Rhizosphere–plant–microbial system under polycyclic aromatic hydrocarbons-induced stress

Kavita Verma[1], Pooja Gokhale Sinha[2], Garima Sharma[1], Surbhi Agarwal[1], Anita Verma[1] and Vartika Mathur[1,3,*]

[1]Department of Zoology, and
[2]Department of Botany, Sri Venkateswara College, Dhaula Kuan, New Delhi 110 021, India
[3]Delhi School of Climate Change and Sustainability, Institute of Eminence, University of Delhi, New Delhi 110 007, India

The rhizosphere–plant–microbial association is a complex and intricate system susceptible to various organic pollutants, including polycyclic aromatic hydrocarbons (PAH). Since the soil acts as a sink of PAH, their accumulation shifts the delicate rhizosphere–plant–microbe equilibrium and enters the food chain through plants. How the presence of PAH in the rhizosphere affects the rhizosphere–plant–microbial system is still unclear. This study aims to understand the effects of PAH on rhizosphere–plant–microbial interactions. It also explores the potential use of microbes to alleviate PAH-induced stress in the soil for effective and sustainable management.

Keywords: Bioaccumulation, microbe-mediated remediation, persistent organic pollutants, polycyclic aromatic hydrocarbons.

POLYCYCLIC aromatic hydrocarbons (PAH) are among the most notorious, cosmopolitan, toxic and persistent organic pollutants. They are ubiquitous in nature, and in the last five decades, their global burden has increased by around 45% (ref. 1). In 2007, the average global PAH emission was estimated to be 504 Gg/year, with major contributions from the developing Asian countries[2]. Africa, Europe, North America, Oceania and South America contribute 18.8%, 9.5%, 8.0%, 1.5% and 6.0% respectively, to worldwide PAH emissions[3]. The distribution and accumulation of PAH are not uniform and show significant regional variation. India (90 Gg) and China (114 Gg) are the major contributors of PAH annually[4]. This is due to rapid industrialization, fossil–fuel-dependent transportation and other anthropogenic activities. Sources of PAH can be broadly classified as petrogenic (petroleum as the source) and pyrogenic (incomplete combustion of fossil fuels and biomass). Most PAH are potential carcinogens, and their exposure or indirect consumption leads to serious health effects. They are considered priority pollutants due to their 'three disease-causing' effects (carcinogenic, teratogenic and mutagenic) on humans[5]. In spite of being volatile and present in the air, the presence of PAH in the soil is of concern as they tend to accumulate in it.

Due to their hydrophobicity, around 90% of the global PAH is adsorbed in the soil, which not only makes it a major sink but also drastically changes the physico-chemical properties of the soil, thereby altering its structure and function[6]. Rhizosphere, the zone of interaction between the soil and roots, is a diverse and intricate habitat hosting a wide range of algae, protozoa, arthropods, nematodes, bacteria and fungi. Among these, microorganisms play a significant role in regulating essential biogeochemical processes and facilitating xenobiotic degradation. Biodegradation of soil pollutants such as pesticides, insecticides, and PAH is a critical ecosystem service provided by rhizospheric microbes[7]. The presence of PAH in the rhizosphere enhances their risk of entering the food chain as well as influences soil microbial diversity and dynamics[8].

Plants are key players that influence the entry, accumulation and movement of PAH in the food chain. They take up PAH directly through the roots or indirectly through the cuticle[9]. The higher the PAH concentration in the soil, the greater the risk of their bioaccumulation and subsequent magnification in the plants. Excess PAH accumulation in plants is responsible for acute, chronic, and latent injuries that eventually disrupt their primary metabolic functions, such as photosynthesis[10]. As plants regulate the growth and diversity of microbial communities through root exudates, when grown in high PAH, the diversity of rhizospheric microbes, as well as their endophytes is observed to be modified[11]. Therefore, the interaction among soil microbes, plants and PAH is a tripartite process; any change in one of them significantly affects not only the other two, but also the food chain.

The interactions among rhizosphere–plant–microbe are delicate and sensitive to the presence of PAH. However, no study has addressed the effect of PAH toxicity on this complex yet important system. This study summarizes the multifaceted interactions among rhizosphere–plant–microbes

---

*For correspondence. (e-mail: vmathur@svc.ac.in) and analyses how this system responds to increased PAH levels. It also explores microbe-mediated, sustainable mitigation measures for PAH-polluted soil to prevent their accumulation and increasing presence in the food chain.

Soil: a sink of PAH

PAH released from various anthropogenic activities accumulate in the soil by wet or dry deposition. The soil serves as their primary and largest steady repository. The lipophilicity of PAH makes them less available for biodegradation, and hence, they accumulate in the soil, increasing their persistence in the ecosystem[12]. The distribution of PAH in the rhizosphere depends on their source and chemical properties, soil characteristics and environmental conditions[12]. The amount of PAH in the soil is inversely proportional to its proximity to the emission source. Industrial and urban soils have more PAH contamination compared to rural or remote areas[13]. The chemical properties of PAH also influence their bioavailability. Low-molecular-weight (LMW) PAH with two or three rings, such as naphthalene, fluorene, phenanthrene and anthracene, are present in lesser amounts as they undergo degradation, leaching and volatilization in the soil[14]. In contrast, high-molecular-weight (HMW) PAH, such as pyrene, chrysene, benzo(*a*)pyrene and benzo(*a*)-anthracene, are abundant in the soil as they are not degraded or transformed completely into simpler products due to their highly lipophilic, persistent and stable chemical composition[15]. It is known that two-, three-, four-, five- and six-ring PAH contribute to >3%, >16%, 45%, >27% and >6% respectively, of the total PAH in the soil of urban parks in China[16]. Thus, HMW PAH are greatly responsible for soil contamination.

Based on the concentration of PAH, the soil is classified as (i) unpolluted (<600 ng g^{-1}), (ii) slightly polluted (600–1000 ng g^{-1}), (iii) polluted (1000–5000 ng g^{-1}), (iv) heavily polluted (5000–10,000 ng g^{-1}) and (v) very highly polluted ($>10,000$ ng g^{-1})[6,17]. Figure 1 summarizes the country-wise prevalence of PAH in the soil based on the literature.

Significance and role of rhizospheric microbes

Diversity of microbes

The rhizosphere is a dynamic zone where numerous biochemical and biophysical processes take place that shape and organize the physical and functional attributes of the soil. Soil characteristics such as texture, pore volume and particle aggregation influence root–microbe association. Interactions between the soil and its microbiome are influenced by the plant species and soil type and are important for plant growth and organic matter turnover[18].

Bacteria are among the most abundant microbes in the rhizosphere, covering nearly 15% of the total root surface, dominated by phyla such as Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes and Acidobacteria[19]. Proteobacteria are present in greater numbers due to their ability to act on labile carbon sources and, thus, grow quickly, making them capable of surviving in diverse rhizospheres[20]. Another dominant phylum is Acidobacteria, which plays a key role in carbon cycling as it is capable of degrading cellulose and lignin[21]. Anaerobic bacteria belonging to *Latescibacteria* and *Planctomycetes* dominate the rhizosphere, whereas aerobic bacteria (Parcubacteria, Firmicutes and Saccharibacteria) are comparatively less in number due to reduced oxygen levels in the rhizosphere[22].

Along with bacteria, the rhizosphere is well represented by fungi primarily belonging to Ascomycota, Basidiomycota and Zygomycota[23]. Arbuscular mycorrhizal (AM) fungi are among the most ubiquitously present fungi in the rhizosphere ecosystem globally and provide an array of services[5,24]. Moreover, several algae, including species of *Arthrospira*, *Chlorella*, *Dunaliella*, *Nostoc* and *Aphanizomenon* are found in the rhizosphere and play a significant role in maintaining soil health by acting as both bioprotective and biostimulant agents[25].

The rhizosphere microbiome is sensitive and quickly responds to any change in its surroundings[26]. The physiochemical properties of the soil, type of vegetation and stage of the plant influence the diversity and abundance of microbes in the rhizosphere.

Rhizosphere microbes in ecosystem services

Rhizosphere microbes play a substantial role in various ecological services such as soil formation, decomposition of organic matter, biogeochemical cycles and degradation of soil contaminants[27]. The ecosystem services performed by microbes are categorized into regulating, supporting and provisioning services (Supplementary Table 1).

Soil bioremediation is an important regulating service performed by the rhizosphere microbes. Genera of bacteria, including *Acinetobacter*, *Burkholderia*, *Pseudomonas*, *Flavobacterium*, *Bacillus* and *Azotobacter* and fungi such as *Aspergillus* are capable of degrading an array of soil contaminants[28,29]. Many species of mycorrhizal fungi are also involved in remediating soil pollutants such as organic hydrocarbons[30]. Microbes either use organic pollutants as the carbon source or degrade the toxic and complex compounds into simple, less toxic forms[31]. Their efficiency and strategy are dependent on the pollution load. A consortium of PAH-degrading microbes removed 97.2% of pyrene from the soil, inhibiting its accumulation in the host tissues[32]. Similarly, up to 90% biodegradation of lindane (organochlorine pesticide) using *Paracoccus* sp. NITDBR1 has been reported[33]. Rhizospheric microbes are also known to degrade diesel-based contaminants efficiently. Diesel oil-contaminated soil was effectively mediated by an artificial consortium containing *Alcaligenes xylosoxidans*, *Pseudomonas*

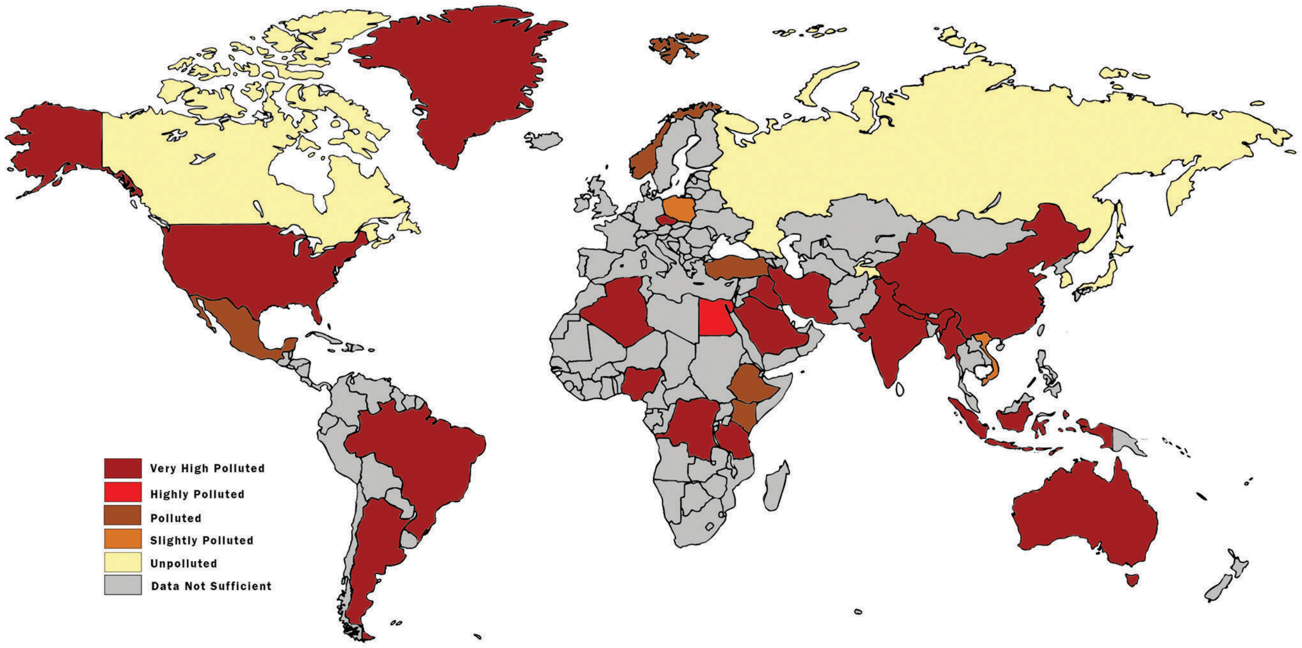

Figure 1. Country-wise polycyclic aromatic hydrocarbons (PAH) contamination in the soil. Source: The map was created by using mapchart.net.

fluorescens, *Pseudomonas putida*, *Stenotrophomonas maltophilia* and *Xanthomonas* sp.[34].

Plant–microbe–rhizosphere system under PAH-induced stress

Physicochemical properties of the soil

Soils across the globe are under constant threat of PAH, which tends to accumulate on these soil particles. The degree of adsorption and desorption of these pollutants depends on redox conditions, pH, organic ligands and inorganic ions[35].

The molecular weight and ring structure of PAH govern their fate in the soil as well as influence soil characteristics[36,37]. HMW PAH tend to alter the physical characters of the soil, such as pore size, rate of filtration and aeration, as they bind more firmly to the particles than LMW PAH. Fine soil particles have less inter-particle space and a porosity-mediated effect that restricts the mobility of HMW PAH due to their greater hydrophobicity[38]. As a result, they tend to completely choke the soil pores or partially replace them, reducing the soil's aeration and filtration capacity.

The presence of PAH affects the physico-chemical properties of the soil, such as pH, cation exchange capacity, humic acid, carbon and nitrogen contents[39,40]. PAH also influence the physical characteristics of the soil, such as grain size, water-holding capacity and porosity, leading to reduced aeration and choking of soil pores[38]. Fine-grained particles, i.e. silt and clay, are more susceptible to PAH binding[41].

The properties of the soil, such as its size, pH and associated organic carbon, also determine the PAH effect[37]. Fine soil particles provide a less scope of PAH movement, resulting in persistent toxicity and enduring effects[38]. The carbon-rich organic and fine-grained acidic soil is more susceptible to PAH contamination and is difficult to bioremediate[42]. Prolonged exposure and subsequent accumulation of PAH in the soil, and by extension, the rhizosphere significantly lower its quality and adversely affect the rate of seed germination, growth, and eventually plant health[43].

In spite of their ubiquitous presence across soils in different parts of the world, there is limited information on the influence of PAH on the soil and its processes. There is a large temporal and spatial variability of types and concentrations of PAH, and therefore, more region-specific studies are required to provide sustainable remediation solutions.

Impact on rhizo-microbiota

Rhizosphere microbes are highly sensitive to any change in the physico-chemical or edaphic properties of the soil. Under the influence of pollutants, a shift in the diversity and growth patterns of the microbial population takes place. Biological activities in the rhizosphere, such as microbial biomass and associated enzymatic activities, are susceptible to organic pollutants, including PAH[44]. The type of PAH influences the community profile of rhizospheric microbiota. Studies have been focused on understanding the effect of PAH on microbial diversity, density and metabolic activity[45]. At high concentration, PAH is detrimental to their growth or even toxic to soil microbes. Contamination of PAH in the rhizosphere may even decrease the diversity of some microbial populations and increase the density of aromatic ring dioxygenase-expressing bacteria (ARDB) due to increased concentration of organic carbon[11]. This could be the result of increased root exudation or accumulation of PAH around the roots due to the transport processes inside PAH-accumulated plants. Soil microflora is highly sensitive to soil perturbation and is therefore known to be a pollution indicator[46,47]. PAH-induced stress in soil can lead to altered microbial diversity, activity and succession[48]. The influence on the microbiome depends upon the type and molecular weight of PAH[49]. For example, pyrene-contaminated soils affect the diversity and abundance of bacteria than fungi. Similarly, the density of Gram-negative bacteria and AM fungi increases around *Echinacea purpurea* grown in PAH-contaminated soil[50]. PAH-mediated change in microbiome is due to altered carbon and nitrogen cycling, and accelerated metabolism of carbon in the soil[51]. These studies indicate that PAH may negatively affect the ecological balance of the rhizosphere. High PAH contamination lowers the capacity of the soil to degrade contaminants due to decreased microbial activity[42,51,52]. Any change in soil microbial diversity and population dynamics may alter the delicate balance of nutrient cycling. Moreover, any shift in rhizospheric community structure and function has direct implications on the growth of plants as well.

Soil enzymes are sensitive indicators of the function and degradation potential of the soil. Enzymes such as urease, alkaline phosphatase, polyphenol oxidase and dehydrogenase are used to determine PAH load by assessing the rhizo-microbiota[53]. There is a positive correlation between the presence of different PAH and the activity of dehydrogenase and urease[54].

Plant response to PAH-induced stress

Increasing PAH concentration in the soil is of concern due to their tendency to bioaccumulate and subsequently biomagnify through absorption by plants. They not only affect the germinability, growth, physiology and metabolic behaviour of the plants but also resource-partitioning[55,56]. Exposure to low PAH concentration increases plant weight and reduces root area[57]. However, high PAH contamination in the soil may inhibit plant growth and have phytotoxic effects, making them prone to other stressors[58,59]. Growth in high PAH soil leads to deformed trichomes, chlorosis, white spots, and impaired root growth and development[54,60]. PAH can penetrate cell membranes and eventually decrease water content, nutrient utilization, inhibit photosynthetic activity and electron transport in plants[56]. LMW PAH can even cause phytotoxic effects in plants, such as impaired growth and development[59].

Uptake of PAH by plants is governed by their concentration, water solubility, physico-chemical and even soil type[36]. Additionally, their molecular weight is a key determinant of their uptake. HMW PAH bind more firmly to soil particles, making their removal through physical means a challenge[61]. PAH uptake and accumulation in the plants, primarily a passive process, are limited due to their high partition coefficients in the soil[62,63]. Root and shoot concentration and transpiration stream concentration factors also determine their uptake and availability in the plants[64].

The rhizosphere significantly influences PAH uptake by the plants directly and/or indirectly[63,65]. Active rhizosphere facilitates PAH degradation and decreases their bioavailability[66,67]. Factors such as microflora, root exudates, soil type, available nutrients and pollutant load influence the rhizosphere effect[68]. Aromatic compounds that are homologous to PAH, as well as surfactant molecules released by the plant roots give rise to the rhizosphere effect that might contribute to an increase in microbial activity and rhizodegradation of PAH in contaminated soils[69,70].

Exposure to PAH induces oxidative stress in plants, leading to increased levels of reactive oxygen species (ROS)[71]. *Arabidopsis thaliana* exposed to high phenanthrene concentration leads to an increase in ROS load, which may surpass the capacity of the antioxidant systems of the plants[72].

A significant amount of PAH is accumulated in the leaves, especially in the cuticle, and is dependent on morphological factors such as size, surface-to-volume ratio and wax content of the leaves, as well as chemical properties such as lipophilicity and volatility of PAH[73]. Adsorption and intake of PAH not only increase toxicity in the plants owing to bioaccumulation but also make them available in vegetables and fruits[74]. Temperature is another important factor that determines the accumulation of PAH in plants. High-temperature conditions enable PAH to exist in the gas phase, while low-temperature conditions facilitate their accumulation in the leaves.

The effect of PAH on plant growth and metabolism is species-specific. For example, the biomass of *Aeschynomene indica* increased, whereas that of *Panicum bisulcatum* decreased to approximately 70% when both species were exposed to the same PAH concentration[68,75]. They not only affect the growth and metabolism of plants but also their endophyte population. Plant endophytes are highly sensitive to PAH contamination, which increases specific PAH-degrading endophytes in the plants. Therefore, endophytes can be explored for better PAH biodegradation in an eco-friendly manner.

PAH-induced stress on the rhizosphere–plant–microbial relationship

Active interactions between plants and rhizo-microbiota have been long recognized and are the fulcrum of biological activity in the rhizosphere. Microbes depend on plant exudates and other associated rhizodeposits for energy, and facilitating critical processes in nutrient cycling, production of growth promoters and xenobiotic degradation. Plants

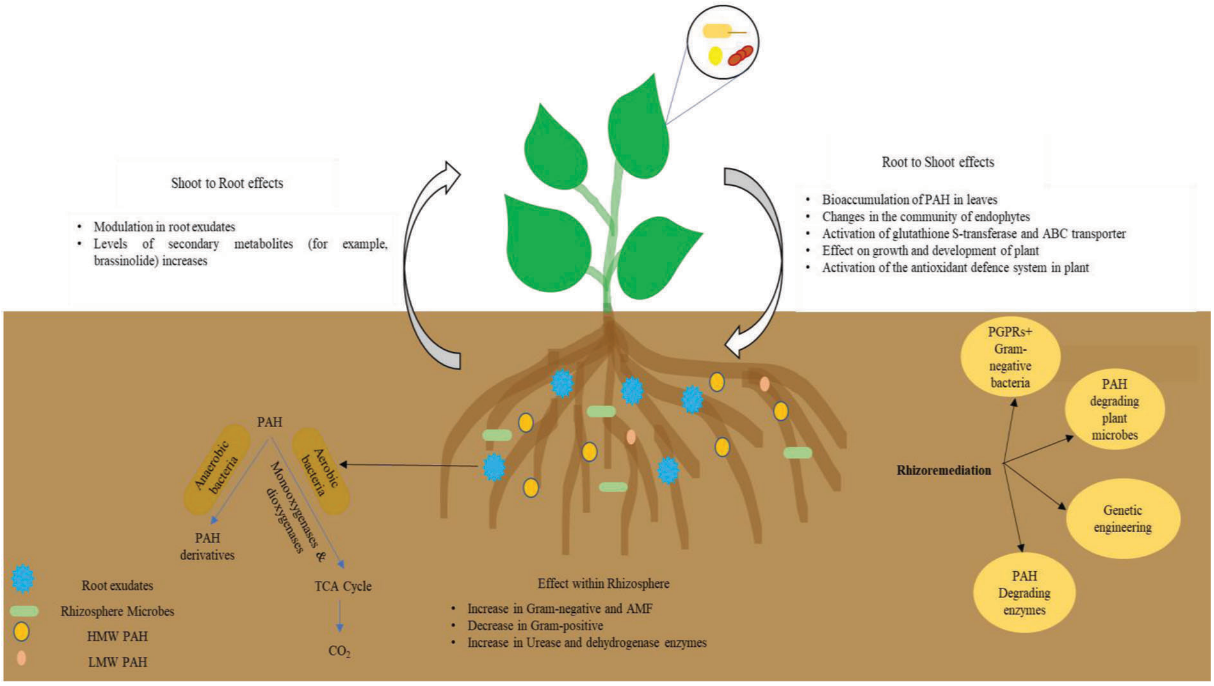

Figure 2. Rhizosphere–plant–microbe system under PAH-induced stress.

under abiotic stress, such as contaminants, influence soil properties through root exudates[76]. This, in turn, affects the microbial communities in the rhizosphere and eventually alters plant performance. This is known as the plant–soil feedback mechanism. Thus, rhizosphere–plant–microbes share an intimate relationship that is not only symbiotic but is more of a cyclic relationship, wherein changes in one of them directly affect the others and ultimately affect all three components. The health of the rhizosphere and its microbial populations are important for plant health and productivity. Plants and rhizospheric microbes are a combined unit of the soil ecosystem; neither can be studied or considered separately.

The rhizosphere microbiome has the capability to degrade pollutants such as PAH[77]. The mere presence of the rhizosphere accelerates the rate of PAH dissipation and degradation[75,78]. Interactions among plant–soil–microbiome are greatly influenced by plant species, physiology and photosystems, and life stages of plants[79,80]. The rhizosphere of grasses provides better degradation of PAH due to their fibrous root system[81]. However, in a comparative study, legumes performed better in the removal of PAH when compared to grasses[75].

This three-component rhizosphere–plant–microbial system quickly responds to any change in the physico-chemical properties and composition of the soil. The addition of carbon-based pollutants such as PAH significantly influences all three components. The effect of PAH on this system is not restricted to morpho-physiological changes in the plants, and their influence can be seen on plant–microbe signalling, nutrient allocation and resource partitioning[82]. A study has shown that increased carbon allocation to the roots led to rapid utilization of carbon by microbes in *Phragmite australis* under hydrocarbon stress[83]. Studies have shown that plant hormones such as ethylene, brassinosteroids, ethane, expansin, cytokinin, cytochrome P450, glutathione-S-transferase and endogenous abscisic acid play a significant role in the signalling pathway of PAH-induced stress[84]. Glutathione S-transferase and ABC transporter play a key role in the transfer of PAH from the rhizosphere into the plant tissues[85]. PAH can affect the plant–rhizosphere–microbial interactions by a two-way process (Figure 2). PAH accumulated in the plants affect their microbiota and physiology. This, in turn, affects the lipophilic composition of root exudates, which facilitate PAH degradation. The presence of glucose, pyruvate and acetate increases PAH accumulation in the rhizosphere. The presence of such compounds in root exudates in the rhizosphere lowers the expression of PAH-degrading genes such as *nahG* in *Pseudomonas fluorescens* HK44 present in the rhizosphere, resulting in increased bacterial biomass[86]. Therefore, the direct or indirect effect of PAH on plants, microbes and rhizosphere may alter their natural interactions temporarily or permanently.

Significance of the plant–microbe–soil system in alleviating PAH-induced stress

Due to their high concentration and prevalence, particularly in some parts of the world, PAH make way into the food chain, augmenting at each trophic level. Their effective

Table 1. Plant–microbial system for effective polycyclic aromatic hydrocarbons (PAH) degradation

Plant–microbial system	PAH degraded	Percentage degradation	Genes involved	Reference
Sorghum × *drummondii* and *Sphingomonadales*	Fluorene, phenanthrene, fluoranthene and pyrene	98	*PAH-RHD*α and *nidA*	90
Fire phoenix and *Mycobacterium* sp.	Total PAH[a]	40.3–53.7	–	91
Orychophragmus violaceus and *Rhodococcus ruber* Em1	Total PAH[b]	17.85	*alkB* and *PAH-RHD*	92
Populus deltoides and *Bacillus* sp. SBER3	Anthracene and naphthalene	>75	–	93
Populus deltoides and *Kurthia* sp., *Micrococcus varian*, *Deinococcus radiodurans* and *Bacillus circulans*	Anthracene and naphthalene	>85		94
Alfalfa (*Medicago sativa* L.), *Ensif meliloti*, *Pseudomonas kunmingensis*, *Rhizobium petrolearium* and *Stenotrophomonas* sp.	*Phenanthrene*	20–60	–	95
Jatropha curcas, Pseudomonas aeruginosa PDB1, *Pseudomonas fragi* DBC, *Klebsiella pneumoniae* AWD5, *Alcaligenes faecalis* BDB4 and *Acinetobacter* sp. PDB4	Pyrene	97.2	*nod*, *nahR*, *nahAF*, *catA*, *kshA* and *hsaC*	96
Ryegrass and *Acinetobacter* sp. or AMF	Phenanthrene and pyrene	>90		97
Ryegrass (*Lolium multiflorum*) and *Arthrobacter pasce* strain (ZZ21) and/or *Bacillus cereus* strain (Z21)	Fluoranthene	74.9		98
Alfalfa (*M. sativa* L.), *Bacillus* sp. and *Flavobacterium* sp.	Total PAH[a]	25.8		99
Vertiveria zizanioides, *Bacillus* sp. and *Pseudomonas* sp.	Total PAH[c]	88–89%		100

[a] Different components of PAH were not studied separately.

[b] Napthalene, Acenaphthylene, Acenaphthene, Fluorene, Phenanthrene, Anthracene, Fluoranthene, Pyrene, Benzo[a]anthracene, Chyrsene, Benzo[b,k]fluoranthene, Benzo[a]pyrene, Indeno[1,2,3-cd]pyrene and Benzo[g,h,i]perylene.

[c] Fluoranthene, Phenantherene, Anthracene, Pyrene, Benzo(a) anthracene, Chrysene, Benzo(b) fluoranthene and Benzo(a) pyrene.

and eco-friendly mitigation is thus the need of the hour. PAH removal through chemical and photolytic oxidation, volatilization and sedimentation is costly and environmentally unsustainable[31]. Conversely, phytoremediation and microbial remediation, although cost-effective and ecologically sustainable, are dependent on the physico-chemical properties of the soil, microbial profile and plant communities present in the rhizosphere and may show incomplete and slow degradation rates. Till now, studies have focused on microbe-assisted phytoremediation, which uses either a single microbe or a consortium for remediation. However, the mechanism of action of a single microbe or consortium within the rhizosphere is not completely understood. Moreover, the rhizospheric ecosystem of higher plants has unique eco-biological characteristics which can be altered due to the addition of such microbe(s). It may also be difficult to provide enough microbial population for complete biodegradation of PAH.

Rhizoremediation is the use of plant and rhizospheric microbiota for the efficient degradation of PAH. The application of plant growth-promoting rhizobacteria (PGPR) provides bidirectional benefits by efficiently degrading PAH and improving plant growth and development, which in turn helps the microbes to grow and survive in the rhizosphere[87]. Various studies have confirmed that the degradation of PAH through rhizoremediation is far more efficient than other remediation techniques due to the exploitation of useful interactions between the host plants and their respective rhizo-microbiota. For example, >70% pyrene degradation was documented in vegetated soil compared to that in unplanted soil conditions (<40%), indicating that rhizo-microbiota, along with the host plants, accelerate the degradation process[88].

The rhizo-microbiota of specific host plants may include microbes significant in plant growth and development and a subpopulation possessing PAH-degrading genes such as ARDB. Such a type of healthy rhizo-microbiota may be formed naturally through microbial interactions within the rhizosphere or artificially through microbiome engineering. The latter includes the establishment of a more efficient microbiome artificially into the rhizosphere, which can completely degrade PAH. *In situ* microbiome engineering may be achieved through augmentation (elevating the levels of a specific microbial community using certain types of supplement), reduction (establishment of a non-conducive environment for undesirable microbial function) or bio-inoculation (application of a mixture of microbes involved in degradation)[89]. Plant–rhizosphere–microbial interactions need to be explored for better remediation of PAH-contaminated soil. Table 1 summarizes some of the beneficial interactions.

Conclusion and future prospects

Prolonged exposure of the soil to high PAH increases the risk of their bioaccumulation and entry into the food chain. PAH-induced stress adversely affects the plant–soil–microbial interactions, ultimately disrupting several ecosystem functions and services. To come up with suitable solution, this tripartite interaction must be completely understood. Being a dynamic system, it is in constant flux, and shows several regional and local variations. Since most PAH emissions are anthropogenic and associated with economic development, there seems to be no imminent near-future solution for this menace. To reduce toxic effects of PAH and minimize the damage to ecosystem and health, sustainable solutions are required. Tapping the potential of soil microbes which can efficiently degrade PAH seems to be the best possible sustainable solution. Rhizoremediation is a promising tool in establishing a healthy host plant microbial zone and developing an efficient PAH-degradation system. However, the diversity of rhizosphere microbes involved in rhizoremediation and their functional genes are still poorly understood. Exploring modern molecular technologies such as genomics, metabolomics, transcriptomics and proteomics for understanding the biochemistry of PAH-degrading microbes will provide adequate knowledge of potential genes and enzymes involved in the degradation process. This will lead to the development of genetically modified microbes or consortia and provide an effective and sustainable solution for soil remediation from PAH-induced stress.

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

---

1. Chen, X. *et al.*, Past, present, and future perspectives on the assessment of bioavailability/bioaccessibility of polycyclic aromatic hydrocarbons: a 20-year systemic review based on scientific econometrics. *Sci. Total Environ.*, 2021, **774**, 145585.
2. Shen, H. *et al.*, Global atmospheric emissions of polycyclic aromatic hydrocarbons from 1960 to 2008 and future predictions. *Environ. Sci. Technol.*, 2013, **47**, 6415–6424.
3. Zhang, Y. and Tao, S., Global atmospheric emission inventory of polycyclic aromatic hydrocarbons (PAHs) for 2004. *Atmos. Environ.*, 2009, **43**, 812–819.
4. Kumar, A., Ambade, B., Sankar, T. K., Sethi, S. S. and Kurwadkar, S., Source identification and health risk assessment of atmospheric PM2. 5-bound polycyclic aromatic hydrocarbons in Jamshedpur, India. *Sustain. Cit. Soc.*, 2020, **52**, 101801.
5. Liu, R., Dai, Y. and Sun, L., Effect of rhizosphere enzymes on phytoremediation in PAH-contaminated soil using five plant species. *PLoS ONE*, 2015, **10**, e0120369.
6. Patel, A. B., Shaikh, S., Jain, K. R., Desai, C. and Madamwar, D., Polycyclic aromatic hydrocarbons: sources, toxicity and remediation approaches. *Front. Microbiol.*, 2020, **11**, 562813.
7. Kuppusamy, S., Thavamani, P., Venkateswarlu, K., Lee, Y. B., Naidu, R. and Megharaj, M., Remediation approaches for polycyclic aromatic hydrocarbons (PAHs) contaminated soils: technological constraints, emerging trends and future directions. *Chemosphere*, 2017, **168**, 944–968.
8. Cristaldi, A., Conti, G. O., Jho, E. H., Zuccarello, P., Grasso, A., Copat, C. and Ferrante, M., Phytoremediation of contaminated soils by heavy metals and PAHs. A brief review. *Environ. Technol. Innov.*, 2017, **8**, 309–326.
9. Fismes, J., Perrin-Ganier, C., Empereur-Bissonnet, P. and Morel, J. L., Soil-to-root transfer and translocation of polycyclic aromatic hydrocarbons by vegetables grown on industrial contaminated soils. *J. Environ. Qual.*, 2002, **31**, 1649–1656.
10. Oguntimehin, I., Eissa, F. and Sakugawa, H., Negative effects of fluoranthene on the ecophysiology of tomato plants (*Lycopersicon esculentum* Mill). Fluoranthene mists negatively affected tomato plants. *Chemosphere*, 2010, **78**, 877–884.
11. Liste, H. H. and Prutz, I., Plant performance, dioxygenase-expressing rhizosphere bacteria, and biodegradation of weathered hydrocarbons in contaminated soil. *Chemosphere*, 2006, **62**, 1411–1420.
12. Kumar, M. *et al.*, Remediation of soils and sediments polluted with polycyclic aromatic hydrocarbons: to immobilize, mobilize, or degrade? *J. Hazard. Mater.*, 2021, **420**, 126534.
13. Krauss, M. and Wilcke, W., Polychlorinated naphthalenes in urban soils: analysis, concentrations, and relation to other persistent organic pollutants. *Environ. Pollut.*, 2003, **12**, 75–89.
14. Hussain, K., Hoque, R. R., Balachandran, S., Medhi, S., Idris, M. G., Rahman, M. and Hussain, F. L., Monitoring and risk analysis of PAHs in the environment. In *Handbook of Environmental Material Management* (ed. Hussain, C. M.), Springer International Publishing, AG, Cham, Switzerland, 2018, pp. 1–35.
15. Kanaly, R. A. and Harayama, S., Biodegradation of high-molecular-weight polycyclic aromatic hydrocarbons by bacteria. *J. Bacteriol.*, 2000, **182**, 2059–2067.
16. Qu, Y. *et al.*, Potential sources, influencing factors, and health risks of polycyclic aromatic hydrocarbons (PAHs) in the surface soil of urban parks in Beijing, China. *Environ. Pollut.*, 2020, **260**, 114016.
17. Duan, Y. *et al.*, Characteristics of polycyclic aromatic hydrocarbons in agricultural soils at a typical coke production base in Shanxi, China. *Chemosphere*, 2015, **127**, 64–69.
18. Berg, G. and Smalla, K., Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol. Ecol.*, 2009, **68**, 1–13.
19. van Loon, L. C., Plant responses to plant growth-promoting rhizobacteria. In *New Perspectives and Approaches in Plant Growth*, Springer, Dordrecht, The Netherlands, 2007, pp. 243–254.
20. Lagos, L. *et al.*, Current overview on the study of bacteria in the rhizosphere by modern molecular techniques: a mini-review. *J. Soil Sci. Plant Nutr.*, 2015, **15**, 504–523.
21. Ward, N. L. *et al.*, Three genomes from the phylum Acidobacteria provide insight into the lifestyles of these microorganisms in soils. *Appl. Environ. Microbiol.*, 2009, **75**, 2046–2056.
22. Liu, F., Mo, X., Kong, W. and Song, Y., Soil bacterial diversity, structure, and function of *Suaeda salsa* in rhizosphere and non-rhizosphere soils in various habitats in the Yellow River Delta, China. *Sci. Total Environ.*, 2020, **740**, 140144.
23. Qiao, Q. *et al.*, Characterization and variation of the rhizosphere fungal community structure of cultivated tetraploid cotton. *PLoS ONE*, 2019, **14**, e0207903.
24. Gai, J. P., Christie, P., Feng, G. and Li, X. L., Twenty years of research on community composition and species distribution of *Arbuscular mycorrhizal* fungi in China: a review. *Mycorrhiza*, 2006, **16**, 229–239.
25. Lee, S. M. and Ryu, C. M., Algae as new kids in the beneficial plant microbiome. *Front. Plant Sci.*, 2021, **12**, 599742.
26. Storey, S., Ashaari, M. M., Clipson, N., Doyle, E. and De Menezes, A. B., Opportunistic bacteria dominate the soil microbiome response to phenanthrene in a microcosm-based study. *Front. Microbiol.*, 2018, **9**, 2815.
27. Singh, M., Awasthi, A., Soni, S. K., Singh, R., Verma, R. K. and Kalra, A., Complementarity among plant growth promoting traits in rhizospheric bacterial communities promotes plant growth. *Sci. Rep.*, 2015, **5**, 1–8.
28. Gupta, A., Gupta, R. and Singh, R. L., Microbes and environment. In *Principles and Application of Environmental Biotechnology for a Sustainable Future*, Springer, Singapore, 2017, pp. 43–84.
29. Eilers, K. G., Lauber, C. L., Knight, R. and Fierer, N., Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. *Soil Biol. Biochem.*, 2010, **42**, 896–903.
30. dos Santos, J. J. and Maranho, L. T., Rhizospheric microorganisms as a solution for the recovery of soils contaminated by petroleum: a review. *J. Environ. Manage.*, 2018, **210**, 104–113.

31. Haritash, A. K. and Kaushik, C. P., Biodegradation aspects of polycyclic aromatic hydrocarbons (PAHs): a review. *J. Hazard. Mater.*, 2009, **169**, 1–15.
32. Singha, L. P. and Pandey, P., Rhizobacterial community of *Jatropha curcas* associated with pyrene biodegradation by consortium of PAH-degrading bacteria. *Appl. Soil Ecol.*, 2020, **155**, 103685.
33. Sahoo, B., Ningthoujam, R. and Chaudhuri, S., Isolation and characterization of a lindane degrading bacteria *Paracoccus* sp. NITDBR1 and evaluation of its plant growth promoting traits. *Int. Microbiol.*, 2019, **22**, 155–167.
34. Szulc, A. *et al.*, The influence of bioaugmentation and biosurfactant addition on bioremediation efficiency of diesel-oil contaminated soil: feasibility during field studies. *J. Environ. Manage.*, 2014, **132**, 121–128.
35. Biswas, B., Qi, F., Biswas, J. K., Wijayawardena, A., Khan, M. A. I. and Naidu, R., The fate of chemical pollutants with soil properties and processes in the climate change paradigm – a review. *Soil Syst.*, 2018, **2**, 51.
36. Abdel-Shafy, H. I. and Mansour, M. S., A review on polycyclic aromatic hydrocarbons: source, environmental impact, effect on human health and remediation. *Egypt. J. Petrol.*, 2016, **25**, 107–123.
37. Ahangar, A. G., Sorption of PAHs in the soil environment with emphasis on the role of soil organic matter: a review. *World Appl. Sci. J.*, 2010, **11**, 759–765.
38. Singh, S. K. and Haritash, A. K., Polycyclic aromatic hydrocarbons: soil pollution and remediation. *Int. J. Environ. Sci. Technol.*, 2019, **16**, 6489–6512.
39. Irha, N., Slet, J. and Petersell, V., Effect of heavy metals and PAH on soil accessed via dehydrogenase assay. *Environ. Int.*, 2003, **28**, 779–782.
40. Włóka, D., Kacprzak, M., Grobelak, A., Grosser, A. and Napora, A., The Impact of PAHs contamination on the physicochemical properties and microbiological activity of industrial soils. *Polycycl. Aromat. Compd.*, 2015, **35**, 372–386.
41. Magi, E., Bianco, R., Ianni, C. and di Carro, M., Distribution of polycyclic aromatic hydrocarbons in the sediments of the Adriatic Sea. *Environ. Pollut.*, 2002, **119**, 91–98.
42. Maletić, S. P., Beljin, J. M., Rončević, S. D., Grgić, M. G. and Dalmacija, B. D., State of the art and future challenges for polycyclic aromatic hydrocarbons is sediments: sources, fate, bioavailability and remediation techniques. *J. Hazard. Mater.*, 2019, **365**, 467–482.
43. Tang, J. C., Wang, R. G., Niu, X. W., Wang, M., Chu, H. R. and Zhou, Q. X., Characterization of the rhizoremediation of petroleum-contaminated soil: effect of different influencing factors. *Biogeosciences*, 2010, **7**, 3961–3969.
44. Labud, V., Garcia, C. and Hernandez, T., Effect of hydrocarbon pollution on the microbial properties of a sandy and a clay soil. *Chemosphere*, 2007, **66**, 1863–1871.
45. Li, S., Hu, S., Shi, S., Ren, L., Yan, W. and Zhao, H., Microbial diversity and metaproteomic analysis of activated sludge responses to naphthalene and anthracene exposure. *RSC Adv.*, 2019, **9**, 22841–22852.
46. Maliszewska-Kordybach, B., Klimkowicz-Pawlas, A., Smreczak, B. and Janusauskaite, D., Ecotoxic effect of phenanthrene on nitrifying bacteria in soils of different properties. *J. Environ. Qual.*, 2007, **36**, 1635–1645.
47. Hou, J., Xu, X., Yu, H., Xi, B. and Tan, W., Comparing the long-term responses of soil microbial structures and diversities to polyethylene microplastics in different aggregate fractions. *Environ. Int.*, 2021, **149**, 106398.
48. Wu, Y., Zeng, J., Zhu, Q., Zhang, Z. and Lin, X., PH is the primary determinant of the bacterial community structure in agricultural soils impacted by polycyclic aromatic hydrocarbon pollution. *Sci. Rep.*, 2017, **7**, 40093.
49. Yi, M., Zhang, L., Li, Y. and Qian, Y., Structural, metabolic, and functional characteristics of soil microbial communities in response to benzo[a]pyrene stress. *J. Hazard. Mater.*, 2022, **431**, 128632.
50. Liu, K. *et al.*, Response of rhizosphere microbial community in high-PAH-contaminated soil using *Echinacea purpurea* (L.) Moench. *Appl. Sci.*, 2022, **12**, 2973.
51. Zhang, L., Yi, M. and Lu, P., Effects of pyrene on the structure and metabolic function of soil microbial communities. *Environ. Pollut.*, 2022, 119301.
52. Mueller, K. E. and Shann, J. R., PAH dissipation in spiked soil: impacts of bioavailability, microbial activity, and trees. *Chemosphere*, 2006, **64**, 1006–1014.
53. Margesin, R., Determination of enzyme activities in contaminated Soil. In *Monitoring and Assessing Soil Bioremediation*, Germany, Berlin, Heidelberg, 2005, pp. 309–320.
54. Shen, G., Lu, Y., Zhou, Q. and Hong, J., Interaction of polycyclic aromatic hydrocarbons and heavy metals on soil enzyme. *Chemosphere*, 2005, **61**, 1175–1182.
55. Maliszewska-Kordybach, B., Klimkowicz-Pawlas, A., Smreczak, B. and Stuczyński, T., Relationship between soil concentrations of PAHs and their regional emission indices. *Water Air Soil Pollut.*, 2010, **213**, 319–330.
56. Kreslavski, V. D. *et al.*, Effects of polyaromatic hydrocarbons on photosystem II activity in pea leaves. *Plant Physiol. Biochem.*, 2014, **81**, 135–142.
57. Calabrese, E. J. and Blain, R. B., Hormesis and plant biology. *Environ. Pollut.*, 2009, **157**, 42–48.
58. Chaîneau, C. H., Morel, J. L. and Oudot, J., Phytotoxicity and plant uptake of fuel oil hydrocarbons. *J. Environ. Qual.*, 1997, **26**, 1478–1483.
59. Henner, P., Schiavon, M., Druelle, V. and Lichtfouse, E., Phytotoxicity of ancient gaswork soils. Effect of polycyclic aromatic hydrocarbons (PAHs) on plant germination. *Org. Geochem.*, 1999, **30**, 963–969.
60. Smreczak, B. and Maliszewska-Kordybach, B., Seeds germination and root growth of selected plants in PAH contaminated soil. *Fresenius Environ. Bull.*, 2003, **12**, 946–949.
61. García-Alonso, S., Pérez-Pastor, R. M., Sevillano-Castaño, M. L., Escolano, O. and García-Frutos, F. J., Influence of particle size on the quality of PAH concentration measurements in a contaminated soil. *Polycycl. Aromat. Compd.*, 2008, **28**, 67–83.
62. Rein, A., Adam, I. K., Miltner, A., Brumme, K., Kästner, M. and Trapp, S., Impact of bacterial activity on turnover of insoluble hydrophobic substrates (phenanthrene and pyrene) – model simulations for prediction of bioremediation success. *J. Hazard. Mater.*, 2016, **306**, 105–114.
63. Su, Y. H. and Zhu, Y. G., Uptake of selected PAHs from contaminated soils by rice seedlings (*Oryza sativa*) and influence of rhizosphere on PAH distribution. *Environ. Pollut.*, 2008, **155**, 359–365.
64. Briggs, G. G., Bromilow, R. H. and Evans, A. A., Relationships between lipophilicity and root uptake and translocation of non-ionised chemicals by barley. *Pestic. Sci.*, 1982, **13**, 495–504.
65. Marchal, G., Smith, K. E. C., Mayer, P., Wollesen De Jonge, L. and Karlson, U. G., Impact of soil amendments and the plant rhizosphere on PAH behaviour in soil. *Environ. Pollut.*, 2014, **188**, 124–131.
66. Pignatello, J. J. and Li, J., Facilitated bioavailability of PAHs to native soil bacteria promoted by nutrient addition. In AGU Fall Meeting Abstracts, 2006.
67. Fu, P. P., Xia, Q., Sun, X. and Yu, H., Phototoxicity and environmental transformation of polycyclic aromatic hydrocarbons (PAHs)-light-induced reactive oxygen species, lipid peroxidation, and DNA damage. *J. Environ. Sci. Health, Part C*, 2012, **30**, 1–41.
68. Ma, B., He, Y., Chen, H., Hai, X., Ming, J. and Rengel, Z., Dissipation of polycyclic aromatic hydrocarbons (PAHs) in the rhizosphere: synthesis through meta-analysis. *Environ. Pollut.*, 2010, **158**, 855–861.
69. Singer, A. C., Crowley, D. E. and Thompson, I. P., Secondary plant metabolites in phytoremediation and biotransformation. *Trends Biotechnol.*, 2003, **21**, 123–130.

70. Goel, G., Pandey, P., Sood, A., Bisht, S., Maheshwari, D. K. and Sharma, G. D., Transformation of pWWO in *Rhizobium leguminosarum* DPT to engineer toluene degrading ability for rhizoremediation. *Indian J. Microbiol.*, 2012, **52**, 197–202.
71. Shen, Y., Li, J., Gu, R., Yue, L., Wang, H., Zhan, X. and Xing, B., Carotenoid and superoxide dismutase are the most effective antioxidants participating in ROS scavenging in phenanthrene accumulated wheat leaf. *Chemosphere*, 2018, **197**, 513–525.
72. Liu, H., Weisman, D., Ye, Y. B., Cui, B., Huang, Y. H., Colón-Carmona, A. and Wang, Z. H., An oxidative stress response to polycyclic aromatic hydrocarbon exposure is rapid and complex in *Arabidopsis thaliana*. *Plant Sci.*, 2009, **176**, 375–382.
73. Mukhopadhyay, S., Dutta, R. and Das, P., A critical review on plant biomonitors for determination of polycyclic aromatic hydrocarbons (PAHs) in air through solvent extraction techniques. *Chemosphere*, 2020, **251**, 126441.
74. Singh, L. and Agarwal, T., Polycyclic aromatic hydrocarbons in diet: Concern for public health. *Trends Food Sci. Technol.*, 2018, **79**, 160–170.
75. Lee, S. H., Lee, W. S., Lee, C. H. and Kim, J. G., Degradation of phenanthrene and pyrene in rhizosphere of grasses and legumes. *J. Hazard. Mater.*, 2008, **153**, 892–898.
76. Rohrbacher, F. and St-Arnaud, M., Root exudation: the ecological driver of hydrocarbon rhizoremediation. *Agronomy*, 2016, **6**, 19.
77. Muratova, A., Hübner, T., Tischer, S., Turkovskaya, O., Möder, M. and Kuschk, P., Plant – rhizosphere-microflora association during phytoremediation of PAH-contaminated soil. *Int. J. Phytoremed.*, 2003, **5**, 137–151.
78. Liu, S., Luo, Y., Cao, Z., Wu, L. and Wong, M., Effect of ryegrass (*Lolium multiflorum* L.) growth on degradation of benzo[a]pyrene and enzyme activity in soil. *J. Food Agric. Environ.*, 2013, **11**, 247–253.
79. Bouasria, A. *et al.*, Changes in root-associated microbial communities are determined by species-specific plant growth responses to stress and disturbance. *Eur. J. Soil Biol.*, 2012, **52**, 59–66.
80. D'Orazio, V., Ghanem, A. and Senesi, N., Phytoremediation of pyrene contaminated soils by different plant species. *Clean-Soil, Air, Water*, 2013, **41**, 377–382.
81. Thomas, F. and Cébron, A., Short-term rhizosphere effect on available carbon sources, phenanthrene degradation, and active microbiome in an aged-contaminated industrial soil. *Front. Microbiol.*, 2016, **7**, 92.
82. Xiang, L. *et al.*, Integrating biochar, bacteria, and plants for sustainable remediation of soils contaminated with organic pollutants. *Environ. Sci. Technol.*, 2022, **56**, 16546–16566.
83. Nie, M., Yang, Q., Jiang, L. F., Fang, C. M., Chen, J. K. and Li, B., Do plants modulate biomass allocation in response to petroleum pollution? *Biol. Lett.*, 2010, **6**, 811–814.
84. Zhao, C. *et al.*, Regulation of endogenous phytohormones alters the fluoranthene content in *Arabidopsis thaliana*. *Sci. Total Environ.*, 2019, **688**, 935–943.
85. Ahammed, G. J. *et al.*, Brassinosteroids induce plant tolerance against phenanthrene by enhancing degradation and detoxification in *Solanum lycopersicum* L. *Ecotoxicol. Environ. Saf.*, 2012, **80**, 28–36.
86. Kamath, R., Schnoor, J. L. and Alvarez, P. J. J., Effect of root-derived substrates on the expression of *nah–lux* genes in *Pseudomonas fluorescens* HK44: implications for PAH biodegradation in the rhiziosphere. *Environ. Sci. Technol.*, 2004, **38**, 1740–1745.
87. Azaizeh, H., Castro, P. M. L. and Kidd, P., Biodegradation of organic xenobiotic pollutants in the rhizosphere. In *Organic Xenobiotics and Plants: From Mode of Action to Ecophysiology*, Springer, Dordrecht, The Netherlands, 2011, pp. 191–2015.
88. Liste, H. H. and Alexander, M., Accumulation of phenanthrene and pyrene in rhizosphere soil. *Chemosphere*, 2000, **40**, 11–14.
89. Kotoky, R., Rajkumari, J. and Pandey, P., The rhizosphere microbiome: significance in rhizoremediation of polyaromatic hydrocarbon contaminated soil. *J. Environ. Manage.*, 2018, **217**, 858–870.
90. Dominguez, J. J. A., Bacosa, H. P., Chien, M. F. and Inoue, C., Enhanced degradation of polycyclic aromatic hydrocarbons (PAHs) in the rhizosphere of sudangrass (*Sorghum × drummondii*). *Chemosphere*, 2019, **234**, 789–795.
91. Zhao, X., Miao, R., Guo, M. and Zhou, Y., Effects of Fire phoenix (a genotype mixture of *Fesctuca arundinecea* L.) and *Mycobacterium* sp. on the degradation of PAHs and bacterial community in soil. *Environ. Sci. Pollut. Res.*, 2021, **28**, 25692–25700.
92. Kong, F. X., Sun, G. D. and Liu, Z. P., Degradation of polycyclic aromatic hydrocarbons in soil mesocosms by microbial/plant bioaugmentation: performance and mechanism. *Chemosphere*, 2018, **198**, 83–91.
93. Bisht, S. *et al.*, Utilization of endophytic strain bacillus sp. SBER3 for biodegradation of polyaromatic hydrocarbons (PAH) in soil model system. *Eur. J. Soil Biol.*, 2014, **60**, 67–76.
94. Bisht, S. *et al.*, Biodegradation of naphthalene and anthracene by chemo-tactically active rhizobacteria of *Populus deltoides*. *Br. J. Microbiol.*, 2010, **41**, 922–930.
95. Muratova, A., Dubrovskaya, E., Golubev, S., Grinev, V., Chernyshova, M. and Turkovskaya, O., The coupling of the plant and microbial catabolisms of phenanthrene in the rhizosphere of *Medicago sativa*. *J. Plant Physiol.*, 2015, **188**, 1–10.
96. Wołejko, E., Jabłońska-Trypuć, A., Wydro, U., Butarewicz, A. and Łozowicka, B., Soil biological activity as an indicator of soil pollution with pesticides – a review. *Appl. Soil Ecol.*, 2020, **147**, 103356.
97. Yu, X. Z., Wu, S. C., Wu, F. Y. and Wong, M. H., Enhanced dissipation of PAHs from soil using mycorrhizal ryegrass and PAH-degrading bacteria. *J. Hazard. Mater.*, 2011, **186**, 1206–1217.
98. Li, W. *et al.*, Combination of plant-growth-promoting and fluoranthene-degrading microbes enhances phytoremediation efficiency in the ryegrass rhizosphere. *Environ. Sci. Pol. Res.*, 2021, **28**, 6068–6077.
99. Zhang, J., Lin, X., Liu, W., Wang, Y., Zeng, J. and Chen, H., Effect of organic wastes on the plant-microbe remediation for removal of aged PAHs in soils. *J. Environ. Sci.*, 2012, **24**, 1476–1482.
100. Dhote, M., Kumar, A., Jajoo, A. and Juwarkar, A., Assessment of hydrocarbon degradation potentials in a plant–microbe interaction system with oil sludge contamination: a sustainable solution. *Int. J. Phytoremed.*, 2017, **19**, 1085–1092.

ACKNOWLEDGEMENTS. We thank the Council of Scientific and Industrial Research, New Delhi, for granting Junior Research Fellowship to K.V. (file no. 09/045(1772)/2019-EMR-I). The study is supported by the Ministry of Environment, Forest and Climate Change (Project Grant Number: 3-6/2020-RE) to VM and PGS.

Received 3 November 2022; re-revised accepted 10 July 2023

doi: 10.18520/cs/v125/i8/837-845