–27. <https://doi.org/10.3390/agronomy6010019>
- Sander mann H (1992) Plant metabolism of xenobiotics. *Trends Biochem Sci* 17:82–84. [https://doi.org/10.1016/0968-0004\(92\)90507-6](https://doi.org/10.1016/0968-0004(92)90507-6)
- Santisi S, Cappello S, Catalfamo M, Mancini G, Hassanshahian M, Genovese L, Giuliano L, Yakimov MM (2015) Biodegradation of crude oil by individual bacterial strains and a mixed bacterial consortium. *Brazilian J Microbiol* 46:377–387. <https://doi.org/10.1002/cfen.200700042>
- Santoyo G, Moreno-Hagelsieb G, del Carmen Orozco-Mosqueda M, Glick BR (2016) Plant growth-promoting bacterial endophytes. *Microbiol Res* 183:92–99. <https://doi.org/10.1016/j.micres.2015.11.008>
- Schindler FV, Mercer EJ, Rice JA (2007) Chemical characteristics of glomalin-related soil protein (GRSP) extracted from soils of varying organic matter content. *Soil Biol Biochem* 39:320–329. <https://doi.org/10.1016/j.soilbio.2006.08.017>

- Siddiqui S, Adams WA, Schollion J (2001) The phytotoxicity and degradation of diesel hydrocarbons in soil. *J Plant Nutr Soil Sci* 164:631–635. [https://doi.org/10.1002/1522-2624\(200112\)164:6<631::AID-JPLN631>3.0.CO;2-E](https://doi.org/10.1002/1522-2624(200112)164:6<631::AID-JPLN631>3.0.CO;2-E)
- Singh M, Pant G, Hossain K, Bhatia AK (2017) Green remediation. Tool for safe and sustainable environment: a review. *Appl Water Sci* 7:2629–2635. <https://doi.org/10.1007/s13201-016-0461-9>
- Singha LP, Sinha N, Pandey P (2018) Rhizoremediation prospects of polyaromatic hydrocarbon degrading rhizobacteria, that facilitate glutathione and glutathione-S-transferase mediated stress response, and enhance growth of rice plants in pyrene contaminated soil. *Ecotoxicol Environ Saf* 164:579–588. <https://doi.org/10.1016/j.ecoenv.2018.08.069>
- Somtrakoon K, Chouychai W (2013) Phytotoxicity of single and combined polycyclic aromatic hydrocarbons toward economic crops. *Russ J Plant Physiol* 60:139–148. <https://doi.org/10.1134/S1021443712060155>
- Sun Y, Zhou Q (2016) Uptake and translocation of benzo[a]pyrene (B[a]P) in two ornamental plants and dissipation in soil. *Ecotoxicol Environ Saf* 124:74–81. <https://doi.org/10.1016/j.ecoenv.2015.09.037>
- Syranidou E, Christofilopoulos S, Gkavrou G, Thijs S, Weyens N, Vangronsveld J, Kalogerakis N (2016) Exploitation of endophytic bacteria to enhance the phytoremediation potential of the wetland helophyte *Juncus acutus*. *Front Microbiol* 7:1–15. <https://doi.org/10.3389/fmicb.2016.01016>
- Taghavi S, Barac T, Greenberg B, Vangronsveld J, Van Der Lelie D, Borremans B (2005) Horizontal gene transfer to endogenous endophytic bacteria from poplar improves phytoremediation of toluene. *Appl Environ Microbiol* 71:8500–8505. <https://doi.org/10.1128/AEM.71.12.8500>
- Tardif S, Yergeau E, Tremblay J, Legendre P, Whyte LG, Greer CW (2016) The willow microbiome is influenced by soil petroleum-hydrocarbon concentration with plant compartment-specific effects. *Front Microbiol* 7:1–14. <https://doi.org/10.3389/fmicb.2016.01363>
- Thijs S, Sillen W, Rineau F, Weyens N, Vangronsveld J (2016) Towards an enhanced understanding of plant-microbiome interactions to improve phytoremediation: engineering the metaorganism. *Front Microbiol* 7:1–15. <https://doi.org/10.3389/fmicb.2016.00341>
- Tian Z, Vila J, Yu M, Bodnar W, Aitken MD (2018) Tracing the biotransformation of polycyclic aromatic hydrocarbons in contaminated soil using stable isotope-assisted metabolomics. *Environ Sci Technol Lett* 5:103–109. <https://doi.org/10.1021/acs.estlett.7b00554>
- Tormoehlen LM, Tekulve KJ, Nañagas KA (2014) Hydrocarbon toxicity: a review. *Clin Toxicol* 52:479–489. <https://doi.org/10.3109/15563650.2014.923904>
- USEPA (2008) Green remediation: incorporating sustainable environmental practices into remediation of contaminated sites. USEPA, Washington, DC
- Uteau D, Hafner S, Pagenkemper SK, Peth S, Wiesenberger GLB, Kuzyakov Y, Horn R (2015) Oxygen and redox potential gradients in the rhizosphere of alfalfa grown on a loamy soil. *J Plant Nutr Soil Sci* 178:278–287. <https://doi.org/10.1002/jpln.201300624>
- van Dam NM, Bouwmeester HJ (2016) Metabolomics in the rhizosphere: tapping into belowground chemical communication. *Trends Plant Sci* 21:256–265. <https://doi.org/10.1016/j.tplants.2016.01.008>
- Varjani SJ (2017) Microbial degradation of petroleum hydrocarbons. *Bioresour Technol* 223:277–286. <https://doi.org/10.1016/j.biortech.2016.10.037>
- Vigneron A, Alsop EB, Cruaud P, Philibert G, King B, Baksmaty L, Lavallée D, Lomans BP, Kyrpidis NC, Head IM, Tsesmetzis N (2017) Comparative metagenomics of hydrocarbon and methane seeps of the Gulf of Mexico. *Sci Rep* 7:1–12. <https://doi.org/10.1038/s41598-017-16375-5>
- Wanapaisan P, Laothamteep N, Vejarano F, Chakraborty J, Shintani M, Muangchinda C, Morita T, Suzuki-Minakuchi C, Inoue K, Nojiri H, Pinyakong O (2018) Synergistic degradation of pyrene



- by five culturable bacteria in a mangrove sediment-derived bacterial consortium. *J Hazard Mater* 342:561–570. <https://doi.org/10.1016/j.jhazmat.2017.08.062>
- Wang H, Wang B, Dong W, Hu X (2016) Co-acclimation of bacterial communities under stresses of hydrocarbons with different structures. *Sci Rep* 6:34588. <https://doi.org/10.1038/srep34588>
- Warembourg FR (1997) The ‘rhizosphere effect’: a plant strategy for plants to exploit and colonize nutrient-limited habitats. *Bioconea* 7:187–194
- Yergeau E, Sanschagrín S, Maynard C, St-Arnaud M, Greer CW (2014) Microbial expression profiles in the rhizosphere of willows depend on soil contamination. *ISME J* 8:344–358. <https://doi.org/10.1038/ismej.2013.163>
- Yergeau E, Tremblay J, Joly S, Labrecque M, Maynard C, Pitre FE, St-Arnaud M, Greer CW (2018) Soil contamination alters the willow root and rhizosphere metatranscriptome and the root-rhizosphere interactome. *ISME J* 12:869–884. <https://doi.org/10.1038/s41396-017-0018-4>
- Zafra G, Absalón ÁE, Anducho-Reyes MÁ, Fernández FJ, Cortés-Espinosa DV (2017) Construction of PAH-degrading mixed microbial consortia by induced selection in soil. *Chemosphere* 172:120–126. <https://doi.org/10.1016/j.chemosphere.2016.12.038>