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Review

Efficient phytoremediation of organic contaminants in soils using plant–endophyte partnerships

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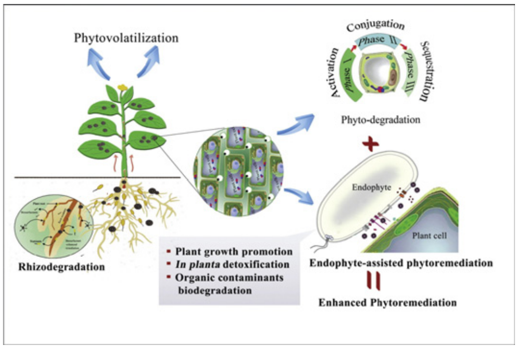
HIGHLIGHTS

- Endophytes are valuable bio-resources for enhancing phytoremediation efficiency.
- The superiority of endophyte-assisted phytoremediation is assessed.
- Mechanisms adopted by plant and endophyte for xenobiotic removal are summarized.
- Cometabolism of plant and endophyte serves a main route for xenobiotic degradation.
- “Omcs” techniques open up new perspectives for plant-endophyte interactions.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil pollution with organic contaminants is one of the most intractable environmental problems today, posing serious threats to humans and the environment. Innovative strategies for remediating organic-contaminated soils are critically needed. Phytoremediation, based on the synergistic actions of plants and their associated microorganisms, has been recognized as a powerful *in situ* approach to soil remediation. Suitable combinations of plants and their associated endophytes can improve plant growth and enhance the biodegradation of organic contaminants in the rhizosphere and/or endosphere, dramatically expediting the removal of organic pollutants from soils. However, for phytoremediation to become a more widely accepted and predictable alternative, a thorough understanding of plant–endophyte interactions is needed. Many studies have recently been conducted on the mechanisms of endophyte-assisted phytoremediation of organic contaminants in soils. In this review, we highlight the superiority of organic pollutant-degrading endophytes for practical applications in phytoremediation, summarize alternative strategies for improving phytoremediation, discuss the fundamental mechanisms of endophyte-assisted phytoremediation, and present updated information regarding the advances, challenges, and new directions in the field of endophyte-assisted phytoremediation technology.

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Contents

1. Introduction

Industrialization, urbanization, and changing agricultural practices have greatly increased the release of anthropogenic hazardous organic contaminants into soils (Table 1), posing a serious threat to the global environment and human health (Kang, 2014). Novel cost-effective and sustainable remediation strategies for removing or detoxifying organic contaminants in soils are urgently needed. Phytoremediation, using plants and their associated microorganisms to eliminate soil contaminants, is a cost-effective, reliable, and promising technology (Arslan et al., 2015; Fester et al., 2014), particularly when the harvested plant biomass can be utilized for bioenergy production (Pandey et al., 2016).

Plants are inhabited by diverse microbial communities, ranging from the rhizosphere and phyllosphere to the endosphere (Compant et al., 2010). These microorganisms maintain contact with their host plants and play vital roles in plant development, growth, and fitness, as well as decontaminating polluted soils. Endophytes engage in these intimate interactions with their host plants without inflicting infections or other negative effects, resulting in mutualistic relationships in most cases (Hardoim et al., 2015). Endophytic microorganisms harbor a plethora

Table 1
Common anthropogenic hazardous organic contaminants detected in soils.

Types	Concentrations	Research areas	Sources of samples	References
Persistent organic pollutants (POPs)				
Petroleum hydrocarbons	400–40,000 μg g^{-1}	Dongying, China	Oilfield	Shi et al., 2015
Polycyclic aromatic hydrocarbons (PAHs)	892–3514 ng g^{-1}	Gdańsk, Poland.	Municipal solid waste landfill	Melnyk et al., 2015
	14.78–2084 ng g^{-1}	Kumasi, Ghana	Communities in metropolis	Bortey-Sam et al., 2014
Polychlorinated biphenyls (PCBs)	11.26–21.89 ng g^{-1}	Oued Souhil, Tunisia	Waste water irrigated soil	Haddaoui et al., 2016
Tetrabromobisphenol A (TBBPA)	ND - 2900 ng g^{-1}	Bui Dau, Vietnam	Electronic (e)-waste recycling workshop	Matsukami et al., 2015
Polybrominated diphenyl ethers (PBDEs)	0.004–4.78 ng g^{-1}	South Korea	Industrial, urban and agricultural soils	Kim et al., 2014
		13.9–13,251.2 ng g^{-1}	Qingyuan, China	E-waste recycling area
Wang et al., 2014				
Polychlorinated dibenzo-p-dioxins/dibenzofurans (PCDD/Fs)	11.5–59.6 pg g^{-1}	Riyadh, Dammam, Saudi Arabia	Industrial area	Al-Wabel et al., 2016
Endosulfans	0.058–8.42 ng g^{-1}	South Korea	Industrial, urban and agricultural soils	Kim et al., 2014
Organochlorine pesticides (OCP)	12.49–310.54 ng g^{-1}	Oued Souhil,Tunisia	Waste water irrigated soil	Haddaoui et al., 2016
	3.22–24.56 ng g^{-1}	Taurus Mountains,Turkey	Forest soil	Turgut et al., 2012
Perfluorinated compounds	5.5-483 ng g^{-1}	Chicago, USA	Biosolid-amended soils	Sepulvado et al., 2011
Endocrine disrupting chemicals (EDCs)				
Phthalic acid esters (PAEs)	0.2–4820 ng g^{-1}	Novi Sad, Serbia	Recreational, residential and industrial area, schools	Škrbić et al., 2016
Bisphenol A (BPA)	12.89–167.9 ng g^{-1}	Hartwood, Lanarkshire, UK.	Sewage sludge amendment	Zhang et al., 2015
Nonylphenol	ND-7.22 ng g^{-1}	Pearl River Delta, Southern China	Vegetable farms	Cai et al., 2012
Nonylphenol monoethoxylate	ND-8.24 ng g^{-1}			
Pharmaceuticals andpersonal care products (PPCPs)				
Acetaminophen	ND-1.8 ng g^{-1}	Valencia, Eastern Spain	Soils irrigated with contaminated waters	Vazquez-Roig et al., 2012
Carbamazepine	ND-1.5 ng g^{-1}			
Tetracycline antibiotics	0.04–184.8 ng g^{-1}	Guangzhou, South China	Organic vegetables farms	Xiang et al., 2016
Clotrimazole	6.5–8.3 ng g^{-1}	Zhejiang, Hunan, Shandong province, China	Biosolid-amended soils	Chen et al., 2013a
Micronazole	7.4–12.5 ng g^{-1}			
Triclocarban	1.20–65.10 ng g^{-1}	Michigan, USA	Municipal biosolid-amended soils	Cha and Cupples, 2009
Tonalide	24.4–67.5 ng g^{-1}	Hunan, Zhejiang province, China	Biosolid-amended soils	Chen et al., 2014

of pollutant-degrading genes for detoxification processes, and are well-suited to *in planta* elimination of toxic organic contaminants (Ijaz et al., 2016). In addition, endophytic microbes can improve plant growth and tolerance to pollutant phytotoxicity due to their plant growth-promoting activities (Santoyo et al., 2016; Table 2). Numerous studies have demonstrated that endophyte-assisted phytoremediation plays an extensive role in soil decontamination (Afzal et al., 2014).

Because many endophytes possess pollutant-degrading activities and plant growth-promoting effects, or a combination thereof, a better understanding of the mechanisms underlying these beneficial endophytic traits could improve the use of endophyte-assisted phytoremediation of organic pollutants in soils. Several review articles and book chapters on endophytes and their assistance in the phytoremediation of organic pollutants in soils have recently become available (Afzal et al., 2014; Arslan et al., 2015; Glick, 2015; Ijaz et al., 2016; Li et al., 2012). However, these published review papers are inadequate for fostering a mechanistic understanding of endophyte-assisted phytoremediation. To our knowledge, there are no reports on the fundamental mechanisms underlying the co-metabolism of recalcitrant organic pollutants by plants and their endophytes or other pathways involved in the phytoremediation of organic-contaminated soils.

Therefore, in the present critical review, we describe the beneficial associations between plants and their associated endophytes. The fundamental mechanisms of endophyte-assisted phytoremediation of organic pollutants in soils are presented in detail, along with three strategies for enhancing this process. We also highlight the potential of metagenomic technologies to advance our understanding of plant–endophyte interactions and their responses to contaminants, which is likely to guide the future use of plant–endophyte partnerships for the enhanced decontamination of polluted soils.

2. Plant–endophyte relationships in phytoremediation

Endophytes are a group of highly varied microorganisms that ubiquitously dwell inside the internal tissues of plants for at least part of their life cycle (Compant et al., 2016; Hardoim et al., 2015). They can be found in nearly every plant species. A wide range of endophytes have established an array of positive, neutral, or negative interactions with host plants, affecting plant growth, health, and survival (Wani et al., 2015). Here, we focus primarily on their beneficial effects. Endophytes can maintain close links with their host plants, often leading to highly co-evolved mutualistic interactions that benefit both endophytes and their hosts. Endophytes obtain rich nutrients and safe habitats from their host plants, protecting themselves from biotic and abiotic stressors (Bacon and Hinton, 2006; Reinhold-Hurek and Hurek, 2011). In return, endophytes produce a wide range of natural bioactive substances facilitating plant growth and development through various mechanisms (Bacon and White, 2016; Santoyo et al., 2016), as illustrated in Fig. 1 and Table 2.

Many endophytes produce phytohormones, probably the best-studied plant growth-promoting mechanism, even under stress conditions (Hardoim et al., 2015), maintaining a dynamic balance of hormones in host plants and modulating host stress response (Khaksar et al., 2016; Khan et al., 2012). Numerous endophytic genera, including *Serratia*, *Enterobacter*, *Acinetobacter*, *Agrobacterium*, *Bacillus*, *Herbaspirillum*, and *Klebsiella* strains, can produce phytohormones such as indole-3-acetic acid (IAA) (Bisht et al., 2014; Kukla et al., 2014), cytokinins (CTKs), and gibberellins (GAs) (Waqas et al., 2015). Some phytohormones, such as IAA, support plant colonization by endophytes, possibly by interfering with the host defense system, which may be an important property for endophytic colonization (Hardoim et al., 2015; Robert-Seilaniantz et al., 2011). It is well documented that under stress

Table 2
List of endophytes for plant growth promotion.

Endophyte species	Host plants	Targeted plants	Plant growth-promoting traits	References
Azotobacter chroococcum Avi2	Rice (*Oryza sativa* L.)	Rice	Nitrogen fixation	Banik et al., 2016
Bacillus sp. SBER3	*Populus deltoides*	*Populus deltoides*	Production of ACC deaminase and IAA Siderophore Phosphate solubilization Biocontrol	Bisht et al., 2014
Paenibacillus spp.	Wheat seeds (*Triticum aestivum* L.)	Wheat and barley seedings	Production of IAA and siderophore Phosphate solubilization Biofilm formation Biocontrol	Herrera et al., 2016
Paecilomyces formosus LHL10	Cucumber (*Cucumis sativus* L.)	Mutant rice cultivar	Production of gibberellins (GAs) and IAA Maintenance of plant water potential Reduction of abscisic acid Accumulation of proline and antioxidants	Khan et al., 2012
Pseudomonas spp.	Ryegrass (*Lolium perenne* L.)	Ryegrass (*Lolium perenne* L.)	Production of ACC deaminase and IAA Siderophore Phosphate solubilization Production of hydrogen cyanide (HCN) Biocontrol	Kukla et al., 2014
Paecilomyces lilacinus *Penicillium* sp. *Penicillium copticola* L3	*Cannabis sativa* L.	*Cannabis sativa* L.	Phytopathogen inhibition Biocontrol	Kusari et al., 2013
Burkholderia phytofirmans PsJN *Enterobacter* sp. FD17	Onion root Maize (*Zea mays* L.)	Maize (*Zea mays* L.)	Maintenance of plant water potential	Naveed et al., 2014
Cladosporium velox	*Tinospora cordifolia*	*Tinospora cordifolia*	Production of chlorogenic acid Biocontrol	Singh et al., 2016
Burkholderia sp. PsJN	Onion root	Carpet grass (*Axonopus affinis*)	Production of ACC deaminase	Tara et al., 2014
Penicillium citrinum LWL4 *Aspergillus terreus* LWL5	Sunflower (*Helianthus annuus* L.)	Sunflower Rice	Production of GAs Siderophore Oxidative stress responses Biocontrol	Waqas et al., 2015
Pseudomonas saponiphila	*Dendrobium candidum*	Pepper plant (*Capsicum annuum* L.)	Production of IAA Solubilizing phosphate Siderophores Production of HCN antibiotics	Wu et al., 2016

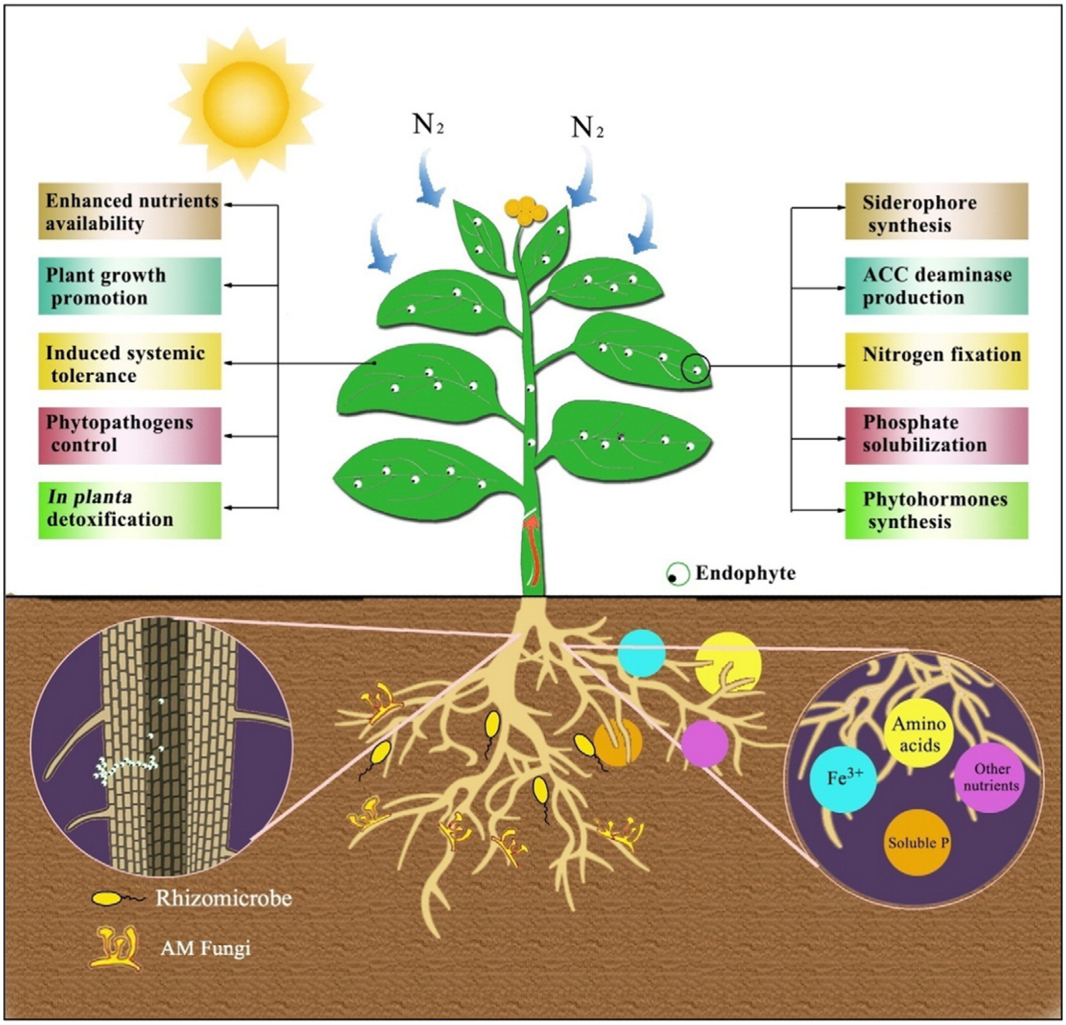

Fig. 1. Mechanisms of plant-growth promoting of endophytes.

conditions, endophytes may also promote plant growth through the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Glick, 2014). This microbial enzyme is responsible for hydrolyzing the plant ethylene precursor ACC into α-ketobutyrate and ammonia, decreasing ethylene levels in host plants (Glick, 2014). Moreover, ACC deaminase plays a key regulatory role in the colonization of plants by endophytes, increasing colonization efficiency (Hardoim et al., 2015; Iniguez et al., 2005).

Aside from the beneficial mechanisms described above, endophytes also promote plant growth by improving nutrient acquisition and water uptake (Santoyo et al., 2016; Naveed et al., 2014), leading to enhanced hardiness and decreased oxidative stress enzyme activities in host plants in contaminated soils. Beneficial endophytes can directly improve host plant nutrition status by facilitating the uptake of nutrients, such as nitrogen, phosphorus, and essential minerals, by fixing nitrogen, solubilizing inorganic phosphate, mineralizing organic phosphorus, and producing siderophores for iron sequestration (Behera et al., 2014; Gaiero et al., 2013; Hardoim et al., 2015).

An increasing body of evidence demonstrates that endophytes can also induce plant growth indirectly, potentially acting as biocontrol agents (Glick, 2012). The proposed indirect mechanisms primarily involve the production of antimicrobial metabolites and lytic enzymes, induction of systemic resistance, competition for nutrients, and niche saturation (Glick, 2015; Robert-Seilaniantz et al., 2011; Zheng et al., 2016). The root endophyte *Bacillus* sp. SBER3 produces siderophores and HCN antibiotics that suppress deleterious microorganisms and induce systemic resistance, protecting the host plant from pathogenic fungal infection, even in environments contaminated with polycyclic aromatic hydrocarbons (PAHs) (Bisht et al., 2014). In general, endophytes have been shown to simultaneously increase nutrient acquisition and suppress phytopathogens in host plants. The medicinal plant endophyte *Pseudomonas saponiphila* is capable of not only producing IAA and solubilizing phosphate but also possesses antifungal activities (*e.g.* production of 2,4-diacetylphloroglucinol, siderophores, and HCN antibiotics) that indirectly benefit plant growth (Wu et al., 2016). Most importantly, the endophytic community as a whole, or just fractions thereof, can play a role in plant growth promotion (Hardoim et al., 2015). The wheat seed endophytic community of *Pantoea* spp. shows potential as a plant growth promoter and biocontrol agent against the pathogen *Fusarium graminearum* (Herrera et al., 2016). Endophytic fungi produce bioactive substrates with growth-inhibitory activities toward plant pathogens and herbivores (Zheng et al., 2016). The endophytic fungus *Cladosporium velos* secretes chlorogenic acid that has potential as a biocontrol agent against polyphagous pests (Singh et al., 2016).

These endophytic plant growth-promoting characteristics facilitate adaptation to biotic and abiotic stressors and increase the biomass of plants suitable for phytoremediation (Ijaz et al., 2016; Ryan et al., 2008). Endophytes can be exploited to improve the effectiveness of phytoremediation of organic pollutants, as they can deliver biodegradative capacities around/inside the host plants, contributing to higher metabolic activities in the rhizosphere and endosphere

(Weyens et al., 2009a). The compatibility of host plants and endophytes and their integral actions are critical factors in their ability to remediate organic-contaminated soils (Ijaz et al., 2016; Saikkonen et al., 2010). Once a plant–endophyte association is established, plant–endophyte partnerships can develop novel phytoremediation strategies for contaminated soils (Afzal et al., 2014).

3. Mechanisms of plant–endophyte phytoremediation of organic contaminants

3.1. Detoxification and degradation of organic contaminants

Current experimental studies on the phytoremediation of soils contaminated with organic pollutants provide an ecologically and economically attractive method for decontaminating a wide range of organic pollutants (Ijaz et al., 2016; Glick, 2015). Although plants, being photoautotrophic organisms, often metabolize or sequester organic compounds, they did not evolve to metabolize organic contaminants as sources of energy or carbon, but can only transform contaminants to more water-soluble forms and/or immobilize them (Burken, 2003; Weyens et al., 2009a). When organic pollutants are at phytotoxic levels, isolated plant species involved in phytoremediation are usually sensitive to these pollutants. Even if the plants can tolerate the organic pollutants, their growth is impaired, and they fail to remediate contaminated soils, possibly due to the phytotoxicity and hydrophobicity of organic pollutants, which inhibit the ability of plants to acquire water and nutrients (Khan et al., 2013).

The beneficial effects of endophytic inoculants on plants growing in contaminated soils have been investigated extensively (Table 2). The highlighted roles of endophytes in the detoxification and degradation of organic contaminants *in planta* include conferring fitness benefits such as increased nutrient acquisition and growth, improved stress tolerance, and efficient degradation of organic contaminants (Table 3; Fig. 2). Pseudomonaceae, Burkholderiaceae, Bacillaceae, and Enterobacteriaceae are among the most common families of cultivable endophytic species found at polluted sites (Afzal et al., 2014). The endophyte *Pseudomonas putida* PD1 was shown to promote root and shoot growth and protect the plants of two different willow clones and a grass against the phytotoxicity of phenanthrene (Khan et al., 2014). Endophytes can also help plants combat the oxidative stress produced by organic contaminants by manipulating the antioxidative stress defense system of host plants (Bacon and White, 2016; Wani et al., 2015). The root endophyte *P. putida* W619 was shown to enhance resistance against Ni-trichloroethylene (TCE) phytotoxicity in poplar, attributed to enhanced plant growth, reduced activities of antioxidative defense-related enzymes, reduced TCE concentration in leaves, and decreased TCE evapotranspiration (Weyens et al., 2015).

These exceptional adaptations and promising remediation efficiencies strongly demonstrate the suitability of pollutant-degrading endophytes for the detoxification and degradation of organic contaminants (Afzal et al., 2014; Ijaz et al., 2016; Table 3). During soil phytoremediation, pollutant-degrading endophytes harboring catabolic genes can effectively detoxify or mineralize organic pollutants. The root endophyte *Pseudomonas* sp. BF1-3, harboring organophosphorus hydrolase gene *ophB*, can efficiently hydrolyze chlorpyrifos (Barman et al., 2014). The endophyte *Burkholderia phytofirmans* PsJN is equipped with glutathione-S-transferase (GST) genes for degrading and detoxifying complex organic compounds (Mitter et al., 2013). On the other hand, external environmental microorganisms can also assist plants in resisting phytotoxic chemicals from within, once they become colonized. *Burkholderia fungorum* DBT1 isolated from oil refinery discharge can transform PAHs in hybrid poplar plants (Andreolli et al., 2013). Moreover, some endophytes can produce chelating agents, siderophores, biosurfactants, low molecular weight organic acids, and various detoxifying enzymes, all of which are favorable for removing organic contaminants from soils (Li et al., 2012; Soleimani et al., 2010; Yousaf et al., 2010).

As outlined above, all of these successful cases provide valuable insights into the mechanisms underlying the detoxification and

Table 3
List of endophytes for degradation of organic pollutants.

Organic pollutants	Endophyte species	Host plants	References
PAHs (anthracene, naphthalene, benzene, toluene, xylene)	*Bacillus* sp. SBER3	*Populus deltoides*	Bisht et al., 2014
Petroleum hydrocarbons, PAHs	*Pseudomonads* spp.	*Halimione portulacoides*, *Sarcocornia perennis*	Oliveira et al., 2014
	Neotyphodium coenophialum *Neotyphodium uncinatum*	Tall fescue (*Festuca. arundinacea Schreb.*), Meadow fescue (*Festuca. pratensis Huds.*)	Soleimani et al., 2010
Petroleum hydrocarbon	*Pseudomonas* spp., *Microbacterium* sp., *Rhodococcus* sp.	Ryegrass (*Lolium perenne* L.)	Kukla et al., 2014
Hydrocarbon	*Bacillus* sp., *Pseudomonas* sp.	*Azadirachta indica*	Singh and Padmavathy, 2015
Alkanes	*Pseudomonas* sp.	Ryegrass (*Lolium multiflorum* L.)	Andria et al., 2009
Pyrene	*Staphylococcus* sp. BJ106	*Alopecurus aequalis*	Sun et al., 2014
Phenanthrene	*Pseudomonas putida* PD1	Poplar	Khan et al., 2014
	Pseudomonas sp. Ph6-*gfp*	Ryegrass (*Lolium multiflorum* L.)	Sun et al., 2015a
	Massilia sp. Pn2	*Alopecurus aequalis* Sobol	Liu et al., 2014
	Paenibacillus sp. PHE-3	*Plantago asiatica* L.	Zhu et al., 2016
Diesel	*Enterobacter ludwigii*	Ryegrass (*Lolium multiflorum* L.) Birdsfoot trefoil (*Lotus corniculatus*) Alfalfa (*Medicago sativa*)	Yousaf et al., 2011
	Pseudomonas sp. J4AJ	*Scirpus triqueter*	Zhang et al., 2014a
Crude oil	*Acinetobacter* sp. BRSI56	*Brachiaria mutica*	Fatima et al., 2015
BTEX, trichloroethylele (TCE)	*Burkholderia cepacia* VM1468	*Populus trichocarpa*	Taghavi et al., 2005
Phenolic pollutants	*Achromobacter xylosoxidans* F3B	*Phragmites australis*, *Ipomoea aquatica*	Ho et al., 2013
TCE	*Pseudomonas putida* W619-TCE	Poplar tree (*Populus deltoids*)	Weyens et al., 2009b, 2015
	Burkholderia cepacia VM1468	Yellow lupine (Lupinus luteus)	Weyens et al., 2010
Chlorpyrifos	*Pseudomonas* sp. BF1-3	Balloon flower	Barman et al., 2014
	Mesorhizobium sp. HN3	Ryegrass (*Lolium multiflorum* L.)	Jabeen et al., 2016
Fenpropathrin	*Klebsiella terrigena* E42, *Pseudomonas* sp. E46	*Spirodela polyrhiza*	Xu et al., 2015
2,2-Bis (p-chlorophenyl)-1, 1-dichloro-ethylene (DDE)	*Stenotrophomonas* sp. *Sphingomonas* sp.	*Cucurbita pepo*	Eevers et al., 2016
2,4,6-Trinitrotoluene (TNT)	*Methylobacterium thiocyanatum* ES2, *Sphingomonas panni* ES4, *Pseudomonas* spp. ER9, *Stenotrophomonas* EL1, *Variovorax* ER18	Bent grass (*Agrostis capillaris*)	Thijs et al., 2014

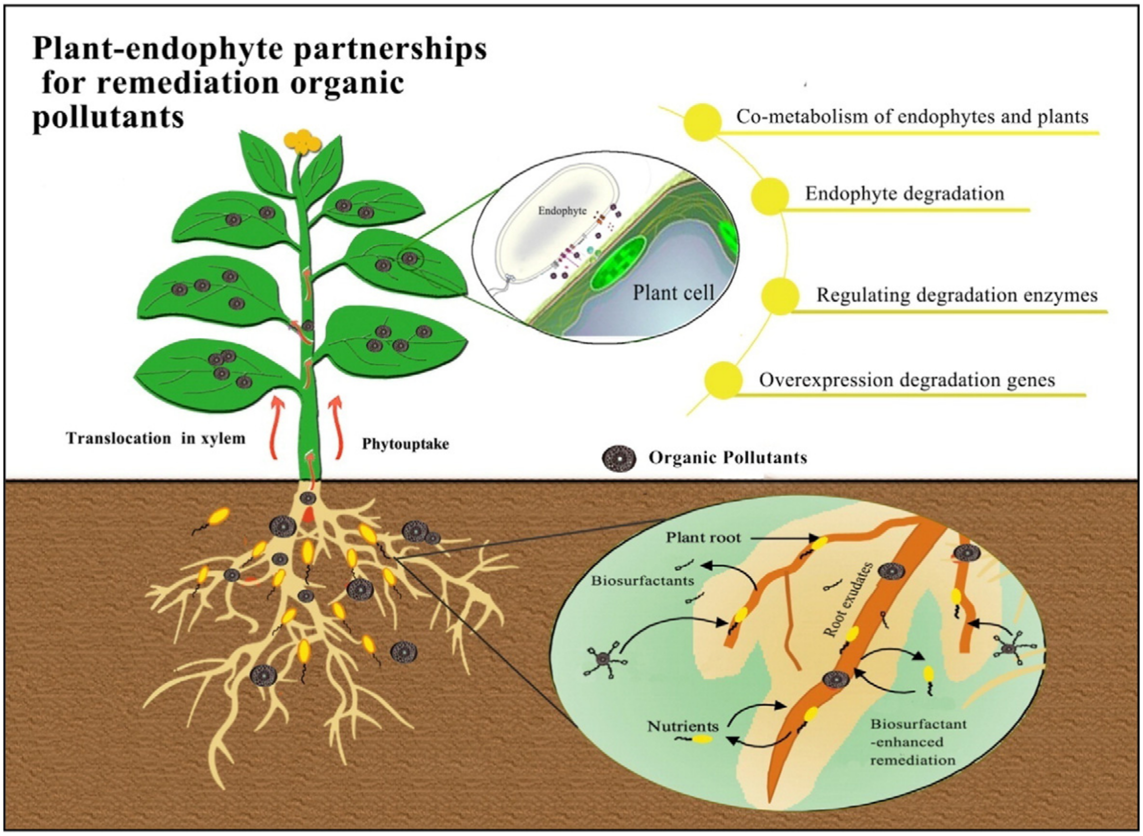

Fig. 2. Plant-endophyte partnerships for phytoremediation of soils contaminated with organic pollutants.

biodegradation of organic contaminants in the plant–endophyte system, providing a basis for successful phytoremediation strategies. However, due to its variability, phytoremediation has not yet achieved the desired outcomes of a viable remediation alternative, namely, exhibiting highly efficient, predictable, and rapid cleanup properties (Stephenson and Black, 2014). Most studies aimed at improving phytoremediation have focused on individual genes, organisms, or groups of organisms in isolation rather than holistically on a large range of organisms in complete ecosystems (Fester et al., 2014). While endophytes have been selected and used for years as single-strain bioinoculants, innovative phytoremediation strategies involving microbial communities or strain mixtures should be developed. Effective turnover of contaminants, or any other chemicals, requires interactions supporting growth and catabolic cooperation among plants and potentially thousands of degradative microbial taxa naturally colonizing the host (Fester et al., 2014). This has led to the concept of the "metaorganism", or plant microbiome, referring to the entirety of a host plant and its associated microbial community (Thijs et al., 2016). One of the key determinants of effective phytoremediation is the relative importance of endophyte microflora in the plant microbiome. In interactions between plants and their environment, endophytes show functional overlap and complex interactions with other groups, such as mycorrhizal fungi, close bacterial symbionts, saprotrophic or oligotrophic fungi, or bacteria colonizing the rhizosphere.

Successful experimental evidence has emphasized the importance of plant microbiome activities in phytoremediation (Hassan et al., 2014). Increasingly, the accessibility of omics tools has facilitated in-depth surveys of the biodiversity and functional characteristics of endophyte communities (Bourdel et al., 2016; Sessitsch et al., 2012). The enormous promise of omics-mediated discoveries that have been translated into usable phytoremediation technologies has been elegantly reviewed elsewhere (Bell et al., 2014; Schenk et al., 2012). However, we still lack an integrated understanding of *in situ* studies of endophyte-assisted phytoremediation at the metaorganismal level. Based on the available omics data sets on phytoremediation, future studies should focus more on plant–microbiome interactions between endophytes and associated organisms, including both plants and other microbes, to elucidate how integrated biological communities interact to adapt themselves to contaminant stress, and to optimize phytoremediation activities (Thijs et al., 2016).

The impressive advent of high-throughput sequencing techniques and omics-based approaches has provided novel insights into the diverse species compositions and community structures of the endophyte microbiome, revealing the abundances of even rare endophytic species (Bell et al., 2014; Desai et al., 2010). However, molecular methods alone cannot reveal the functions or putative roles of endophytic microorganisms in phytoremediation, either in the laboratory or in nature (Prakash et al., 2013). Further developments in phytoremediation must be anchored with corresponding developments in the isolation, characterization, and preservation of novel endophytic microbes. A polyphasic strategy that closely couples laboratory-based cultivation with molecular techniques is needed to decipher the complex interactions between endophyte community members and their hosts and their interplay with the environment during phytoremediation.

3.2. Biosurfactants from endophytes and their roles in phytoremediation

Phytoremediation provides only a partial solution for decontaminating soil polluted with organic contaminants (Ijaz et al., 2016). The persistence of organic pollutants in the environment is linked with their different hydrophobic properties, as described by octanol–water partition coefficients (K_{ow}). Plant uptake of organic compounds is the first and most crucial step in phytoremediation, and is, in general, governed by the hydrophobicity of these organic contaminants (Chakraborty and Das, 2016). Moderately hydrophobic compounds with a log K_{ow} ranging from 0.5 to 3.0 tend to be taken up by plant roots before their degradation by rhizospheric microflora (Arslan et al., 2015). These compounds readily enter the xylem stream for subsequent accumulation or degradation. Therefore, after this class of contaminants accumulates within plant tissues for a significant amount of time, endophytes seem to be well-suited for *in planta* detoxification of these compounds (Afzal et al., 2014; Ijaz et al., 2016). In the case of soils contaminated with highly hydrophobic xenobiotics with a log K_{ow} greater than 3.0, phytoremediation is not a suitable solution, because plants are unable to degrade these organic chemicals in their rhizosphere or tissues (Arslan et al., 2015). It is well established that bioavailability is one of the most limiting factors in the phytoremediation of persistent organic pollutants in soils (Wenzel, 2009). The poor water solubility of highly hydrophobic organic pollutants limits their mobility and bioavailability, which is determined by the rate at which the substrates reach the cell surface with regard to the rate of uptake and metabolism. The presence of biosurfactants released by microorganisms or plants may facilitate the removal of such organic contaminants in soils by increasing their bioavailability, uptake by plants, or microbial degradation, and thus enhance the efficiency of phytoremediation *in situ* (Shekhar et al., 2015; Zhang et al., 2014a).

Recently, attention toward biosurfactants has doubled (Shekhar et al., 2015). Several studies have shown that endophytes can produce biosurfactants, increasing the bioavailability of organic contaminants and increasing bioremediation efficiency (Zhang et al., 2014a; Kukla et al., 2014). The efficiency of the phytoremediation of organic-contaminated soils can thus be increased by inoculating plants with biosurfactant-producing endophytes (Fig. 2). The root endophyte *Bacillus subtilis* K1 secretes biosurfactants that exhibit good emulsification activity, excellent surface-active properties, as well as high stability, making it suitable for bioremediation of oil-contaminated soils (Pathak and Keharia, 2014). Interestingly, a novel endophytic actinomycete, *Nocardiopsis* sp. mrinalini9, from leaf tissues of the medicinal plant *Hibiscus rosasinensis*, was found to possess both biosurfactant production and hydrocarbon biodegradation capacities, showing great potential for the bioremediation of diesel-contaminated soils (Singh and Sedhuraman, 2015). Many other known endophytic microbes of the *Acinetobacter*, *Bacillus*, *Kocuria*, *Microbacterium*, *Pseudomonas*, and *Rhodococcus* genera have been investigated for production of biosurfactants and bioemulsifiers and their potential applications in phytoremediation (Kukla et al., 2014; Pathak and Keharia, 2014).

Endophytic microorganisms with remarkable biosurfactant capacities have been isolated from plants, as described above. However, little is known about the potential biosurfactant production by endophytes *in situ*, as most of the studies were performed *in vitro*. Based on these studies, it is reasonable to speculate that endophytes can produce biosurfactants *in vivo*, facilitating the degradation of organic contaminants in plant tissues. Recent indirect evidence suggests that PAH-degrading endophytic bacteria could significantly reduce the accumulation of hydrophobic PAHs in plant tissues (Liu et al., 2014; Sun et al., 2015a). It is well known that the efficiency of any phytoremediation system depends on the bioavailability of the targeted pollutants and root-microbial modifications of their solubility and chemical speciation in the rhizosphere (Wenzel, 2009). Another possibility is that biosurfactants derived from endophytes colonizing root tissues are released into the rhizosphere soils from the roots; this has a significant effect on rhizosphere processes (Read et al., 2003; Sun et al., 2012), leading to enhanced rhizodegradation of organic pollutants in soils (Juwarkar et al., 2010). Perhaps more importantly, biosurfactant-producing endophytes recruited by biophysical or host-derived metabolic cues can surround root surfaces and thrive there to enhance the degradation of xenobiotics by releasing biosurfactants directly into the rhizosphere (Thijs et al., 2016). Such rhizosphere processes are an important strategy for circumventing the limitations of xenobiotic hydrophobicity, and may mobilize hydrophobic pollutants from soil particle surfaces (Vergani et al., 2017; Wenzel, 2009), enabling their degradation in the rhizosphere or in tissues. The application of biosurfactant-producing endophytic inoculants is a promising approach for improving the efficiency of the phytoremediation of organic-contaminated soils. Yet, there is no convincing evidence for the direct stimulation of biosurfactant-producing endophytes *in situ*. Further research, in the form of a series of bench-scale and potted plant experiments, should focus not only on endophyte biosurfactant production under different controlled conditions but also on existing phytoremediation processes, because there is a need for more informative data.

Based on the concept of bioaugmentation, inoculation with biosurfactant-producing microorganisms is a promising strategy for enhancing the bioremediation of organic-contaminated soils (Banat et al., 2010; Mnif et al., 2015). This practice avoids the high costs of producing and preparing biosurfactants and offers the advantage of a continuous supply of non-toxic biodegradable surfactants. In fact, the use of microbes with concurrent capacities to degrade hydrophobic contaminants and produce biosurfactants can effectively speed up the bioremediation of organic-contaminated soils (Kumari et al., 2012; Zhang et al., 2014a). In most cases, microbes naturally coexist in consortia that provide robust and broad metabolic capacities, and these traits are attractive for the bioremediation of organic-contaminated soils (Hays et al., 2015). Endophytes can coexist in plant tissues, and are physiologically compatible and mutually complementary. In *Scirpus triqueter*, the biosurfactant-producing endophyte *Bacillus subtilis* U-3 coexists with the diesel-degrading endophyte *Pseudomonas* sp. J4AJ, exemplary candidates for the remediation of oil-contaminated environments (Zhang et al., 2014a). A diversity analysis of endophytic bacteria in *Lolium perenne* from Kukla et al. (2014) found five biosurfactant-producing endophytes coexisting with other endophytic bacteria, including plant growth-promoting strains and hydrocarbon-degrading strains. The combined activities of these strains may be responsible for the effectiveness of phytoremediation by this plant–endophyte system. The continuous interplay between different microbial species may be either cooperative or antagonistic. However, incompatibilities among inoculated microorganisms can cause antagonism in the rhizosphere and/or endosphere due to competition for nutrients or other resources (Lutz et al., 2004). Clearly, further detailed investigations into microbial interactions within constructed consortia are necessary to achieve the desired enhancement of their pollutant-degrading potential, enabling more effective bioremediation.

3.3. Plant metabolism of organic contaminants

Plant metabolism of organic contaminants can offer an environmentally benign, cost-effective, feasible option for soil bioremediation (Glick, 2015; Schwitzguébel, 2015). Plants adapt themselves to stresses induced by organic contaminants by establishing detoxifying systems inside their cells where organic pollutants are reduced, converted, catabolized, or even eliminated, giving plants an ability to minimize the deleterious effects of pollutants known as the "green liver" model (Sandermann, 1994). This model was proven in studies of the carrot (*Daucus carota* var. *Sativus*), which demonstrated the ability to degrade phthalate esters (PAEs) (Sun et al., 2015b). Enzymes in higher plants can detoxify organic contaminants through degradation and conjugation processes (Kvesitadze et al., 2009; Glick, 2015). Enzymes such as peroxidase, polyphenol peroxidase, catalase, cytochrome P450 monooxygenases, dehalogenase, nitroreductase, laccase, hydrolase, and glutathione-S-transferase participate directly in the tolerance, stabilization, deposition, and detoxification of organic contaminants (Kvesitadze et al., 2009; Schwitzguébel, 2015; Yu and Powles, 2014).

Oxygenases such as cytochrome P450 monooxygenases and peroxidases can mediate the initial metabolism of organic contaminants in plants, including ring-breaking activities necessary for benzene derivatives such as toluene (Kvesitadze et al., 2009; Sandermann, 1994). Plants also carry out aryl and alkyl hydroxylation, ester hydrolysis, and N- or O-dealkylation reactions (Schwitzguébel, 2015; Sun et al., 2015b). These processes modify organic compounds by introducing functional groups, resulting in more polar and active compounds with increased solubilities (Komives and Gullner, 2005). The activated compounds are conjugated to plant polar molecules such as glutathione, amino acids, carbohydrates, malonic acid, or sulfate. Covalent modifications include peptide conjugation and ether, ester or thioether linkages, catalyzed by transferases such as glycosyltransferases and glutathione S-transferases (Aken et al., 2010; Kvesitadze et al., 2009). Soluble conjugates are routed to vacuoles or apoplasts *via* GST or ATP binding, or can be completely mineralized into CO_2 and H_2O. Bound conjugates are moved out of the cell *via* exocytosis to the apoplast and incorporated into the cell wall (Komossa et al., 1995; Kvesitadze et al., 2009).

Cytochrome P450 monooxygenases, peroxidases, and Remazol Brilliant Blue R oxidases can transform PCBs in plants (Chroma et al., 2002, 2003; Vergani et al., 2017). Glycosyltransferases and glutathione S-transferases are conjugated to PCBs using glucose and glutathione as substrates, respectively (Sandermann, 1994; Vergani et al., 2017). Conjugates with a suitably reactive functional group are sequestered into different cellular compartments for catabolism or storage. The plant cytochrome P450-containing monooxygenases and dioxygenases are critical for the oxidation of BTEX compounds (benzene, toluene, ethylbenzene, and xylenes), using NADH or NADPH as electron donors to break benzene rings (Kvesitadze et al., 2009; Thiravetyan et al., 2015). Additionally, cytochrome P450 monooxygenase, glycosyl-transferase, and glutathione S-transferase are involved in both detoxification and signaling functions in promoting herbicide metabolic resistance in weedy plant species (Cummins et al., 2013; Yu and Powles, 2014). In ryegrass, pumpkin, and maize, nitroreductase and glutathione-transferase are the essential enzymes for polybrominated diphenyl ethers (PBDEs) transformation *via* debromination (Huang et al., 2013). Cytochrome P450 monooxygenase, glutathione, and laccase also play roles in phytooxidation and covalent modifications for the removal of hexachloroethane (HCA) and dichlorodiphenyldichloroethane (DDD) (Dhir, 2013). Other enzymes, including dehalogenase, glutathione S-transferase, and Fe-S clusters in chloroplast ferredoxin are also involved in the removal of HCA and DDD.

The "green liver" model has unequivocally illustrated the transformation processes of organic contaminants in plants, and common degradative enzymes used for biotransformation, such as peroxidase and cytochrome P450, have been identified (Glick, 2015; Sun et al., 2015b; Vergani et al., 2017). However, the exact regulatory mechanisms have not been elucidated at a molecular level, making the prediction and manipulation of xenobiotic transformation impossible. These xenobiotic-degrading enzymes can be engineered with transgenes to improve their stability or efficiency with respect to various organic compounds (Doty, 2008). Next-generation sequencing and omics technologies present a fundamental tool for revealing the molecular mechanisms behind phytoremediation. By enabling important insights into the genes and metabolic pathways involved in contaminant catabolism by plants, new functional genomics studies of pollutant-degrading microorganisms and model microbial communities have improved our understanding of the genetic and molecular bases of the reactions involved in transformation processes (Bell et al., 2014; Bouhajja et al., 2016; Ufarté et al., 2015).

To date, few omics investigations have been aimed at plant responses to organic contaminants. One study found that hexahydro-1,3,5-trinitro-1,3,5-triazine (RDX) induced differential expression of five major genes involved in the detoxification of xenobiotic pollutants in poplar (Tanaka et al., 2007). Knowledge of the processes involved in plant metabolism of organic contaminants is still limited. Discovering new degradation pathways of xenobiotic pollutants is still challenging. Despite this, the wealth of data provided by omics approaches allows for broad mapping of genetic, enzymatic, and metabolic networks involved in phytoremediation at the plant level. Further studies elucidating the metabolic pathways of xenobiotic degradation in plant–microbial associations, particularly in plant–endophyte partnerships, and the underlying feedback mechanisms that lead to xenobiotic degradation and transformation in plant tissues, at both the genetic and biochemical levels, are conceivable.

3.4. Plant–endophyte partnerships for cleaning up organic contaminants

3.4.1. Endophyte colonization and survival

Beneficial plant endophytes are useful for studying plant growth-promoting mechanisms (Hardoim et al., 2015; Santoyo et al., 2016), and are also of interest for their potential as xenobiotic-degrading microorganisms for phytoremediation (Afzal et al., 2014; Ijaz et al., 2016). The use of plants and their associated endophytes in treating organic-contaminated soils is gaining increasing acceptance as a feasible cleanup technology (Afzal et al., 2014; Ijaz et al., 2016). However, in many cases, inoculants fail to induce the desired effects when re-inoculated in the field. This may be due to insufficient rhizosphere and/or plant colonization and survival of the endophytes, which has been identified as a crucial step (Lugtenberg et al., 2001). Therefore, successful execution of these versatile endophyte-assisted phytoremediation strategies requires a thorough understanding of the factors governing endophyte colonization of the rhizosphere and/or plant tissues, to improve the efficiency and reliability of inoculant strains in contaminated soils.

The "competition-driven" model may explain the colonization and survival of beneficial endophytic inoculants in a contaminated rhizosphere and/or plant tissues (Thijs et al., 2016). Plants actively recruit, or at least exhibit preferences toward, a specialized microbial flora to colonize their rhizosphere and/or interior tissues. This complex microbial community is often referred to as the second genome of the plant, extending the functional potential of the host (Berendsen et al., 2012). Endophytes that can colonize internal plant tissues may have an advantage over microorganisms inhabiting the rhizosphere, as they have close contact with plant cells and receive a direct supply of carbon, and therefore exert a direct beneficial effect on plant growth. Of course, rhizosphere microorganisms may also have the potential to enter and colonize plant roots and then spread throughout the plant, which is well known as one of the primary routes of endophytic colonization (Hardoim et al., 2008). Following rhizosphere colonization, endophytes may invade specific plant tissues and colonize various plant compartments (Compant et al., 2011; Fig. 1). In light of this, endophytic diversities represent a subset of complete rhizosphere microbial communities (Compant et al., 2010; Santoyo et al., 2016).

The processes of plant colonization by beneficial endophytes include rhizosphere and rhizoplane colonization, and subsequent plant tissue colonization. Before they can confer any beneficial effects on a plant, endophytic inoculants must be competent root colonizers, characterized by strong microbial competition (Compant et al., 2005). The combined actions of microbe–microbe and host–microbe interactions drive root microbiota differentiation through physiological processes occurring at the root–soil interface. Chemotaxis toward root exudates and root mucilage plays an important role in successful rhizosphere and rhizoplane colonization, which is highly dependent on plant phenotype, the exposure of the plant to stress, and agricultural practices (Compant et al., 2010; Kristin and Miranda, 2013). In addition, some root exudates are repulsive compounds that have negative effects on inoculant colonization (Bais et al., 2006). Root exudation and root mucilage are spatially heterogeneous, leading to spatial and temporal differences in rhizosphere and rhizoplane colonization (Lareen et al., 2016). Aside from chemotaxis toward root exudates, several other factors are involved in colonization processes, including biocontrol activities, bacterial flagella, quorum sensing, and the production of specific compounds and enzymes, which have been discussed in detail previously (Alquéres et al., 2013; Compant et al., 2010; Kusari et al., 2015).

Efficient colonization in the rhizosphere and rhizoplane of a host plant is the first step for endophytes engaging in plant–microbe interactions (Compant et al., 2010). Endophytic inoculants can, therefore, become successful endosphere colonizers if they have the ability to deal with the vagaries of their changing surroundings, from the external environment to inside plant tissues, where different tissues require different microbial responses (Compant et al., 2011; Hardoim et al., 2008). Competent inoculants utilize active or passive mechanisms in their translocation processes that allow them to progress from the rhizoplane to the cortex of the root system through primary and lateral root cracks, fissures, and diverse tissue wounds (Hardoim et al., 2008). Alternative sources may be the caulosphere for stem endophytes and the phyllosphere for leaf endophytes (Compant et al., 2016; Sun et al., 2015a). Important factors such as lipopolysaccharides, flagella, pili, twitching motility, and the secretion of cell wall-degrading enzymes facilitate endophytic colonization and mobility within the host plant (Compant et al., 2010). Studies have also shown that additional genes, various metabolic pathways, and transport systems are all involved in endophytic colonization (Fouts et al., 2008). In particular, the modulation of ethylene levels in plant tissues by microbial-derived ACC deaminase is a key factor influencing plant physiology (Glick, 2014), and the ability of inoculants to modulate plant ethylene concentrations is imperative for their competence as endophytes (Hardoim et al., 2008). Once they are inside the plant, endophytes respond to plant-derived assembly signaling cues to enter the endophytic life stage and spread to other root cortex tissues and beyond (reviewed in Compant et al., 2010; Hardoim et al., 2008). A single colonization event by one competent endophytic cell will be followed by its multiplication inside the plant, often reaching high population density, particularly in the roots, where endophytes can establish subpopulations of 10^5–10^7 CFU g^{-1} FW (Hallmann, 2001).

Effective root colonization leads to dense populations of diverse heterotrophic microorganisms inhabiting the rhizosphere, rhizoplane, and interior plant tissues. These competent microbial associations increase the capacity for the stepwise transformation of organic contaminants by consortia in the rhizosphere and/or within plants, providing opportunities for genetic exchange and gene rearrangements (Jha et al., 2015). The reed endophyte *Achromobacter xylosoxidans* F3B successfully inoculated the model species *Arabidopsis thaliana* and vetiver (*Vetiveria zizanioides*), improving toluene degradation in vetiver (Ho et al., 2013). In an attempt to investigate the patterns and sites of entry of endophytes, fluorescence microscopy technology was used to study green fluorescent protein (GFP)-labeled strains after inoculation (Gaiero et al., 2013). With this technique, the phenanthrene-degrading endophyte *Pseudomonas* sp. Ph6-*gfp* was found to actively colonize inoculated ryegrass roots, stems, and leaves, showing a natural capacity to reduce the risk of plant phenanthrene contamination by decreasing the concentration and accumulation of phenanthrene *in planta* (Sun et al., 2015a). GFP-based techniques have successfully formed the foundation for investigating endophyte colonization patterns. A new technique based on fluorescence resonance energy transfer (FRET) was developed to visually confirm the intracellular presence of endophytic species in plant tissues as an alternative when the use of GFP is restricted (Banik et al., 2016).

Describing dispersal in microbial communities is often a difficult task, as endophytic communities are dynamic over time and rather unpredictable in plant tissues (Hardoim et al., 2015). Moreover, using conventional cultivation-dependent techniques, we often miss the endophytes with low abundance or exhibiting slow growth and fail to assess or access the uncultivable microbial majority (Prakash et al., 2013). Aside from GFP-based techniques, a number of cultivation-independent molecular techniques analyzing the colonization, taxonomic and functional diversity, and metabolic activities of pollutant-degrading endophytes are compatible with high-throughput setups such as genetic fingerprinting, real-time PCR, DNA microarrays, and pyrosequencing-based metagenomics (reviewed by Jha and Jha, 2015). The cultivation-independent 454 pyrosequencing technique was used to investigate changes in endophytic bacterial communities following exposure of zucchini (*Cucurbita pepo* ssp. *pepo*) to 2,2-bis(p-chlorophenyl)-1,1-dichloro-ethylene (DDE), confirming the improved phytoremediation of DDE-contaminated soils by *C. pepo* with endophytic assistance (Eevers et al., 2016).

Soil characteristics such as soil type, particle size, or organic matter content not only affect plant growth but also substantially influence microbial colonization and activities (Afzal et al., 2014; Pandey et al., 2009). For example, sand, loamy sand, and loam soil types significantly influence colonization by root endophyte *Pseudomonas* sp. strain ITRI53, promoting variations in hydrocarbon degradation (Afzal et al., 2011). The inoculation method is another crucial factor affecting the colonization and survival of endophytes and ultimate phytoremediation efficiency. Ryegrass was inoculated with the root endophyte *Burkholderia phytofirmans* PsJN by four different methods, and soil inoculation was found to be the most efficient in facilitating plant biomass production, hydrocarbon degradation, and toxicity reduction, compared with seed inoculation, rhizosphere inoculation, and foliar inoculation (Afzal et al., 2013). On the other hand, root soaking was recognized as an optimal method for colonization and phenanthrene removal efficiency by the endophyte *Pseudomonas* sp. Ph6-*gfp in planta* compared with seed soaking and leaf painting (Sun et al., 2015a). The plant species can also affect the colonization patterns and metabolic activities of inoculated endophytes during phytoremediation. The colonization and metabolic activities of an oil-degrading endophytic consortium were higher in the rhizosphere and endosphere of *Brachiaria mutica* than in *Leptochloa fusca*, two grass species planted in crude oil-contaminated soil (Fatima et al., 2016). Moreover, host plant origin, plant development stage, density of the inoculum, timing and frequency of inoculation, and contaminant concentrations in different soil substrates have considerable influence on endophytic inoculant colonization and survival, and subsequent phytoremediation efficiency (Afzal et al., 2011; Hardoim et al., 2008; Khan et al., 2013). Variable outcomes indicate that our understanding of endophytic colonization is still incomplete.

A particularly important aspect to consider is prioritization (Thijs et al., 2016). Studies are inconclusive as to whether a plant with an established microbial community changes its associations or keeps the ones already formed when new inoculants are introduced (Kristin and Miranda, 2013). Further analysis of sequenced genomes, characterization of unknown genes, and the identification of genes expressed during colonization will aid in predicting the dynamics of endophyte-plant interactions and whether endophytes are likely to establish themselves in the plant environment after field applications for phytoremediation. Metagenome sequence analysis of rice root endophytic bacteria deduced several putative functions in motility, plant polymer degradation, iron acquisition and storage, quorum sensing, and detoxification of reactive oxygen species, which are important factors in colonization by the root microbiome (Sessitsch et al., 2012). From the genomes of the analyzed endophytic strains, a list of genes is predicted to be involved in determining the endophytic colonization of *Burkholderia* spp. (Ali et al., 2014). Various inherent properties necessary for efficient colonization of plant environments could explain sufficient plant host colonization by rhizosphere and/or endophytic inoculants. An improved understanding of how beneficial endophytes colonize different plant niches will further our knowledge of plant–endophyte interactions and enable the design of treatments that specifically promote colonization for effective bioremediation. However, the genetic principles governing the differential colonization of endophytes are still unknown and require further investigation.

3.4.2. Mutualistic symbiotic relationships between host plants and endophytes

Instead of the “individual plant” approach, the use of assemblages of plants and associated endophytes with complementary or synergistic traits will likely provide more effective and consistent phytoremediation

(Afzal et al., 2014). This concept of so-called "concerted plant–endophyte synergisms" is gaining more and more momentum. The symbiotic system of oil-degrading endophyte *Pseudomonas* sp. J4AJ and *Scirpus triqueter* increased the height and stem biomass of *S.triqueter* and enhanced diesel oil removal rates compared with individual plants (Zhang et al., 2014b). The inoculation of carpet grass, *Axonopus affinis*, with a mixture of microorganisms, two hydrocarbon-degrading *Pseudomonas* sp. ITRH25, *Pantoea* sp. BTRH79, and one plant growth-promoting endophyte, *Burkholderia* sp. PsJN, resulted in enhanced plant growth and improved phytoremediation (Tara et al., 2014). However, not all plant species and their associated endophytes are suitable candidates for improving phytoremediation. When the aquatic plant *Spirodela polyrhiza* was inoculated with three endophytes, *Pseudomonas* sp. E46, *Klebsiella terrigena* E42, and *Pseudomonas* sp. E1, fenpropathrin degradation was only 17.5% higher in *Pseudomonas* sp. E46 inoculated plants, and little effect was observed in the two other treatments (Xu et al., 2015).

Considering the additional contribution to enhancing phytoremediation, the compatibility between endophytes and host plants should merit more consideration (Saikkonen et al., 2010). Endophytes residing mutualistically within the internal tissues of host plants are capable of maintaining bi- and tripartite synergistic associations with host plants and associated microbes (Kusari et al., 2013). To understand and eventually manipulate these synergistic relationships, the molecular interaction mechanisms underlying compatible relationships between the partners must be elucidated (Reinhold-Hurek and Hurek, 2011). Admittedly, such data are still limited. There is compelling evidence that endophytes co-evolve with host plants to recognize each other by quorum sensing-like cell-to-cell communication (Kusari et al., 2015). Endophytes and host plants constantly communicate either with each other or with associated microflora and macroflora *via* quorum-sensing systems, thereby maintaining mutualistic associations (Kusari et al., 2015). Interpreting the trafficking of quorum-sensing signaling molecules in multispecies crosstalk remains a huge challenge. Plants from various genera reportedly may produce acyl-L-homoserine lactones (AHLs), mimicking compounds for interacting with associated microflora, both within and outside plant tissues (Pérez-Montaño et al., 2013). Comparative genome analysis revealed that the endophyte *Burkholderia phytofirmans* PsJN possesses genes for quorum-sensing compounds 3-hydroxy-C8-homoserine lactones, 3-hydroxy-C14-homoserine lactones, 3-oxo-C12-homoserine lactones, and 3-oxo-C14-homoserine lactones, allowing them to associate with various host plants and improve plant root systems (Mitter et al., 2013; Sessitsch et al., 2005).

Admittedly, there is currently a dearth of data pertaining to quorum-sensing system-mediated multispecies communication between endophytes and host plants at the molecular level (Kusari et al., 2015). A deeper appreciation of plant–endophyte interaction signaling at a cellular level may provide novel therapeutic strategies for enhancing beneficial synergistic relationships. The complementary metabolic effects of plant–endophyte communities on their environment have great potential in endophyte-assisted phytoremediation. Therefore, we propose that a balanced and compatible plant-endophytic symbiosis is required. However, our current understanding of the co-evolution, trophic relationships, and functioning of these mutualistic symbiotic interactions is still poor, impeding the development of such applications (Frey-Klett et al., 2011). Further studies addressing these issues will have major implications for plant-endophytic biology and ecology in relation to phytoremediation.

3.4.3. Co-metabolism of organic contaminants

Due to their toxicity and limited bioavailability, some organic contaminants, especially recalcitrant compounds such as polychlorinated biphenyls (PCBs) and PAHs, cannot be used as carbon and energy sources for endophytic communities during phytoremediation (Kuiper et al., 2004; Musilova et al., 2016). Meanwhile, a lack of catabolic enzyme induction and low levels of growth-supporting substrates may limit the growth and proliferation of endophytes. In fact, co-metabolism of pollutants and interspecies metabolism are the rule, rather than the exception (Thijs et al., 2016). Biodegradation of recalcitrant compounds can occur through co-metabolism involving the oxidation of organic contaminants (non-growth substrates) in the presence of growth substrates (Kuiper et al., 2004; Martin et al., 2014; Soleimani et al., 2010), the major mechanism used by endophytes and plants for the degradation of recalcitrant pollutants. Complementary biodegradation associated with a mixed-species community within plant tissues is known as the metabolome (Bell et al., 2014). In the case of phytoremediation of organic contaminants, plants can benefit from endophytes equipped with appropriate degradation pathways and metabolic capacities, and *vice versa*, both of which may lead to the enhanced phytoremediation of organic contaminants through co-metabolism (Thijs et al., 2016; Weyens et al., 2009a).

Cooperation to achieve novel catabolic reactions should be seen within host plants (Ijaz et al., 2016). The close link between endophyte fitness and its host plant may be ascribed to the alignment of interests of both partners toward mutually beneficial cooperation (Saikkonen et al., 2010), leading to co-metabolism during phytoremediation. When using plant-associated endophytes, an inoculated plant can efficiently increase its metabolic activity by furnishing growth substances derived from photosynthesis such as organic acids, sugars, and amino acids (Bacon and Hinton, 2006; Soleimani et al., 2010). These substances provide carbon and energy sources for microbial degradation and/or induce the synthesis of degradation enzymes and coenzymes (NADH, NADPH), ultimately leading to enhanced degradation of organic pollutants. Endophytes that chronically inhabit plant interiors obtain pollutant-degrading genes through horizontal gene transfer (Thijs et al., 2016), and thus share a diverse array of catabolic enzymes with their host plants. These catabolic enzymes are perfectly suited to metabolizing and detoxifying xenobiotic compounds in plant tissues (Dhir, 2013; Kvesitadze et al., 2009). There is direct evidence that cytochrome P450 monooxygenase enzymes are commonly found in animals, plants, and endophytes that play roles in the detoxification of their environments (Singer et al., 2003).

Additionally, many plant secondary metabolites such as terpenes, flavonoids, salicylic acid, and lignin derivatives are important natural substrates readily used by endophytes within plant tissues, and play an important role in developing the myriad organic pollutant-degrading enzymes found in nature (Gilbert and Crowley, 1997; Jha et al., 2015; Musilova et al., 2016; Singer et al., 2003). These naturally occurring chemicals in plants share structural similarities with many hazardous organic chemicals, and some of them are intermediates or inducers of degradation pathways produced during the degradation of other contaminants (*e.g.*, PCBs, pyrene, or 2,4-dichlorophenoxyacetic acid) (Jha et al., 2015; Khan et al., 2013; Passatore et al., 2014). These plant secondary metabolites may serve as analogues or co-metabolites of organic contaminants to stimulate endophytic degradation of xenobiotics and broaden the spectrum of their activities (Jha et al., 2015). In particular, salicylate, involved in inducing systemic acquired resistance in plants, has been linked to the microbial degradation of naphthalene (Singer et al., 2003). Therefore, plant secondary metabolites as appropriate co-substrates may enable endophytes to facilitate bioconversion or neutralize the phytotoxicity of contaminants by modulating degradative gene expression and activating microbial metabolic pathways (Liu et al., 2014; Siciliano et al., 2001; Yousaf et al., 2011). For these reasons, considerable attention has been given to the potential applications of plant-associated endophytes for their innate biodegradation of organic contaminants, their distinct physiological and biochemical characteristics, and their potential as vectors for pollutant-degrading gene delivery (Afzal et al., 2014; Doty, 2008). Exemplifying this strong specificity, several PAH-degrading endophytes that can co-metabolize PAHs in plant tissues have been isolated from plants grown in PAH-contaminated soils (Liu et al., 2014; Sun et al., 2014; Zhu et al., 2016).

Plant secondary metabolites are undoubtedly one of the main driving forces generating highly diversified interactions between plants and their associated microorganisms, which offer the unique opportunity to enhance phytoremediation of xenobiotic contaminants (Jha et al., 2015; Musilova et al., 2016). The co-inoculation of bent grass (*Agrostis capillaris*) with a CAP9 consortium of microorganisms, one root endophyte *Variovorax ginsengisola*, three *Pseudomonas* spp. rhizobacteria, and one endo-phyllosphere *Stenotrophomonas chelatiphaga*, resulted in more efficient TNT co-metabolism and enhanced plant growth (Thijs et al., 2014). However, studies directly linking the composition and quantity of plant secondary metabolites to the co-metabolism of organic contaminants within plant tissues are scarce. The mechanisms regulating co-metabolism between plants and associated endophytes are still unknown. The mechanisms of directly cooperative plant–endophyte interactions in the co-catabolism of pollutants, which will aid in developing novel catabolic reactions for degrading recalcitrant compounds, also require more research.

Finding a suitable experimental setup for investigating phytoremediation processes occurring at the dynamic interface between a plant and its endophytes in the microenvironment of plant tissues still represents a major challenge. This knowledge is critical to fully optimize endophyte-assisted phytoremediation processes. The use of novel omics approaches may provide a detailed understanding of the effects of plants on the activities of endophytes involved in transforming specific organic contaminants (Bell et al., 2014; Schenk et al., 2012). Furthermore, applying DNA-based stable isotope probing (DNA-SIP) techniques to $^{13}CO_2$-exposed plants will be incredibly useful in identifying the endophytic transformation pathways for xenobiotic compounds of interest (Jha et al., 2015). Combining DNA-SIP with omics approaches permits us to track organic contaminants co-metabolized by a broader set of endophytic species or functional groups in multi-species consortia (reviewed in Martin et al., 2014; Uhlik et al., 2013), paving a new avenue in the field of endophyte-assisted phytoremediation of organic contaminants.

3.4.4. Enzymes for organic contaminant degradation

All plants have the capacity to be host plants harboring a great diversity of endophyte species (Compant et al., 2016; Wani et al., 2015), and specific endophytes colonizing plants can stimulate certain transcription levels of pollutant-degrading genes and thus exert a significant potential impact on the metabolic activities of degrading enzymes (Siciliano et al., 2001). These endophytes represent a huge natural reservoir of degrading enzymes for identifying pollutants and the complete bioremediation of organic-contaminated soils (Afzal et al., 2014). When exposed to organic contaminants, some endophytes have the potential to trigger and regulate both basal and inducible enzymes in plants or endophytes (Bacon and White, 2016; Kusari et al., 2015), accelerating the metabolic processing of organic pollutants *in planta* or enhancing the secretion of pollutant-degrading enzymes from roots into the rhizosphere, leading to accelerated *ex planta* degradation of organic pollutants (Khan et al., 2013; Sun et al., 2015a). Most pollutant-degrading enzymes, such as peroxidases, dioxygenases, P450 monooxygenases, laccases, dehalogenases, nitrilases, and nitroreductases, are known to be present in both endophytes and plants (Gerhardt et al., 2009). These enzymes directly participate in the biotransformation of many xenobiotic compounds (Kvesitadze et al., 2009). With the help of endophytic fungi *Neotyphodium coenophialum* and *Neotyphodium uncinatum*, inoculated plants *Festuca arundinacea* Schreb. and *Festuca pratensis* Huds. create more highly water-soluble phenols and increase the activity of dehydrogenase, an important enzyme for the degradation of PAHs (Soleimani et al., 2010).

On the other hand, some plant species grown in organic-contaminated soils also have the ability to selectively augment the abundance and activity of necessary catabolic enzymes produced by themselves and their associated endophytes (Siciliano et al., 2001). The synergetic action of catabolic gene-bearing plants and endophytes has co-evolved a diverse array of catabolic enzymes, perfectly suited to metabolizing organic pollutants present in plant tissues and the root zone and decreasing both the phytotoxicity and evapotranspiration of volatile organic pollutants (Fatima et al., 2016; Jabeen et al., 2016; Weyens et al., 2015). A higher abundance of PAH-ring hydroxylating dioxygenases was isolated from the root endophytes of *Spartina alterniflora* following treatment with high concentrations ($100\ mg\ kg^{-1}$) of phenanthrene, suggesting that the endophyte may play an important role in the phytoremediation of PAH-contaminated soils (Hong et al., 2015).

Although there are some microorganisms that can completely degrade certain organic pollutants, individual strains generally do not possess complete metabolic pathways (Gerhardt et al., 2009). In many cases, the degradation of organic pollutants requires the concerted action of several enzymes. For certain complex organic pollutants like PCBs, monooxygenases and peroxidases are unable to completely metabolize them in plants, but their intermediates can serve as substrates for bacterial *BphC* enzymes (Francova et al., 2004). Thus, endophytes harboring *bphC* genes may develop efficient plant–endophyte partnerships for the complete removal of PCBs through phytoremediation (Ijaz et al., 2016; Vergani et al., 2017).

Endophyte-assisted phytoremediation of organic-contaminated soils depends on the breakdown of organic contaminants into stable, innocuous end-products by pollutant-degrading enzymes. In plant–endophyte partnerships, the presence of large amounts of plant secondary metabolites possibly exerts a biostimulatory effect to induce degradative enzyme activities, and therefore may provide cells with energy (Jha et al., 2015; Musilova et al., 2016). This can be partly explained by the exogenous addition of plant litter significantly increasing indole degradation by inducing the endophyte *Phomopsis liquidambari* to produce the non-specific oxidases laccase and lignin peroxidase (LiP) (Chen et al., 2013b). Some endophytic fungi can produce extracellular oxidases including laccase, manganese peroxidase (MnP), and LiP, which are involved in the degradation of various phenolics (Promputtha et al., 2010). The O_2-dependent initial oxygenase attack on aromatic hydrocarbon structures is the most critical step in the degradation of aromatic pollutants (Fuchs et al., 2011). Moreover, catalase and dehydrogenase activities are enhanced in diesel-contaminated soils when *Scirpus triqueter* is inoculated with endophyte *Pseudomonas* sp. J4AJ, compared with the control treatment (without *S. triqueter*) (Zhang et al., 2014b).

Although we have presented some evidence supporting the “secondary compound hypothesis” as the explanation of endophyte-assisted phytoremediation of organic-contaminated soils (Musilova et al., 2016), these studies are based mostly on experiments using pure cultures. There are still considerable knowledge gaps regarding which plant-released chemicals stimulate the enzymatic activities of endophytes toward the degradation of specific contaminants. The implementation of meta-omics approaches provides new insights into the trophic interactions within plant tissues, thereby improving our understanding of the genes and enzymatic pathways involved in pollutant catabolism by plant–endophyte partnerships (Bell et al., 2014; Bouhajja et al., 2016). Particularly, many enzymes have been unearthed through functional metagenomics, a highly efficient technology for discovering novel enzymes from a huge diversity of microbial communities without requiring isolation and cultivation (reviewed by Ufarté et al., 2015). The SIP technique enables researchers to track the incorporation and degradation pathways of ^{13}C-, ^{15}N-, or ^{18}O-labeled compounds derived from plants in the community, to identify enzymatic expression patterns in both plants and endophytic microorganisms, and assess the role of plant secondary metabolites in the plant–endophyte system (Martin et al., 2014; Musilova et al., 2016; Uhlik et al., 2013).

3.4.5. Abundance and expression of pollutant-degrading genes

Plants coupled with their associated endophytes hold great potential for decontaminating soils polluted with toxic organic contaminants (Ijaz et al., 2016). The efficiency of a phytoremediation process depends primarily upon the presence (or colonization) and metabolic activity of the plant-associated microflora, which harbor biodegradative genes required for the enzymatic breakdown of organic pollutants (Mitter et al., 2013; Thijs et al., 2016). Many xenobiotic-degrading endophytes may serve as vectors to introduce biodegradation genes inside the host plants (Fatima et al., 2015; Ryan et al., 2008), contributing to the detoxification of the organic pollutants and improving survival of the plants under stress conditions. Plants grown in soil contaminated with xenobiotics selectively recruit endophytes with pollutant-degrading genes. In the presence of nitroaromatics, two genes encoding nitrotoluene degradation, 2-nitrotoluene reductase (*ntdAa*) and nitrotoluene monooxygenase (*ntnM*), were more prevalent in endophytes than within rhizospheric or bulk soil microbial communities (Siciliano et al., 2001). At petroleum hydrocarbon-contaminated sites, two genes encoding hydrocarbon degradation, alkane monooxygenase (*alk*B) and naphthalene dioxygenase (*ndo*B), were found to be much more prevalent in root endophytes than in the surrounding bulk soil communities (Siciliano et al., 2001).

Inoculation with pollutant-degrading endophytes efficiently enhances the abundance and expression of degrading genes in the rhizosphere and/or endosphere of the inoculated plants vegetated in contaminated soils, resulting in improved phytoremediation. Italian ryegrass, an endophyte colonized by *Pseudomonas* sp. strain ITRI53, showed high expression of *alkB* genes, suggesting more efficient degradation of alkanes (Andria et al., 2009). Furthermore, *alkB* gene expression was higher in the shoot interior than in the root interior of Italian ryegrass, possibly because varied metabolites in the root and shoot influenced *alkB* gene expression (Andria et al., 2009). Similar effects, that hydrocarbon-degrading endophytes showed higher abundance and expression levels of *alk*B and CYP153 (cytochrome P450 hydroxylase) genes in the endosphere of different plant species as well as in the rhizosphere, were observed; this indicates a strong positive relationship between gene expression and hydrocarbon degradation (Fatima et al., 2016; Yousaf et al., 2011). The abundance and expression of *alkB* and CYP153 genes of endophytes involved in hydrocarbon degradation varied markedly with inoculant strains, plant species, plant development stages, and plant compartments (Yousaf et al., 2011). The host plant origin, which influences endophytic colonization in different plant compartments, and its various secondary metabolites, which provide nutrients for microbial growth and co-metabolites for xenobiotic degradation, may be responsible for the varied abundance and expression of pollutant-degrading genes (Musilova et al., 2016; Yousaf et al., 2011). In addition, some abiotic factors such as soil type, pollutant concentrations, and even inoculation method may affect the abundance and expression of pollutant-degrading genes in the rhizosphere and endosphere of inoculated plants (Afzal et al., 2014). Plant–endophyte partnerships certainly enhance the abundance and expression of catabolic genes in plant interior tissues as well as in the rhizosphere, leading to increased phytoremediation (Ijaz et al., 2016). Monitoring gene abundance and expression during the phytoremediation of organic-contaminated soils will provide indications of the presence of specific inoculated endophytes and the functional activity of pollutant-degrading genes (Oliveira et al., 2015).

However, the molecular mechanisms manipulating the abundance and expression of pollutant-degrading genes between host plants and their endophytes are largely unknown. The integration of SIP with metagenomics could help to identify novel genes, gene products, and degradation pathways involved in plant–endophyte interactions and to assess the potential of biodegradation by plant–endophyte systems (Bouhajja et al., 2016; Uhlik et al., 2013). The combination of DNA-SIP labeling and metagenomic sequence analysis has revealed the effects of ring-hydroxylating dioxygenase gene expression on PAH degradation (Chemerys et al., 2014). The universality of highlighted omics technologies will demystify the molecular mechanisms and their regulation of the expression of degradative genes; and the complex plant-endophytic interactions during phytoremediation will be exploited in more detail, enabling new breakthroughs in bioremediation technologies.

4. Strategies for enhancing phytoremediation by plant–endophyte partnerships

Endophyte-assisted phytoremediation of contaminated soils relies on the immense metabolic capacities of plants and their associated endophytes to transform organic pollutants into essentially harmless end products. Although plant–endophyte partnerships can cope with a wide range of organic contaminants and can adapt themselves to many different inhospitable polluted environments (Ijaz et al., 2016; Table 3), unfavorable environmental conditions still hamper their applications in the phytoremediation of organic-contaminated environments. In such cases, the solutions for successful bioremediation may be biostimulation, bioaugmentation, and genetic modification, all of which focus on hastening the kinetics of pollutant removal.

4.1. Biostimulation

Intentional biostimulation manipulates physicochemical parameters to stimulate the plants and indigenous microbes degrading organic pollutants (Adams et al., 2015). It can be done by adding various growth-promoting nutrients such as carbon, nitrogen, and phosphorus to improve metabolic activities. In some cases, biostimulation can be achieved using selected supplemental nutrients such as crude plant extracts or plant exudates that act as co-substrates inducing enzymes for co-metabolism (Jha et al., 2015; Reinhold-Hurek and Hurek, 2011). Additives such as electron acceptors or donors, oxidants, and bulking agents can also be used in biostimulation (Kuppusamy et al., 2016). Alternatively, successful biostimulation can be obtained by generating an optimal balance of physical factors such as aeration, temperature, and buffering of environmental pH by altering the redox state and electrokinetic state of contaminated soils (Pandey et al., 2009). These findings point to the possibility of diverse applications of biostimulation for *in situ* decontamination of polluted environments.

The primary advantage of biostimulation is that the stimulated indigenous microorganisms adapt well to the contaminated sites being treated. However, such an approach is not always effective. The challenges include the delivery of additives in a manner readily available to indigenous microbial communities, and the density and diversity of indigenous microbes capable of degrading high concentrations of pollutants (Adams et al., 2015). Biostimulation can be more effective when combined with bioaugmentation methods. Both indigenous and exogenous microorganisms can benefit from biostimulation by the addition of energy sources or electron acceptors (El Fantroussi and Agathos, 2005). However, any such planned intervention must be followed by site-specific evaluations of the contaminated site. There are few reports on the effects of biostimulation on endophyte-assisted phytoremediation of organic-contaminated soils. At any rate, biostimulation is a highly effective strategy for increasing the population densities of pollutant-degrading endophytes, as well as the rate of pollutant degradation in the rhizosphere and/or endosphere of plants, especially in contaminated soils with limited nutrients.

4.2. Bioaugmentation

Bioaugmentation, which has become a widely accepted practice, can be defined as the deliberate inoculation with specific competent strains or consortia microorganisms to improve the capacity of a contaminated soil to remove pollutants (El Fantroussi and Agathos, 2005). Successful application of the bioaugmentation technique depends on the selection of appropriate microbial strains, and their subsequent persistence, activity, and migration once introduced into polluted sites slated for bioremediation (Thompson et al., 2005). Bioaugmentation with endophytes would have several benefits over traditional bioaugmentation, as endophytes harboring appropriate metabolic pathways can improve *in planta* degradation of organic contaminants. *In situ* bioaugmentation of poplar trees growing on a TCE-contaminated soil with the TCE-degrading endophyte *Pseudomonas putida* W619-TCE resulted in the reduction of TCE evapotranspiration by 90% under field conditions and horizontal gene transfer of TCE degradative activity to members of the poplar's endogenous endophytic population (Weyens et al., 2009b).

Bioaugmentation can also be obtained with suitable plant growth-promoting endophytes, providing large and active beneficial microbial populations serving as plant growth promoters and biofertilizer (Hardoim et al., 2015). The inoculation of ryegrass with a chlorpyrifos (CP)-degrading endophyte, *Mesorhizobium* sp. HN3, which belongs to plant growth-promoting rhizobia, led to efficient colonization in the rhizosphere, enhanced plant growth and degradation of CP, and lower CP residues in plants (Jabeen et al., 2016). In addition, bioaugmentation of soils polluted with hydrophobic organics, with endophytic strains or consortia selected specifically for their biosurfactant production, has been highly successful (Pathak and Keharia, 2014).

Despite these successes, it is naive and unrealistic to expect that by simply picking the “right” organisms or tailoring the right field parameters, bioaugmentation will suddenly become reliable and predictable (Thompson et al., 2005). Inevitably, a plethora of barriers such as adaptations of microbial strains or microbial consortia, competition between introduced and indigenous biota, use of other organic substrates instead of the pollutant, and the availability of the contaminant to the microorganisms, determine the activity, persistence, and performance of bioaugmented inoculants (Adams et al., 2015). It bears mentioning that, by far, bioaugmentation does not achieve the desired outcomes at the field scale owing to the complexity of the environment. It is not practical to tailor microbial consortia specifically for every site and application. However, it is clear that the identification and isolation of strains should be made on the basis of a comprehensive understanding of the composition, population dynamics, and physiological profiles of the source communities, as well as those in the target habitats (Thompson et al., 2005). Apart from selecting well-adapted and catabolically competent strains, one should also consider environmental conditions in the target habitats, to achieve appropriate results.

4.3. Genetic modification

Desirable pollutant-degrading genes from microbes or higher organisms can be engineered into either plants or their endophytes (Doty, 2008). Successful transgene expression may improve the phytoremediation of organic contaminants by complementing the metabolic properties of plant–endophyte partnerships, leading to enhanced tolerance of phytotoxic chemicals and increased removal of organic contaminants, compared with wild types (Abhilash et al., 2009; Taghavi et al., 2011).

4.3.1. Engineering endophytes to improve phytoremediation

Endophytic microorganisms engineered with genetic information required for catabolic pathways can promote the degradation of pollutants in the rhizosphere and/or in plant vascular systems (Ijaz et al., 2016). Inoculation of plants with recombinant endophytic bacteria engineered with appropriate catabolic pathways resulted in efficient colonization, protection against the phytotoxic effects of naphthalene, and increased naphthalene degradation, compared with uninoculated plants (Germaine et al., 2009). Inoculation of poplar and yellow lupine plants with the engineered endophyte *Burkholderia cepacia* VM1468 increased biomass and decreased the phytotoxicity and evapotranspiration of toluene and TCE, respectively (Taghavi et al., 2005; Weyens et al., 2010). Engineered endophytes can act as vectors for delivering degradative abilities to improve the phytoremediation of organic contaminants in soils in two ways, or a combination thereof (Taghavi et al., 2011; Weyens et al., 2009b): the straightforward construction of an engineered endophytic strain among the endogenous community by conjugation, or the horizontal transfer of degrading genes to the endogenous endophytic community. Horizontal gene transfer of the pTOM-Bu61 plasmid (coding for constitutive toluene and TCE degradation) among plant-associated endophytic bacteria *in planta* has been observed (Taghavi et al., 2005). Such transfer could be used to modify endogenous endophytic communities and thus improve the bioremediation of environmental insults.

Being subject to selection pressure, the engineered endophytes with the appropriate degradation characteristics have a selective advantage over the indigenous community. Nevertheless, selective pressure cannot guarantee that an endophytic inoculum will become an integrated part of the endogenous endophytic community (Taghavi et al., 2005, 2011). Natural horizontal gene transfer plays an important role in the development of naturally engineered endophytes with appropriate catabolic genes and heterologous expression, thus allowing endogenous endophytic communities to rapidly adapt themselves to new environmental stressors (Taghavi et al., 2005). The prevalence of *nah* (naphthalene dioxygenase) genes and the detection of catabolic plasmids in plants indicate that horizontal gene transfer can drive the spread of *nah* genes in these habitats, which probably facilitates bacterial endophytic adaptation and *in planta* petroleum hydrocarbon degradation (Oliveira et al., 2014). It is of practical significance that endophytes are transgenically altered through horizontal gene transfers to enhance their degradation capabilities. We believe that genetically engineering indigenous endophytic strains by horizontal gene transfers within endogenous microbial populations should have superior adaptability to environmental stress over introducing entirely new strains.

4.3.2. Transgenic plants for enhanced phytoremediation

Transgenic plants expressing bacterial or mammalian genes involved in xenobiotic metabolism can be used to enhance the phytoremediation of herbicides, explosives, PCBs, *etc.* (Abhilash et al., 2009; Kawahigashi, 2009). The first transgenic plants with enhanced metabolism of organic pollutants targeted explosives and halogenated compounds in tobacco plants (Doty et al., 2000; French et al., 1999). Transgenic alfalfa plants expressed the 2,3-dihydroxybiphenyl-1,2-dioxygenase (*BphC.B*) gene cloned from a soil metagenomic library, resulting in improved disposal and tolerance of complex contaminants of PCBs/2,4-DCP, which were used to help achieve the phytoremediation of soils contaminated with a mixture of PCBs and 2,4-DCP (Wang et al., 2015). The combination of this transgenic alfalfa and the bioemulsifying protein, AlnA, as a biosurfactant, led to higher removal rates of PCBs (Ren et al., 2016). In the case of improved PCB degradation, it should be noted that the *Pseudomonas*-like PCB-degrading gene, *bphC*, was significantly more abundant in the transgenic alfalfa/AlnA treatment compared with unplanted soils (Ren et al., 2016). Transgenic *Arabidopsis* and rice plants expressing four *Pseudomonas* genes encoding a naphthalene dioxygenase system provide an efficient and environmentally friendly technology for cleaning up soils contaminated with PAHs (Peng et al., 2014).

Transgenic plants that express a bacterial gene encoding ACC deaminase (*acdS*) under the regulation of a root-specific promoter can reduce stress-related ethylene, facilitating plant growth (Heydarian et al., 2016). It is hoped that the resultant increase in biomass production provided by ACC deaminase will be an attractive alternative to improved phytoremediation (Abhilash et al., 2009). The combination of multiple genes related to the different phases of xenobiotic degradation within plant tissues and the gene encoding ACC deaminase may improve the phytoremediation competence of transgenic plants (Kawahigashi, 2009). As transgenic plant studies advance, it is important to note that transgenes may influence the diversity and functional abilities of colonizing endophytes (Rasche et al., 2006). More studies are necessary for understanding how the interactions between transgenic plants and inoculated endophytes influence the phytoremediation of xenobiotic pollutants.

5. Conclusions and perspectives

Endophytes have attracted worldwide attention due to their unique plant growth-promoting activities and pollutant-degrading abilities.

Endophyte-assisted phytoremediation is the most sustainable and environmentally friendly approach for cleanup, mainly because this technology is compatible with the major biogeochemical cycles. The application of plant–endophyte partnerships is gaining more and more popularity in phytoremediation. Mechanism-based studies from all over the world have improved our understanding of the various mechanisms of endophyte-assisted phytoremediation of organic-contaminated soils. Considerable effort has been invested in exploring endophyte-assisted phytoremediation, enabling greater insights into the integrated activity patterns of plants and their associated endophytes in phytoremediation. The recent omics advances have undoubtedly led to great leaps in our understanding of how plants and endophytes can be harnessed to maximize growth, appropriately assemble the plant microbiome, and direct phytoremediation strategies.

Despite the enormous progress already made in endophyte-assisted phytoremediation, several challenges remain. A major concern that has not been addressed in this review is the infrastructure required to screen hundreds of competent endophytes for desired functions, as it is not easy to imitate the living conditions of endophytes *in vitro*. The persistence and stability of transgenic plants or engineered endophytes in decontaminating polluted soils still need to be resolved before field application. Moreover, most studies on endophytes are commonly based on experimental manipulations and are rarely based on variable, field-realistic conditions. Further research should move beyond these limitations and identify how plant–endophyte partnerships are working in tandem under different scenarios. The mechanisms involved in endophyte-assisted phytoremediation still require further evaluation, and more investigations are needed to better realize the potential of these fascinating endophytes for improving the soil environment.

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