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Plant–bacteria partnerships for the remediation of persistent organic pollutants

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Abstract High toxicity, bioaccumulation factor and widespread dispersal of persistent organic pollutants (POPs) cause environmental and human health hazards. The combined use of plants and bacteria is a promising approach for the remediation of soil and water contaminated with POPs. Plants provide residency and nutrients to their associated rhizosphere and endophytic bacteria. In return, the bacteria support plant growth by the degradation and detoxification of POPs. Moreover, they improve plant growth and health due to their innate plant growth-promoting mechanisms. This review provides a critical view of factors that affect absorption and translocation of POPs in plants and the limitations that plant have to deal with during the remediation of POPs. Moreover, the synergistic effects of plant–bacteria interactions in the phytoremediation of organic pollutants with special reference to POPs are discussed.

Keywords Persistent organic pollutants · Phytoremediation · Plant–bacteria partnerships · Endophytic bacteria · Rhizosphere bacteria · Bacterial assisted phytoremediation

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Introduction

After World War II, economic boost due to advances in science and technology has resulted in the use of a wide range of synthetic chemicals and thus, in an exponential increase in their production. Although these chemicals proved to be beneficial in agricultural and industrial processes, several studies reported their harmful effects on living organisms and the environment. Among these chemicals, POPs are of increasing concern due to their persistent behavior and high toxicity in natural settings. POPs are defined as "intentionally or unintentionally produced lipophilic chemicals capable of accumulating in the environment and are resistant to photochemical degradation with long-range dispersal potential" (Sharma et al. 2014a). POPs are categorized into three major groups on the basis of their origin and use: organochlorine pesticides (OCPs), industrial chemicals (ICs), and unintended by-products (UIBPs) (UNEP 2003) (Table 1).

The first report of harmful effects of POPs was the publication of Carson and Darling "Silent Spring" (Carson and Darling 1962). They traces the impact of DDT as it is absorbed by creature after creature in the food chain, until eventually birds' eggs are unable to hatch, because their shells have become so brittle that they break when the birds sit on them. As a result of this report, DDT was banned in 1973 (Staniforth 2013). In later years, mass-poisoning episodes by diseases, Yusho and Yu-Cheng, in Japan and Taiwan, respectively, strengthened the discouragement of the release of POPs in the environment (Bradberry et al. 2014). Considering the aspects of human and environmental health deterioration, the Stockholm Convention of POPs was organized by the United Nations Environment Program (UNEP) in 2001. The convention was signed to regulate and ban the use of a preliminary list of 12 chemicals—collectively referred to as the dirty dozen—that showed high persistence, bioaccumulation in fatty tissues,

Table 1 List of POPs, including dirty dozen chemicals, their usage, toxicity, and persistence

Group name	Generic name	Usage	Toxicity (LD_{50})	Persistence (half-life)
OCPs	Aldrin[a]	Insecticide	39 mg/kg	5 years
	Dieldrin[a]	Insecticide	49 mg/kg	5 years
	Chlordane[a]	Pesticide	83–590 mg/kg	1–3 years
	DDT[a]	Pesticide	113–800 mg/kg	2–15 years
	Endrin[a]	Pesticide	43.4 mg/kg	12–15 years
	Heptachlor[a]	Pesticide	40–162 mg/kg	Up to 2 years
	Mirex[a]	Pesticide	740 mg/kg	Up to 10 years
	Toxaphene[a]	Pesticide	80–293 mg/kg	1–12 years
	Hexachlorobenzene[a]	Fungicide	19–245 mg/kg	2.7–22.9 years
	Chlordecone	Insecticide	126–132 mg/kg	Up to 50 years
	Lindane (γ-HCH)	Insecticide	88–190 mg/kg	Up to 2 weeks
	α, β-Hexachlorocyclohexane	Insecticide	88 mg/kg	–
	Endosulfan	Pesticide	18–160 mg/kg	Up to 50 days
ICs	PCBs[a]	Insulating fluid	1010–4250 mg/kg	0.9–7.2 years
	Commercial pentaBDE	Flame retardant	2640–6200 mg/kg	10–20 days
	Commercial octaBDE	Flame retardant	–	14–70 days
	Hexabromocyclododecane	Flame retardant	10 gm/kg	–
UIBPs	Perfluorooctane sulfonic acid	Coating	–	4 years
	Perfluorooctane sulfonyl fluoride	Clothing	–	4 years
	Dioxins–dibenzodioxins[a]	Byproduct of chlorine	22 μg/kg	20 years
	Furans–dibenzofurans[a]	Herbicide	22 μg/kg	20 years
	Pentachlorobenzene	Pesticide	125–1080 mg/kg	–

Sources: Haffner and Schecter (2014), Ritter et al. (1995), WWF (2005)

[a] Indicates dirty dozen chemicals

and toxicity (Johansen 2003; Xu et al. 2013) (Table 1). The dirty dozen included aldrin, dieldrin, DDT, chlordane, mirex, endrin, heptachlor, toxaphene, hexachlorobenzene (HCB), polychlorinated biphenyls (PCBs), dibenzodioxins, and dibenzofurans. In the following years, 11 more chemicals (Table 1) were added to the list due to their persistence and toxicity (Haffner and Schecter 2014). Although many of the developed countries have banned the production of most of the POPs, their use is still a common practice in most of the developing countries (Sharma et al. 2014b).

Phytoremediation is a promising approach for the remediation of soil and water contaminated with organic and inorganic pollutants (Khan et al. 2014; McCutcheon and Schnoor 2004; Schwitzguébel and Schröder 2009). However, the presence of organic pollutants including POPs in soil and water decreases plant growth and phytoremediation efficacy (Gerhardt et al. 2009; Ibáñez et al. 2012; Mench et al. 2009; Saleh et al. 2004). Moreover, plants have certain limits with respect to their capabilities to remove organic pollutants from the environment (Carvalho et al. 2014; Chaudhry et al. 2005; Khoudi et al. 2013). The combined use of plants and bacteria has been recently proposed to enhance the efficiency of remediation of soil contaminated with organic pollutants including POPs (Becerra-Castro et al. 2013; Glick 2010; Haslmayr et al. 2014; Weyens et al. 2009a). Rhizobacteria colonize the roots, whereas endophytic bacteria reside inside the plant tissues (Compant et al. 2010). Plants provide the space and nutrients to the bacteria. In return, rhizosphere and endophytic bacteria improve the bioavailability and allow to mineralization of organic pollutants. The bacteria also improve plant growth due to their plant growth-promoting activities such as siderophore and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase production and nitrogen fixation. Moreover, the bacteria reduce the toxicity and evapotranspiration of the pollutants in the environment (Afzal et al. 2014a; Khan et al. 2013a; Shehzadi et al. 2015; Vangronsveld et al. 2009; Weyens et al. 2009b; Yousaf et al. 2014).

This review is structured to discuss the occurrence, fate, and degradation of POPs by plant and plant–bacteria synergism. Moreover, the role of rhizosphere and endophytic bacteria to accelerate the phytoremediation of POPs is emphasized.

POPs in the environment

POPs are carbon-based compounds that show resistance to degradation under natural conditions and thus stay in the environment for long periods of time (Weber et al. 2011). The

fundamental reason behind their stability is the presence of carbon–chlorine bond that resist against hydrolysis (El-Shahawi et al. 2010). The stability is further increased by increasing the number of chlorine atoms in the compound. Therefore, the compounds with higher halogenation are more resistant to degradation as compared to the compounds with lower halogenation (Wikoff et al. 2012).

In addition to stability, the semivolatile and insoluble nature of POPs allow their long distance dispersal and worldwide distribution (Wang 2012). They have been found in the areas where they were never used, e.g., the Arctic of Alaska. This unexpected occurrence is because of the transportation of many of the POPs from the USA and Canada to Alaska, where they sank and settled in the ice sheets without being degraded (Braune et al. 2005; Newton et al. 2014). In general, POPs tend to evaporate in hot places and then condense back in colder regions (Nurzhanova et al. 2013; Qiu 2013).

Due to high stability and long-range transportation characteristics, POPs find their ways from water and air into the soil ecosystem where they are taken up by plants and living organisms (Hao et al. 2014; McLeod et al. 2014; Morris et al. 2014). They follow the usual process of bioaccumulation and biomagnification as they move up in each trophic level of the food chain. The first report on the bioaccumulation of POPs in biotic elements was put forward in 1970 when polar bears were found to have pesticides in their fat tissues (Lie et al. 2003). Later on, many studies highlighted the trans-boundary nature of POPs along with their deteriorating effects on wildlife and human health (Bowes and Jonkel 1975; El-Shahawi et al. 2010; Li and Macdonald 2005; Muir et al. 1988; Norstrom and Muir 1994; Voldner and Li 1995). Although most of the studies were related to arctic region, these findings reduced the release of these chemicals in natural environments.

Humans along with other tertiary carnivores reside at the top of the food chain and, thereby, are at high risk of exposure to POPs as compared to the organisms at lower trophic levels (Lee et al. 2014a; Wang et al. 2014). Human exposure to POPs begins prenatally as many of them possess ability to cross the placenta. Soon after birth, exposure occurs through breastfeeding and later by ingestion, inhalation, and dermal contact (Man et al. 2014; Vafeiadi et al. 2014). Once they are within the body, POPs are taken up by adipocytes due to their lipophilic nature where they finally become a part of the adipose tissues and liver (Dewailly et al. 1999; Lee et al. 2014b). Their continuous accumulation can lead to metabolic disorders triggering cardiovascular diseases and physical health illness including larger body burdens. Usually, the accumulated POPs are slowly released into the blood stream. However, during the period of large mobilization of adipose tissue, such as pregnancy, weight loss, and breastfeeding, they are released at a faster rate and cause severe damages to fetuses or infants (La Merrill et al. 2012). Therefore, the remediation of POPs-contaminated soil and water is one of the key topics in the field of environment science and engineering (Abhilash et al. 2013; Agyekum et al. 2014; Becerra-Castro et al. 2013; Chhikara et al. 2010; Florence et al. 2015).

Phytoremediation of POPs

Phytoremediation is an eco-friendly technology that utilizes plants, to transform, translocate, sequester, extract, and/or detoxify the pollutants present in sediments, soil, groundwater, surface water, and even in the atmosphere (Chigbo and Batty 2014; Samardjieva et al. 2015; Susarla et al. 2002) and thus remediate or restore the contaminated sites. Plants may take up POPs from the environment and translocate in their different tissues (Ahmad et al. 2012; Chhikara et al. 2010; Germaine et al. 2009). The uptake of POPs in plants depends on a number of physicochemical characteristics of these compounds (Admire et al. 2014; Campanella et al. 2002; Zhan et al. 2015). These physicochemical characteristics are octanol–water partition coefficient (log K_{ow}), acidity constant (pK_a), aqueous solubility (S_w), octanol solubility (S_o), and the concentration of the pollutant (Admire et al. 2014; Alkorta and Garbisu 2001; Zeng et al. 2012). Among all these characteristics, the role of log K_{ow} value is of significant concern due to its direct involvement in determining how hydrophobic or lipophilic the compound is. Usually, the compounds having lower log K_{ow} values (0.5–3.0) are easily taken up by plants as compared to those having higher log K_{ow} values. In the case of POPs, log K_{ow} value of most of the compounds range between 3.0 and 8.3, making them resilient for phytouptake (Takaki et al. 2014; White and Zeeb 2007) (Table 2). Consequently, POPs bind to lipid membranes of plant roots (Chaudhry et al. 2002; White and Zeeb 2007).

In addition to log K_{ow} value, the uptake and translocation of POPs in plants depend upon POP and plant type (Gleba et al. 1999; Mitton et al. 2014; Pilon-Smits 2005). POPs, like aldrin, dieldrin, heptachlor, chlordane, lindane, DDT, etc., have been found to be taken up at different rate by different plants irrespective of their high log K_{ow} values (Agyekum et al. 2014; Calabrese and Blain 2009; Mattina et al. 2000). Moreover, plant physiology and transpiration rate affect the uptake of POPs in plants. For example, lichens accumulated higher levels of POPs than pine needles (Ockenden et al. 1998). Similarly, zucchini and pumpkin accumulated high concentration of DDT than tall fescue, alfalfa, and rye grass (Lunney et al. 2004). In conditions where uptake of POPs is not feasible, the main route of POP uptake could be the direct absorption by plant roots, volatilization from soil and absorption by leaves, and particle-facilitated transportation along with deposition on aerial parts (Ficko et al. 2010; Ockenden et al. 1998; Smith and Jones 2000; Whitfield Åslund et al. 2007).

Although POPs could enter plants through roots and leaves (Wang and Liu 2007), these are mainly taken up by roots and

Table 2 The log K_{ow} values for POPs

Generic name	Log K_{ow}	Reference
Aldrin	5.52	Garten and Trabalka (1983)
Dieldrin	5.48	Mackay (1982)
Chlordane (α, β, γ)	5.66, 5.62, 5.44	Simpson et al. (1995)
DDT	6.2	Weyens et al. (2009b)
Endrin	4.71	Finizio et al. (1997)
Heptachlor	6.10	Simpson et al. (1995)
Mirex	6.89	Mackay (1982)
Toxaphene	4.77 to 6.64	Fisk et al. (1999)
Hexachlorobenzene	5.23	Mackay (1982)
Chlordecone	4.5	Cabidoche et al. (2009)
Gamma-hexachlorocyclohexane	3.85	Mackay (1982)
Hexachlorocyclohexane	3.89 and 3.95	Isnard and Lambert (1988)
Endosulfan	3.5	DeLorenzo et al. (2002)
PCBs	3.76 to 8.26	Wu et al. (2008)
Hexabromobiphenyl	6.39	Mackay (1982)
Commercial pentaBDE	6.64 to 6.97	Rahman et al. (2001)
Commercial octaBDE	5.5 to 8.9	Rahman et al. (2001)
Hexabromocyclododecane	5.62	Hayward et al. (2006)
Dioxins–dibenzodioxins	4.20	Wang and Wong (2002)
Pentachlorobenzene	5.19	Mackay (1982)

translocated to the aboveground parts (Lunney et al. 2004; Mo et al. 2008). As POPs are manmade chemicals, specific transporter proteins for their transportation are absent in plants; hence, their uptake by roots occurs via simple diffusion through the cell wall from where they enter the xylem stream (Campos et al. 2008). Different plant species can absorb different POPs at different extents (Burken et al. 2005; Mikes et al. 2009; Nash and Beall 1970). The detailed description of different plants and their abilities to absorb and/or translocate different POPs has been presented in Table 3.

After uptake and translocation, to avoid the toxicity associated with absorbed pollutants, plants usually follow one of the two procedures, evapotranspiration and/or phytodegradation. For most of the pollutants, evapotranspiration is the major mechanism in which plants release the pollutants in the atmosphere through their leaves. During the course of evolution, plants were not under selection pressure and hence have not adopted pathways for mineralization of organic pollutants (Burken 2003; Gerhardt et al. 2009). Regarding phytodegradation, partial degradation of pollutants within plants takes place through *in planta* detoxification mechanisms, i.e., transformation (phase 1), conjugation (phase 2), and compartmentalization (phase 3) (Fig. 1).

This mechanism is generally termed as green-liver model (Sandermann 1992, 1994). Phytodegradation of POPs takes place by the virtue of oxidation reactions, hydrolysis, and epoxide formation (Chaudhry et al. 2002). Among these, oxidation is more prevalent and takes place by the action of different plant-derived microsomal enzymes such as cytochromes P450, peroxidases, and flavin-dependent monooxygenases (Durst and Benveniste 1993; Khandare et al. 2012; Naumann et al. 2002). These plant-derived microsomal enzymes are capable of degrading numerous POPs due to their reactive nature. For example, cytochrome P450 can act on organophosphate (P=S→P=O) insecticides with the release of atomic sulfur (Neal 1980). This mechanism of desulfuration has been observed as a cytochrome P450-catalyzed reaction in maize and sorghum during the degradation of methidathion, malathion, diazinon, and isozafos (Moreland et al. 1993, 1995). Furthermore, the cytochrome P450 system is reported to be involved in the metabolism of different PCB congeners and carbamate compounds (Chaudhry et al. 2002; Lee and Fletcher 1992).

To improve the overall potential of plant-based phytoremediation, the combined use of plants and bacteria has been recently proposed which can significantly enhance the degradation of organic pollutants including POPs *in planta* as well as *ex planta* (Afzal et al. 2014b; Glick 2010; Khan et al. 2013a; Mitter et al. 2013). The following sections elucidate the importance of plant-bacteria partnerships for the remediation of POPs-contaminated environment.

Plant–bacteria partnership for the remediation of POPs

In plant–bacteria partnerships, POPs could be degraded by plant-associated bacteria, mainly rhizobacteria (Afzal et al. 2014a; Glick 2010; Mackova et al. 2009; Weyens et al.

Table 3 Absorption/translocation of different POPs in different plants along with the target organ

POPs	Plant	Plant uptake	Target	Reference
Lindane	*Brassica napus*	Absorbed and translocated	Shoot	Westcott (1985)
	Zea mays			Heinrich and Schulz (1996)
	Coffea liberica	Absorbed	Root	Ruegg et al. (1977)
Hexachlorobenzene	*Picea abies*	Translocated	Needles	Weiss et al. (1998)
	Oryza sativa		All parts	Liu et al. (2013)
Dieldrin	*Glycine soja*	Translocated	Shoot	Nash and Beall (1970)
	Rhizophora mangle			Walsh et al. (1974)
	Lolium perenne	Absorbed	Root	Voerman and Besemer (1975)
Endrin, heptachlor	*Glycine max*	Translocated	Shoot	Nash and Beall (1970)
DDT	*Vigna unguiculata*	Absorbed and translocated	Shoot	Kiflom et al. (1999)
	Phragmites australis, *Oryza sativa*			Chu et al. (2006)
	Lolium perenne	Absorbed	Root	Voerman and Besemer (1975)
	Lpomoea batatas			Talekar et al. (1985)
Heptachlor epoxide	Forage crops	Translocated	Shoot	Singh et al. (1992)
T-chlordane	Forage crops	Translocated	Shoot	Singh et al. (1992)
DDE	*Lolium perenne*	Absorbed	Root	White (2000), Voerman and Besemer (1975)
	Phaseolus coccineus			White (2000)
	Cucurbita pepo	Translocated	Shoot	White et al. (2003)
Chlordane	*Daucus carota*, *Beta vulgaris*, *Solanum tuberosum*	Absorbed	Root	Mattina et al. (2000)
	Spinacia oleracea, *Lactuca sativa*, *Cucurbita andreana*, *Taraxacum*	Translocated	Shoot	Mattina et al. (2000)
2,2-Bis(p-chlorophenyl)-1, 1-dichloroethylene	*Cucurbita andreana*, *Cucurbita pepo*	Translocated	Shoot	White et al. (2005)
PCBs	*Phragmites australis*, *Oryza sativa*,	Absorbed and translocated	Shoot	Chu et al. (2006)
Polybrominated diphenyl ethers	*Nicotiana tabacum*, *Solanaceae*	Translocated	Shoot	Vrkoslavová et al. (2010)
Aldrin	*Ipomoea batatas*	Absorbed	Root	Talekar et al. (1985)
Organochlorine	*Ipomoea batatas, Colocasia esculenta*, *Ipomoea batatas*	Accumulation	Root	Florence et al. (2015)

2009a). In this association, bacteria possessing catabolic genes survive and proliferate in the close vicinity of roots and in some cases in the internal tissues of host plant without causing pathogenicity (Naveed et al. 2014; Sessitsch et al. 2005). Plants provide optimum conditions to these microorganisms to proliferate by offering nutrients and residency while allowing them to feed upon pollutants in the rhizosphere as well as in the endosphere. Therefore, the combined use of plants and the associated bacteria (pollutant-degrading and/or plant growth-promoting) strengthens the role of each partner. In this sense, bacteria help host plant to overcome contaminant-induced stress responses and develop high shoot and root biomass, which ultimately enhances microbial population and the degradation of organic pollutants including POPs (Weyens et al. 2009a). Furthermore, it is well established that, in this partnership, the rate of pollutant degradation is higher than the individual contribution of each partner in remediation processes (Khan et al. 2013b; Lunney et al. 2004).

The interactions between plants and bacteria having catabolic genes have led to the evolution of a diverse variety of catabolic enzymes that can metabolize and detoxify the xenobiotics (Hong et al. 2015; Singer et al. 2003; Xun et al. 2015). These synergistic relationships between plants and plant-associated bacterial communities in rhizosphere and/or endosphere have been widely investigated (Compant et al. 2010; Fahad et al. 2015; Khan et al. 2013a). Recently, the combined use of plants and bacteria has been exploited to enhance the phytoremediation of soil and water contaminated with different organic pollutants (Afzal et al. 2014b; Arslan et al. 2014; Khan et al. 2013b; Shehzadi et al. 2014). Similarly, several studies were performed to explore the potential of plant–bacteria partnership for the remediation of POPs-contaminated soil and water (Aken et al. 2009; Becerra-Castro et al. 2013; Jha and Jha 2015; Jha et al. 2014). Both rhizosphere and endophytic bacteria can enhance plant growth and POP degradation.

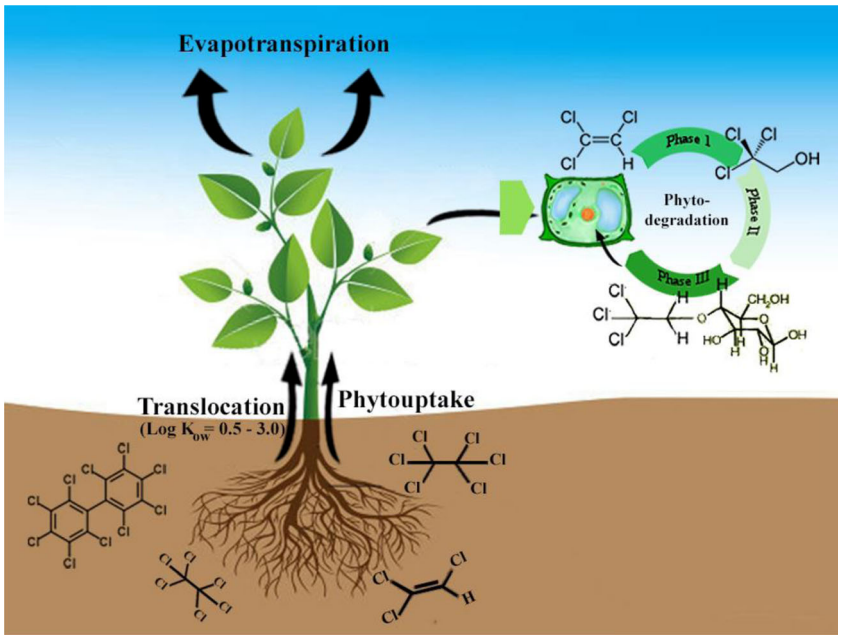

Fig. 1 Up take and degradation of organic pollutants within the plant tissues

Plant–rhizobacteria partnerships

Although rhizobacteria have previously been studied for their plant growth-promoting mechanisms, they have recently gained attention for improving the efficiency of phytoremediation of contaminated soil and water (Glick 2010; Gurska et al. 2009; Khan et al. 2013a). Rhizobacteria capable of degrading different POPs have been isolated from rhizospheric soil of different plants and well-studied for POP degradation pathways and genes involved in POP degradation have been identified (Brazil et al. 2005; Fatima et al. 2015; Nicoară et al. 2014). Although these bacteria showed high potential to degrade different POPs, these are unable to survive and proliferate in the contaminated soils (Pandey et al. 2009). Therefore, effective mineralization and degradation of the pollutants can be achieved by employing rhizobacteria in association with plants. In such a relationship, rhizobacteria having catabolic genes feed upon the organic pollutants as a sole carbon source for their cell functioning and metabolism, whereas plants facilitate the survival of rhizobacteria by adjusting the rhizosphere environment through production of root exudates, rhizosphere oxidation, co-metabolite induction, H^+/OH^- ion excretion, organic acid production, and release of biogenic surfactants (Fig. 2) (Afzal et al. 2013a; Hinsinger et al. 2003; Khan et al. 2013a).

The plant–rhizobacteria interactions enhance the abundance and expression of catabolic genes in the rhizosphere, leading to an increase in mineralization, degradation, stabilization, and/or sequestration of variety of organic compounds including POPs (Jha and Jha 2015; Passatore et al. 2014; Sprocati et al. 2014; Yateem 2013). In addition to this, rhizobacteria possessing plant growth-promoting activities improve plant health and biomass production. Improved plant growth facilitates the colonization of rhizobacteria in rhizoplane leading an increase of the organic pollutants degradation (Afzal et al. 2013b; Compant et al. 2010; Khan et al. 2013a; Yousaf et al. 2010). Importantly, during degradation of recalcitrant compounds, most of the pollutants cannot be used as carbon and energy sources for rhizobacteria; therefore, their degradation is often facilitated by co-metabolism of a similar but harmless structural analog that is a secondary metabolite of the host plant. The structural analogs act as inducers and enhance the bacterial population which then could degrade the organic pollutant (Singer et al. 2003; Bedard et al. 1986). Plant terpenes, flavonoids, and salicylic acid have also been found to act as inducer and enhance the degradation of different POPs (Gilbert and Crowley 1997, 1998; Hernandez et al. 1997; Koh et al. 2000; Master and Mohn 2001; Singer et al. 2000; Tandlich et al. 2001).

Recently, several studies have been conducted to explore the potential of plant–rhizobacteria partnerships for the remediation of POPs-contaminated soil and water (Abhilash et al. 2013; Gerhardt et al. 2009; Jha and Jha 2015; Qin et al. 2014). Among POPs, PCBs that released into the environment as a consequence of their use as hydraulic fluids, plasticizers, adhesives, flame retardants, etc. are well-studied pollutants. They have been reported to be successfully degraded by the combined use of plants and rhizobacteria (Leigh et al. 2002). The partnerships of alfalfa with *Pseudomonas fluorescens* sp. strain F113 and *Arabidopsis* with *Pseudomonas putida* strain Flav1-1 enhanced the degradation of a variety of PCBs (Villacieros et al. 2005; Narasimhan et al. 2003). Similarly, enhanced biotransformation of a number of aroclor compounds (e.g., 1242, 1248, 1254, and 1260) by alfalfa

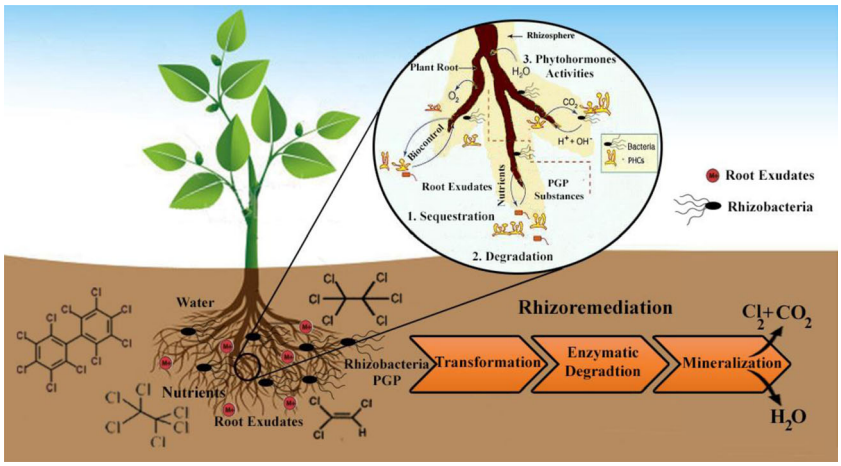

Fig. 2 Plant–rhizobacteria partnership and mineralization of POPs

inoculated with a symbiotic N_2-fixing rhizobacterium, *Sinorhizobium meliloti* strain A-025, has been reported (Mehmannavaz et al. 2002). Many other studies also reported the enhanced degradation of POPs by plant–rhizobacteria partnerships as shown in Table 4.

Many chemicals in the root exudates of plants stimulate rhizospheric microbes to perform degradation of xenobiotic pollutants including POPs (Donnelly et al. 1994; Isidorov and Jdanova 2002). Degradation of POPs is attributable to the chemical composition of root exudates as well as the rate of exudation, which facilitates pollutant-degrading rhizobacteria enormously in the rhizosphere (Rao 1990; Salt et al. 1998). More importantly, these factors tend to vary from one plant to another as most of the plant species contain phenols in their exudates, which support the proliferation of POPs-degrading rhizobacteria (Fletcher and Hegde 1995; Salt et al. 1998). Similarly as in the case of PCBs, a common component of root exudates, salicylate, is reported to elevate the expression of *bphA* gene encoding biphenyl dioxygenase in *Pseudomonas* sp. Cam-1, while inhibition of the same gene occurs by the presence of terpenes in root exudates (Master and Mohn 2001).

Another factor that governs the removal of POPs from the contaminated environment is the bioavailability of the pollutant (Federici et al. 2012). A number of mobilizing agents such as plant oils, synthetic surfactants and biogenic surfactants have been applied to enhance the bioavailability of POPs in the soil (Berselli et al. 2004; Fava and Ciccotosto 2002; Fava and Gioia 1998, 2001; Federici et al. 2012). A rhizobacteria having potential to produce biosurfactants can enhance the bioavaiability of POPs and ultimately their degradation (Aslund and Zeeb 2010). Biosurfactants make POP-H_2O soluble aggregates which ultimately release the pollutant from soil particles. However, the release of surfactants in the root exudates seems more promising as it may provide easy solubilization of POPs in plant rhizosphere (Passatore et al. 2014). These studies reveal that the combined use plants and biosurfactant-producing bacteria can improve the bioavailability of organic pollutants through biosurfactant exudation and/or production and consequently the remediation of POPs-contaminated environment. Recently, rhizoengineering has gained attention to enhance the removal of POPs from the environment (Thijs and Vangronsveld 2015). In rhizoengineering, the aim is to favor the population of rhizobacteria by adopting many possible strategies including nutrient adjustments, flavonoid regulations, and facilitating degradation by the inoculation of transgenic strains (Fu et al. 2012). Many POPs, especially PCBs, have been reported to be successfully remediated by the adjustment of flavonoids, apigenin, and naringenin (Narasimhan et al. 2003).

Plant–endophyte partnership

Plant–endophyte partnership is a promising approach for the remediation of a wide range of xenobiotics (Afzal et al. 2014a; Glick 2010; Weyens et al. 2009b). In plant–endophyte partnership, plants provide nutrients and residency to endophytic bacteria whereas endophytic bacteria protect plants from the toxic effects of the pollutants taken up by the plants (Afzal et al. 2014a; Rylott 2014). Endophytic bacteria degrade the pollutants in the rhizosphere as well as in the endosphere and contribute significantly in pollutant degradation (Afzal et al. 2011; Compant et al. 2010; Yousaf et al. 2011). Furthermore, endophytic bacteria were found to have significant effects on plant growth and development in the contaminated soil and water, especially due to their plant growth-promoting activities (Afzal et al. 2012; Ryan et al. 2008; Shehzadi et al. 2014). Usually, endophytic bacteria can be found in plant endosphere, mainly root cortex and/or xylem, and are involved in the mineralization of pollutants as shown in Fig. 3 (Schulz and Boyle 2006; Sessitsch et al. 2005; Weyens et al. 2009b). Due to beneficial effects of endophytic bacteria, their innate immune system facilitates the colonization of the bacteria in root and shoot (Moore et al. 2006).

Table 4 Examples of successful POPs degradation using plant–rhizobacteria partnerships

Rhizospheric bacteria	Host plant	Target pollutant	Reference
Rhodococcus sp. *Arthrobacter*, *Oxydans*, *Rhodococcus erythreus* type strain	*Robinia pseudoacacia, Betula pendula*, *Fraxinus excelsior*	PCBs	Schell (1985)
Pseudomonas fluorescens	*Medicago sativa*		Brazil et al. (1995)
Burkholderia cepacia	*Hordeum aestivum*	2,4-D	Jacobsen (1997)
Sphingomonas herbicidovorans, AB042233, *Sphingomonas* sp. DS3-1, *Sphingomonas taejonensis*, *Sphingomonas*, *Herbicidovorans*, *Sphingomonas* sp. D12	*Zea mays*	α, β, γ, δ-hexachlorocyclohexane	Abhilash et al. (2013), Böltner et al. (2008)
Indigenous degraders	*Panicum virogatum* L.	PCBs	Chekol et al. (2004)
Pseudomonas fluorescens	*Medicago sativa*		Villacieros et al. (2005)
Achromobacter sp.	*Salix caprea*		Leigh et al. (2006)
Microbacterium oxydans type strain	*Pinus nigra*		Siciliano and Germida (1998)
Microbacterium oxydans type strain	*Pinus nigra*		Siciliano and Germida (1998)
Pseudomonas mendocina, *Pseudomonas fluorescens*	*Solanum nigrum*		Ionescu et al. (2009)
Bacillus pumilus	*Armoracia rusticana*		Ionescu et al. (2009)
Sphingobacterium mizutae, *Burkholderia cepacia*	*Salix caprea*		Ionescu et al. (2009)
Achromobacter sp.	*Nicotiana tabacum*		Ionescu et al. (2009)
Pseudomonas, *Rhodococcus*, *Rhizobium*	*Medicago sativa*		Ionescu et al. (2009)
Pseudomonas putida Flav1-1, *Pseudomonas putida* PML2	*Arabidopsis*		Narasimhan et al. (2003)
Sphingobium chlorophenolicum ATCC 39723	*Triticum aestivum*	Pentachlorophenol	Dams et al. (2007)
Microbacterium foliorum, *Gordonia*, *alkanivorans*, and *Mesorhizobium*	*Sesbania cannabina*	TPH	Maqbool et al. (2012)

Recently, plant–endophyte partnership has gained popularity compared to other mechanisms of remediation (Afzal et al. 2014a; Weyens et al. 2009b; Zhu et al. 2014). Plant–endophyte partnership has advantages over plant–rhizobacteria partnership during the remediation of organic pollutants which are easily taken up by plants (Weyens et al. 2009c; Afzal et al. 2014a). In such circumstances, although rhizoremediation seems possible, the pollutant is not available to the rhizospheric microfloradue to its lower residency time in rhizosphere and optimum lipophilicity. Consequently, endophytic communities get the opportunity to degrade the contaminants by the action of intracellular dioxygenases before the contaminants are evapotranspired (Trapp et al. 2000; Weyens et al. 2009b). Furthermore, a major advantage of endophytic bacteria over free-living rhizobacteria is that they reside in internal tissues of the host plant and hence have less

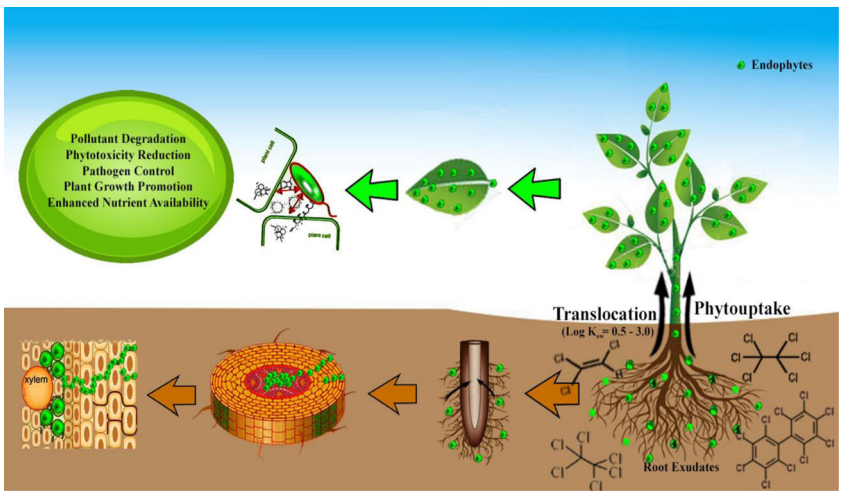

Fig. 3 Plant–endophyte partnerships for the remediation of POPs

Table 5 Examples of successful POP degradation using plant–endophyte partnerships

Endophytic bacteria	Host plant	Target pollutant	Reference
Pseudomonas aeruginosa R75 *Pseudomonas savastanoi* CB35	*Lolium perenne*	Chlorobenzoic acids	Siciliano et al. (1998)
Methylobacterium populi BJ001	*Populus alba*	2,4,6-Trinitrotoluene, hexahydro-1,3,5-trinitro-1,3,5-triazine, octahydro-1,3,5,7-tetranitro-1,3,5-tetrazocine	Van Aken et al. (2004)
Pseudomonas putida VM1450	*Populus alba* and *Salix babylonica*	2,4-Dichlorophenoxyacetate	Germaine et al. (2006)
Pseudomonas spp., *Brevundimonas*, *Pseudomonas rhodesiae*	*Medicago sativa*, *Puccinellia nuttaalliana*, *Festuca altaica*, *Lolium perenne*, *Thinopyrum ponticum*	n-Hexadecane	Phillips et al. (2008)
Enterobacter sp. 12J1	*Triticum* and *Zea mays*	Pyrene	Sheng et al. (2008)
Pseudomonas putida	*Pisum sativum*	Naphthalene	Germaine et al. (2009)
Pseudomonas sp. strain ITRI53, *Rhodococcus* sp. strain ITRH43	*Lolium perenne*	Hydrocarbons	Andria et al. (2009)
Enterobacter ludwigii	*Lolium multiflorum*, *Lotus corniculatus*, and *Medicago sativa*		Yousaf et al. (2011)
Achromobacter xylosoxidans	*Ipomoea aquatica*, *Chrysopogon zizanioides*, *Phragmites australis*	Catechol and phenol	Ho et al. (2009)
Pseudomonas putida W619-TCE	*Populus alba*	Trichloroethylene	Weyens et al. (2009a)
Burkholderia cepacia VM1468	*Lupinus luteus*		Weyens et al. (2010a)
Pseudomonas putida W619-TCE	*Populus alba*		Weyens et al. (2010b)
Enterobacter sp. strain PDN3	*Populus alba*		Kang et al. (2012)
Burkholderia cepacia strain FX2	*Zea mays* and *Triticum*	Toluene	Wang et al. (2010)
Rhodococcus erythropolis ET54b, *Sphingomonas* sp. D4	*Cytisusstriatus*	Hexachlorocyclohexane	Becerra-Castro et al. (2013)
Consortium CAP9	*Agrostis*	2,4,6-Trinitrotoluene	Thijs et al. (2014)

competition for nutrients and space, whereas rhizobacterial population have more competition by a large numbers of soil microorganisms which often results in reduction of the desired species (Doty 2008).

The first laboratory study on the degradation of POPs using plant–endophyte partnership was conducted by Germaine and coworkers (2006), who applied endophytic bacterium, *Pseudomonas putida* VM1450, to pea plant for the degradation of 2,4-dichlorophenoxyacetic acid (2,4-D). The strain was able to colonize plant endosphere resulting in significant degradation of 2,4-D in plant tissues. Furthermore, a naphthalene-degrading endophytic bacterial strain, *Pseudomonas putida* VM1441, has been reported to efficiently colonized root and shoot interior of the host plant and enhanced plant growth and naphthalene degradation (Germaine et al. 2009). In later years, several endophytic bacteria having POPs-degrading catabolic genes and having potential to degrade POPs were isolated and characterized (Andria et al. 2009; Wang et al. 2014; Weyens et al. 2010a; Yousaf et al. 2011). Recently, the combined use of plants and endophytic bacteria has been found to remediate hexachlorocyclohexane (HCH) (Becerra-Castro et al. 2013). Two endophytic bacteria, *Rhodococcus erythropolis* ET54b and *Sphingomonas* sp. D4, were inoculated to *Cytisuss triatus* vegetated in HCH-contaminated soil. Bacterial inoculation improved plant growth and HCH degradation both in the rhizosphere and endosphere. Examples of successful degradation of a number of POPs by the application of endophytic bacteria in association with different plants are listed in Table 5.

Abovementioned studies reveal that both rhizospheric and endophytic bacteria have potential to facilitate and enhance the degradation of POPs. Until now, relatively less number of endophytes with POP degradation abilities have been isolated as compared to rhizobacteria. Therefore, further studies are needed to explore the ecology of POPs degrading endophytic bacteria.

Conclusions

The combined use of plants and POPs-degrading rhizosphere and/or endophytic bacteria provides an effective approach for the remediation of POPs-contaminated sites. In bacterial-assisted phytoremediation of POPs, rhizobacteria and endophytic bacteria that possess appropriate genes for the degradation, transformation, and mineralization of pollutants allow to alleviate toxicity to the plant or their direct phytovolatilization. Although many POPs, especially PCBs, have been remediated from a wide range of ecosystems through bacterial-assisted phytoremediation, this endeavor still faces

numerous challenges. A better understanding of improving bioavailability of POPs by bacteria, the mechanisms by which these POPs are tolerated by certain plants or bacterial species, and how relevant traits like the survival of the inoculated bacteria in POPs environments as well as maximum detoxification by the use of combinations of different POPs-degrading bacteria will provide a broader and more efficient application of phytoremediation of POPs-contaminated environment. Moreover, the knowledge about metabolic activities of the bacteria and their diversity by using metagenomic techniques can further help us to design more sustainable bacterial assisted phytoremediation strategies.

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