Phytoremediation of indoor air: mechanisms of pollutant translocation and biodegradation

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Abstract

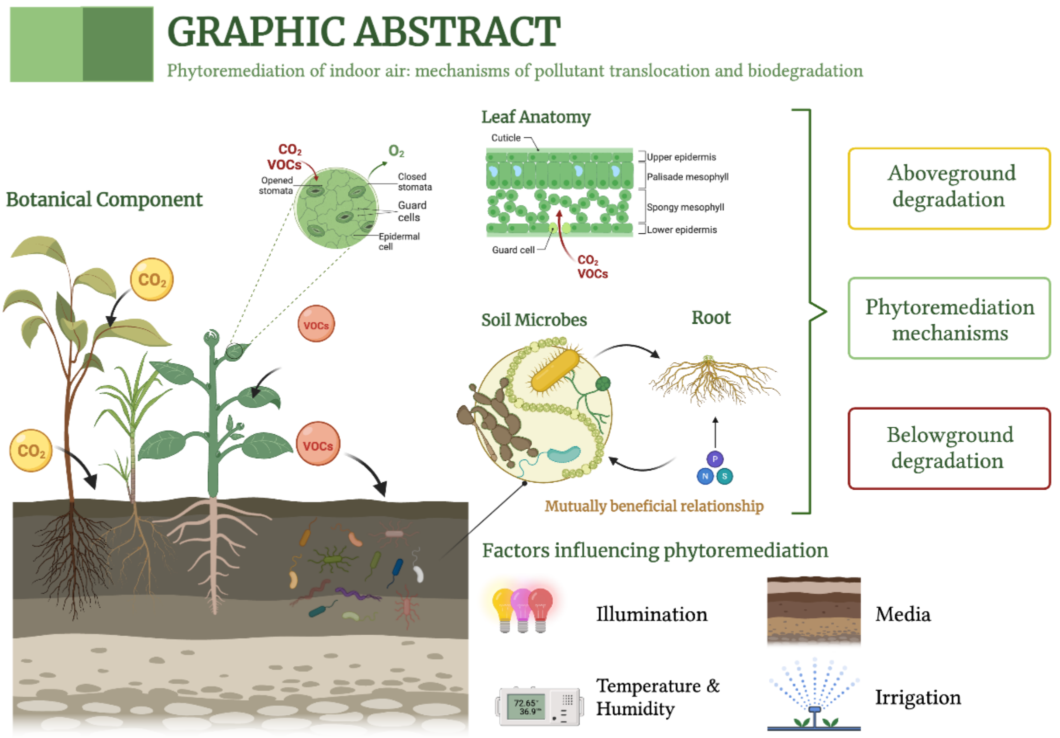
The built indoor environment, including domestic housing and commercial offices, has significantly lower air quality relative to ambient outdoor air. Methods of air purification typically rely on traditional mechanical filtration methods such as heating, ventilation and air conditioning systems (HVAC), which are energetically intensive and require routine maintenance to ensure adequate filtration. To reduce energy demands and to improve urban sustainability, phytoremediation technologies have emerged as a promising method for the remediation of indoor air quality. Due to the need to identify and optimise sustainable methods to improve air quality, we present a comprehensive review on the mechanisms for plant-driven and microbial-driven removal of gaseous contaminants (i.e. volatile organic compounds) is warranted. The literature indicates that indoor air phytoremediation systems rely on complex of both the biological aspects (plant parts, substrate, microbial community, substrate moisture) and abiotic factors (airflow, moisture content), however it is evident that the method for optimal application of these factors within systems is currently significantly understudied, especially in relation to research done *in-situ*. The authors recommend future research directions should be targeted at plant biochemical analysis of phytoremediation systems exposed to real world pollutants like petroleum vapour, vehicle emissions, and mixed synthetic furnishings of-gassing, as well as the

dynamics of the substrate microbial community within root systems. The assessment and developed understanding of these key areas are not only essential for the progression of the field of research but also for continued wide spread adoption for these phytoremediation systems.

Keywords

Active green walls, Air pollution, Metabolic pathways, Microbial degradation, Phytoremediation, Rhizosphere

Graphical abstract



1. Indoor air pollution

The rise in globalisation and increasing population size has led to densely populated urban spaces where modern dwellers typically spend 80% of their time within indoor urban centres for both housing and business (Morawska et al., 2020). Due to elevated levels of indoor-sourced contaminants, such as volatile organic compounds (VOCs), indoor air pollutant levels are consistently 3–5 times higher than outdoors (Jafari et al., 2015). Indoor exposure to certain VOC contaminants has become a significant health concern worldwide (Ninyà et al., 2022), with short-term exposure known to cause respiratory and dermatological health issues, as well as psychological discomfort (Jansz, 2011). Due to the highly sealed nature of modern buildings, chronic long-term exposure to these pollutants can result in increased pulmonary pathology, nasopharyngeal, and lung cancer (J. M. Adams et al., 2001). This phenomenon has been coined as 'sick building syndrome' which is the term used to describe scenarios where individuals in a building experience immediate health and comfort issues that seem to be related to the time they spend in the building, yet no specific cause can be determined (Sarkhosh et al., 2021). The recent global pandemic of COVID-19 has only amplified this issue as large proportions of the global population were required to spend up to 100% of their time indoors during mandatory lockdowns (Ninyà et al., 2022). High indoor occupancy rates are also an issue for the urban work force, as the majority of urban commercial structures often rely on HVAC systems to regulate the indoor environment (Wargocki, 2011). HVAC systems commonly incorporate air filters with minimum efficiency reporting values (MERV) of 8-13, which are effective for particulate matter (PM) removal but are incapable of gaseous pollutant filtration (Z. Wang et al., 2004). It is therefore essential that energy-efficient solutions capable of addressing this indoor air quality (IAQ) issue be investigated in order to reduce the current health burden. Plant-based air pollution remediation systems are finding increasing attention as potential candidates for indoor air quality management.

1.1 Phytoremediation of indoor air pollution

Plant-based air pollutant removal systems function much like bio-scrubbers, bio-trickling filters and industrial biofilters (Burgess et al., 2001; Delhoménie & Heitz, 2005; Iranpour et al., 2005; Revah & Morgan-Sagastume, 2005), which dissolve or otherwise capture air pollutants into an aqueous phase, that can then be metabolized or sequestered by microbial or other biological activity. Plant-based green wall biofilters utilise plants and their rhizosphere (the 1-3mm thick region of substrate immediately surrounding root surfaces) microbial communities to metabolise gaseous contaminants and convert toxic chemicals to a nutrient source for both the plant and the associated microbial community(Irga et al., 2018; Pettit et al., 2018a; F. Torpy et al., 2017). The remediation properties of plants and their rhizosphere have a high potential to remove VOCs from sealed environments. Compared to alternative solutions to pollutant removal, phytoremediation is considered a sustainable, cost-effective, and eco-friendly technology (Irga et al., 2018).

Whilst plant mediated remediation of NO_x, CO_2, CO and PM have been demonstrated, most air phytoremediation research has been focussed on the removal of VOCs (Matheson et al., 2023; Pettit et al., 2018a). It is generally understood that the great majority of VOC removal is performed by the actions of substrate microorganisms, with the plant playing a role to support the microflora (Aydogan & Montoya, 2011; Wei et al., 2017).Nonetheless, there is evidence of some VOC removal by the plants themselves in passive systems, based on the absorption of pollutants into plant cells, which are consequently sequestered, metabolised or transferred to other plant parts and thus degraded (Giese et al., 1994; Komives & Gullner, 2005). Therefore, understanding the metabolic pathways of VOC degradation by plants may be of value for developing further improvements to phytoremediation systems for indoor air purification.

Air purification via botanical biofiltration was established by NASA scientists (B. C. Wolverton et al., 1984), while investigating potted plants for their innate ability to phytoremediate toxic compounds, they found passive potted plant systems to significantly reduce ambient VOC concentrations within model spacecraft that were used by NASA. Since these initial studies a plethora of literature investigating the removal of VOCs by a number of different plant species has been published in the field, dominance of certain plant species in phytoremediation research is often owing to their resilience to indoor environments and growing conditions (Brilli et al., 2018), as well as their popularity due to their aesthetic qualities (Dravigne et al., 2008).

Phytoremediation systems for the indoor environment are currently categorised into two forms: passive and active systems. Passive remediation systems rely primarily on the diffusion of indoor pollutants to complete absorption and purification (Bandehali et al., 2021; Y. Han et al., 2022; Teiri et al., 2022). The limitations of this system are obvious, as the concentration of pollutants in indoor environments is generally low, passive systems have a limited capacity to remediate indoor air (Bandehali et al., 2021; Y. Han et al., 2022; Teiri et al., 2022). While it is likely that the microbial community residing in the rhizosphere is responsible for the majority of chemical removal in these systems, there is some evidence of endophytic and epiphytic bacteria in/on the leaves assisting in gaseous contaminant removal (Barac et al., 2004; De Kempeneer et al., 2004; Khaksar et al., 2016; Knief et al., 2012).

Active bioremediation systems have been developed to address the pollutant diffusion rate limitations of passive systems and have been studied extensively in recent years (for a detailed review, see

Matheson et al. (2023)). Active systems combine plants and their substrates with a mechanical ventilation system, directing the polluted airstream through the rhizosphere and foliage (Bandehali et al., 2021; González-Martín et al., 2021; Moya et al., 2019; Pettit et al., 2018b; Teiri et al., 2022), resulting in greatly enhanced filtration efficiency. As the primary removal mechanism (i.e. the substrate) is being directly supplied with polluted air, the above-ground plant parts in active systems play a smaller role in their pollutant removal efficiency (González-Martín et al., 2021). Therefore, the metabolic pathways employed by rhizospheric microbial communities are the primary driver of pollutant remediation by these systems.

To date, there have been few published studies demonstrating the pollutant removal efficiency of phytoremediation systems in realistic indoor environment (Mannan & Al-Ghamdi, 2021). However, these studies have provided a proof of concept for these systems, (Z. Wang & Zhang, 2011), revealed satisfactory single pass removal efficiencies of an active green wall prototype for formaldehyde and toluene (90% and ~33%; respectively, for 4 days) within real office building conditions. Pettit et al., (2019), tested a piolet scale active green wall against a compartmentalised HVAC system containing a MERV H13 rated filter within a school classroom located in Chaoyang District Beijing, China. The piolet green wall was shown to outperform the control HVAC system removing 72.5% more TVOCs over the experimental period. Considering these preliminary studies, the amount of commercially available botanical indoor air filtration systems such as, the Naava (Naturvention, Finland) interior air filter system, is continuing to increase every year. While the commercial desire for these indoor air phytoremediation systems is promising, to date, reviews on the underlying the key mechanisms for degradation within these systems, and how VOCs enter plant-based systems to become degraded, are less common. The objective of the current review is thus to present information on the phytoremediation of common air pollutants, and to identify the main factors influencing the efficacy of botanical air purification.

The review has several objectives,

1. outline the pathways and mechanisms of different plant organs in phytoremediation, with a focus on the foliage and the root rhizosphere.
2. provide an analysis of the remediation performance of the microbiota and the plant in phytoremediation.
3. Provide a detailed overview of the metabolic pathways employed by plant rhizosphere bacteria to degrade a range of gaseous contaminants.
4. Provide potential solutions to improving indoor air purification rates.

2. Degradation of VOCs in phytosystems

2.1 VOC uptake processes

To date, most studies determining the drawdown potential of phytoremediation systems for gaseous air pollutants have been conducted in static sealed chambers (Dela Cruz et al., 2014; Irga et al., 2018; K. J. Kim et al., 2018). The rhizosphere microbial community has been credited with the bulk of VOC degradation efficiency, but many studies have found that the aboveground phytomass, the rhizosphere, and the substrate itself all play specific roles in the removal of VOCs (Figure 1).

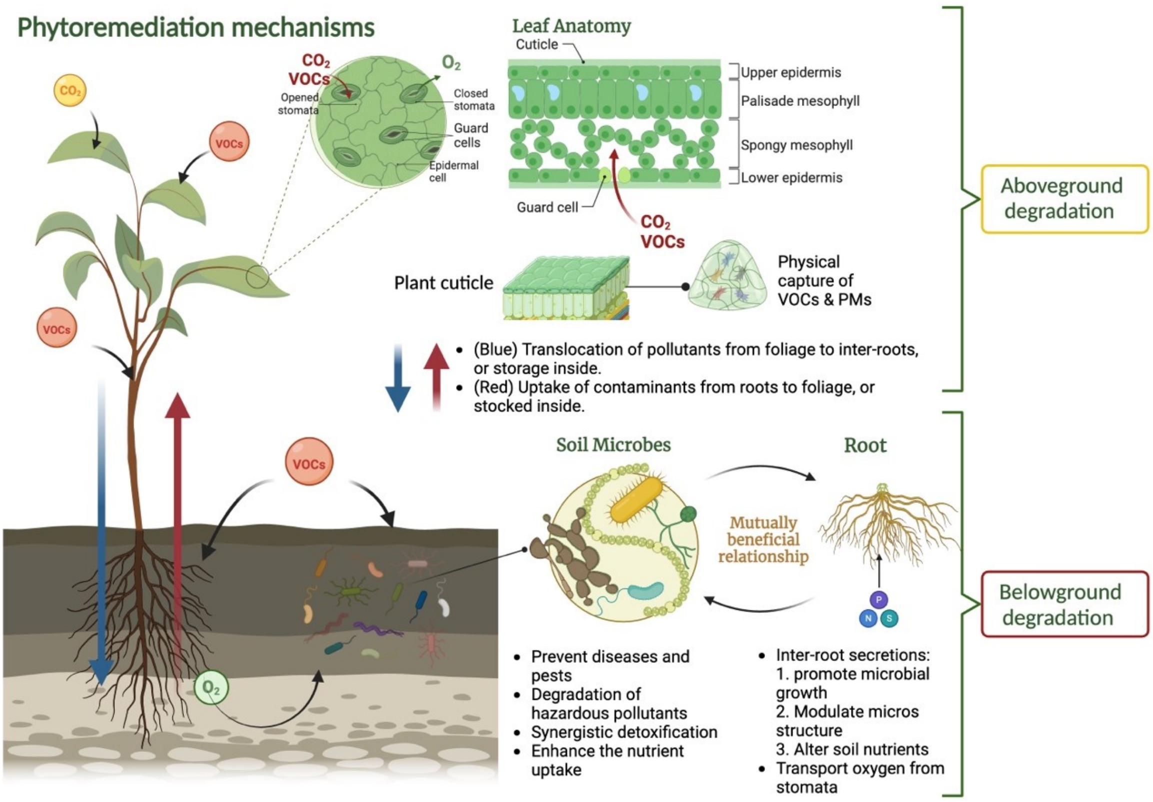


Figure 1. Mechanisms of plant-microorganism synergistic degradation of VOCs. Image by author

For example, one of the first studies to suggest the microbial activity in the rhizosphere was contributing to VOC removal by Wolverton et al. (1993) demonstrated a removal of formaldehyde and xylene by 50.5% and 67%, respectively. Similarly, Xu et al. (2011)recorded similar soil contributions in a comparative experiment using the plant species *Chlorophytum comosum*, *Aloe vera* and *Epipremnum aureum*. It was later documented by Kim et al. (2018) that the removal of formaldehyde was increased 10-fold during the night, suggesting that photosynthesis driven plant respiration was not a major contributor to the removal of gaseous formaldehyde. Thus, there is evidence for at least some VOC removal by the phytomass, whether above or below ground, at least for passive systems tested by the abovementioned studies.

The aboveground portions of the plant involved in phytoremediation are primarily the foliage, where the specific plant responses are largely driven by the properties of each individual pollutant, such as dipole moment and molecular mass (Pettit et al., 2019). While there is the potential for epiphytic bacteria to metabolise some VOCs on the plant leaf surface(Kandel et al., 2017), the primary mechanism for plant foliage-mediated removal of gaseous contaminants is thought to be absorption into the plant tissue through stomates (gas exchange) (Ugrekhelidze et al., 1997) and adsorption to the waxy cuticle of the plant leaf (Treesubsuntorn & Thiravetyan, 2012). As stated previously, the rate of stomatal uptake is dependent on the concentration gradient between the leaf and atmosphere (Oikawa & Lerdau, 2013). The chemical structure and properties of the VOC may thus affect the rate of transport within the plant as interactions with mesophyll and stomatal resistance may differ (Wesely & Hicks, 2000). However, there are some studies that have suggested that epiphytic bacteria (communities that reside on the external surfaces of plant tissue) can contribute to the removal of pollutants by driving a VOC intracellular gradient (Seco et al., 2007). Internal plant metabolism maintains a concentration gradient and ensures continuous uptake for VOCs, and the lipophilicity or hydrophilicity (specific K_{ow}) of various VOCs within the leaves allows for certain chemicals to pass through the cell structure and into the cytoplasm (Matsui, 2016), where they are thought to be detoxified by participating in glycosylation, glutathionylation and reductive oxidation reactions (Karl et al., 2010; Tani et al., 2013).

In addition to the physiochemical properties of plant structures that can influence VOC removal, abiotic environmental factors such as relative humidity, light intensity and temperature can all act on both the plant and the contaminant to create an environment where adsorption, absorption or adhesion rates are affected. Chemical contaminants that are either dry or wet deposited onto leaf surfaces accumulate (Treesubsuntorn & Thiravetyan, 2012) and can be incorporated into the leaf's waxy cuticle for either uptake by the plant or utilisation by any endophytic or epiphytic bacteria (Hörmann et al., 2018; Seco et al., 2007; Zuo et al., 2022a). However, there is conflicting literature regarding the waxy cuticle's role in phytoremediation. Yeats & Rose (2013) hypothesised that toluene is only retained in the plant cuticle and does not undergo any translocation within the leaf tissue, or degradation, contradicting previous work (Ugrekhelidze et al., 1997).

2.2 Translocation of VOCs in plant tissues

There are currently two primary modes of translocation of VOCs in plants, depending on the direction of VOC flow relative to the aboveground and belowground plant parts. The first mode of transport is from the above-ground plant parts to the roots via the phloem after the absorption of gaseous contaminants by the leaves (Su & Liang, 2015). VOCs are consequently transported out of the plant to the rhizosphere and surrounding soil. This has been observed by Liang et al. (2019)who exposed tomato plants and hanging orchids to carbon labelled 3.1 Formaldehyde (HCHO), detecting the labelled VOC in the root zone, despite only having foliar exposure to the gaseous contaminant (Liang et al., 2019). Once again, these results have not been consistently found in all plants, with wheat not displaying labelled HCHO in the root zone after foliar exposure (Liang et al. 2019). It is currently unclear exactly how leaf-to-rhizosphere transport occurs, and why it differs amongst plant types. Further studies with a wider range of plant and chemical species are thus required.

The most studied mode of VOC transport in plants is upward transport from the roots to the leaves via the xylem (Pettit et al., 2020; Schröder & Collins, 2002). Flow through the xylem is an integral part of plant growth (K. J. Kim et al., 2020), and is driven by evapotranspiration, where substrate moisture is absorbed by the roots and exported via the stomata during transpiration (Schröder & Collins, 2002). It is therefore likely that pollutants that have become solubilised in the substrate are drawn into the roots in the same way (Kim et al. 2020). Interestingly, most studies have not observed the re-emission of substrate absorbed VOCs from the leaves, evidence that contaminants absorbed through the roots are either degraded or stored in plant tissue. A study by Briggs et al. (1982) developed a mathematical model referred to as “transpiration stream concentration factor” that can be used to quantify the uptake of compounds by plants through the roots, stems and leaves ((Dominici et al., 2021). This model indicates that chemical transport for compounds from the rhizosphere to other plant parts will occur via transpiration flow for compounds with log K_{ow}~2, with VOC lipophilicity also affecting transport efficiency (Mankiewicz et al., 2022; Mura et al., 2005). Nevertheless, high log K_{ow} compounds may block the plant's transport process and thus be trapped in the plant's stem by components with an affinity for the VOC molecules, such as lignin (Llewellyn & Dixon, 2011).

Currently, no study has determined the relative contribution of these two transportation routes to the purification of pollutants from polluted air. Due to the still quantitatively unknown importance of transport throughout the plant system to gross VOC removal, further research into this field is warranted, and may lead to technological advancement that improves phytoremediation efficiency.

2.3 Belowground degradation – plant contribution

The primary mechanism for the removal of VOCs is broadly believed to be through microbial degradation in the rhizosphere (Bais et al., 2006; Cheng et al., 2019; Philippot et al., 2013). However, there is also some evidence that substrate-located VOCs can also be remediated by plant activity. This may occur through absorption of substrate moisture containing dissolved VOCs into root systems and thence transport through the transpiration flow from the roots to the above-ground plant parts and xylem cell wall or cellulose-based interactions (i.e. ion exchange) (Darlington et al., 2001; Dolan & Glynn, 1997; Llewellyn & Dixon, 2011; Pilon-Smits, 2005; J. Yang et al., 2009). Pollutants that diffuse into substrates may enter the cytoplasm of root cells via the plasma membrane driven by transpiration flows, diffusive transport and/or microbially facilitated transport (McCorquodale-Bauer et al., 2023). Additionally, VOCs have been observed to bind to lignin in the cell walls of roots and humus, subsequently leading to their sequestration and conversion into insoluble compounds (B. X. Y. Lee et al., 2020). This process has been implicated in decreasing the mobility of pollutants in the soil, which reduces leaching and prevents contaminants from entering ground water systems and the food chain (Lee et al., 2021).

The physical characteristics of plant roots may also lead to species differences in VOC removal rates due to varying complexity of root matrices, root exudate properties, and variations in the rhizosphere microbial community among different plant species (Bais et al., 2006; Moya et al., 2019). Extensive research has demonstrated that plants can utilize their root systems to exude carbohydrates, amino acids, and organic acids into the rhizosphere, thereby facilitating the stabilisation and equilibrium of microbial communities (Hütsch et al., 2002; Martínez-Lavanchy et al., 2015). This process is particularly critical in the context of phytoremediation systems, where wetland plants have been documented to facilitate oxygen transport to their roots through specialised aerenchyma structures, thereby enhancing aerobic microbial activity (Wießner et al., 2005). Additionally, root system architecture has also been identified as a key factor influencing the efficacy of bioremediation processes (Fatima et al., 2017; Iori et al., 2017; Pettit et al., 2017). These well-developed root architectures provide increased surface area for interaction with contaminated soils, optimize water absorption, and confer higher tolerance to environmental stress(Iori et al., 2017). This principle of root system dynamics can further inform strategies for phytoremediation of airborne pollutants, as illustrated by Pettit et al., (2017), who found that plants like *C. comosum*, characterized by shallow fibrous root structures, exhibit improved pollutant removal efficacy in active green wall applications. Due to the often-symbiotic relationship between individual plant species and their rhizospheric microbial communities, it can be difficult to differentiate between the metabolic effects of the plant and the rhizospheric microbial community. The role of rhizosphere microorganisms in bio- and-phytoremediation will be described in the following section.

2.4 Belowground degradation – substrate and rhizospheric microbial contributions

Substrate properties can have a profound impact on the adsorptive capacity for VOCs (Ruiz et al., 1998), with pH and organic carbon content thought to be of significance (Insam & Seewald, 2010). It has been previously demonstrated that manipulating the substrate in both potted plants and active green walls can alter the VOC remediation potential of plant (Orwell et al., 2006; Panke-Buisse et al., 2015; Pettit et al., 2018b; Rappert & Müller, 2005). In addition to the physical and chemical properties, substrate choice can serve to benefit or limit the rhizospheric microbiome, either improving or reducing VOC interception and degradation (Pettit et al., 2018b).

Plant-rhizosphere interactions occur through chemical signalling and the provision of carbon resources through exudates and other rhizo-deposits, generated through photosynthesis (Bais et al., 2006). Due to the close relationship between plants and their rhizospheric microbial communities, the bacterial composition of the rhizosphere is distinct from the surrounding bulk soil and the rhizospheric microenvironment is often reported to enrich certain microbial functions including denitrification and methanol oxidation (Ling et al., 2022). Generally, all rhizospheric bacterial communities have been found to be capable of degrading gaseous VOCs (Rappert & Müller, 2005)and through exposure to contaminants, VOC-degrading species are selectively enhanced, resulting in higher rates of degradation on subsequent exposure. While there are certain bacterial species that possess well known metabolic pathways for VOC degradation, it has been observed in active green walls that bacterial abundance and composition shifts with geographical region (Fleck et al., 2020), indicating variability in rhizospheric communities with known VOC degrading capabilities. As such, there may be the potential for bacterial enrichment or biostimulation of active green wall systems to promote gaseous VOC degradation, although this has received limited attention (Rappert & Müller, 2005; Shahriari Moghadam et al., 2017; Y. Yang et al., 2020). A study conducted by Yang et al., (2020) observed a 288.8% increase in HCHO removal after inoculating *Vigna radiata* with soils that had been previously exposed to the VOC. However, in the same study, the increased removal of HCHO by *Aloe vera* was only 24.9% using the same soil inoculation (Y. Yang et al. 2020) suggesting the efficacy of biostimulation varies with plant species. It may be plausible that *Aloe vera* could not sustain the bacterial communities (i.e. abundance of specific VOC-degrading bacteria) in the soil as effectively as *Vigna radiata* and therefore did not perform as well. Variable effects associated biostimulation in green wall systems is currently critically understudied. Some studies outside of the VOC remediation field have associated plant microbial community inoculations as a technique to alter plant flowering time and improve plant fitness under drought conditions , due to the symbiotic relationship of plant and microbial biomes it is plausible that whole-microbial community innoculations with VOC degrading bacteria may be a promising technique to further optimise VOC removal of plant based green wall systems (Lau et al., 2012; Panke-Buisse et al., 2015).

Rhizoremediation is a process describing the synergistic interaction between plants and microorganisms to remediate contaminants in soil matrices (Bhatia et al., 2011; Kuiper et al., 2004) This process has received considerable attention and research in the fields of water and soil pollution. The primary rhizospheric microorganisms involved bacteria and fungi. Dominant rhizospheric microbial groups are represented by phyla such as Firmicutes, Proteobacteria, Actinobacteria, and genera like Bacillus, Pseudomonas, and Arthrobacter (Agarwal et al., 2020; Pires et al., 2017) Plant Growth-Promoting Rhizobacteria (PGPR) are a category of beneficial rhizobacteria that have become a focal point of recent studies for their role in promoting plant growth (Bhatia et al., 2011; Kloepper & Schroth, 1978). In the context of phytoremediation, PGPR may also provide effective solutions for plant detoxification and maintaining plant health during the remediation of pollutants (Bhatia et al., 2011; Thouron et al., 2017; L. Zhao et al., 2021a). PGPR contribute to plant defence against pathogens (Guo et al., 2004; Raj et al., 2003), facilitate nutrient absorption from the soil (Çakmakçi et al., 2006; Siddiqui, 2001), and participate in the decomposition and synthesis of pollutants (Glick, 1995). Some Research has indicated that the strategic augmentation of PGPR can enhance the efficiency of removing polycyclic aromatic hydrocarbons (PAHs) and creosote(X. D. Huang et al., 2004a, 2004b). The underlying mechanisms may involve the modulation of plant hormones, including auxin, gibberellin, cytokinin, and ethylene pathways—and to reduce stress ethylene levels by consuming 1-aminocyclopropane-1-carboxylate (ACC), thus promoting plant germination and growth (Hall et al., 1996; Reed & Glick, 2005; Safronova et al., 2006). Regarding VOC remediation, hydrocarbon-degrading bacteria are a focal point of study. It has been observed that hydrocarbon-degrading bacteria naturally occur in low proportions (0.1%) in the environment, and even in areas with severe contamination, their abundance ranges from only 1% to 10% (Ferradji et al., 2014; Mnif et al., 2014; Nazina et al., 2005; Varjani et al., 2015). Nonetheless, many studies have emphasized that bioremediation is a collaborative process involving multiple microbial species (Fatima et al., 2017), as the degradation capacity of a single bacterial strain is limited and substrate-specific, necessitating the involvement of diverse microbial consortia for efficient enzymatic activity (Alkhatib et al., 2011; Mukred et al., 2008). Detailed information on common air pollutants and their associated microbial communities can be found in Supplementary table 1.

Fungi can constitute a crucial element of the bioremediation process within contaminated sites as well (Baldantoni et al., 2017; L. Zhao et al., 2021a). The *Basidiomycota* and *Ascomycota* represent the two most commonly encountered groups of fungi in pollutant remediation(Agarwal et al., 2020). Despite this, there remains a substantial research gap regarding the role of fungi in bioremediation, especially concerning air pollutants. It has been observed (Gadd, 2010) that *arbuscular mycorrhizal* fungi (AMF) are abundant in highly polluted, nutrient-deficient soils, exhibiting resilience in harsh environments. These fungi have been theorised to facilitate detoxification by altering metal availability in the soil and aiding plants in water and nutrient uptake under stress conditions (Agarwal et al., 2020; Alka et al., 2020; Gadd, 2010). (Purohit et al., 2018a)confirmed that fungi enhance nutrient acquisition by plants in lead-contaminated soils. A potential mechanism for fungal remediation of soil pollutants, particularly PAHs, involves the production of ligninolytic enzymes capable of degrading these compounds (Baldantoni et al., 2017; Purohit et al., 2018b; L. Zhao et al., 2021a). Thus, the role of fungi in bioremediation warrants further attention, especially in exploring air pollution remediation, as fungi may offer additional degradation pathways.

There is also a possibility that certain microorganisms with specific metabolic pathways for VOC degradation could be used for single-species inoculation of plant substrates. For example, a study by (Khaksar et al., 2016) found that the bacterium *Bacillus cereus* (strain ERBP) increased HCHO removal by nearly 3-fold over uninoculated media, and consequently ameliorated plant formaldehyde stress. While this research suggests promising potential, the study was limited in that the strain was introduced into a sterile substrate. It is therefore likely that in practise, the biostimulation of a more complex system, such as an already functional rhizosphere, would elicit different outcomes, especially due to competition with indigenous microorganisms and the challenges of adapting to the new environment (Kaminsky et al., 2019; King & Bell, 2022).

2.5 Plant and Microbial Enzyme-Gene Networks in Phytoremediation Response

In most bioremediation environments, pollutants typically do not exist as single entities; instead, they are often present as complex mixtures, all degrade concurrently within the environment (Cerniglia, 1992a, 1992b; Fatima et al., 2017; Heitkamp & Cerniglia, 1987; Ka¨stner & Mahro, 1996). This complexity makes it highly challenging to monitor each compound and further explore the degradation pathways, especially when attempting to understand how microbial communities interact and coordinate in bioremediation(Agarwal et al., 2020; Fatima et al., 2017; Khan et al., 2013). Research has demonstrated that interactions such as competition or synergy among pollutants can occur when plants and microorganisms are involved in bioremediation, leading to variations in degradation efficiency (Cerniglia, 1992a, 1992b; Ferradji et al., 2014; Ka¨stner & Mahro, 1996; Ma et al., 2016; Mnif et al., 2014; Nazina et al., 2005; Rahman et al., 2003; Varjani et al., 2015). Further analysis reveals that the enzymes mediating these processes play a pivotal role (Alvarez-Cohen &

Speitel, 2001; Schäffner et al., 2002). Some enzymes exhibit high specificity, being capable of degrading only particular pollutants, while others can act on a broader range of substrates (Alvarez-Cohen & Speitel, 2001; Kennedy & Law, 1999; Tegge, 1984). Despite variations in microbial species, key enzymes responsible for degradation are often conserved (Alvarez-Cohen & Speitel, 2001; Bollag, 1992; Gianfreda & Rao, 2004). For example, laccase is capable of breaking down phenols (Ullah et al., 2000), PAHs (Dodor et al., 2004), polychlorinated biphenyls (PCBs)(Novotn~ et al., 1997). Utilizing this characteristic, enzymes with broader compatibility can be considered for genetic modification to enhance the efficiency of phytoremediation (Bhatia et al., 2011; Fatima et al., 2017; Rahman et al., 2003; Varjani, 2017a). However, in natural ecosystems, the growth of target microorganisms is often constrained by factors such as microbial competition, cooperation, and environmental limitations, making it difficult to substantially increase their abundance even in polluted soils (Agarwal et al., 2020; Baldwin et al., 2003; Bhatia et al., 2011; Cerniglia, 1992a, 1992b; Fatima et al., 2017; Tallis et al., 2011). Furthermore, applying genetic engineering technologies may play a role in accurately monitoring the activity and responses of different enzymes to varying levels of pollutants (Agarwal et al., 2020; Ducrocq et al., 1999; Ghosh et al., 2018; Janke et al., 1981; Khan et al., 2013; S.-Y. Lee et al., 1996; Mesarch et al., 2000; Yousaf et al., 2011). Techniques such as gene sequencing and PCR allow for a more detailed understanding of these enzymes (Baek & Kenerley, 1998; Borneman et al., 1996; Ducrocq et al., 1999; Ghosh et al., 2018; Kurata et al., 2001; S.-Y. Lee et al., 1996; Raeymaekers, 1998). The specific sequence probes enable tracking of degradation processes during bioremediation, which is crucial for unraveling the complexities of bioremediation mechanisms (Agarwal et al., 2020; Borneman et al., 1996; Ghosh et al., 2018; Purohit et al., 2018a; Yousaf et al., 2011). While the majority of studies focus on rhizospheric microbes and their enzymes, plants themselves also play a role through specific enzymatic reactions and gene sequences.

One of the plant mediated detoxification processes that has been proposed is through enzymatic reactions predominantly occuring in the chloroplasts and cytosol of plant cells (Canaval et al., 2020; Omasa et al., 2000; Takagi et al., 2016; TANI & MOCHIZUKI, 2021; B. C. Wolverton et al., 1989; Yamane & Tani, 2024; Yamauchi et al., 2011). Pollutants are initially transformed through enzymatic catalysis, such as oxidation by cytochrome P450 monooxygenases, reduction by dehydrogenases, or hydrolysis by esterases (Coleman et al., 1997; Sandermann, 1994; Schäffner et al., 2002). Following this, conjugation reactions occur, in which glutathione-S-transferases or glycosyltransferases facilitate the attachment of glutathione or sugars to the metabolites, reducing their toxicity (Coleman et al., 1997; Sandermann, 1994; Schäffner et al., 2002). Subsequently, these intermediates may be conjugated with glutathione or sugars through the action of glutathione-S-transferases (GSTs) or glycosyltransferases, thereby detoxifying and neutralizing less toxic compounds (Coleman et al., 1997; Muramoto et al., 2015; Sandermann, 1994; Schäffner et al., 2002; Yamane & Tani, 2024). Most of these transformed molecules are either polymerized or stored within vacuoles, where they participate in further metabolic reactions (Coleman et al., 1997; Omasa et al., 2000; Sandermann, 1994; Schäffner et al., 2002; TANI & MOCHIZUKI, 2021; Yamane & Tani, 2024). Metabolites that cannot be further degraded or detoxified are expelled from the cell through ATP- or proton-dependent transporters or via exocytosis (Coleman et al., 1997; Sandermann, 1994; Schäffner et al., 2002).

Supplementary table 2 provides a comprehensive overview of the key enzymes involved in various enzymatic reactions and their corresponding genetic information. Overall, during the bioremediation process, it is evident that microorganisms work in synergy with plants (Agarwal et al., 2020; Baldwin et al., 2003; Bhatia et al., 2011; Fatima et al., 2017; Tallis et al., 2011; L. Zhao et al., 2021a). The degradation of various pollutants often necessitates the involvement of multiple microbial communities, which cooperate to break down contaminants into nutrients and non-toxic substances. Plants play an active role in this process by releasing root exudates, which help to shape microbial community dynamics and enhance degradation efficiency. The degradation of specific compounds is primarily determined by specialized enzymes, which are derived from both microorganisms and plants (Agarwal et al., 2020; Fatima et al., 2017; Khan et al., 2013). These enzymes are adaptable, with their activity being influenced by environmental conditions such as pH and temperature, and their activity can be further enhanced through manipulating microbial communities or employing genetic engineering techniques. Therefore, a thorough understanding of the specific enzymes involved in the breakdown of various substances, as well as the genetic information that regulates these enzymes, is essential.

3. Removal of common gaseous VOCs

3.1 Formaldehyde (HCHO)

The stomata of plant leaves appear to be responsible for the majority of HCHO uptake, after which it may be at least partially converted into non-toxic substances through plant metabolism or concentrated within the stem, or otherwise expelled through the root system (K. J. Kim et al., 2010). While plant metabolism can remove gaseous HCHO, it requires the use of several enzymes and metabolic processes (Y. Han et al., 2022; Rachmadiarti et al., 2019; L. Wang et al., 2020). There is evidence, however, that the majority of HCOH degradation occurs in the rhizosphere after downwards transport by the plant (Aydogan & Montoya, 2011; K. J. Kim et al., 2010; Panyametheekul et al., 2019; Salthammer et al., 2010; Xu et al., 2011).

HCHO detoxification in plants depends on C1 metabolism (Iba, 2002), where HCHO is oxidised and converted to formate by the enzymes glutathione-dependent formaldehyde dehydrogenase (FDH) and S-formylglutathione hydrolase (SFGH) (Giese et al., 1994). Formate then enters the chloroplasts and mitochondria, where it is further oxidised to CO_2. The CO_2 is diffused into the cytoplasm or assimilated into glucose and fructose through the Calvin cycle (Sun et al., 2015)(Figure 2).

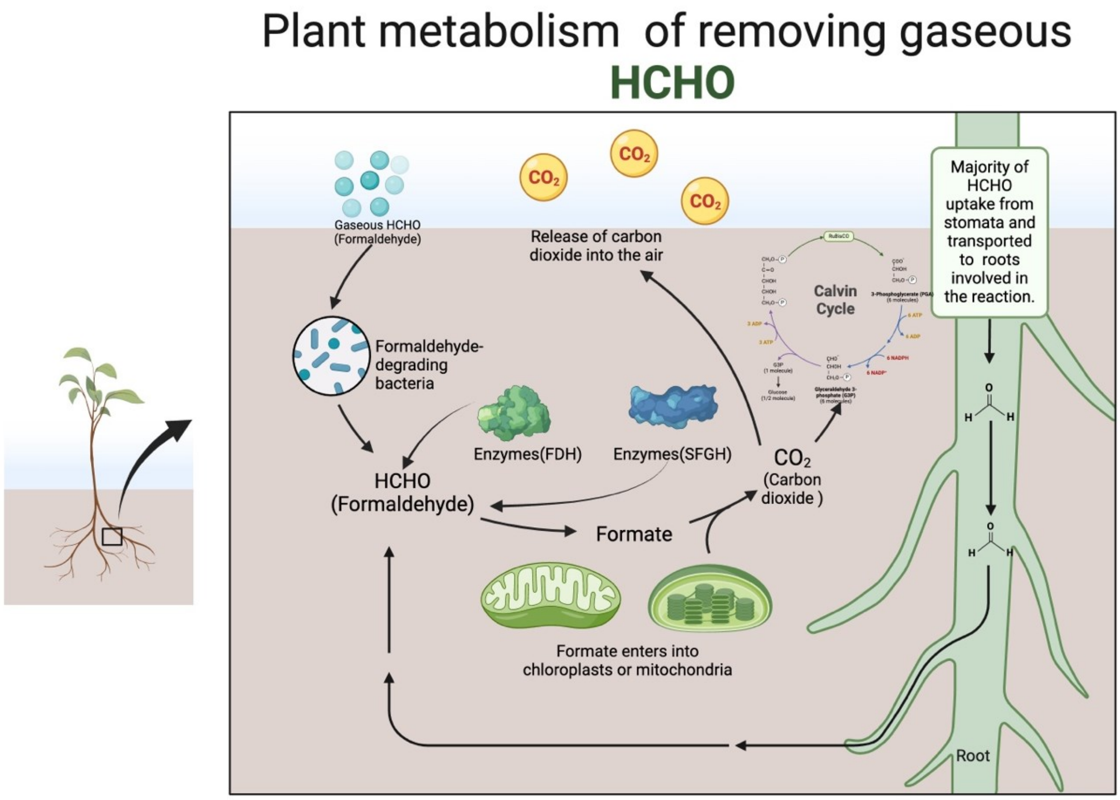


Figure 2. The chemical processes for the degradation of formaldehyde (HCHO) by plant. Image by author.

Currently, the metabolites of formaldehyde degradation differ between studies (S. Zhao et al., 2019), and it is unclear whether these are biological or methodological effects. Through the use of radiolabeled formaldehyde, researchers have elucidated the complete pathway by which indoor plants catalyze formaldehyde, sequentially converting it into sugars, amino acids, cell wall components, and other natural compounds (Giese et al., 1994; Schäffner et al., 2002). Studies have demonstrated that the FDH (formaldehyde dehydrogenase) gene sequence in plants exhibits high homology with those found in microorganisms and animals, indicating that FDH is a precursor within the large alcohol dehydrogenase gene family (Fliegmann & Sandermann, 1997; Schäffner et al., 2002). In *Chlorophytum* species ‘ foliage, it has been confirmed that formaldehyde detoxification relies on a glutathione-dependent formaldehyde dehydrogenase (FDH; EC 1.2.1.1), which serves as a critical enzyme in this process (Giese et al., 1994; Schäffner et al., 2002). Further studies have confirmed similar findings in other common indoor plants, such as *Ficus*, *Schefflera*, and *Spathiphyllum* (Schäffner et al., 2002). In *Ficus benjamina,* sucrose is mainly produced (Schmitz et al., 2000), while other studies have found that the primary metabolite of foliar HCOH exposure is mainly glucose (Seco et al., 2007). In the case of *Epipremnum aureum*, most of the leaf metabolites are composed of fructose, less than half of the metabolites in the stems are fructose, and in the roots, sucrose is mainly produced (Irga et al., 2018).

In a study conducted by Zuo et al. (2022), it was observed that during the purification of HCHO by plant leaves, the concentration of CO_2 would increase, either as a biproduct of HCHO degradation, or because of plants being unable to photosynthesise as effectively while dealing with HCHO metabolism. This raises the question of gas interference in the purification process of VOCs by plant processes.

3.2 PAHs & BTEX

Benzene, xylene, toluene, and ethylbenzene (BTEX) are main components of air pollution, primarily arising from the combustion and evaporation of petroleum-based products (Atashgahi et al., 2018; Fatima et al., 2017; Y. Huang et al., 2013; Li et al., 2013; Yan et al., 2019; Y. Zhang et al., 2021). Consequently, when addressing the bioremediation of air pollutants, particularly in underground part, it is essential to consider petroleum-derived contaminants. Soil pollutants stemming from petroleum combustion, wildfires, and other air pollution sources are primarily characterized by PAHs and BTEX (Yan et al., 2019; Y. Zhang et al., 2021; L. Zhao et al., 2021a). PAHs are high molecular weight polycyclic hydrocarbons that, compared to the low molecular weight of BTEX, exhibit greater resistance to environmental degradation and absorption (Bihari et al., 2006; C. Zhao et al., 2021; L. Zhao et al., 2021a, 2021b). BTEX is more volatile and mobile within air and soil, whereas PAHs exhibit a tendency to adsorb onto soil particles, leading to prolonged retention(Y. Huang et al., 2013; Li et al., 2013; L. Zhao et al., 2021b). The degradation of PAHs involves a cooperative metabolic process between plants and soil microorganisms, which utilize enzymatic reactions to break down these compounds (H. Zhang et al., 2020; L. Zhao et al., 2021b)(figure 3). A few microbial species can also degrade PAHs directly (H. Zhang et al., 2020). The breakdown of PAHs is typically initiated through oxidation reactions, which convert complex polycyclic structures into smaller molecular units (e.g., BTEX), which are subsequently broken down via similar pathways into nutrients, CO_2, and H_2O (Varjani, 2017b; L. Zhao et al., 2021b). It is important to note that during the co-remediation of PAHs by plants and microbes, compounds with lower molecular weights are degraded preferentially, whereas larger, benzene-ring-rich structures exhibit lower degradation efficiency (Atlas, 1981; Fatima et al., 2018; Glick, 2010; Salanitro, 2001; Sessitsch et al., 2013). This might be due to the stronger adsorption affinity of these high-molecular-weight PAHs to soil particles (Chen et al., 2018; L. Zhao et al., 2021b).

in phytoremediation research, BTEX are aromatic hydrophobic VOCs that have been frequently studied due to their relative toxicity and problematic concentrations in indoor air (Gong et al., 2019; Jindrová et al., 2002; Sriprapat & Thiravetyan, 2013; F. R. Torpy, Irga, Brennan, et al., 2013). While there have been many studies on the degradation of BTEX by potted plants (Fooladi et al., 2019; Gong et al., 2019; Orwell et al., 2004), few to date have explored the physiological processes involved in the degradation of BTEX in plant cells (Sriprapat, Boraphech, et al., 2014; Sriprapat & Thiravetyan, 2013). Some studies have hypothesised that due to structural similarity, there are similar enzymatic pathways for the degradation of all BTEX compounds (Orwell et al., 2006; Pettit et al., 2018a). It has been proposed that BTEX and possibly other aromatic VOCs may have competitive or synergistic relationships during plant absorption (Irga et al., 2018; Setsungnern et al., 2019). Toluene has been shown to be absorbed by the stomata and cuticles on plant leaves (K. T. Han & Ruan, 2020), where it was hypothesised that it was translocated to the roots for metabolism by rhizospheric bacteria. Leaf cuticles also have some toluene absorption capacity, which is thought to lead to subsequent leaf uptake (Wei et al., 2017), although other studies have found that toluene may be stored in the cuticle without participating in any reactions (Hörmann et al., 2018).

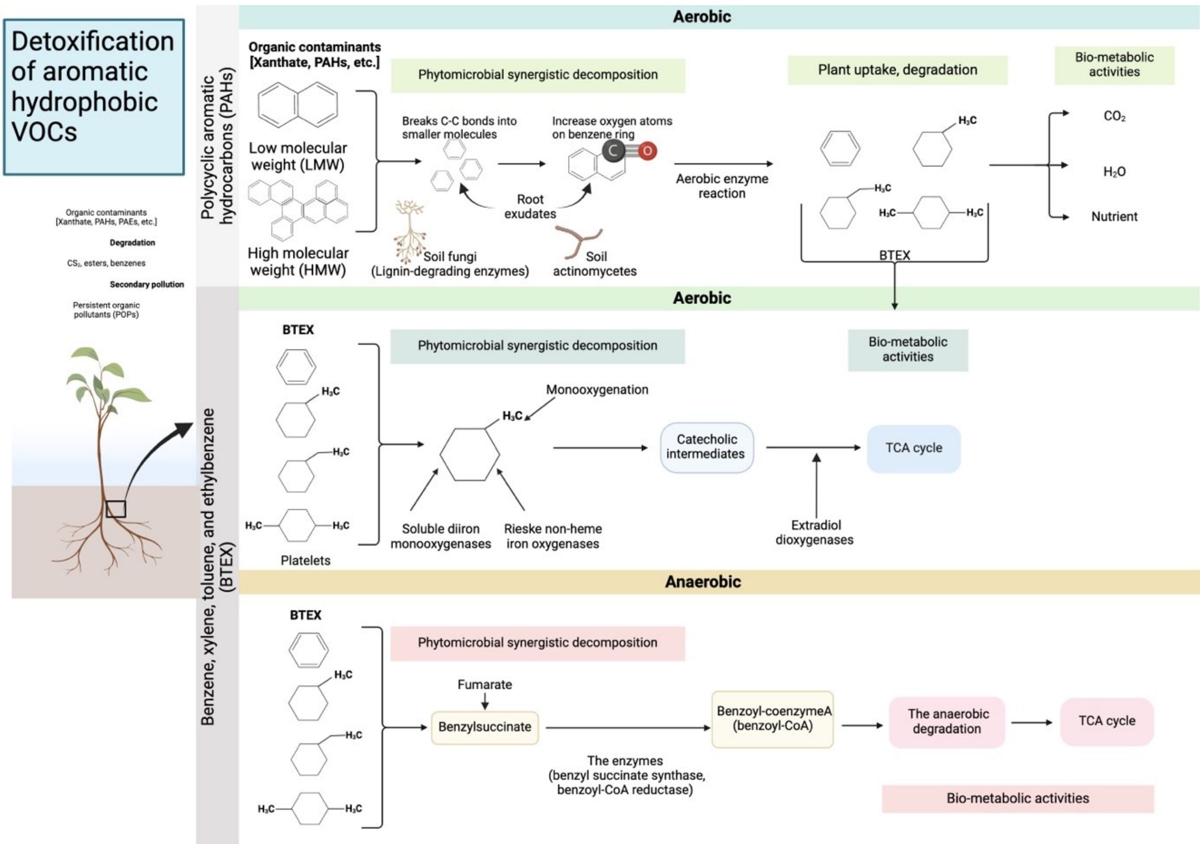


Figure 3. Degradation pathways of PAHs and BTEX in in phytosynthetic microbial remediation

As depicted in Figure 3, BTEX are first oxidised in the plant with the enzymatic hydrolysis of the aromatic ring (Varjani, 2017b). The transformation of BTEX within plants is essentially dependent on the activity of the relevant enzymes, where the transformation rate can be influenced by a variety of factors such as penetration rate, localisation site, type of reaction catalysed, oxidising enzyme activity and specificity and the chemical properties of the hydrocarbon (Ugrekhelidze et al., 1997). Setsungnern et al., (2019) found that the CYP90B1 enzyme increased 2-8-fold relative to a blank control when *C. comosum* was exposed to increasing concentrations of benzene gas, evidence that CYP90B1 enzyme is at least one of the critical enzymes for plant-mediated aromatic VOC degradation (Setsungnern et al., 2019). In related transgenic plant experiments, overexpression of genes in the presence of benzene has been demonstrated, e.g. ferredoxin-NADP reductase (FNR), glutathione s-transferase Theta 1 (GSTT1), glutathione synthase (GS) and homologous phytate transferase (HPT) (Setsungnern et al. 2019). Additionally, after translocation to the roots, benzene, toluene, ethylbenzene and xylene degradation is initiated with the facilitation of mono- and dioxygenases (Y. Yang et al., 2020), and thus follow similar pathways to those previously mentioned. While the metabolic process of BTEX degradation is understood in plants, there is an absence of detailed literature that describes and documents the upregulation of BTEX degrading genes and enzymes in laboratory and field settings, and thus further research in this area would be of value.

3.3 Halogenated hydrocarbons

Halogenated hydrocarbons such as tetrachloroethylene and trichlorethylene (TCE) are common volatile industry pollutants commonly used within textile processing, degreasing and dry cleaning (Burken & Schnoor, 1997; Nwoko, 2010; T. Shang et al., 2004). While they readily volatilise into the atmosphere, the majority of literature concerning the phytoremediation of these compounds is associated with plants ability to remove them from environmental matrices such as soil and water (Gordon et al., n.d.; Moccia et al., 2017a; Newman et al., 1997; T. Shang et al., 2004; T. Q. Shang et al., 2001; T. Q. Shang & Gordon, 2002; Y. Zhang et al., 2013). These studies associate removal via phytodegradation mainly operated through plant hormone metabolism utilising cytochrome P450 monoxygenases and dehalogenases and following the green liver model proposed bySandermann (1994). The halogenated hydrocarbons are transformed through oxidation and conjugated with carbohydrates, gluthione and carboxylic acids via Glycosyltransferases, glutathione-S-transferases, carboxylic acids and acyltransferases before being compartmentalised within plant cells vacuoles or apoplast through exocytosis, ATP binding cassette (ABC) and multi drug and toxic compound extrusion (MATE) transporters (Susarla et al., 2002), here the transformed compounds can enter other plant biological processes or be excreted (Moccia et al., 2017b; Schäffner et al., 2002). While these metabolic processes are seemingly well understood within literature, the studies almost solely investigate pollutant removal from soil and water matrices rather than air contamination. There is also a lack of recent publications on the topic, leaving the understanding of these processes within recent phytoremediation technologies such as active green walls, highly understudied.

4 Factors affecting VOC removal

Phytoremediation for gaseous contaminants, especially within the indoor environment, is a rapidly expanding field of research. However, it remains unclear what characteristics of botanical systems have the greatest influence on VOC removal rates. Thus, a comprehensive summary of the relevant phytoremediation studies and the characteristics studies that were found to be related to VOC removal has been detailed below (Table 1).

The main factors that affect biofiltration performance thus appear to relate to: plant selection (Aydogan & Montoya, 2011; K. J. Kim et al., 2010; Muhammad et al., 2019; Paull et al., 2019; Sæbø et al., 2012), light availability and photosynthetic potential (Dominici et al., 2021; Y. Huang et al., 2016; Lin et al., 2013; Sun et al., 2015; Treesubsuntorn & Thiravetyan, 2018; Wannomai et al., 2019), airflow for active systems (Abdo et al., 2019; Mankiewicz et al., 2022; Pettit et al., 2019; Yoon & Park, 2002), temperature and humidity (Gubb et al., 2018; Poórová et al., 2020; Poorova & Vranayova, 2021; Ruiz et al., 1998), substrate composition and performance (Mankiewicz et al., 2022; Pettit et al., 2018b), and substrate moisture content and irrigation (Barac et al., 2004; B. X. Y. Lee et al., 2020; Mankiewicz et al., 2022)(Figure 4).

These influencing factors have been shown to indirectly affect bioremediation efficiency by altering the chemical and physical characteristics of soil, thereby impacting the living conditions of plants and microorganisms (Boopathy, 2000; Fatima et al., 2017; Klein et al., 2010; Mohan et al., 2006). However, recent studies have uncovered more profound mechanisms behind these effects, particularly concerning microbial communities (G. O. Adams et al., 2014, 2015; J. M. Adams et al., 2001; Afzal et al., 2014; Agarwal et al., 2020; Boopathy, 2000; Klein et al., 2010; Shukla et al., 2010). For instance, changes in soil properties often lead to fluctuations in the availability of essential nutrients—such as nitrogen, phosphorus, and iron—especially in polluted environments ((Agarwal et al., 2020; Fatima et al., 2017; Foght et al., 1996; Fulekar et al., 2009). This can lead to conditions where nutrient concentrations are either excessively high or markedly depleted (Agarwal et al., 2020; Alka et al., 2020; Foght et al., 1996; Fulekar et al., 2009). Such variations impair the nutrient uptake by plants, potentially reducing the effectiveness of phytoremediation or even leading to plant death (Fatima et al., 2017; Foght et al., 1996). These nutrient shifts can also restructure microbial community structures, causing changes in microbial populations. Temperature is another factor; within the temperature range suitable for plant growth, the efficiency of biodegradation typically decreases as temperatures drop (Fatima et al., 2017; Srivastava et al., 2014). This reduction is attributed to the temperature sensitivity of enzymatic reactions and the tendency of most microorganisms to thrive in warmer conditions (Fatima et al., 2017; Srivastava et al., 2014). Soil moisture is additionally important; while many plants can tolerate varying moisture levels, the stability of microbial communities requires a narrower range (around 25%) (Das & Chandran, 2011; Fatima et al., 2017). Saturated soils, or substrates with poor aeration, can further restrict air circulation, inhibiting the activity of aerobic microorganisms (Fatima et al., 2017; Khan et al., 2013). Additionally, compacted soils can make it more challenging to separate and remove organic pollutants (Fatima et al., 2017; Mohan et al., 2006).

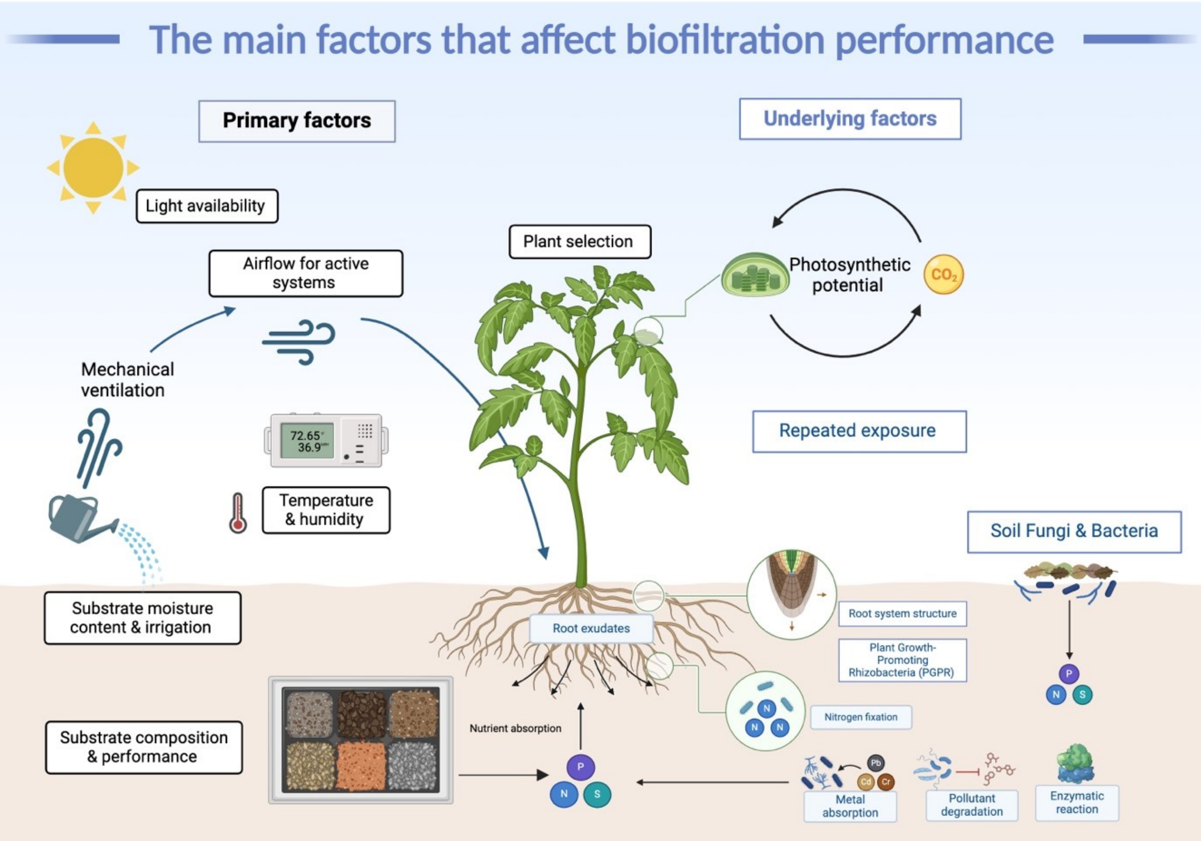


Figure 4. Various factors influence the potential of botanical systems to phytoremediated gaseous VOCs. Image by author.

An understudied factor affecting VOC removal performance is the effect of repeated exposure. As the mechanism for removal is primarily rhizosphere-driven, repeated exposure to gaseous contaminants will selectively up-regulate the microbial populations that are capable of processing those specific pollutants. For example, Jen et al. (1995)noted a 4-fold increase in carbon-labelled toluene after repeated exposure. Similarly, in a study conducted byKim et al. (2011), toluene was removed at significantly greater rates in 27 out of 28 plant species after repeated exposure. Therefore, it is essential to consider the influence of repeated exposure when assessing the removal potential of botanical systems for gaseous VOCs as experimentation may be confounded by repeated exposures, leading to an over estimation of performance, particularly in the absence of independent replication. Studies that assess the effect of repeat exposure on the degradation of a range of VOCs should also consider the time taken for microbial reset in the plant rhizosphere, and how this differs between plant species and VOC exposures.

Table 1. Summary of literature on different types of bioremediation, for various VOCs (TVOCs = total ambient VOCs)

Authors & Year	Type of System	Plant Species	Plant part	Pollutant	Removal Rate/ %	Driving Factor
Irga et al., 2013	Hydroponic plant	*Syngonium podophyllum*	Rhizosphere and subtrate microoganisms	Benzene	50% removal at 1444 $\mu g/m^3/h/pot$ 50% removal at 739 $\mu g/m^3/h/pot$ 50% removal at 519 $\mu g/m^3/h/pot$	Light Temperature and relative humidity Substrate composition and performance Substrate moisture content and irrigation Botanical component
Torpy et al. 2018	Active Green Wall	*Philodendron scandens* *Philodendron scandens 'Brazil'* *Asplenium antiquum* *Syngonium podophyllum*	Aerial parts and rhizosphere	Methyl ethyl ketone (MEK)	56.6 ± 0.86% in 8 hours	Light Airflow, Temperature and relative humidity Substrate composition and performance Substrate moisture content and irrigation
Ibrahim et al. 2021	Active Green Wall	*Epipremnum aureum*	Aerial parts and rhizosphere	TVOCs	54.5%, 65.42%, 46% In 16 minutes	Airflow Temperature and relative humidity Substrate composition and performance
Suárez-Cáceres et al. 2021	Green Wall	*Nephrolepis exaltata*	Aerial parts and rhizosphere	TVOCs	12.8%-77.3% In 3 hours	Light Airflow Substrate composition and performance Repeated exposure
Treesubsuntorn et al., 2013	Leaf only	*Chamaedorea seifrizii* *Scindapsus aureus* *Sansevieria trifasciata* *Philodendron domesticum* *Ixoraebarbata craib* *Monster acuminate* *Epipremnum aureum* *Dracaena sanderiana*	Leaves (stomata, cuticle wax)	Benzene	1.10 – 23.46 µmol/g of plant material over 3 days.	Botanical component Airflow Temperature and relative humidity Repeated exposure
Hörmann et al., 2018	Potted Plant	*Dieffenbachia maculate* *Spathiphyllum wallisii* *Asparagus densiflorus*	Aerial part	Toluene 2-ethylhexanol	1.4 – 1.5 $L\ h^{-1}\ m^{-2}$	Botanical component Light Airflow Repeated exposure
Kondo et al, 1995	Potted Plant	*Nerium indicum*	Stomata and rhizosphere	Formaldehyde	103 $ng\ dm^{-2}\cdot h^{-1}.ppb^{-1}$	Light Airflow
Orwell et al., 2004	Potted Plant	*Dracaena, Epipremnum aureum, Dracaena marginata, Schefflera 'Amate', Spathiphyllum 'Petite', Spathiphyllum 'Sensation', Howea forsteriana*	Leaves rhizosphere and subtrate microoganisms	Benzene	12 – 27 ppm/day	Botanical component Light Temperature and relative humidity Repeated exposure
Orwell et al., 2006	Potted Plant	*Spathiphyllum, Dracaena*	Rhizosphere and subtrate microoganisms	Toluene *m*- xylene	0.68 – 1014 $mg/m^2/day$	Airflow Repeated exposure
Sriprapat et al., 2013	Potted Plant	*Zamioculcas zamiifolia*	Stomate and cuticle	Benzene, Toluene, Ethylbenzene, Xylene	Stomatal pathways: Benzene 80%; Toluene 76%; Ethylbenzene 75%; and Xylene 73%. Non-stomatal pathways: 20%, 23%, 25%, and 26%, respectively.	Light Temperature and relative humidity Substrate moisture content and irrigation

Teiri et al., 2018	Potted Plant	*Chamaedorea elegans*	Rhizosphere and subtrate microoganisms	Formaldehyde	1.47 $mg/m^2/h$	Light Airflow Temperature and relative humidity Substrate composition and performance Substrate moisture content and irrigation
Torpy et al., 2013	Potted Plant	*Spathiphyllum wallisi*	Rhizosphere and subtrate microoganisms	Benzene	Bio stimulation increased removal rates by around 27%	Light Substrate composition and performance Repeated exposure
Treesubsuntorn et al., 2012	Potted Plant	*Chamaedorea seifrizii, Scindapsus aureus, Sansevieria trifasciata, Philodendron domesticum, Ixoraebarbata craib, Monster acuminate, Epipremnumaureum and Dracaena sanderiana*	Leaves (cuticle wax)	Benzene	Removal at 72h range from 43 – 77% depending on species.	Botanical component Light Airflow Temperature and relative humidity Substrate composition and performance
Wood et al., 2002	Potted Plant	*Howea forsteriana, Spathiphyllum wallisii and Dracaena deremensis*	Rhizosphere	Benzene and *n*-hexane	367 – 4032 $mg/m^3/day/$	Botanical component Light Airflow Substrate composition and performance
Zhou et al., 2011	Potted Plant	30 species fromArceae, Agavaceae and Liliaceae families	Plant morphology	Formaldehyde	2.21 – 4.60 mg/m^3 over 7 days	Botanical component
Zuo et al., 2022	Potted Plant	*Epipremnum aureum and Rohdea japonica*	Aerial parts and rhizosphere	Formaldehyde	The underground part and the aerial part of *E. aureum* was 0.152 and 0.163 $mg·m^{−3}·h^{−1}$, respectively, and the rate of purification of formaldehyde was 68.6% and 73.8%, respectively. The underground part and the aerial part of *R. japonica* was 0.136 and 0.131 $mg·m^{−3}·h^{−1}$, and the rate of purification of formaldehyde was 61.1% and 58.9%, respectively.	Botanical component Airflow Temperature and relative humidity Substrate composition and performance Repeated exposure
Aydogan & Montoya, 2011	Potted Plant	*Hedera helix,Chrysanthemum morifolium,Dalea compacta, Epipremnum aureum*	Aerial parts and rhizosphere	Formaldehyde	Formaldehyde removal of activated carbon (AC),clay and growstone in a pot under wet conditions, were at about 98%, 62.6% and 62.3%, respectively,for a 10h period expanded.	Botanical component Airflow Substrate composition and performance Substrate moisture content and irrigation
Kim et al., 2010	Potted Plant	86 different plant species representing general classes (fern, woody foliage plants, herbaceous, Korean native and herbs)	Aerial parts and rhizosphere	Formaldehyde	6.64 $µg/m^3$ in 5h (O.japonica) 0.13 $µg/m^3$ in 5h (D.deremensis)	Botanical component Light Temperature and relative humidity Substrate composition and performance
Kim et al., 2014	Potted Plant	*Fatsia japonica and Dracaena fragrans*	Roots	Toluene, Xylene	N/A	Botanical component Airflow Substrate composition and performance Repeated exposure
Kim et al., 2016	Potted Plant	*Schefflera actinophylla and Ficus benghalensis*	Plant stem with rhizosphere	Toluene, xylene	both S. actinophylla and F. benghalensis, average toluene transported ratio via the stem and by direct diffusion from the air into the medium was 47 and 53 %, and	Botanical component Airflow Substrate composition and performance Repeated exposure

					the ratios of m,p-xylene transported was 60 and 40 %. The ratio of o-xylene transported via the stem and by direct diffusion from the air into the medium was 61 and 39 % in both species.	
Setsungnern et al., 2017	Hydroponic plant	*Chlorophytum comosum*	Aerial parts and rhizosphere	Benzene	31.37% removal under 1:1 LED light. 24.75% removal under fluorescent light	Light Temperature and relative humidity Repeated exposure
Sriprapat et al., 2014	Potted Plant	*Alternanthera bettzickiana, Drimiopsis botryoides, Aloe vera, Chlorophytum comosum, Aglaonema commutatum, Cordyline fruticosa, Philodendron martianum , Sansevieria hyacinthoides , Aglaonema rotundum, Fittonia albivenis , Muehlenbeckia platyclada, Tradescantia spathacea, Guzmania lingulata, Zamioculcas zamiifolia,and Cyperus alternifolius*	Cuticle wax, aerial parts and rhizosphere	Toluene, Ethylbenzene	About 77% removal in 72h (Toluene) across 12 plants. About 70% removal at 72h (Ethylbenzene) across 12 plant.	Botanical component
Sriprapat et al., 2016	Hydroponic plant	*Epipremnum aureum, Chlorophytum comosum, Syngonium podophyllum, Hedera helix, Dracaena godseffiana and Nicotiana tabacum*	Aerial parts and rhizosphere	Benzene	25.3 – 34 µmol $m^{-2}h^{-1}$	Botanical component Substrate composition and performance Repeated exposure
Su & Liang, 2015	Hydroponic plant	*Chlorophytum comosum*	Plant leaves and roots	Formaldehyde	135 µg/h/plant (maximum)	Substrate composition and performance Repeated exposure

5 Performance enhancement

5.1 Passive green walls

The major limitation of passive systems remains as the limited rate at which pollutants diffuse from indoor ambient air into the plants functional removal zones, while the primary resolution for this rate limiting step is the provision of adequate air circulation through indoor zones containing these systems (Soreanu, 2015)there have been a few potential performance enhancement techniques proposed within literature to increase natural phytoremediation capabilities of these systems. With the absence of active airflow, the process of translocation of VOCs through plant foliage to the rhizosphere is paramount for delivery of pollutants towards plants primary removal zones (Irga et al., 2013), thus some have proposed the selection of specific plants species which show highest removal rates for desired pollutants. (Sriprapat, Suksabye, et al., 2014)investigated airborne uptake of toluene and ethylbenzene by 12 ornamental plants revealing highest removal by *Sansevieria trifasciata* and *Chlorophytum comosum* respectively. It was proposed that the higher hexadecenoic acid contents within plants waxy cuticle may be involved in increased uptake of these aromatic hydrocarbons. Rhizospheric biostimulation has also been proposed as a possibly effective method for performance enhancement, Torpy et al., (2013) investigated the removal of benzene by potted systems both with and without an added biostimulate solution. While effective biostimulation was observed with increased benzene removal rates of ~15%, repeated exposure has also been observed to result in increased performance due to the natural up-regulation of VOC degrading bacteria, by giving them a competitive advantage over non-VOC degrading species (De Kempeneer et al., 2004; Khaksar et al., 2016; Sriprapat & Thiravetyan, 2016). While this body of work has demonstrated the potential of performance enhancement of natural phytoremediation of passive green walls, the application of active airflow remains the most effective abiotic factor that has increased the performance of phytoremediation systems.

5.2 Active green walls

Active airflow through the substrate provides a direct delivery of gaseous contaminants to the roots and rhizosphere, as well as a physical matrix for particle impaction and the solubilisation of VOCs and other gaseous pollutants (J. M. Kim et al., 2008; Orwell et al., 2006; Paull et al., 2018; Wood et al., 2002). In active green walls, the direction of airflow is fixed – either from ambient, across the foliage and into the substrate, or from ambient and into the substrate, and then out via the foliage (Abdo et al., 2019; Darlington & Dixon, 1999; Irga et al., 2017). It has been hypothesised that the direction of airflow may not have a measurable effect on performance, however there are some concerns that drawing air through the plant foliage first may bring moist air into the ducting behind the walls and promote the development of problematic biofilms (Abdo et al., 2019; Darlington & Dixon, 1999; Pettit et al., 2020; F. Torpy et al., 2017).

While active airflow allows for pollutants to be directly exposed to the rhizosphere, the second most important factor is moisture and irrigation (Delhoménie & Heitz, 2005). The provision of adequate moisture not only maintains normal physiological activity of the plants, but also contributes to removal of pollutants (Keller, 1986; Panyametheekul et al., 2019). Plants and their rhizospheric communities depend on water for major metabolic mechanisms such as CO_2 assimilation, photosynthesis, nutrient transport, productivity, production and cell membrane stability (González & González-Vilar, 2006). During exposure to gaseous contaminants, the cell membranes of plant tissues are affected by water loss (González and González-Vilar 2006), which may result in diminished performance with reduced water availability for the plants. Additionally, water content in the substrate can help to maintain microbial carrying capacity and retain the metabolic cross-feeding processes which have been hypothesised to assist in contaminant remediation (Willey et al., 2008).

In the absence of appropriate moisture, active green walls will have a substantially reduced capacity for remediating contaminants. A dry substrate will not only impact plant performance, but will also create excessive airflow channels, reducing the residence time of pollutants and filtration efficiencies (Pettit et al., 2018b). Additionally, depending on the composition of the substrate, critically low moisture content over an extended period of time can cause some substrates to become hydrophobic that will resist rehydration (Sabo et al., 1993; Thompson et al., 1996), leading to problematic maintenance. In contrast, excessive watering can also inhibit airflow with the substrate matrix, creating anaerobic zones for microbes (Young & Ritz, 2000), reducing the relative surface area for gas exchange (Abdo et al., 2019), increasing the pressure drop across the substrate 'filter' (Abdo et al., 2019), contribute to substrate compaction and generally reduce the lifespan of the green wall. It has therefore been recommended that green wall substrate moisture content should be maintained between 40-60% by weight, depending on plant species (Irga et al., 2023).

6 Advancements in air Phytoremediation

There are several avenues of research that show promising results for the further enhancement of phytoremediation technology, however in their current form they are complex and potentially expensive. One such method is the application of exogenous phytohormones, such as methyl jasmonate (MeJA) which has been shown to increase benzene removal in the plant *Zamioculcas zamiifolia* by affecting the production of indoleacetic acid (IAA) (Khaksar et al., 2017). Similarly, the application of biologically active 24-epibrassinolide (EBR) in the plant *Chlorophytum comosum* has been shown to increase the removal of benzene by affecting the expression of related reductases and genes, enhancing the activity of glutathione synthase, and leading to an increase in NADPH biosynthesis (Setsungnern et al., 2019). The application of exogenous phytohormones clearly warrants further investigation.

Another alternative technology to increase phytoremediation potential is the application of genetic modification (GM) which has been used extensively in agriculture and has yielded significant performance enhancement (Herdt, 2006; Panesar & Marwaha, 2013; Ray, 2020). It has been suggested that GM technology can be applied to green walls to improve indoor air quality for urban dwellers (Lee et al., 2015), with some studies on transgenic plants already showing promising results. A study on *Petunia sp.* which expressed FALDH from *Arabiopsis* was observed to have a 26% increased removal rate for HCHO (Lee et al. 2015), which was higher than the removal rates of several other common indoor plants (K. J. Kim et al., 2010). In another study, transgenic *Petunia sp*. carrying the CYP2E1 gene from mammalian cells showed significantly improved HCHO removal and resistance, likely due to its increased ability to oxidise VOCs (Man et al., 2015). The main concerns regarding transgenic plants targeted at VOC removal relate to their costs and the challenges with registering their use in the general environment. If these challenges can be overcome, there may be significant potential for performance enhancement from this area.

7 Conclusions and future work

Phytoremediation has been demonstrated as an effective way to remediate indoor air pollutants while improving other environmental qualities such as humidity and thermal comfort. While our understanding of the physical, physiochemical and metabolic pathways for VOC degradation are increasing, there is a distinct lack of literature that directly investigates these factors. While the plant rhizosphere and substrate-based microorganisms have proved to be essential for the reduction of most air pollutants, our understanding of the between-microbe interactions in the rhizosphere is lacking. Overall, evidence shows that phytoremediation relies on the complex interactions of biological systems (plant parts, substrate, microbial community, substrate moisture etc) and abiotic factors (mechanically assisted airflow, moisture content etc). While there are many promising findings to date, further research is needed to optimise this technology within our indoor environments. To further validate the efficacy of these systems, research should focus on the ideal inclusion of both biotic and abiotic factors, specifically, plant biochemical analysis of phytoremediation systems exposed to real world pollutants, petroleum vapour, vehicle emissions, and mixed synthetic furnishings of-gassing, as well as how this effect the dynamics of the substrate microbial community within root systems. Continued contributions within this field, especially in relation to studies performed *in-situ* and active green wall technology, will serve to further promote these systems as a priority sustainable building practice for the reduction of indoor air pollution and associated human health impacts.

Conflict of interest

The authors declare that they have no known competing personal or financial interests that could have influence the current research.

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LL drafted the original manuscript, SM, RF, WK, TB, FT and PJ wrote and edited the final manuscript.

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Supplementary

Table 1. Synergistic microbial species and degradation pathways for bioremediation of different pollutants.

Synergistic Microorganisms	Target Pollutant	Degradation pathways	Source from	References
Comamonas testosteroni R5, Methylibium petroleiphilum, Ralstonia pickettii PKO1 , Burkholderia vietnamensis G4	Toluene	Aerobic and anaerobic	Freshwater sediments ，Soil	((Fliegmann & Sandermann, 1997; Kukor & Olsen, 1990; Martínez-Lavanchy et al., 2015; Nakatsu et al., 2006; Teramoto et al., 1999)
Xanthomonadaceae family	petroleum hydrocarbon	Aerobes	Freshwater sediments ，Soil	(Cerqueira et al., 2011; Martínez-Lavanchy et al., 2015; Myeong et al., 2008)
Magnetospirillum sp. strain TS-6	Toluene	Anaerobic	Freshwater sediments ，Soil	(Geelhoed et al., 2009; Martínez-Lavanchy et al., 2015)
Biphenyl dioxygenase(Comamonas testosteroni , Pseudomonas sp., Rhodococcus sp., Burkholderia sp.,) Isopropylbenzene and ethylbenzene Dioxygenases(Rhodococcus erythropolis , Pseudomonas sp.) Naphthalene dioxygenase(Pseudomonas sp., Burkholderia sp., Alcaligenes faecalis, Cycloclasticus sp., Neptunomonas naphthovorans, Rhodococcus sp.,) Toluene/benzene/chlorobenzene Dioxygenase(Pseudomonas putida, Pseudomonas sp.) Toluene monooxygenase(Pseudomonas putida, Pseudomonas sp.) Ring hydroxylating	Aromatic pollutants	Aerobic and anaerobic	Soil	(Baldwin et al., 2003)

monooxygenases(Pseudomonas sp., Ralstonia picketti, Burkholderia cepacian) Phenol hydroxylase(Pseudomonas putida, Comamonas testosteroni , Comamonas sp., Burkholderia cepacian, Ralstonia sp.)				
Family: *Nevskiaceae, Patulibacter-aceae* and *Xanthobacteraceae* the genera: *Devosia, Prosthecomicrobium* and *Hyphomicrobium*	VOCs	Aerobic and anaerobic	Soil of Active green wall	(Fleck et al., 2020; Mikkonen et al., 2018; Russell et al., 2014)

- Table2. Enzyme types involved in bioremediation of different pollutants and potential genetic information.

Pollutants source	**Primary enzymes**	**Primer to detect catabolic genes**	**Microorganisms or plants**	**References**
Toluene	side-chain monooxygenases（pathway 1 in Fig） soluble diiron monooxygenases,（pathways 2, 3, and 4 in Fig） Rieske non-heme iron oxygenases,（pathway 5 in Fig） toluene 4-monooxygenase (pathway 4) extradiol dioxygenases benzoyl-CoA (pathway 6)	xylene monooxygenase (xylM-AET01-F/-R), toluene dioxygenase (TOD-AET18-F/-R), catechol-2,3-dioxygenase (EXDO-AET18-F/-R) , toluene monooxygenase (TMO-AET14-F/-R), phenol hydroxylase (PHE-AET14-F/-R) , catechol-2,3-dioxygenase isolate(EXDO-AET14-F/-R)	The families *Xanthomon-adaceae, Comamonadaceae*, and *Burkholderiaceae*	(Martínez-Lavanchy et al., 2015)

Aromatic pollutants	biphenyl dioxygenase	Naphthalene dioxygenase(NAH-F/-R), Toluene dioxygenase(TOD-F/-R), Xylene monooxygenase(TOL-F/-R), Biphenyl dioxygenase(BPH1-F/-R, BPH2-F/-R,BPH3-F/(3/4)-R Toluene monooxygenase(RMO-F/-R,RDEG-F/-R), Phenol monooxygenase(PHE-F/-R)	Biphenyl dioxygenase(Comamonas testosteroni , Pseudomonas sp., Rhodococcus sp., Burkholderia sp.,)	(Baldwin et al., 2003)
	naphthalene dioxygenase		Isopropylbenzene and ethylbenzene Dioxygenases(Rhodococcus erythropolis , Pseudomonas sp.)	
	toluene dioxygenase		Naphthalene dioxygenase(Pseudomonas sp., Burkholderia sp., Alcaligenes faecalis, Cycloclasticus sp., Neptunomonas naphthovorans, Rhodococcus sp.,)	
	toluene/xylene monooxygenase		Toluene/benzene/chlorobenzene Dioxygenase(Pseudomonas putida, Pseudomonas sp.)	

	phenol monooxygenase		Toluene monooxygenase(Pseudomonas putida, Pseudomonas sp.) Ring hydroxylating monooxygenases(Pseudomonas sp., Ralstonia picketti, Burkholderia cepacian)	
	ring-hydroxylating toluene monooxygenase		Phenol hydroxylase(Pseudomonas putida, Comamonas testosteroni , Comamonas sp., Burkholderia cepacian, Ralstonia sp.)	
Exogenous organic chemicals	Transformation phase(Cytochrome P450 monooxygenases, esterases, reductases, dehalogenases) Conjugation phase(Glycosyltransferases, glutathione-S-transferases, acyltransferases)	Maize Fdh cDNA (J. Fliegmann and H. Sandermann, 1997, Plant Mol Biol 34: 843±854)	The chloroplasts and cytosol of plant cells	(Fliegmann & Sandermann, 1997; Yamane & Tani, 2024)
Formaldehyde	Glutathionedependent formaldehyde dehydrogenase (FDH; EC 1.2.1.1)		Chlorophytum, various common indoor plants, including Ficus benjamina, Schefflera arboricola and Spathiphyllum wallisii	(Mitter et al., 2013)
Pentachlorophenol, PAHs such as pyrene or benzo[a]pyren, trinitrotoluene, various industrial chemicals and	Cytochrome P450 monooxygenases, glutathione-S-transferases, glucosyl-O-transferases and acyltransferases	an amino acid signature motif WAPQXXXXXHXXXXXFVTHCGWNSXXEXXXXGVPMXXXPFFGDQ (single letter amino acid code)	Mainly wheat and soybean cell culture cells	(Ayangbenro & Babalola, 2017; Checcucci et al., 2017; Gupta & Diwan, 2017; Mishra et al., 2017)

many plant protection agents				
Phenols and anilines, DDT or herbicide metabolites	pentachlorophenol conjugating O-glucosyltransferase, soybean isoenzyme, N-glucosyltransferase conjugating the amino group of3,4-dichloroaniline , O-glucosyltransferases	an amino acid signature motif WAPQXXXXXHXXXXXFVTHCGWNSXXEXXXXGVPMXXXPFFGDQ (single letter amino acid code)	Mainly wheat and soybean cell culture cells	(Khare et al., 2018; Lata et al., 2018; Madhaiyan et al., 2007; Wan et al., 2012)
pentachlorophenol, different trichlorophenols, 2,2-(bis)-4-chlorophenyl-acetic acid, 3-chloroaniline, 3,4-dichloroaniline or 4-chlorothiophenol as potential xenobiotic substrates, and indole-3-acetic acid as a potential endogenous substrate	glucosyltransferases, glutathione-S-transferase and cytochrome P450 monoxygenase	• r glucosyl-transferase UGT75D1 from Arabidopsis expressed in yeast	a large subset ofplant species including several algae and mosses	(Flocco et al., 2004; Ghosh et al., 2018; Saleem et al., 2018)
Reactive carbonyls, acrolein, saturated aldehydes and methylglyoxal as well as unsaturated aldehydes	predominant NADPH-dependent acrolein-reducing enzyme, a homolog of Arabidopsis (At1g23740), aldo-keto reductase (At2g37770) and aldehyde reductases (At1g54870 and At3g04000)	cDNA encoding an alkenal/one oxidoreductase (AOR) catalyzing reduction of an α,β-unsaturated bond	Cucumber leaves, *Arabidopsis*	(Yamauchi et al., 2011)
Isoprene	alkenal/ one oxidoreductase (AOR)	AORchl, AORcyt-I, and AORcyt-II genes	Terrestrial plants	(Canaval et al., 2020)
methacrolein (MACR)	NADPH-dependent enzyme,	cDNA encoding an alkenal/one oxidoreductase (AOR) catalyzing reduction	Tomato leaves (Solanum lycopersicum)	(Muramoto et al., 2015)

Lipid-derived reactive carbonyl species (RCS)	chloroplast-localized alkenal/one oxidoreductase (AtAOR)	387-bp fragment of the AtAOR cDNA (59-caccgagcgagaaagcattggaag-39 and 59-gcgtcaaagacaacatcgta-39)	chloroplasts of Arabidopsis (Arabidopsis thaliana) in dark enviroment	(Takagi et al., 2016)

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