

Review

Plant-Bacteria Interactions for the Elimination of Atmospheric Contaminants in Cities

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Abstract: One of the major health risks for humans, especially for those living in large cities, is air pollution. Air pollution consists mainly of emissions of particulate matter (PM), nitrogen oxides, sulphur dioxide, ammonia and volatile organic compounds (VOCs). The organic carbon fraction of particulate matter is a mixture of hundreds of organic compounds, such as polycyclic aromatic hydrocarbons (PAHs), or polychlorinated dibenzo-*p*-dioxins and dibenzofurans (PCDD/Fs), some of which are mutagenic and/or carcinogenic. Because this particulate matter represents a serious threat for human health, measures to reduce emissions and to eliminate contaminants need to be strongly reinforced, with a focus on novel biotechnologies. In this review, we will explore the possibilities that bacteria associated with plants may offer the amelioration of atmospheric contaminants in cities, and we will discuss this strategy in the context of “Green Architecture”.

Keywords: atmospheric pollutants; plant-bacteria interactions; rhizoremediation; phylloremediation; “Green Architecture”

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1. Introduction

Around 55% of the global population (4.2 billion people) live in urban areas, and by 2050 it has been projected that 68% of the population will be urban (<https://population.un.org/wup/> (accessed on 3 March 2021)). The number of megacities (those with more than 10 million inhabitants) is predicted to increase from 33 to 43 by 2030. The management of urban growth in the context of sustainable development must, therefore, maximize the benefits of agglomeration whilst minimizing the potential adverse impacts. One of the major negative impacts for citizens living in large cities is air pollution. Metropolitan area emissions constitute 52% of total emissions by weight; however, they cause nearly 75% of the gross annual damage (GAD) in the USA [1]. Health impacts related to air pollution are predicted to increase worldwide, and by 2030 it is estimated that total premature deaths due to air pollution will reach 3.1 million annually (OECD Environment Outlook to 2030). The estimated cost to the National Health Service and social care of diseases associated with air pollution is estimated to be £5.56 billion between 2017 and 2025 in the UK [2]. In addition to the health problem, the dispersion and deposition of particulate matter (PM) also provoke negative effects on visibility, as well as on cultural heritage and agricultural and natural ecosystems [3–6].

The major source of air pollution in big cities is on-road vehicles [7], although waste incinerators, biomass burning, secondary aerosols, oil combustion, industrial exhaust and suspended road dust are also important sources of contamination [8,9]. Air pollution consists mainly of emissions of particulate matter (PM), nitrogen oxides, sulphur dioxide (SO₂), ammonia (NH₃) and volatile organic compounds (VOCs). Atmospheric PMs are complex mixtures of elemental carbon (EC), organic carbon (OC), ammonium, nitrates, sulphates, mineral dust, trace elements and water. Fine particles (PM_{2.5}), NH₃, SO₂ and

VOCs represent almost 50% of all emissions by weight [1]. Within PM_{2.5}, OC, consisting of a mixture of hundreds of different organic compounds, may represent 10–70% of the dry mass [10]. Therefore, OC and VOCs are some of the main elements in air pollution. Aerosol particles, in particular PM_{2.5}, have serious adverse effects on respiratory and cardiovascular systems, and although they represent only 6% of the emissions, they cause 23% of total damage [11–13]. PM_{2.5} concentrations in many metropolitan areas exceed the limits (15 µg m⁻³) recommended by the USA National Ambient Air Quality Standard [14]. Some of the VOCs and OC associated with PM_{2.5}, such as benzene, toluene, ethylbenzene, and xylenes (BTEX), polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs) and polychlorinated dibenzo-*p*-dioxins and dibenzofurans (PCDD/Fs) [15,16], are mutagenic and/or carcinogenic.

Consequently, air pollution has a clear negative effect on the economy; it decreases labour productivity and increases the costs of public health (OECD outlook for 2030). Activities to decrease emissions are being promoted by different national and international organizations, which include taxes and tradable permits, development of eco-innovation businesses and key actions in sectors such as energy, transport and agriculture. These actions should be complemented with new strategies to ameliorate air quality.

In this review, we will focus on the removal of the main OC and VOCs in air pollution by bioabsorbing and/or biodegrading and, therefore, detoxifying associations between plants and bacteria in the context of “Green Architecture”, which is based on the inclusion of green infrastructures to make citizen-friendly, energy-saving and climate-resilient cities.

2. BTEX, PAHs, PCBs and Dioxins: Origin and Toxicity

Among the most abundant contaminants in air pollution are BTEX, PAHs, PCBs and dioxins (Figure 1). BTEX and PAHs are petroleum-derived compounds that are released into the atmosphere as emissions from motor vehicles and aircraft exhaust systems, waste incinerator smoke, fossil fuel home-heating systems, losses during petrol manufacturing, accidental oil spills in gas stations or oil refineries and cigarette smoke, amongst others [9]. However, many are natural products that can also be released during volcanic eruptions or forest fires [17,18]. PAHs and BTEX are considered carcinogenic, mutagenic and teratogenic [15,16]. Global atmospheric emissions of the 16 PAHs listed as priority pollutants by the US EPA (United States Environmental Protection Agency) were estimated to be 520 kilotons per year during the first decade of the 21st century [19,20]. PAHs are potential carcinogens; in general, as the number of aromatic rings in the molecule increases, the risks for health increase concomitantly. PAHs induce reactive oxygen species and PAH-DNA adducts that are linked to lung, skin and bladder cancers in adult populations exposed to high levels of ambient PAHs [21]. BTEX compounds are among the most abundantly produced chemicals worldwide, with an annual production of 8–10 million tons of benzene, 5–10 million tons of toluene, 5–10 million tons of ethylbenzene and 10–15 million tons of xylenes. Benzene has been classified by the International Agency for Research on Cancer (IARC) as a class 1 carcinogen for humans. It causes acute and chronic leukaemia, although the toxicity mechanisms are not well understood [22–24]. Toluenes, ethylbenzenes and xylenes are toxic for humans (irritating to the skin, eyes and respiratory tract, and can cause systemic toxicity by unknown mechanisms).

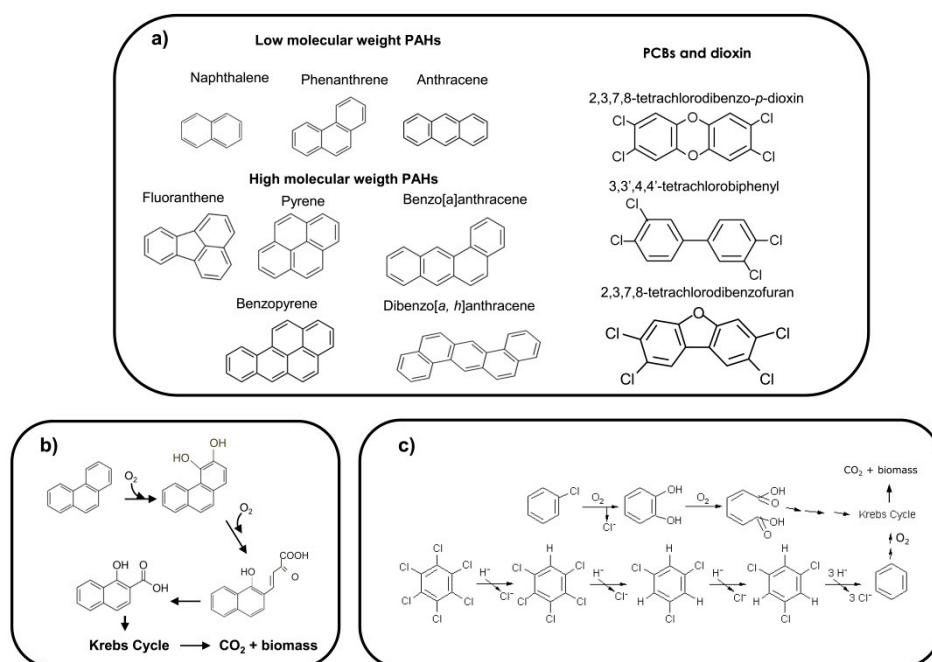


Figure 1. (a) Chemical structures of different polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), dioxin and dioxin-like molecules; (b) Scheme for the aerobic bacterial degradation of phenanthrene. (c) A general scheme for the aerobic bacterial degradation of monochlorobenzene and for the anoxic bacterial dehalogenation and degradation of hexachlorobenzene to benzene and its oxidative mineralization to CO₂. Both contaminants end up in the central bacterial metabolism pathways from which energy and biomass are obtained. In both cases, chlorine is released as an environmentally friendly chloride ion.

PCBs were banned in 1978 in the US and later on in many other countries, but prior to banning they were produced in huge amounts (megatons) as insulators and dielectric or coolant fluids for cables, electrical apparatus and heat transfer systems [25]. Trade names of specific PCB mixtures include Aroclor, Clophens, Phenoclor and Pyralenes. Chlorinated dioxins are generated as unwanted by-products in the chemical syntheses of several pesticides, disinfectants and wood preservatives [26]. A predominant source of chlorodioxin-contamination is the incineration of PCB-containing plastic insulators of electrical cables or other halogenated organic compounds. Many municipal solid waste incinerators are still emitting dioxin-contaminated fly ash. Both chlorodioxins and co-planar PCBs cause immunotoxic and endocrine effects, as well as the induction of malign tumours, whilst non-coplanar PCBs can cause neurotoxic and/or immunotoxic effects. High concentrations of chlorodioxins and also of some PCB congeners cause chloracne and anaemia. Chronic or sub-chronic exposition to low concentrations may lead to liver damage and reproductive effects, as well as cognitive deficiencies, affect levels of thyroid hormones, and may cause several types of cancer [26,27].

The toxicity of PAHs, PCBs and chlorodioxins for animals and humans is based on their capacity to bind to the aryl hydrocarbon receptor (AhR), which leads to the transcription of target genes, among them, the genes of the cytochrome P450-monoxygenases (CYP) [27,28]. CYPs are generally found in the liver and are normally responsible for the detoxification of toxic compounds taken up by the body. CYPs activate these contaminants, including BTEX, by partial oxidation, transforming the poorly water-soluble compounds into easily secreted soluble ones or organo-soluble metabolites such as phenols, dihydrodiols, quinones or epoxides [29–31]. The epoxide intermediates can be converted through the action of an epoxide hydrolase into highly reactive diols that are mutagenic, carcinogenic and teratogenic [30,32]. These metabolites bind to and disrupt DNA and RNA, leading to tumour formation and genotoxic effects.

Not all the contaminants have the same capacity to produce deleterious effects; for example, the binding of chlorinated dioxins and PCBs to the AhR depends on the number of chlorines and their position in the molecule. 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (Figure 1a) is the most toxic dioxin [33]; however, in molecules that contain the chlorine atoms in other positions of the aromatic ring structure (i.e., 1,2,3,4-tetrachlorodibenzo-*p*-dioxin), the resulting chemical compounds are less toxic. Similarly, the non-chlorinated dioxin molecule is nearly non-toxic. In both cases, the above-mentioned molecules are not able to bind or bind poorly to the AhR-receptor. The so-called co-planar PCBs that carry chlorine substituents on their lateral position, similar to the Seveso dioxin, as shown for 3,3',4,4'-tetrachlorobiphenyl (Figure 1a), are toxic whilst, in general, the toxicity is reduced when the four chlorines are in other positions as they no longer bind to the Ah receptor, or if they do it is to a much lesser degree [34]. Similarly, if more chlorine atoms are present than only those of the depicted co-planar PCB molecule, a lower tendency exists to form a complex with the Ah receptor, and thereby reduce the induction of detrimental effects.

3. Deposition, Transport and Detoxification of Contaminants in Plants

Although contamination by these toxic compounds can occur locally at high concentrations, for instance, by leakages of PCBs from technical equipment or by accidental oil-spills, atmospheric contaminants mainly occur from a number of processes of technical usage, dumping, burning, etc., leading to distribution by wind, sometimes over long distances, and they are finally deposited as PMs on all the surfaces of the environment [35,36]. Transportation of these contaminants in PMs is different depending on their physico-chemical properties and on meteorological factors [15,37]. The vapour-pressure of the different PAHs determines their behaviour in the atmosphere; in general, low-molecular-weight PAHs (LMW-PAHs) remain in the gas phase, whilst medium- to high-molecular-weight PAHs (HMW-PAHs) tend to bind to small particles, mainly to PM_{2.5}. PAHs, such as fluoranthene or pyrene (both of 4 rings, Figure 1a), are equally distributed between both phases, depending on ambient air temperature and on the carbonaceous composition of the particles [38–40].

Atmospheric contaminants can be deposited directly from the air onto leaves or can be deposited in soils, and are then adsorbed to roots [41]; they can also be mobilized from soil to leaves by evaporation or wind, or be transported from roots to leaves (Figure 2) [42–44]. The direct relationship between PAH concentrations in soil and in plants suggests that soil-to-root transfer dominates over atmosphere-to-plant transfer [45]. Relatively volatile organic compounds, such as BTEX, anthracene and phenanthrene, are more likely to be deposited on the leaf cuticle through gaseous depositions whilst less volatile compounds, such as benzo[a]pyrene, are deposited by particulate depositions [46].

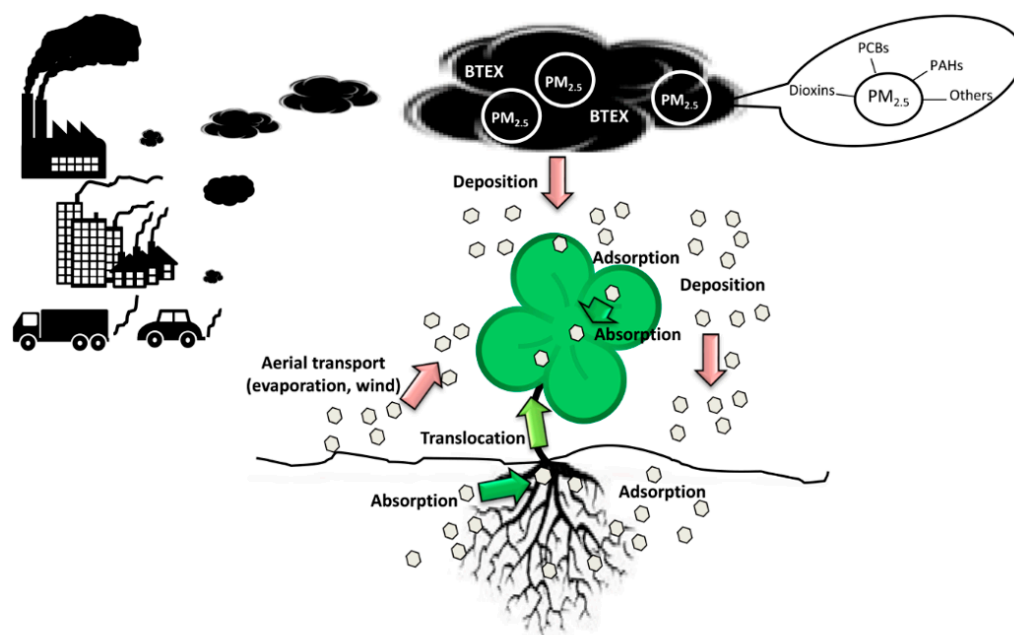


Figure 2. Schematic representation of the fate of contaminants. In green are shown plant-dependent processes; in pink, physical processes. Contaminants are deposited on surfaces (plants and soil) where they can be adsorbed. Parts of these contaminants are absorbed and then enter the plant structures. Contaminants can also be translocated from the roots to the shoots. Wind and evaporation can also mobilize contaminants from soil to leaves. BTEX (benzene, toluene, ethylbenzene and xylenes); PM_{2.5} (fine particulate matter); PCBs (polychlorinated biphenyls) and PAHs (polycyclic aromatic hydrocarbons).

The amount of contaminants which finally accumulates in vegetation depends not only on the physico-chemical properties of the particular contaminant, but also on the characteristics of leaf surfaces and root architecture, as well as on many other environment-related parameters such as wind, rain, temperature, sorption to soils, organic content of soils, composition of root exudates and others [47–49].

After deposition on soils and because of the high lipophilicity and low solubility in water of PAHs, PCBs and chlorodioxins, some authors have indicated that they must be adsorbed to the epidermis of roots which are in contact with soil particles, without entering the inner root. However, there are many reports about the mobilization of contaminants from roots to shoots; i.e., for polychlorinated dibenzo-*p*-dioxins and dibenzofurans in *Cucurbitaceae* [50], total petroleum hydrocarbon in rice [51] or benzo[*a*]pyrene in ornamental plants [52]. Although the extent of contaminant uptake and transport from roots to shoots is still being debated in the literature, it is accepted that mobilization of contaminants through the plant is a consequence of two different processes: (i) the accumulation of contaminants in plant tissues mainly correlated to their hydrophobicity and plant lipid contents, and (ii) the transfer between plant tissues driven mainly by transpiration and the concentration gradient of the contaminant across plant-cell components [53]. Contaminant translocation is generally associated to the vascular system of the xylem with the transpiration stream acting as an important driving force, but it was recently demonstrated that PAHs are also acropetally transported via the phloem [54].

PAHs accumulate in different cells and plant tissues because of their varying solubility in the water of the tissues [55]. Although it is accepted that chemicals with logK_{ow} (logarithm of the *n*-octanol/water partition coefficient) between −1 and 4 are suitable for the transpiration stream, many contaminants are poorly transferred from the root to the shoot because of their high logK_{ow} values. In studies using different plants, it was demonstrated that pyrene (logK_{ow} = 5.32) accumulated in cell walls more than phenanthrene (logK_{ow} = 4.46), probably due to the higher logK_{ow} of pyrene [53,56,57]. LMW-PAHs seemed to show

a stronger linear correlation between soil and shoot concentrations than HMW-PAHs, suggesting that the translocation of LMW-PAHs is faster from soil to shoots than the translocation of HMW-PAHs. Accordingly, translocation of LMW-PAHs and MMW-PAHs (pyrene, anthracene and phenanthrene) has amply been demonstrated [56], whilst there are few reports about the translocation of HMW-PAHs [55,58]. Although there is a correlation between the contaminant concentration in soil and in plants, some discrepancies have been observed between plant species.

The transport of contaminants can be symplastic (through the cell cytoplasm or vacuoles and to interconnected cells via the plasmodesmata) or apoplastic (diffusion between cell walls, without entering the cells) [59,60]. Wild et al. were pioneers in demonstrating the symplastic entrance of phenanthrene in spinach [59]. They observed that phenanthrene was mostly deposited on leaves via gas-phase transfer in maize (*Zea mays* L.) and spinach (*Spinacia oleracea*). After one or two days, phenanthrene diffused through the cuticles into the maize cell walls (indicative of apoplastic transport), being mainly located in the apoplast and moving through the cell walls and intercellular spaces of the epidermis. In spinach, they observed phenanthrene in the cellular cytoplasm (indicative of symplastic transport) and in the vacuole, with both acting as reservoirs for phenanthrene. After 12 days, most of the phenanthrene was located in the maize xylem (mostly bound to the walls), but it was not found in the spinach xylem. In soil, the symplastic uptake was also demonstrated to be the major entrance pathway of phenanthrene into wheat and of pyrene into *Agropyron cristatum* L. [61,62], whilst, in both cases, the apoplastic transport was also detected but at lower levels. The active absorption of contaminants involved H⁺ transport and energy conversion processes, and the passive transport, was associated with water led/directed through protein channels; i.e., there was a stronger correlation between the PCB concentration in soil and in carrots than in potatoes, probably because the carrots presented oil channels that could be used for PCB transport [63].

The distribution of contaminants within plants can determine their fate: to be metabolized, stored in the aerial parts of the plants or even returned (desorbed) to the atmosphere or soil. Once located in the plant interior, contaminants are mainly activated by cytochrome P450 monooxygenases (CYP). The resulting compounds are later conjugated with glucose, glucuronic acid or glutathione moieties. These conjugates are then sequestered in the cell wall or in vacuoles [64].

Despite evidence for the accumulation and subsequent biotransformation of organic contaminants in plants, it is believed that the contribution of plant uptake for their removal from the environment is very low. Soil-bound contaminants, such as PAHs, are strongly associated with soil organic matter and poorly transferred to plant roots. Furthermore, contaminants or derived products accumulating in plant cell walls or vacuoles may return to the environment after plant decay. However, plants may stimulate organic contaminant degradation through several processes such as by increasing the bioavailability of the contaminants, influencing desorption from soil particles and stimulating the biodegrading microbiota in the rhizosphere [65–71].

4. Degradation of BTEX, PAHs, PCBs and Dioxins by Bacteria

Biodegradation of BTEX, PAHs and, to lesser extent, PCBs is performed by a large number of different microorganisms, including bacteria, fungi and algae that have been isolated from very diverse edaphic and aquatic, aerobic and anaerobic environments, and many reviews have been published on the subject since the 1980s [72–75]. Among BTEX- and PAH-degrading bacteria, *Pseudomonas*, *Sphingomonas*, *Burkholderia*, *Mycobacterium*, *Rhodococcus* and *Bacillus* have been extensively studied. *Stenotrophomonas* and *Pasteurella* species, and some anoxic PAH-degrading bacteria belonging to the Delta-proteobacteria, have also been reported. Aerobic bacterial biodegradation of these compounds requires the presence of O₂ to initiate the enzymatic attack on the aromatic rings of PAHs [76,77]. In the initial step, dioxygenase catalyses the oxidation of an aromatic ring to yield non-

aromatic *cis*-dihydrodiols. These initial dioxygenases are multi-component enzyme systems that catalyse the dihydroxylation of PAHs ranging in size from two to five fused rings. These dihydroxylated intermediates are then, upon enzymatic rearomatization to diols, cleaved by monocomponent intradiol or extradiol ring-cleaving dioxygenases (through either an *ortho*-cleavage pathway or a *meta*-cleavage pathway). Further breakdown then leads to central intermediates such as *cis,cis*-muconic acids or hydroxymuconic semi-aldehydes in the case of the degradation of monoaromatic rings, or to salicylates, catechol-like structures or protocatechuates in the degradation of higher annelated aromatics. All these intermediates are then further converted to tricarboxylic acid (TCA) cycle intermediates, used for anabolic biomass formation and mineralized to CO₂ (Figure 1b) [73,76]. Compounds such as naphthalene (two aromatic rings), anthracene or phenanthrene (three aromatic rings) can be completely mineralized by many of these bacteria; however, the mineralization of HMW-PAHs has not completely been elucidated, and in some bacteria, only partially degraded, dead-end products have been detected [78].

Only a single specialized bacterium, *Sphingomonas wittichii* strain RW1, can use the non-chlorinated dibenzo-*p*-dioxin molecule as its sole carbon- and energy source [79] and co-metabolize several of its chlorinated derivatives [80,81]. Other bacterial isolates, with highly similar catabolic genes to that of the *Sphingomonas wittichii* strain RW1, are capable of growing with diphenyl ether, dibenzofuran, carbazol or structurally similar compounds, and they can also attack the dibenzo-*p*-dioxin molecule, including low- to mid-chlorinated dibenzo-*p*-dioxins and dibenzofurans [82,83]. All these strains possess a special angular dioxygenase system [84,85].

For the biodegradation of other haloorganic contaminants (e.g., polyhalogenated benzenes or toluenes) of the ecosphere, numerous bacteria have been described, even when a single aromatic benzene ring system carries up to four chlorine atoms. A few bacteria can dehalogenize such molecules aerobically with molecular oxygen [86,87]. A general scheme for the aerobic metabolism of a monochlorobenzene is shown in Figure 1c. Fully, or almost very highly chlorinated aromatic compounds, such as hexachlorobenzene, octachlorodibenzo-*p*-dioxin, octachlorodibenzofuran or decachlorobiphenyl are highly recalcitrant, and only a few aerobic bacterium have the potential to degrade hexachlorobenzene [88,89]. However, such completely or almost fully halogenated aromatics can be degraded anaerobically, under sequential dehalogenation, to the mono- or even non-halogenated aromatic or alkene structure. In this case, these compounds are being utilized by special anaerobic bacteria as electron acceptors in the presence of hydrogen, thereby releasing a benign chloride ion in every single reaction step [90–92]. Figure 1c shows such a simplified reaction sequence, where the model compound hexachlorobenzene is dehalogenated anoxically and the resulting benzene is then aerobically mineralized.

5. Plant-Bacteria Associations for the Elimination of Atmospheric Contaminants

Whilst bacteria are armoured with a battery of degradative genes encoding catabolic biocatalysts, plants offer a large surface area to collect air particles, and they are able to stimulate bacterial activities in their rhizosphere [93]. Therefore, the combination of both organisms could be a good solution for the elimination of contaminants [94]. Radwan et al. were pioneers in demonstrating the elimination of oil contaminants by a combination of plant and soil microorganisms under natural conditions [95]. However, this natural remediation, in general, takes a long time and, for this reason, there is a pressing need to engineer more efficient bio-systems for the elimination of contaminants.

5.1. Rhizoremediation

Rhizoremediation consists of the elimination of contaminants from the soil surrounding the plant root and is based on the fact that plant tissues, especially roots, secrete different metabolites that microbes can use as a nitrogen, carbon, sulphur or phosphorus

source, and on the influence that root exudates exert over the bioavailability of contaminants. Bacteria which live near root surfaces may be attracted by these root exudates [96,97] and use such rhizospheric compounds as nutrients, thereby resisting the toxicity of certain secondary metabolites secreted by plants and the presence of reactive oxygen species produced by the respiration of root cells [98,99]. Plant roots provide a large surface area on which microorganisms can proliferate and reach high cell densities. Some roots can transport microorganisms through the soil to depths where aerobic microorganisms are normally unable to thrive, and provide oxygen for the initial attack of mono- and dioxygenases for (aromatic) contaminant degradation. Although many microorganisms exhibited specific biodegradation properties, their reintroduction into the soil to remove pollutants has sometimes been unsuccessful. It is thought that nutrient limitation, competition with indigenous microbiota or poor performance under environmental stressful conditions may limit the success of (re)introduced microorganisms in contaminated soils [100]. However, in the presence of contaminants, these microorganisms have a crucial advantage over indigenous microbiota; in general contaminant-degrading microorganisms are adapted to the toxic effects of the contaminant and they can use it as an additional carbon and energy source. There are, therefore, two crucial aspects in rhizoremediation: (i) the pathways for the degradation of contaminants have to be operative and free of catabolite repression effects [101–105], and (ii) the contaminant has to be bioavailable in a form that can be taken up by the bacterial cell [67–69,71].

The elimination of contaminants by bacteria decreases their concentration in the rhizosphere and, therefore, improves plant growth [106]. In addition, some rhizospheric bacteria can solubilize phosphate, facilitate iron uptake and/or synthesize plant hormones to promote plant growth. These two actions promote soil fertility during rhizoremediation [107]. Therefore, a mutual benefit for both organisms exists during the association of plants and bacteria for the elimination of contaminants (Figure 3). The identification of plant microbiomes has confirmed that microbial populations in the rhizosphere depend on the age of the plant, its physiological status and even the cultivar, supporting the idea that plant roots exert a certain selection toward the microorganisms living in their rhizosphere [108–110]. It has been demonstrated that plants can attract specific degradative bacteria toward their rhizosphere in the context of rhizoremediation [111–113]. It is becoming clear that plant-microbe interactions influence the effectiveness of rhizoremediation and, therefore, the selection of the best plant-bacteria combination for a specific contaminant is crucial for its effective elimination [114].

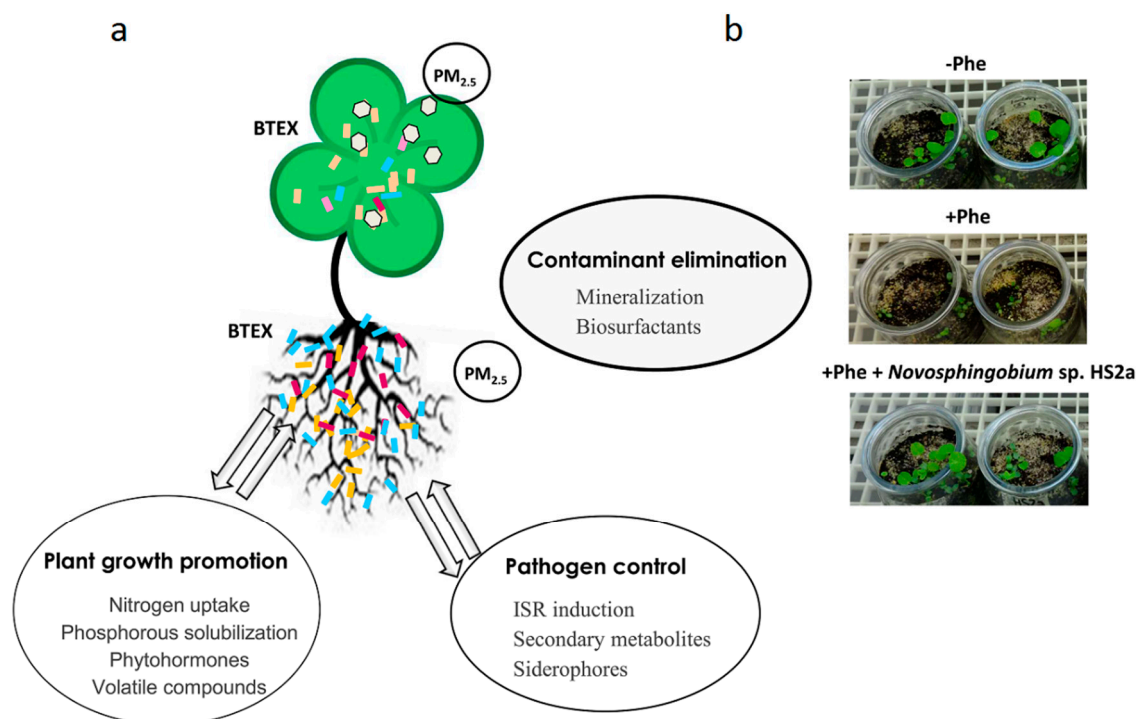


Figure 3. Schematic representation of bacterial activities in the rhizosphere and phyllosphere (a). ISR (induced systemic resistance); BTEX (benzene, toluene, ethylbenzene and xylenes); PM_{2.5} (fine particulate matter). The bioaugmentation of soil with *Novosphingobium* sp. HS2a, a bacterium able to mineralize phenanthrene (Phe), promotes clover growth on phenanthrene-contaminated soils (b) [106].

Prairie grasses, which have an extensive fibrous root system, are among the best studied plants for the remediation of hydrocarbon-polluted soils [115,116]. Although well-known bacteria could be used in rhizoremediation, in general they are not well-adapted to survive and compete in the rhizosphere. Bacteria isolated from contaminated soils have also been used for bioaugmentation, although there is, in general, a lack of information about the degradative abilities of these bacteria and about their ability to persist in specific plant environments [117,118]. Certain types of degradative bacteria that are commonly found in contaminated environments have been reported to be good candidates for rhizoremediation, amongst them *Arthrobacter*, *Rhodobacter*, *Rhodococcus*, *Pseudomonas*, *Burkholderia*, *Bacillus*, *Mycobacterium* or members of the *Sphingomonadacea* family [106,119–121]. Certain endophytes have also been reported as good choices for bioremediation as they are adapted to a specific plant and have fewer competitors in their natural environment. However, in this case, the transport of contaminants into the plant interior is crucial for effective bioremediation [122]. In the last five years, there have been many publications dealing with different aspects of rhizoremediation, suggesting the maturity of this research field [62,123–131]. As a result, a large number of different bacteria which are able to remove pollutants from soil have been described; Table 1 shows some examples of bacteria-plant combinations for the degradation of contaminants.

Table 1. Examples of rhizoremediation of pollutants using plant-microbe pairs.

Plants	Pollutants	Microbes	References
<i>Senecus glaucus</i>	Oil	<i>Arthrobacter</i>	[95]
<i>Alfalfa</i>	PAHs	Not identified	[132]
<i>Barley</i>	2,4-D	<i>Burkholderia cepacia</i>	[133]
Oat, lupin, rape, pepper, radish, pine	Pyrene	Not identified	[134]
Poplar	2,4-D	<i>Amycolata</i> sp. CB1190	[135]
<i>Lolium multiflorum</i>	PAHs	<i>Pseudomonas putida</i> strain PCL1444	[136]
<i>Zinnia angustifolia</i>	Mefenoxam	<i>Pseudomonas fluorescens</i> <i>Chrysobacterium indologenes</i>	[137]
<i>Hordeum vulgare</i>	Phenanthrene	<i>Pseudomonas fluorescens</i> , <i>Pseudomonas aureofaciens</i>	[138]
<i>Trifolium repens</i>	Chrysene	<i>Rhizobium leguminosarum</i>	[139]
<i>Triticum aestivum</i>	Phenanthrene	<i>Pseudomonas</i> sp. strain GF3	[140]
<i>Hordeum vulgare</i>	PAHs	<i>Mycobacterium</i> sps.	[141]
<i>Sorghum bicolor</i>	Phenanthrene	<i>Sinorhizobium meliloti</i> strain P221	[142]
<i>Lolium multiflorum</i>	Diesel oil	<i>Rhodococcus</i> sp. strain ITRH43	[143]
<i>Secale cereale</i> , <i>Medicago sativa</i>	Crude oil	<i>Azospirillum brasilense</i> strain SR80	[144]
<i>Lotus corniculatus</i>	Diesel oil	<i>Pantoea</i> sp. strain BTRH79	[145]
<i>Zea mays</i>	Phenanthrene, pyrene	<i>Pseudomonas</i> sp. strain UG14Lr, <i>Pseudomonas putida</i> strain MUB1	[146]
<i>Lolium multiflorum</i>	PAHs	<i>Acinetobacter</i> sp.	[147]
<i>Medicago sativa</i>	PAHs	<i>Rhizobium meliloti</i> strain ACCC 17519	[148]
<i>Zea mays</i>	Diesel oil	<i>Gordonia</i> sp. strain S2RP-17	[149]
<i>Lolium perenne</i>	Diesel oil	<i>Pantoea</i> sp. strain BTRH79	[150]
<i>Festuca</i>	PAHs and diesel	<i>Azospirillum</i> sp. and <i>Pseudomonas stutzeri</i>	[151]
<i>Populus deltoides</i>	PAHs	<i>Kurthia</i> sp. <i>Micrococcus</i> sp. <i>Bacillus</i> sp. <i>Dienococcus</i> sp. Endophytic <i>Bacillus</i> sp.	[152]
<i>Salix purpurea</i>	Phenanthrene	<i>Pseudomonas putida</i> PD1	[153]
<i>Sorghum</i> and <i>Onobrychis sativa</i>	Phenanthrene, pyrene	Bacterial consortium	[154]
Annual grasses	Monoaromatics, PAHs	<i>Pseudomonas putida</i> strains	[155]
Clover	Phenanthrene	<i>Novosphingobium</i> sp. HS2a	[106]
<i>Lolium multiflorum</i>	PAHs	<i>Mycobacterium gilvum</i>	[156]
<i>Avicennia schaueriana</i>	Oil	Bacterial consortium	[157]
<i>Arabidopsis thaliana</i>	PCBs	<i>Rhodococcus</i>	[121]
<i>Echinochloa crus-galli</i> , <i>Cynodon dactylon</i>	Monoaromatics	<i>Pseudomonas</i> sp. J10	[158]
<i>Chromolaena odorata</i>	Lead, petroleum	<i>Micrococcus luteus</i> .	[159]
Grasses	PAHs	<i>Mycobacterium vanbaalenii</i> PYR-1	[160]
<i>Morus alba</i>	Biphenyl	<i>Rhodococcus</i> sp. MAPN-1	[161]
Poplar	1,4-Dioxane	<i>Mycobacterium dioxanotrophicus</i> PH-06, <i>Pseudonocardia dioxanivorans</i> CB1190	[162]
<i>Festuca arundinacea</i> L.	PAHs	<i>Mycobacterium</i> sp.	[163]

5.2. Phylloremediation

For the elimination of atmospheric contaminants, it is noteworthy that the surface area of leaves can be 6–14 times greater than the land the vegetation is growing upon and, therefore, the phyllosphere, which is the aerial part of plants consisting of the stems and leaves, is an important environment to study [164]. The phyllosphere is a hostile habitat for microorganisms; the microbial communities established on the phyllosphere are affected by environmental factors such as UV radiation, temperature variations, climatic factors (e.g., precipitation), low nutrients and pollution [165–169]. Generally, the most important factors determining the structures of phyllosphere bacterial communities are the season, the plant species and biogeography [166,170–175]. One of the factors by which plant species affect phyllosphere bacterial communities is the composition and type of waxy cuticle which covers the leaf surfaces. This waxy cuticle can be comprised of lipid components, cutin and waxes, but also contains hydrocarbons and amino acids [176]. However, the limited diffusion of nutrients and water, as well as the spatially heterogeneous nutrient availability, result in leaf surfaces being largely oligotrophic with localized “oases” of nutrients [166]. Nevertheless, leaves can support bacterial populations of 10^4 – 10^5 bacteria mm^{-2} of leaf surface or up to 10^8 bacteria g^{-1} leaf material together with smaller fungal populations [177]. Bacterial communities established on leaf surfaces of different plant species are typically dominated by Proteobacteria, especially Alphaproteobacteria such as *Sphingomonas* and *Methylobacterium* [178,179], and Gammaproteobacteria such as *Pseudomonas* [180,181].

The accumulation of air pollutants and airborne PMs on leaf surfaces is dependent on the plant species, leaf size and structure, but is also affected by the types of waxes which make up the cuticle, the hairs covering the leaf and leaf smoothness [46,47,182,183]. Both PMs and hydrocarbon contaminants accumulating on the leaf surface affect bacterial communities. For instance, the analyses of the microbial communities on the leaves of *Platanus* trees revealed that tree location (city vs. rural) explained the largest differences, and that the amounts of PM on the leaves acted as partial drivers of the bacterial community structure [184]. In another study, more particulate matter (PM) was found on hornbeam tree leaves in cities, but when the authors looked at the functional diversity of hydrocarbon degradation genes of the phyllosphere communities, they found statistically more of these type of genes in the phyllosphere of a natural forest [185]. Therefore, the response of bacterial communities to PM and hydrocarbon contaminant deposition may not always be linked. Nevertheless, in a study by Franzetti et al., in which they observed seasonal differences in PAH concentrations in Milan (with maxima in winter and minima in summer), the gene coverage of dioxygenases for the catabolism of PAHs and aromatic compounds found in metagenomic data of communities of the phyllosphere of magnolia was higher in winter than in summer [186]. Similarly, the diversity of bacterial communities and of the abundance of a gene encoding hydrocarbon degradation by the phyllospheric bacteria on the leaves of *Platanus* in different parts of Milan was affected more strongly by the season than by the sampling location (park/road) [187].

Other studies demonstrated that phyllospheric bacteria participate directly in the removal of hydrocarbon-related air pollutants [84,181]. For instance, Sandhu et al. [188,189] showed that phyllosphere communities mineralized significantly more phenol than bean leaves which had been surface sterilized. Ali and collaborators found that bacterial communities on legume leaves could consume more crude oil, phenanthrene and *n*-octadecane compared to sterilized leaves [190]. Similarly, Sorkhoh et al. observed that the leaves of broad beans and American grass removed 80% more volatile crude oil hydrocarbons than leaves which had been surface sterilized [191]. Waight et al. found that phenanthrene sprayed on the leaves of *Ixora* plants disappeared faster than on surface-sterilized leaves [192]. Sangthong et al. demonstrated the role of epiphytic bacteria in xylene degradation [193]. Similarly, phyllospheric bacteria on the unsterilized leaves of ornamental plants enhanced phenanthrene removal [194]. Endophytes have also been used for the elimination of gaseous ethylbenzene [195]. An extensive list of plant associated bacteria which are able

to degrade or biotransform air pollutants can be found in the review by Wei et al. [181]. All these findings show the involvement of phyllospheric bacteria in the elimination of air pollutants (Table 2).

Table 2. Phylloremediation of pollutants using plant–microbe pairs.

Plants	Pollutants	Microbes	References
<i>Azalea indica</i>	Toluene	<i>Pseudomonas putida</i> TVA8	[196]
Bean	Phenol	<i>Pseudomonas</i> sp. strain CF600	[188]
<i>Ixora</i> sp	Phenanthrene	<i>Pseudomonas oleovorans</i> <i>Mycobacterium</i> sps. <i>Rhizobium</i> sps. <i>Deinococcus</i> sp.	[192]
Ornamental plants	Phenanthrene	Indigenous population	[194]
Beans and peas	Hydrocarbon vapors	Not identified	[190]
<i>Bougainvillea buttiana</i>	Xylene	<i>Enterobacter cloacae</i> LSRC11, <i>Staphylococcus</i> sp. A1, <i>Pseudomonas aeruginosa</i>	[193]
Urban trees	Phenanthrene, benzo[a]pyrene	Non identified	[197]

More importantly, these studies also open up the possibility that the manipulation of phyllosphere bacterial communities by bioaugmentation with air pollutant-degrading bacteria could be used to remove contaminants from the air [198]. The finding by Scheublin et al., that a chlorophenol degrading *Arthrobacter* strain originating from soil showed good phyllosphere colonization and that it expresses degradation genes, suggests that even non-phyllospheric bacteria may successfully be used for phylloremediation [199].

6. Removal of Air Pollutants and the Role of Green Architecture

Growing awareness about indoor and outdoor air contamination has promoted research in the phytoremediation of this type of pollution [198,200,201]. Furthermore, PAHs, PCBs and VOCs are now considered as re-emerging contaminants [202,203]. However, many of the studies dealing with this subject do not specifically investigate the plant-bacteria interactions involved, although the role of the bacteria is usually acknowledged [204,205]. For many authors, plants are passive accumulators of contaminants, and their role as biomarkers has been thoroughly investigated [206,207]. However, as mentioned above, the inoculation of plants with the appropriate microbes improves contaminant removal and mineralization.

The green infrastructures of traditional cities, which include gardens, parks, open corridors and ornamental vegetation, provide services that benefit urban populations [208,209]. These services include the psychological well-being of urbanites by providing space for sports activities, relaxation and socialization [210–212], noise attenuation and flood mitigation [213], and increase the value of cultural heritage [214]. They also contribute to the control and spread of air pollution and to the microclimate regulation of the urban environment [215–217]. However, growing urban populations have forced planners for urban environments to find new strategies for public transport, employment and urban amenities, as well as for the creation and maintenance of green infrastructures [218,219]. The current urbanization trend toward a more compact and dense urban form leaves less space for green infrastructures [220–222]. Green Architecture is a relatively new concept that involves the construction of eco-friendly buildings and infrastructures to minimize the harmful effects of urbanization on the environment, including outdoor and indoor air pollution. According to these practices, the elements that have traditionally been used for aesthetic reasons are now one of the best ecological methods for sustainable edification, with vegetation being incorporated in very innovative ways (i.e., incorporation of vegetation surrounding or connecting skyscrapers, in vertical gardens or roof gardens and botanical sculptures) [223]. Due to the importance of health problems caused by

atmospheric contaminants and the increase in the number of citizens living in megacities, there is a growing interest in the utilization of green elements for contaminant dissipation. Several studies have demonstrated that the surface with green-coverage is inversely correlated with the amount of PM contamination in the air, although the type of green coverage is also important [205,224–226].

Some architectural elements to mitigate air pollution are being developed, such as green wall biofilters [227], or green belts, established around industrial areas [228]. At the laboratory scale, many studies have shown that biofilters are capable of removing indoor VOCs (such as formaldehyde, toluene, ethylbenzene and xylene) [229,230]. Two different biofiltration systems can be installed in green infrastructures. In passive biofiltration, the simple diffusion of air to green wall components is used to eliminate the contaminants. These systems consist of the use of potted plants, biocovers, green roofs and green walls [231–234]. One of the problems of these systems is their limited capacity for remediating high levels of air pollution, in particular PM, but their main advantage is their low cost [235]. In active botanical biofilters, the transfer of polluted air through active systems improves the amount of the contaminant elimination [231].

Green-walls are already being commercially installed in many buildings as biofiltration systems to alleviate indoor pollution. However, there are mixed results about the efficiency of green infrastructures such as green roofs, green-walls and others in the elimination of outdoor atmospheric contamination, at least, as passive biofilters [236,237]. In most of these studies, PM elimination or adsorption to plant material has been studied, but there are not many reports about the elimination of the specific contaminants contained in PM.

Although the importance of microorganisms in green infrastructures is becoming more evident [186,238–241], few examples of manipulated plant-microorganism combinations have been reported in the literature, and those that have mainly deal with microbes that improve plant growth [242,243]. Phyllo- and rhizoremediation are good strategies for air pollutant elimination and, therefore, improving rhizosphere and phyllosphere bacterial communities with tailor-made bacterial consortia, which attack diverse organic contaminants, could be considered a way of improving the capacity of plants to remove these air pollutants within a Green Architecture strategy [237,244,245].

7. Research Needs

There are a number of issues that need to be solved in order to successfully implement the utilization of plant-bacteria combinations as a strategy to ameliorate air pollution in cities. First of all, although there has been a spectacular increase in the number of publications regarding the fate of contaminants in plants and the mechanisms of deposition on leaves and soil [246], more research will be necessary to improve our knowledge about the bioaccumulation and fate of contaminants in vegetation [247]. Depending on the location, the bioremediation strategy will require the utilization of endophytic, phyllospheric or rhizospheric bacteria capable of dealing with these target contaminants [248,249]. Because of the close proximity of green structures to citizens, detailed safety analyses of degrading microorganisms and studies about the accumulation of possible toxic intermediates from degradative pathways should be investigated [250]. The plant and its associated microbiome have co-evolved throughout time, establishing complex interrelationships to function almost as a single unit. The development and health of this supra-organism (holobiont) depends on the environmental conditions and the balance between its different components [251]. During bioremediation, the presence of pollutants and bioaugmentation with exogenous bacteria can affect the functioning of this holobiont [113,252]. Phenanthrene, for example, is able to induce the hypersensitive (HR) and systemic acquired responses (SAR), characterized by the overproduction of reactive oxidative species by the plant [253,254]. The study of these new interactions and how the degradation potential of contaminants could be altered by the complex signalization existing in these niches is a novel research field to be explored. Therefore, the molecular communication between the

plant and its associated microbiota is crucial to ensure efficient contaminant elimination under changing environmental conditions [114]. Plants and their associated microbiota are able to produce multiple chemical signals (quorum sensing molecules, quorum quenching enzymes, VOCs, hormones and other secondary metabolites) that affect the equilibrium of the holobiont [165,255,256]. Unfortunately, little is known about the effects of these complex signalling cascades on the establishment and biodegradation potential of bacteria used in phyto-/rhizo-/phyllorremediation. However, a better understanding of this environmental complexity, with the aid of high throughput -omics tools, is nowadays feasible [257,258].

Up to now, most of the research related to plants used in Green Architecture has focused on the tolerance of the plants toward atmospheric contaminants [259,260]. As mentioned previously, the associations of plants with contaminant-degrading bacteria promote plant growth by alleviating the toxicity of the contaminants and are increasing the number of plant species that could be used in Green Buildings. However, how to find the best plant-bacteria combinations for each location is a topic still to be resolved to achieve the successful elimination of contaminants. Moreover, these bacteria or bacterial consortia will need to be well adapted and robust, and this might be aided by a recently described adaptation strategy for the plant environment [261]. Improved engineering, architectural and agricultural practices to implement these strategies will also be required for successful implementation of this biotechnology.

8. Conclusions

The successful utilization of plant-bacteria combinations in Green Architecture is a promising technology that will have clear economic implications and lead to less public expenditure in citizens' healthcare, and it could also lower the costs of contamination control.

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