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REVIEW ARTICLE

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Plant-Microbes' Interactions and their Roles in Bioremediation: A Case Study of *Phragmites australis* in Acid Mine Condition

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ABSTRACT

The interactions between plants and microbial communities are vital in shaping the dynamism of a particular ecosystem toward ecological sustainability. In an acid mine drainage (AMD) system characterized by the abundance of heavy metals and physicochemical parameters, the survival of plants could be limited. Hence, plants surviving in such environmental conditions tend to develop a particular microsystem that promotes their growth. Plant-microbes interaction is among the systems that most plants develop to enhance their ability to withstand the toxicity of heavy metals and possibly grow. The common reed (CR), *Phragmites australis*, an invasive weed, has been found to withstand the toxicity of heavy metals and survive in AMD environments. In addition, the association between CR and the microbial communities at the rhizosphere level plays a crucial role in the growth of CR by reducing the toxicity of the heavy metals. These interactions culminate in the release of diverse metabolites by the plant and microbial communities controlled by specific genes. This review collated information on the different microbial communities associated with CR and the metabolites released to promote the growth of CR and enhance their remediation potential. Although the interactions were under the influence of secreted metabolites, a gap still existed in elucidating the specific metabolites secreted either by the microbes or the CR. Further study is recommended that could cut across interdisciplinary approaches, including molecular docking, to enhance the elucidation of diverse metabolites from the microbes and CR.

Keywords: Common reed; *Phragmites australis*; Metabolites; Acid mine drainage; Bioremediation

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INTRODUCTION

Phragmites australis, also known as common reed (CR) is a plant that thrives in wetland ecosystems globally. As a tall, productive macrophyte, it exhibits significant genetic diversity, functional traits, and haplotypes within its own species (Bickford et al., 2023; Xu et al., 2023). The CR, capable of remediating polluted sites such as mine dumps (Kalu et al., 2021), is confronted with challenges like Reed Die-Back Syndrome (RDBS) in specific regions, which has the potential to affect its growth form and cause premature aging (Haldan et al., 2023). However, the interaction between the reed and the associated microbial communities plays crucial in the reed's health status. The root zone of the CR plant contains a high concentration of dissolved oxygen and organic carbon, which provides an optimal environment for the growth and proliferation of microorganisms and promote plant-microbes' interaction (Toyama et al., 2011).

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In general, the interaction between plants and diverse microbial communities both at the rhizosphere level or endophytic level could be positive as well as negative. The negative relationship tends to enhance development of diverse survival mechanisms with the host plant as well as the microbes involved (Fatima & Senthil-Kumar, 2015). The positive interaction between the microbes and the host plants plays crucial role in the health status of the plant and promote their development in diverse harsh environment condition such as acid mine drainage (AMD) culminating in their potential to remediate the environment. The CR is an exceptionally efficient aquatic plant in terms of nutrient and heavy metal accumulation, surpassing other plants of its kind. Additionally, it displays remarkable stress resistance and metal accumulation mechanisms, allowing it to thrive in acid mine drainage (AMD) environments (Ding et al., 2021). Studies suggest that the leaf sheaths of CR possess superior metal storage capacity, and various plant organs exhibit distinct functions in stress resistance (Guo & Cutright 2014). Furthermore, citric acid has been demonstrated to enhance metal uptake in CR, thereby increasing metal accumulation in plant tissues and improving phytoremediation efficiency (Shaw et al., 2022).

The microbes interacting with CR enhanced their ability to survive in diverse harsh conditions, including AMD, as well as promoting their ability to remediate the environment (Cangioli et al., 2022). The interaction between the microbes and CR is controlled by diverse metabolic pathways under the influence of diverse metabolites and the associated genes. Phytohormones, siderophores, and chelating agents are among the chemical substances secreted by bacteria and fungi in association with host plants that aid in the plants' bioremediation capabilities (Kaundal et al., 2023). With the aid of these chemicals, the microbes mobilize pollutants through the co-interaction of the exudates and enzymes from the plant in the rhizosphere and support the bioremediation processes (García-Sánchez et al., 2018). In light of this, the objective of this present review is to unveil plant microbes interactions involved in the bioremediation of contaminated environment with CR as a case study in the bioremediation of AMD. An overview of plant-microbes' interaction was provided, encompassing different types of interactions that occur between plants and microbial communities, molecular and biochemical mechanisms underlying plant-microbes' interactions, roles of key molecules in shaping plant-microbes' interactions, positive impacts of plant-microbe interactions to plants, and plant-microbe interactions in environmental remediation. In addition, information on CR-microbe interaction was collated to provide insights into microbes that associates with the CR, genes that could promote the CR and microbes' interaction to enhance their bioremediation potentials, and the role of the CR-microbes' interaction that promotes the remediation of AMD.

Overview of Plant-Microbe Interactions

Different Types of Plant-microbe Interactions

Plants are autotrophs which represent the most important organism in the ecosystem. Improvement in plant health is pivotal to the effective functioning of the ecosystem since they are the primary producers. Consequently, the diversity of interactions occurring between plants and microbes is therefore a key element in determining plant health and maintaining plant holobiont homeostasis (Hassani et al., 2018). These various types of interactions can be classified based on the specific nature existing between plants and microbes. One of the commonest symbiotic interactions between two species in nature is mutualism. This is a highly complex and dynamic ecological interaction between two species, resulting in a net benefit for both organisms. Several mutualistic interactions between plants and microbes have been reported (Kim et al., 2019; Li et al., 2021). One of such well-documented mutualistic interactions is the tripartite symbiotic relationship between leguminous plants, nitrogen-fixing bacteria, and arbuscular mycorrhizal fungi (Primieri et al., 2021). This symbiotic association results in the formation of nodules on plant roots, a passage by which rhizobia (nitrogen-fixing bacteria) converts atmospheric nitrogen into usable ammonia for plant use, while the plant in turn provides carbohydrates from photosynthesis utilizable by the bacteria (Jones et al., 2007). Effective uptake of plant nutrients such as nitrogen, phosphorus, potassium, calcium, and water are also enhanced by the arbuscular mycorrhizal fungi in exchange for plant-derived carbon compounds (Khaliq et al., 2022). Fungi and bacteria endophytes living in plant tissues are also examples of mutualistic interactions. While endophytic fungi have been reported to improve the production of secondary metabolites in their host plants, resulting in the enhancement of the plant's resistance against pathogenic microbes (Fadiji & Babalola, 2020; Omomowo et al., 2023), molecular studies on endophytic bacteria have reportedly contributed to improved plant growth and tolerance to environmental stress conditions (Shah et al., 2022; Kaur and Karnwal, 2023).

Unlike mutualism, the parasitic plant-microbe interaction is a one-sided relationship that provides exclusive trophic benefits to the microbe at the detriment of the plant host or vice-versa. This relationship represents a complex interplay between organisms at the confluence of plant physiology, microbial ecology, and the dynamics at play in the prevailing ecosystem. Several pathogenic microorganisms such as oomycetes, fungi, nematodes, viruses, viroids, bacteria, and parasitic plants cause plant diseases by colonizing the host metabolic machinery (Fatima & Senthil-Kumar, 2015), disrupting their cellular functions and fleecing their resources (Toruño et al., 2016) ultimately results in conditions such as wilting, stunted growth and necrosis. There are also reports of parasitic plants also plundering resources from their microbial partners (Rasmussen & Rasmussen, 2009).

In the study of plant-pathogen interactions, a relatively rare type of relationship occurs called commensalism. The symbiont, which is the typical beneficiary in the relationship, trophically interacts with the host organism without providing any apparent benefit or inflicting any potential harm on the later. The rarity of this interaction is a result of few incidences in nature where an organism is truly unaffected by the dependency of another in a symbiotic relationship (Mathis & Bronstein, 2020). Roper et al. (2019) reported the commensal relationship that the bacterium *Xylella fastidiosa* has with its diverse hosts. Studies conducted on the interaction of various *Colletotrichum* species on different hosts showed a commensal lifestyle demonstrated by the fungi (Redman et al., 2001).

Molecular and Biochemical Mechanisms Underlying Plant-microbes' Interactions

Plants and microbes are involved in constant, intricate and complex evolutionary adaptations, which results in an interplay of various biochemical and molecular mechanisms. This interaction, which may be broadly pathogenic or mutualistic, begins with the exchange of a series of signal transmission molecules within the plant's apoplast, a compartment where the compatibility of this interaction is first determined (Du et al., 2016). Signal transduction pathways are series of complex networks that are ubiquitous throughout plant cells, enabling them to respond effectively to external stimuli. The bidirectional interactions between plants and microorganisms both at molecular and biochemical level involving diverse signal transduction pathways begin mostly at the three main points of entry which include, the stomata (Toruño et al., 2016), roots (dos Santos et al., 2018) and wounds on the plant epidermis (Pfeilmeier et al., 2016). The release of chemical signals in form of biochemical molecules from both partners facilitates recognition mechanisms and ultimately modulates interaction between them. These molecules, referred to as microbial effectors include avirulence proteins (Avr), which are produced by both fungi and bacteria creates a microenvironment that promote the microbial interaction with the host plants to ensure their survival (Laugé & De Wit, 1998). In the parasitic interaction between plants and microbes, a notable effector protein called type III secretion system (T3SS) effectors is often secreted by bacteria into the host cells to infect and colonise the plant (Ramos-Morales, 2012). An immune response is induced by the invasion, resulting in hypersensitive cell death (Jonathan & Dangl, 2006). T3SS exhibit divers role such as the suppression of the host defence mechanism (Coburn et al., 2007), promotion of nutrient uptake from the plant (Stringlis et al., 2019) and manipulation of plant development (Macho, 2016). Another effector is the chitins and chitin-related compounds which are important component of the fungal cell wall. The uniqueness of these compounds makes the recognition of conserved microbe-associated molecular patterns (MAMPs) in response to fungi invasion easy, which induces MAMP triggered immunity in plants (Pusztahelyi, 2018). Symbiotic interactions, such as those with nitrogen-fixing bacteria (rhizobia) and mycorrhizal fungi, require specialized signalling molecules. Examples of such molecules are Nodulation factors (Nod factors), which are chitooligosaccharides produced by nitrogen-fixing bacteria as a chemical signal in response to plants' metabolites such as flavonoids (Diarra Mbengue et al., 2020). The Nod-factors stimulate morphological changes in their host plant, creating root nodules for effective bacteria colonization (Jones et al., 2007). In hormonal cross-talks between plants and microbes, plants' secondary metabolites, such as salicylic acid, jasmonic acid, and ethylene, are crucial in regulating defense responses (Yang et al., 2019). Salicylic acid is commonly associated with defence against biotrophic pathogens (Ullah et al., 2023), whereas jasmonic acids and ethylene are related with defence against necrotrophic pathogens and herbivorous insects (Macioszek et al., 2023).

Roles of Key Molecules in Shaping Plant-microbes' Interactions

Plants produce a variety of compounds collectively known as secondary metabolites (SM) to protect themselves against pathogens, predators such as herbivores, and stressful environmental conditions. The broad categories of secondary metabolites include alkaloids, phenolic compounds, terpenoids, and sulphur-containing compounds (Adolfo & Elena, 2009). Plant-microbe interactions are shaped by these metabolites and small molecules called microbial effectors, released by pathogens in parasitic association with plants. Effectors, which are small, secreted molecules that alter host cell structure and function, facilitate infection or trigger defence responses from the plant host (Keen et al., 2000). The dynamic interplay between plants' secondary metabolites and microbial effectors is a key determinant of plant health and susceptibility to diseases. There are two broad categories of plant defences with regards to microbial attack: the preformed is the structural component of the plant cells such as cell walls and waxy cuticles, and inducible defence. Preformed defence represent the first line of defence action against plant pathogens, denying them access into the cell. SM such as phytoanticipins are also examples of preformed antimicrobial compounds that are synthesized in healthy plants before pathogenic attack or invasion (Soledade et al., 2015). Inducible defences are responses triggered by a previous interaction with a pathogen which ultimately provides some level of resistance to subsequent attacks (Riessen & Trevett-Smith, 2009). Examples of such defences include Pathogen-associated Molecular Patterns (PAMPs). When microbe-derived PAMPs are identified by plant pattern recognition receptors (PRRs), a variety of defensive reactions are triggered, including the formation of reactive oxygen species (Lee et al., 2020), antimicrobial proteins (Bhandari et al., 2023), and cell wall strengthening (Bacete et al., 2018; Wan et al., 2021). Another example of inducible defences is Effector-Triggered Immunity. This is the identification of specific microbial effectors by plant resistance proteins that elicit defence strategies (Bacete et al., 2018), which frequently results in a localized response known as the hypersensitive response (Depotter & Doehlemann, 2020). This can lead to programmed cell death to mitigate further pathogenic attack (Balint-Kurti, 2019).

Pathogenic microbes, such as bacteria, fungi, and viruses, use a wide range of effector chemicals to disrupt host plant metabolic activities and spread infection. Host plant cells receive effectors via specific secretion systems such as type III secretion system found in bacteria (Coburn et al., 2007; Mak & Thurston, 2021). Once translocated within the plant cells, they can control cellular processes by interfering with plant signaling, suppressing immune responses, and facilitating pathogen colonization (Lucke et al., 2020; Wu & Derevnina, 2023). A well-reported mechanism of microbial effectors is the prevention of PTI by targeting PRRs or signaling components which results in diminishing the host plant's defense and increasing microbial virulence (Thomma et al., 2011; Zhang & Zhou, 2010). Some effectors, for example, degrade or block PRRs, whilst others disrupt signalling pathways, resulting in immune responses being suppressed (Harris et al., 2023; Kazan & Lyons, 2014; Zhang & Zhou, 2010).

Positive Impacts of Plant-microbe Interactions to Plants

Interactions between microbes and plants, which primarily occur in the rhizosphere, on plant surfaces and inside plant tissues are essential for improving plant health and yield. These interactions have profound positive impact on plants, providing them with great benefits such as better nutrient uptake (Jacoby et al., 2017; Das et al., 2022; Singh et al., 2022), stronger disease resistance (Amoo et al., 2023; Schirawski & Perlin, 2018; Wille et al., 2019), and better stress tolerance (Kumar & Verma, 2018; Etesami, 2020; Inbaraj, 2021). Two of the well-known and widely studied plant-microbe interactions are the symbiotic relationship between mycorrhizal fungi (MF) and nitrogen-fixing bacteria (NFB). Throughout their life cycles, MF are almost exclusively associated with the roots of terrestrial plants, forming a symbiotic relationship that is mutually beneficial with them. The fungi invade two types of environments, notably the roots of host plants and the surrounding soil (Read et al., 2000), where they fetch mineral resources via the mycelium for the plants and increase the surface area for water uptake and promote nutrient absorption (Selosse & Roy, 2009). MF are recompensed by receiving plant photosynthates in form of sucrose or hexose through their mycorrhizal intraradical structures, and subsequently transported as glycogen or triacylglycerol via the extensive extraradical hyphae network (Bago et al., 2002, 2003; Parniske, 2008). Since green plants are incapable of extracting nitrogen from the soil for their photosynthetic needs, they form symbiotic relationships with NFB. These can fix inert, atmospheric nitrogen anaerobically by combining it with elements such as oxygen or hydrogen using the enzyme nitrogenase, resulting in nitrogen conversion to NH_3 bioavailable to plants. The pathway for this conversion is represented by the following equation (Mahmud et al., 2020):

$$N_2 + 8H^+ + 8e^- + 16\text{Mg-ATP} \rightarrow 2NH_3 + H_2 + 16\text{Mg-ADP} + 16\ P$$

In nitrogen-deficient soils, this biological, microbe-assisted nitrogen fixation process is essential for plant growth, lowering the demand for chemical fertilizers and advancing sustainable agriculture.

Phosphorus is an important plant nutrient that is found in soil and is necessary for plant growth and health. As a component of plant cells, it is vital for the growth of the plant's growing tip and cell division (Kavanová et al., 2006). However, plants cannot utilize organic phosphorus from the soil, it is rather taken up in the form of inorganic phosphate and reconverted to organic forms such as adenosine triphosphate (ATP) and adenosine diphosphate (ADP) (Khan et al., 2023). Phosphate-solubilizing bacteria (PSB) help convert insoluble, organic phosphates into soluble, inorganic forms that plants may absorb (Leyval & Berthelin, 1989).

Microbes also play a significant role in increasing plant disease resistance through different mechanisms. In a plant-pathogen-assisted mechanism, rhizomicrobes interact directly with plant pathogens, secreting chemical compounds that limit their growth and/or render them avirulent, thus safeguarding the host plant (Dey et al., 2014; Martínez-Hidalgo et al., 2015). Many studies have reported that various microorganisms have demonstrated the ability to induce systemic resistance by triggering plants' immune system. Bacteria such as *Bacillus* spp. and *Pseudomonas* spp., and certain fungi species can assist plants in their defence responses by acquiring broad-spectrum disease resistance (Zeilinger et al., 2016). Specific examples include the treatment of beans root with *Trichoderma harzianum* T39, which induced a systemic resistance against *Botrytis cinerea* (De Meyer et al., 1998), and the induction of local and systemic resistance against *Phytophthora parasitica* by arbuscular mycorrhizal fungi in tomato roots (Cordier et al., 1998).

Several studies have shown that microbes, through various mechanisms, assist in mitigating the effect of abiotic stress on plant. Caused by drought and salinity. Endophytes such as *Streptomyces albidoflavus* OsiLf-2, an osmolyte producing bacteria have been reported to induce drought and salt tolerance via a multi-level mechanism that included improvement of the photosynthetic system of its rice host under stress (Niu et al., 2022). Furthermore, plants can also withstand abiotic stress via phytohormones produced by endophytic bacteria such as abscisic acid, cytokinins, gibberellic acid, indole acetic acid, jasmonic acid, salicylic acid, as well as the enzyme 1-aminocyclopropane-1-carboxylate deaminase that reduces ethylene (Singh et al., 2023; Ameen et al., 2024). These microorganisms can also help improve soil structure, composition, and fertility by increasing water penetration, thereby giving plants better access to water and nutrients. They can also excrete exudates and byproducts by enhancing soil aggregation, resulting in better water infiltration and reduced erosion, and contribute to the production of organic material available to the plant (Coban et al., 2022; Iqbal et al., 2023).

Plant-microbe Interactions in Environmental Remediation

Anthropogenic activities have heightened since the dawn of industrial revolution, undoubtedly leading to increased production of wastes and pollution. The primary sources of environmental contaminants include industrial and commercial facilities, as well as domestic sewage systems. Some of the more commonly encountered contaminates from these sources are heavy metals such as arsenic, cadmium, chromium copper, lead, manganese, mercury, molybdenum and zinc (He et al., 2005; Tchounwou et al., 2012). Organic pollutants, including aldrin, chlordane, dichlorodiphenyltrichloroethane, dieldrin, heptachlor, mirex, polycyclic aromatic hydrocarbons, polychrlorinated biphenyls toxaphene, are threats to human health and are hazardous to the environment (Harner et al., 2006). Pesticides and herbicides used as chemical weed control in agricultural practices are also important environmental contaminants (Aktar et al., 2009; Pathak et al., 2022). These contaminants find their way into the food chain and pose a severe threat to human health (Shetty et al., 2023). It is therefore imperative to implement environmental remediation for the protection of human health and to safeguard the environment.

Many studies have highlighted the crucial role of plant-microbe interactions in the remediation of terrestrial and aquatic environmental contamination. These interactions promote eco-friendly environmental sustainability through degradation and detoxification of toxic compounds, and immobilization of contaminants usually called rhizoremediation. Soil pollutants are biodegraded into less toxic contaminants by the activities of plant root microorganisms. Plants provide nutrients in form of root exudates such as amino acids, sugars and organic acids, a carbon and energy source for microorganisms to thrive (Eze & Amuji, 2024). The exudates attract plant-growth promoting microorganisms (PGPMs) such as plant-growth promoting rhizobacteria (PGPB) and arbuscular mycorrhizal fungi (Rizaludin et al., 2021; Rolli et al., 2021). Microbes with biodegrading enzymes in turn degrade the contaminants which exist in various forms such as hydrocarbons, polyaromatic compounds, herbicides, and pesticides, using them as energy source or transforming them into less toxic compounds (Laura et al., 2013; Yadav et al., 2021). Examples of microbes reported to have rhizoremediation potentials include genera of the bacteria *Bacillus* spp., *Enterobacter* spp., *Flavobacterium* spp., *Pseudomonas* spp., *Stenotrophomonas* spp. (Aryal & Liakopoulou-Kyriakides, 2013; Sivaram et al., 2019) and fungal genera *Aspergillus* spp. (Venkatesh et al., 2021), *Cladosporium* spp. (Bonhomme et al., 2003), and *Penicillium* spp. (Volke-Seplveda et al., 2002). Heavy metals (HMs) regarded as one of the most important pollutants in the soil environment (Ahmad et al., 2015) often binds tightly to soil particles, resulting in oxidative stress and causing damage to plants' cellular structure (Dube et al., 2001; Nyiramigisha, 2021). The symbiotic interaction of plants and microbes ensures the loosening of soil particles from HMs attachment for further phytoremediation by plants (Khanna et al., 2023). PGBP alleviate the toxicity of HMs by transforming them into bioavailable forms through various mechanistic processes such as methylation of the metals (Ma et al., 2016), production of biosurfactants for their degradation (Mishra et al., 2021; da Silva et al., 2023) and altering the soil pH leading to metal precipitation for effective phytoremediation (Jamil & Clarke, 2013; Shah & Daverey, 2020).

Molecular Insights into Plant–microbes' Interactions for Sustainable Remediation of Contaminated Environment

"Omics" technologies and studies such as meta-genomics, meta-transcriptomics, metabolomics, and meta-proteomics have enhanced the understanding of the plant-microbes' interactions as well as the enzymatic interactions between the plants and the associated microbial communities that could promote the remediation of contaminated environment and the sustainability of the bioremediation techniques (Chettri et al., 2021; Kochhar et al., 2022; Rane et al., 2022). Meta-genomic studies that cut across amplicon gene sequencing and Next-generation sequencing that include 454 pyrosequencing and MiSeq platforms promoted the knowledge of the microbial communities associated with plants growing in the contaminated environment (Rane et al., 2022). For example, Zhan et al. (2021) unveil the presence of Phyllospheric fungal and bacterial community and their association with *Schoenoplectus tabernaemontani* that promotes their plant's growth. Through meta-transcriptomics, microbial community functions and the associated genes that enhanced the interactions between plants and the microbes in the bioremediation of contaminated environment has been unveiled (Dubey et al., 2020). For example, an upregulation of genes responsible of black spot's defence in rose plant leaves and downregulation of genes responsible for photosynthesis and cell wall modification for powdery mildew was obsevered (Neu et al., 2019).

According to Huang et al. (2019), through metabolomic studies, alcohol dehydrogenase activity and pathways were observed in the interaction between *Agromyces* sp. Strain A475-1 and small mustard plant *Arabidopsis thaliana*. This alcohol dehydrogenase activity promoted the release of diverse metabolites that help to modulate the root microbiota of *A. thaliana* and ensure the plant's growth and proliferation of the microbial communities. Meta-proteomics studies reveal the proteins responsible for the interaction between plants and microbial communities in a contaminated environment as well as promote the bioremediation of the environment. A detailed information on the molecular insights into plant-microbes' interaction for sustainable remediation of contaminated environment is provided in the review study done by Rane et al. (2022).

Plant–microbe Interactions for Bioremediation of Pesticides

FAO (2020) termed any substance (chemical mixture or biologically made ingredients) with the potentials to cause the destruction or control as well as repel any pest (insects, weeds, pathogenic fungi, rats, etc,) including regulation of plant growth as pesticide. Despite the usefulness of the pesticides, their residues become the major pollutant in agricultural areas and the spread of the contamination in soil and to groundwater is facilitated by rain, rivers, and hydric basins (Gill and Garg 2014; Wilkinson et al. 2017). Due to the toxic nature of the residues of pesticides, it becomes pertinent to develop sustainable remediation techniques. Phytoremediation and microbial remediation approaches have been reported to be a promising tool for the removal of the residual pesticides that are toxic to both plants, animals, and soil microbial ecosystems (dos Anjos dos Santos et al., 2021).

The interaction between plants and microbial communities in pesticides contaminated environment has been reported to promote better remediation of the environment. For example, Zhang et al. (2014) and Asemoloye et al. (2017) reported that bacteria and fungi interaction at the root levels of plant play pivotal role in the bioremediation of organic pesticides in agricultural area. The review study done by dos Anjos dos Santos et al. (2021) provided in-depth insight into plant-microbes' interactions and their role in the remediation of pesticides.

Phragmites Australis-Microbe Interaction

Overview of *Phragmites australis*

Phragmites australis, commonly known as common reed, is a cosmopolitan grass species found in wetland ecosystems globally. The ubiquitous wetland plant is one of the world's most invasive plants (Uddin & Robinson, 2017). It has both negative and positive effects. Negatively, non-native subspecies threaten wetland biodiversity in North America (Bickford et al., 2023), while in freshwater systems, they disrupt ecosystems, displace species, and affect fish conditions (Zhang et al., 2023). Robichaud & Rooney (2017) found that the invasion of CR in a Lake Erie coastal marsh had long-term effects on birds, threatening their ecological integrity. The dense growth of these plants alters their habitats and disrupts their ecological connectivity, restricting the movement of wildlife (Leonard et al., 2021). Additionally, CR can modify hydrological equilibrium, increase the likelihood of flooding, and obstruct water flow. Furthermore, dense stands of CR can limit access to water bodies and reduce recreational opportunities such as fishing, boating, and bird watching in coastal areas, negatively impacting tourism, property values, and infrastructure (Tripathi et al., 2022). The spread of invasive CR can also alter the aesthetics and functionality of affected regions (Hazelton, 2018; Krzton-Presson et al., 2018). On the positive side, CR can enhance nitrogen storage in salt marshes, benefiting soil organic N storage and microbial processes (Jacobs, 2022). Additionally, the plant response to climate change factors, such as salinity, temperature, and CO_2 levels, is crucial for understanding its behaviour and implementing sustainable management strategies (Pardis, 2022). The environmental benefits of CR have been substantial, demonstrating the capacity to reduce environmental pollution in its surroundings (Srivastava et al., 2014). Researchers have extensively studied CR, particularly their role in mitigating environmental contamination (Milke et al., 2020; Chitimus et al., 2023). CR's ability to thrive under extreme environmental conditions, such as high temperature and elevated CO_2 levels, is attributed to several factors, including changes in carbon trapping mechanisms (from C_3 to C_4 and vice versa), microbial associations, and biochemical adaptations. CR is a particularly preferred plant system for wastewater treatment in ecological engineering, owing to its unique characteristics (Srivastava et al., 2014; Wu et al., 2023).

Microbes Associated with *Phragmites australis*

Microbes play a significant role in the growth of plants including CR (Ding et al., 2023). Several studies have indicated that many microbes associated with CR behave as saprophytes (Zhao et al., 2017; Shearin et al., 2018; Ding et al., 2023), with only a small percentage being strong pathogens (Schroeder et al., 2020), whereas the majority are non-pathogenic (DeVries et al., 2020). These microbes interact with plants in various ways, such as enhancing organic nitrogen uptake by degrading proteins into a form that is easily absorbed by CR roots, promoting growth, and activating root-produced enzymes that aid in nutrient absorption (Kumar et al., 2023). Endophytic bacteria residing inside the plant, such as certain *Bacillus* species, can promote growth and defensive mechanisms in CR, potentially contributing to its aggressive nature and rapid growth in dense stands, outcompeting other plant species (Kumar et al., 2023). Additionally, the microbial communities surrounding CR can stimulate their growth in polluted environments, showcasing the beneficial role of these microbes in supporting the development of the plant (DeVries et al., 2020). Overall, the diverse array of microbes associated with CR influences its growth by aiding nutrient uptake, promoting growth, and potentially contributing to its invasive nature. The review done by Kalu et al. (2021) provided a comprehensive role of the rhizospheres' microbes associated with CR in diverse environment including acid mine drainage.

The microbes associated with CR include *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, *Fusobacteria*, *Actinobacteria*, and *Planctomycetes* (Kalu et al., 2021). The microbial communities surrounding CR can be utilized in land reclamation as they can stimulate the growth of reeds in polluted environments (Kalu et al., 2021). The rhizosphere microbiome of CR has been studied in various locations globally, with most reports coming from Europe and North America (DeVries et al., 2020). The microbial spectra associated with the rhizosphere of CR vary depending on environmental stress and the reed-microbes interaction (Kalu et al., 2021). Differences in rhizosphere microbial communities between native and non-native CR may depend on stand density (Bickford et al., 2020). The invasiveness of non-native CR does not result from the differential cultivation of beneficial or antagonistic rhizosphere microorganisms, but rather from altering the composition and function of root-associated microbial communities in the soil (Bickford et al., 2020). The soil microbiome may change because of ongoing invasion, potentially being important in the later stages of invasion or expansion (Bickford et al., 2020).

Genes Associated with the *Phragmites* and Microbe

The relationship between CR and microbes is complex, with known mutualistic and pathogenic symbionts associated with CR, although the specific roles of many of these microbes remain to be evaluated. The microbiome associated with CR plays a crucial role in its success, and a deeper understanding of these relationships and the associated genes could lead to new insights into invasive species control strategies (Wang et al., 2021; Bickford et al., 2022). The genes associated with CR and microbes include unique and essential genes that could be targeted in genetic control approaches using RNAi (Oh et al., 2022). CR interacts with various microbes in its environment, and these interactions can have significant ecological implications. These interactions could be linked to the presence or absence of the following genes:

Plant Defence Genes

CR, a plant species with high adaptation capacity, may express genes involved in defence responses against microbial pathogens. These defence-related genes include receptor-like protein/kinases, such as cysteine-rich receptor-like protein kinases and lectin receptor-like kinases (Ho et al., 2023). Additionally, genes associated with biotic stress and defence responses are expressed at higher levels in invasive genotypes of CR, indicating a basal defence mechanism (Wang et al., 2021). These findings highlight the plant's ability to combat microbial threats through a variety of defence-related gene expressions. In addition, the down-regulation of these genes could signal a positive as well as compatible common reeds-microbe interaction.

Microbial Recognition Genes

Microbes interacting with CR may possess genes involved in recognizing plant surfaces, such as those encoding for adhesion proteins or receptors that recognize plant-derived signals. CR may express genes involved in recognition against microbes such as *Pseudomonas*. These genes could include those encoding for ethylene response factors like ATERF-1, which have been identified as potential pathogen-binding proteins in plants (Rioja et al., 2013). Additionally, genes related to peptidoglycan recognition proteins (PGRPs) could play a role in microbial recognition and enhance the interaction between the CR and the microbes (Zhang et al., 2020). Understanding the molecular mechanisms underlying salt tolerance in CR can shed light on the genes involved in microbial recognition in these plants (Sun et al., 2014).

Plant-microbe Degradation Genes

Some microbes associated with CR may possess genes encoding for enzymes as well as protein that promote their compatibility with the common reeds which will enhance nutrient sharing and substrate breakdown in any contaminated environment. Studies have shown that CR can up-regulate genes related to oxidoreductase activity and glutathione metabolism when exposed to stress (Zhang et al., 2020). Additionally, indigenous oil-degrading bacteria effectively respond to oil contamination in CR marsh soil, with specific genes like alkane monooxygenase and PAH-ring hydroxylating dioxygenase alpha subunit playing crucial roles in biodegradation (Wang et al., 2019). Furthermore, CR roots have been found to enhance reductive dehalogenation of contaminants like 1,2,3,4-tetrachlorobenzene, with important bacterial populations like Desulfitobacterium sp. and Dehalococcoides sp. strain CBDB1 contributing to effective degradation (Alvarez, 2006). This implied that there could be gene-engineered environment created by the co-released gene/proteins/enzymes from both the common reeds and the associated microbial community. Although these findings underscore the potential of CR to degrade contaminants through microbial association, more studies could unveil more genes interaction between the reeds and the microbes in remediation of environment.

Plant-microbe Signalling Genes

Both CR and associated microbes likely possess genes involved in intercellular communication and signalling. These genes regulate the establishment and maintenance of both symbiotic and pathogenic interactions. CR is a versatile plant species that expresses genes involved in signalling pathways against microbial pathogens. These genes play crucial roles in defence mechanisms. Studies have suggested that CR utilizes root exudates for allelopathy, releasing chemicals that suppress neighbouring plants (Wang et al., 2021). Moreover, the response of plants to environmental stress involves the upregulation of signalling genes that could promote plant-microbe interaction and enhance the survival of the plant through diverse mechanism which include sequestration of the contaminants (Rudrappa & Bais, 2008; Yu et al., 2022). Furthermore, the adaptation of plants to high-salinity habitats involves the upregulation of signalling genes that promotes the coding of oxidoreductase activity and glutathione metabolism, enhancing their ability to scavenge reactive oxygen species and resist salt stress (Zhang et al., 2020). Overall, CR demonstrated a sophisticated molecular response to microbial challenges, highlighting its potential for ecological restoration in degraded wetlands through interactions that favours compatible microbial community.

The Role of the *Phragmites* and Microbes’ Interaction in the Remediation of AMD

The interaction between CR and microbes plays a significant role in the remediation of AMD. This interaction has been elaborated in several ways. CR are known for their ability to thrive in harsh environmental conditions, including those contaminated with heavy metals and acidic conditions typical of AMD (Milke et al., 2020). Through a process called phytoremediation, these plants can absorb metals and other contaminants from the soil and water through their roots. This helps reduce the concentration of pollutants in the environment (Kalu et al., 2021). CR, a common plant used in phytoremediation, interacts with microbes to effectively remediate pollutants. Microorganisms in the rhizosphere of CR play a crucial role in facilitating the removal of contaminants (Bali et al., 2022; Bhatt et al., 2023). Microbes, such as bacteria and fungi, aid in growth promotion, stress alleviation, and degradation of pollutants, enabling plants to thrive in contaminated environments (Augusta et al., 2022; Rabani et al., 2022). Through various mechanisms, such as phytohormone production and chelation, these microbes mobilize pollutants in the rhizosphere, which are then absorbed by plants (Rabani et al., 2022). Additionally, plants release exudates and enzymes that stimulate microbial activities in the soil, further supporting the bioremediation process. This synergistic CR-microbe interaction demonstrates the potential of phytoremediation as a sustainable and eco-friendly approach for environmental cleanup.

Microbes, particularly certain bacterial and fungal strains, play a crucial role in AMD treatment. These microbes can catalyze reactions that transform toxic metals into less harmful forms or immobilize them, making them less available for uptake by plants or other organisms. The interaction between CR and microbial activity is intricate and depends on the specific plant lineage and soil conditions. Research indicates that various lineages of CR, both native and non-native, can have varying impacts on soil microbial communities (Bickford et al., 2022; Wang et al., 2023). While the introduced lineage of CR in North America tends to attract more orchid mycorrhizal fungi, the native lineage gathers more plant pathogenic and ectomycorrhizal fungi (Kim et al., 2018). Additionally, the microbial enzyme activities and functional gene abundances in terrestrial and aquatic environment associated with different CR lineages vary, affecting the carbon storage potential and methane emissions (Shrestha et al., 2021). Furthermore, the presence of CR in aquatic environments can improve the elimination of bisphenols through their association with microorganisms (Zhao et al., 2020). These findings explain the complex relationships between CR and soil microbial communities, which influence ecosystem dynamics and biogeochemical processes.

The rhizosphere, which is the zone of soil around plant roots, is a hotspot for microbial activity. CR roots release organic compounds, such as root exudates, which serve as food sources for various microorganisms. This creates a microenvironment conducive to microbial growth and activity, thereby enhancing their ability to remediate AMD contaminants. Rhizosphere interaction between CR and microbes plays a crucial role in nutrient cycling, plant growth, and environmental remediation (Li et al., 2022; Wang et al., 2023; Zhang, 2023). Studies have shown that the addition of different substrates to soil can enhance nitrogen removal in winter, affecting root metabolites and microbial community composition (Zhou et al., 2022). Furthermore, the symbiotic relationship between CR and microbes, such as arbuscular mycorrhizal fungi (AMF), significantly affects plant growth by facilitating nutrient uptake and promoting root development (Li et al., 2022). Specific bacteria, such as *Devosia,* associated with AMF hyphae play a vital role in enhancing nitrogen uptake and promoting plant growth. The active bacterial community in the rhizosphere of CR responds to environmental variations, showing changes in diversity and composition based on seasonal and flooding conditions (Zhou et al., 2022). These interactions highlight the importance of rhizospheric crosstalk in the regulation of plant health, nutrient cycling, and environmental sustainability.

Symbiotic interactions between CR and microbes play a crucial role in the invasive behaviour of this species (Schroeder et al., 2020; Kumar et al., 2021). CR cultivate root and soil fungal communities with higher richness, diversity, and pathogen abundance than those of native species, indicating a unique symbiotic relationship (DeVries et al., 2020). The plant-microbe association is essential for the remediation of environmental pollutants, such as petroleum hydrocarbons, where microbes effectively degrade these contaminants and aid in soil and environmental reclamation (Ratna et al., 2021). Additionally, the rhizosphere serves as a hub for microbial activities, where plants release metabolites that shape microbial communities and biofilm-forming rhizobacteria thereby establishing symbiotic relationships with host plants, benefiting from each other through nutrient exchange and enhancing plant immunity (Tariq & Ahmed, 2023). This symbiotic association is crucial for plant growth and environmental cleanup.

Microbes often form biofilms on the surface of CR root. These biofilms act as barriers that trap and immobilize contaminants, preventing their migration and uptake by plants and other organisms. The interaction between CR and microbes during biofilm formation is critical for phytodepuration processes. The roots of CR and *Typha latifolia* host a diverse microbiota that forms biofilms on the rhizoplane, aiding pollutant removal (Jishma & Radhakrishnan, 2023). These biofilm-forming microbes play a significant role in phytodepuration by enhancing the breakdown of pollutants and supporting plant health (Degiambattista, 2022). The microbiota associated with CR and *Typha* spp. roots tends to converge towards a common taxonomic composition dominated by *Actinobacteria*, *Firmicutes*, *Proteobacteria*, and *Planctomycetes*, indicating a selective process at the root-soil interface (Tariq & Ahmed, 2023). The enrichment of biofilm-forming bacteria on the rhizoplane suggests specific metabolic capabilities that contribute to the phytodepuration process, highlighting the importance of plant-microbiota interactions in environmental clean-up strategies (Pietrangelo et al., 2018). An overview of the bioremediation processes and potentials of CR is provided in Fig. 1.

Future Perspective

Globally, industrialization has led to the production and release of toxic pollutants including acid mine water into the environment leading to the deterioration of the environment. Protection of the environment from the damage caused by the acid mine water is a great challenge despite the adoption of diverse physicochemical methods such as ion exchange, precipitation, reverse osmosis, evaporation, and sorption (Ouyang et al., 2019). The proliferation of CR in the acid mine water prompted into more research into their ability to survive in the environment as well as the plant-microbes' interaction between CR and the microbial communities that could promote their survival and proliferation. Plant-microbes' interactions both at the rhizosphere and endophytic level of CR has enhanced their ability to survive, grow, and promoted the remediation of acid mine water (Kalu et al., 2021). However, further studies are needed that could adopt the combination of "omics" technologies (meta-genomics, meta - transcriptomics, metabolomics, and

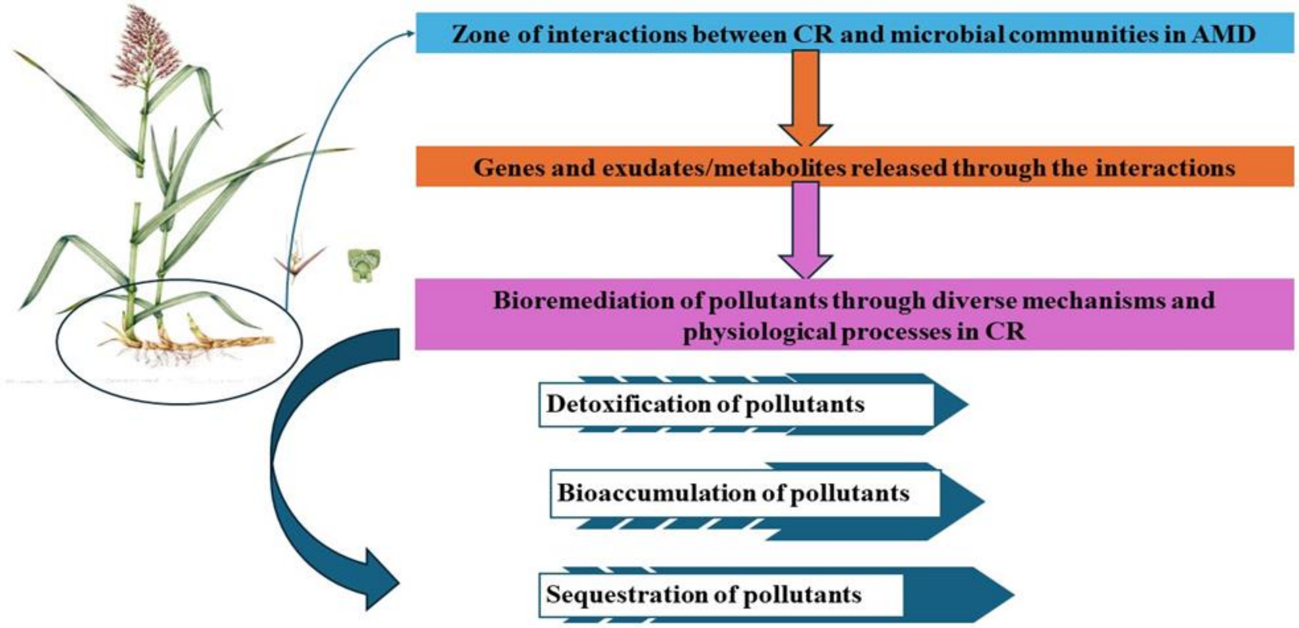

Fig. 1: Overview of bioremediation potential and process in CR through the interactions between the microbial communities and the reed.

meta-proteomics) and advance biotechnology (systems metabolic engineering, synthetic biology and nanotechnology) to provide more insights into the development of sustainable bioremediation techniques for acid mine water contaminated environment through genetic reprogramming of the microbial communities associated with CR in acid mine water conditions.

Conclusion

Plant-microbes' interaction is a complex and crucial interaction that tends to shape diverse ecosystems that are embedded in both terrestrial and aquatic environments to ensure sustainability of the environment. Diverse beneficial roles as well as negative impact of these interactions including different interactions are highlighted in the study of Chauhan et al. (2023). Notably, microbes-microbes and plant-microbes' interactions at the rhizosphere level culminate into the enhancement of the plant to survive unfavourable conditions in the environment. Although the microbes-microbes interaction could be antagonistic, the plant exudates tend to be specific in enhancing the survival of the microbes that promotes their growth, survival, and remediation of the environment. CR, an invasive weed known to grow well in wetland environments have been reported to thrive successfully in AMD conditions with the potentials to sequester heavy metals, the major contaminants in AMD and reduce the acidic condition of AMD. Solely, the CR may not withstand the harsh conditions except through the aid of diverse microbial interactions which could be symbiotic. These interactions are believed to be possible through diverse metabolic pathways controlled by specific genes co-produced by both plants and microbial communities. The limitations in the co-production of the genes controlling the metabolic pathways that enhanced the remediation potentials of CR is the paucity of information of the particular genes that comes from the microbial communities and the ones that comes from the plants. This will deter any augmentation or molecular manipulation through molecular docking approaches that can promote or optimise the bioremediation potential of CR. Further studies are recommended in these areas to provide solutions to the limitations.

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