



Advances in Chemotactic and Non-chemotactic Bioremediation of Water: A Comprehensive Review

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Abstract

Pollution has reached to a critical threshold affecting the climate and diversity of the planet Earth. All global authorities have included pollution control in their agenda for near future. Most of the environmental research nowadays is focused on removing waste generated by anthropogenic activities, may it be solid, liquid or gaseous waste. Bioremediation is believed to be the most eco-friendly approach for reducing or removing pollutants contaminating different matrices of the environment. There are various methods covered under the umbrella term of bioremediation. Chemotaxis-mediated bioremediation attracted attention of several research groups since early decade of twenty first century due to improved efficiency achieved by this strategy. There is very limited literature available on comparative account of non-chemotactic and chemotactic bioremediation. In this review, authors have extensively discussed about research developments in non-chemotactic and chemotaxis mediated bioremediation comparing the efficiency and scale of the processes.

Keywords: Bioremediation; Chemotaxis; Chemotactic bioremediation; Water; Microbial degradation

Introduction

The atmosphere on the planet Earth has made it possible for life to flourish. All life forms live in a delicate balance depending on the limited resources available on our planet. The technological revolutions have changed the quality and demands of human life since last few decades. But this change in demands is accompanied with its own cost; the damage to the environment. The intricate balance between

environment and the life thriving on it is being disturbed by anthropogenic activities. These activities are knowingly and unknowingly leading to explosion of pollution on the planet Earth and are ultimately challenging our own as well as other species' survival. The crisis of pollution of almost all resources; air, soil, water, food, has led to recognition of this issue at the global front. The university of South Australia, in their proposal for global contamination

initiative, have stated that the extent of contamination is so great to adversely affect stratosphere, deep oceans, wildlife, polar regions, rural area to modern cities, individual persons to newborn babies [1]. The World Health Organization has released a report on 'Contaminated sites and Health' (2012) which chalked down current and future risk involved due to exposure to environmental contaminants and strategies to be adopted for risk assessment and containment [2]. Global alliance on health and pollution partnered by many public and private organizations such as UNICEF, UNEP, the World Bank and others, have come forward to establish a contaminated sites database which is the largest database of polluted sites [2]. Such initiatives now help us to have easy access to information pertaining to pollution and its management. Another report on 'Contaminated land' (2021) published by The United States Environmental Protection Agency (USEPA), extensively talks about causes, categories and effects of contaminated lands, human exposure and environment indicators [3]. Considering the enormous impact of pollution on present and future of this planet and its diversity; reduction in pollution has been included in the Sustainable Development Goals and action plan of the United Nations. The present review discusses efforts taken through bioremediation for reclamation of resources with special attention to water.

Strategies for reclamation of contaminated sites

There are different strategies and approaches to reduce the level of contamination of a given site or ecosystem (Figure 1). Digging the upper layer of contaminated soil and taking it to landfills, incineration, chemical based dechlorination, oxidation using ultraviolet light, use of ion exchange resins, adsorption on activated carbon and other natural materials, biosorption, coagulation and reverse osmosis are some of the approaches [3–7]. These approaches are asso-

ciated with several limitations such as risk of exposure during treatment, sensitivity to environment conditions, time consumed for treatment and inefficiency at low concentrations of pollutants. Land-filling is simply taking the contaminants to another site. UV oxidation is difficult to be applied on large scale and has a reach only to upper layers. Moreover physical and chemical methods may lead to formation of toxic by-products and hence the whole idea of detoxification is not achieved. One approach to achieve eco-friendly removal of pollutants is Phytoremediation. Phytoremediation is a process where fast growing plants are used to reclaim contaminated soil or water matrix through holding or degradation of pollutants to less toxic or non-toxic form by plants, plant roots or associated biotic-abiotic factors [8]. Although this is the greenest approach to bioremediation, the limitations are numerous, to name a few, finding the most appropriate plant which is able to grow in contaminated site, less tolerance by plants towards stress induced by contamination and time consumed in the process. A more suitable alternative that overcomes many of the previously stated disadvantages is microbial bioremediation.

Microbial bioremediation is a method of degradation of pollutants using microorganisms thereby reducing their concentration and hazards. Microorganisms have ability to utilize a myriad of compounds as energy source. In doing so, they breakdown, transform or accumulate these compounds decreasing their levels in the ecosystem [9]. The process of bioremediation has several advantages over the other methods, such as, bioremediation can be done on-site in native conditions; it can be used for variety of environmental matrices such as soil, fresh water, marine water and others; natural flora of the ecosystem can be used for remediation purpose; external addition of harmful chemicals is not required making it an eco-friendly approach. With the advent of recombinant DNA tech-

nology, organisms can be engineered to maximize the degradation of targeted pollutant and minimize toxic metabolic products of degradation. Rhizoremediation is another approach where plant-microbe associations and use of root exudates as food for rhizospheric pollutant remediating microorganisms can be efficiently employed in bioremediation [10]. Extremophiles are the category of microorganisms that can survive and multiply in extreme environmental conditions such as high/ low pH, temperature, salinity and a combination of these, where other organisms cannot thrive. Since contaminated sites and wastewater can exhibit such harsh conditions, for example, oil spillage in ocean, petroleum waste, pH and salinity of textile industry waste, increased salinity of soil due to accumulation of chemical fertilizers and pesticides and so on; extremophiles have proved very useful in bioremediation of such habitats. Therefore, many researchers have focused their studies on utilization of unique capabilities of

these organisms. Extremophiles have grabbed special attention in textile dye bioremediation owing to their sustainability to adverse conditions in terms of pH and salinity of effluent [11–12] and thus some examples of extremophiles are included in this review. Chemotaxis based bioremediation is an upcoming approach for efficient removal of pollutants. Chemotaxis is movement of microorganisms, especially bacteria, towards a chemical attractant (here, a pollutant), under the influence of chemical gradient. A microorganism, which is attracted to a pollutant and also degrade it, can have obvious advantages over non-chemotactic degraders. There are several reports indicating higher efficiency of chemotactic bioremediation. The present review will discuss new researches in the area of non-chemotactic and chemotaxis based bioremediation and comment on its potential for application with advantages and limitations.

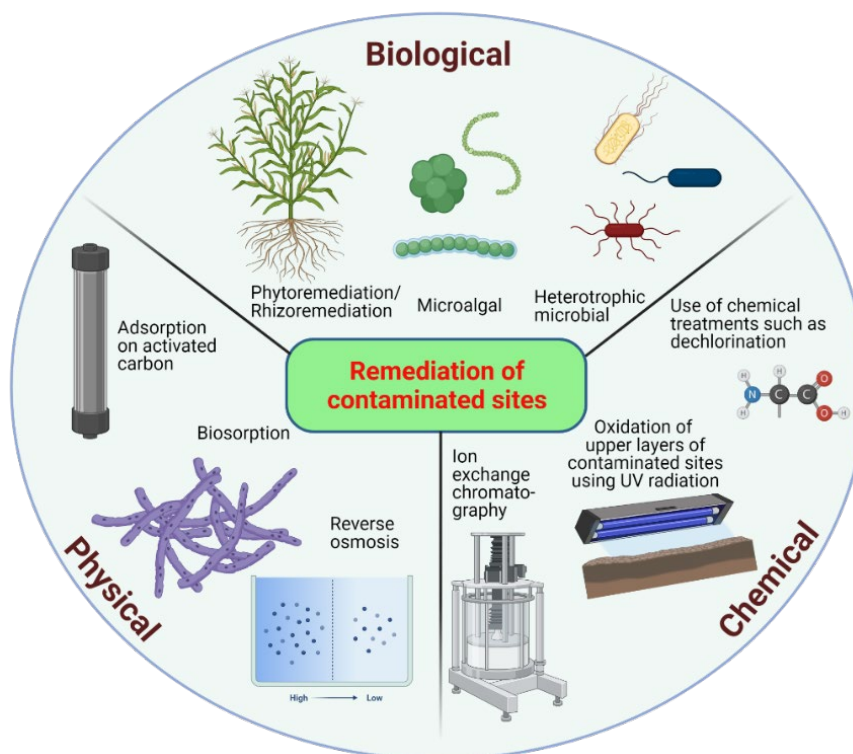


Figure 1 Major strategies that can be adopted for remediation of different environmental matrices.

Non- chemotactic microbial bioremediation

Bioremediation has attracted enormous research due to its feasibility in applied aspects such as low cost, convenient operation, *in situ* application without harming the habitat and low consequential pollution [13]. Bioremediation using microorganisms can take place via adsorption, biosorption, bioaugmentation, biodegradation, physico-chemical and biological mechanisms [14]. The term ‘non-chemotactic microbial bioremediation’ used in present review implies to bioremediation reports using organisms which have one or more characteristics such as, non-chemotactic mutants of the study organisms stated in original articles, known non-chemotactic organisms taken for comparative study with chemotactic organisms stated in original articles, non-motile and known to lack chemotaxis or do not possess chemotaxis genes necessary to exhibit chemotactic response and use of immobilized or dead biomass where cell movement is not possible. Relevant explanations are stated with references for various examples of non-chemotactic bioremediation discussed in this review. Bioremediation of some important groups of pollutants by major mechanisms other than chemotaxis is discussed in following sections.

1) Hydrocarbons

The analysis of published articles and patents related to bioremediation showed that oils are major contaminants (38%) as compared to organic waste, metals and others [15]. Use of petroleum in day to day life, automotive industries, oil extraction sites and spillage of oil on land and oceans create pollution as well as ecological problems due to hydrophobic nature, less bioavailability and recalcitrant nature of these pollutants. In petroleum hydrocarbon contaminated sites, organisms belonging to α and γ -proteobacteria have been found frequently associated and aiding in remediation of hydrocarbon in aerobic conditions. Whereas, in anaerobic

conditions of petroleum contaminated groundwater, ϵ -proteobacteria were found to be dominant [16]. In order to treat such hydrocarbon contaminated sites, special attention has been given to biosurfactant producing bacteria that can degrade hydrocarbons to obtain energy. Polycyclic aromatic hydrocarbons (PAHs) are another group of contaminants of emerging concern. Bacteria belonging to different genera reported to be non-motile and non-chemotactic were found to degrade PAH [17]. Some authors have also used laboratory scale bioreactors with good efficiency of degradation of contaminants using fungal cultures [18]. Fungi are regarded as non-chemotactic organisms [19]. Fungi *Trametes versicolor*, *Phanerochaete chrysosporium*, *Irpex lacteus*, *Phlebia radiata* and several other genera have been recognized for eco-friendly remediation of PAH. Adeola and Forbes (2021) have given an extensive review on technologies for PAH removal from water [20]. In a study on Ascomycetous and Basidiomycetous cold adapted yeasts isolated from Antarctica, many isolates were able to degrade phenol, n-hexadecane and methanol as sole carbon source and were found to be tolerant to 1mM concentration of different heavy metals [21]. Zhao et al. (2017) reported a novel species of a haloarcheon *Halorientalis hydrocarbonoclasticus* sp. nov. that could degrade hydrocarbon n-hexadecane in hypersaline habitats at almost 60% efficiency [22]. In a different approach to bioremediation of hydrocarbons, n-alkanes (C-16, C-18, C-19, C-26, C-28) and PAH (naphthalene and pyrene), salt tolerant *Corynebacterium variabile* HRJ4 immobilized on biochar showed higher efficiency than free living organisms [17].

2) Heavy metals

Heavy metals are very frequently found contaminants nowadays and are of special concern as they are toxic even at trace concentrations. Chromium is a carcinogenic heavy metal originating from leather and electroplating indust-

ries and is extremely harmful to ecology; mercury is toxic and radioactive waste from nuclear weapons. Arsenic, lead, cadmium, zinc are among the other heavy metals found in polluted sites [23] including treated drinking water [24]. α -Proteobacteria and Actinobacteria were reported in remediation of Cadmium [16]. The chemotaxis genes are rarely found associated with Actinobacteria and thus this group of organisms is regarded as non-chemotactic with few exceptions [25]. Xia et al. (2019) have given an extensive review on bioremediation of chromium [13]. Genetically engineered micro-organisms have been demonstrated to be very useful for heavy metal remediation purposes. A non-motile organism *Sphingomonas desiccabilis* [26], with over-expression of *arsM* gene encoding arsenite methyltransferase enzyme required for arsenic remediation had potential for remediation of arsenic [27]. *Methylococcus capsulatus*, a capsulated non-motile non-chemotactic organism [28], over-expressing *CrR* gene for Cr (IV) reductase yielded efficient Cr (IV) remediation [29]. *Deinococcus* genus is reported to be lacking chemotaxis genes and thus unlikely to exhibit chemotaxis [30–31]. Brim et al. (2000) genetically engineered *Deinococcus radiodurans* with *merA* gene giving resistance to Hg (II) and thus had improved mercury remediation [32]. Another study reported a combined phytoremediation of mercury using *Aeschynomene fluminensis* and endophytic fungal bioremediation using *Aspergillus* sp. A31 and *Lindgomycetaceae* P87 to almost 60% reduction [33]. Several microalgae have shown promising application in phycoremediation of arsenic, chromium, cadmium, lead and mercury [34]. Use of *Chlorella vulgaris* for arsenic remediation [35], *C. sorokiniana* for chromium remediation [36], *Parachlorella* sp. for cadmium remediation [37], *Phormidium* sp. for lead remediation [38] are some of the highly efficient microalgae reported in phycoremediation of heavy metals.

3) Pesticides and herbicides

Reducing pollution by chemical pesticides has been one of the forefronts of bioremediation research. Many authors have reported remediation of pesticides such as organophosphorus pesticides [39], atrazine, carbofuran, glyphosate, 2,4-D and diazinon [40], terbutryn, diuron, imidacloprid [41], cadusafos, DDT, lindane, endosulfan, aldrin, dieldrin, and chlordane [42]. Non-motile *Staphylococcus* sp. DAB-1W was reported to degrade lindane by 98% in 8 days with 10 mg L⁻¹ initial concentration of lindane [43]. In another report, *Staphylococcus succinus* HLJ-10 was found to degrade insecticide D-cyphenothrin at the efficiency of 90% in 7 days in laboratory scale experiments with 50 mg L⁻¹ initial concentration of insecticide [44]. Several genera of actinomycetes are reported to degrade pesticides such as aldrin, chlorpyrifos, carbofuran, diazinon, diuron [45], lindane co-polluted with chromium (IV) [46]. An *ex-situ* approach to degrade organophosphorus pesticides, chlorpyrifos and diazinon, utilized mixed culture of *Streptomyces* species immobilized on polyurethane foam. This immobilized culture was used as inoculum for continuous stirred tank bioreactor with 800 ml working volume. Authors reported 100% removal of pesticides within 72 hours with 50 mg L⁻¹ initial concentration [47]. Fungi are well reported for degradation of pesticides [45]. Bhatt et al. (2020) reported *Fusarium proliferatum* CF2 for degradation of allethrin with complete degradation in within 144 hours [48]. Use of microalgae in pesticide remediation is also well reported [49].

4) Dyes

Textile industry is one amongst the largest industries and thus is major contributor of pollution. Textile dyes pollute diverse milieu and are known to be toxic, carcinogenic and interfere in photosynthesis. Bioremediation of these dyes has been studied on a wide scale and various bacteria and fungi are reported in

biosorption and biodegradation using *in situ* approaches through biostimulation and bioaugmentation, whereas, *ex situ* approaches through use of bioreactors, composting and land farming [50]. Consortia [51–52] or co-cultures [53] of bacteria have shown increased efficiency of degradation in some studies. *Aspergillus*, *Trichoderma*, *Trametes*, *Cladosporium* are reported to remediate habitat from dyes using one or multiple mechanisms of bioaccumulation, biodegradation and biosorption [54]. In a study by Lalnunhlmi and Krishnaswamy (2016), a consortium of extremophilic bacteria was reported to be highly efficient in removal of Azo dyes Direct blue 151 and Direct red 31 at an efficiency of 97.57% and 95.25% respectively from saline habitat [55]. As per the report of Rathod and Pathak (2018), consortium of halophiles isolated from sea water showed good efficiency, 68.88% and 70.78% respectively in remediation of textile dyes Direct red 81 and Direct orange 34 [56]. Table 1 includes examples of bioremediation involving mechanisms other than chemotaxis.

Bacterial consortia have been found to play a significant role in bioremediation of multiple pollutants within waste treatment plants. Use of biosorbents is gaining popularity in bioremediation and Singh et al. (2020) have presented an extensive review on use of biosorbents and strategies to enhance its efficiency in bioremediation [66]. However, biosorption comes with an inherent disadvantage of treating and disposing the sorbed pollutants and biomass.

Despite of the examples, methods and technologies discussed above, there are certain limitations demanding more research in the field of bioremediation, such as, spiking the environment with non-native microorganisms, their

survival, degradability of pollutants, accessibility, bioavailability of pollutants to microorganisms and concentration dependency of the process efficiency as many pollutants occur in lower concentrations. Juwarkar et al. (2010) have extensively discussed elements, merits and demerits of bioremediation [67]. Bioavailability of pollutants can be limited due to physico-chemical sorption, binding to humic acids, diffusion and solubility. All these factors affect the mass transfer coefficient of pollutants to microbial cells on which the rate of biodegradation largely depends. The supply of other essential nutrients and oxygen to the degrading organisms may be limited due to lower mass transfer ratios as we reach deep in the contaminated sites [68]. The bioavailability problems can be minimized using several approaches such as reducing the size of the suspended solids in water, use of biosurfactants and increasing solubility of pollutants. However, there can be different dynamics of *in vitro*, *ex situ* and *in situ* applications of bioremediation. Azubuike et al. (2016) have discussed the advantages and disadvantages of *ex situ* and *in situ* approaches [69]. Many comparative studies between non-chemotactic and chemotactic bioremediation have concluded that if the organisms itself responds to the cues of pollutants, the problems of bioavailability and mass transfer can be effectively minimized which in turn improves the process efficiency considerably. Figure 2 represents some of the advantages and limitations of bioremediation mechanisms depending on and independent of chemotaxis. The subsequent section of review will cover chemotaxis-mediated bioremediation with examples and how it overcomes some of the disadvantages of non-chemotactic bioremediation.

Table 1 Examples of bioremediation involving mechanisms other than chemotaxis

Contaminant	Initial concentration of contaminant and matrix used if any	Methods used for remediation study	Organisms involved	Efficiency	Reference
Heavy metals					
Vanadium	1130.1 ± 9.8 mg kg ⁻¹ in surface soil 0.13 ± 0.02 mg L ⁻¹ in groundwater	Bioremediation in laboratory scale bioreactor using natural flora.	Microbial community	65.2 ± 1.9% to 98.7 ± 3.6% of 75 mg L ⁻¹ within 72 h in soil 78.0 ± 3.5% to 88.3 ± 3.7% of 10 mg L ⁻¹ within 12 h in water	[57]
	50 mg L ⁻¹	Laboratory scale	Cell debris of <i>Bacillus cereus</i> strain XMCr-6	97%	[58]
	100 ppm	100 ml flask culture	<i>Chlorella sorokiniana</i>	99.68%	[39]
Lead	10 mg L ⁻¹	Semi-batch packed bed adsorption (15 cm x 4.8 cm glass column)	Powdered biomass of <i>Phormidium</i> sp.	92.2%	[36]
Arsenite and nitrate (combined removal)	33 mg L ⁻¹ nitrate, 5 mg L ⁻¹ arsenite (III)	Microbial electrochemical technology using continuous flow bioelectrochemical reactor	<i>Achromobacter</i> sp.	92±-5% for arsenite oxidation at hydraulic retention time (HRT) of 1.6 h, 100% for nitrate at HRT of 2.3 h,	[59]
Hydrocarbons					
n-alkanes, naphthalene (NAP) and pyrene (PYR)	n-C16 (0.1%), n-C18 (0.1%), n-C19 (0.1%), n-C26 (0.05%), n-C28 (0.05%), NAP (0.05%) and PYR (0.05%).	25 mL flask culture	<i>Corynebacterium variabile</i> HRJ4 immobilized on biochar	78.9% in 7 d	[17]
n-hexadecane	5 g L ⁻¹	50 mL flask culture	<i>Halorientalis hydrocarbonoclasticus</i> sp. nov.	57 ± 5.2%	[22]

Table 1 Examples of bioremediation involving mechanisms other than chemotaxis (*continued*)

Contaminant	Initial concentration of contaminant and matrix used if any	Methods used for remediation study	Organisms involved	Efficiency	Reference
Hydrocarbons (<i>continued</i>)					
Hexadecane, tetradecane, phenanthrene, pyrene	2.5% hexadecane and tetradecane; 100 mg g ⁻¹ phenanthrene, pyrene	Laboratory scale	Passive extracellular biosorption by dead cells of <i>Pseudomonas synxantha</i>	Always less than chemotactic extracellular biosorption	[60]
Naphthalene	Saturated naphthalene solution	Capillary assembly	<i>Pseudomonas putida</i> G7, mutant non-chemotactic to naphthalene	90 % in 30 h	[61]
Naphthalene and anthracene	0.5, 0.8 and 1.0 mg/50ml)	50 mL flask culture	<i>Micrococcus varians</i> SBA8, <i>Deinococcus radiodurans</i> SBA6	4-5 % in 6 d	[62]
Pesticides and herbicides					
Pesticides Atrazine, carbofuran, glyphosate, 2,4-D and diazinon	50 mg L ⁻¹ (mixture of all pesticides)	30 mL in glass vial	Microbial consortium	>90% for Atrazine, carbofuran, glyphosate	[40]
2,4-D, Diazinon, 2-methyl-4-chlorophenoxyacetic acid (MCPA)	0.1–1000 ng L ⁻¹	10 L tubular horizontal photobioreactor	Microalgae	2,4-D: 100%, Diazinon: 100%, MCPA: 89% after 5 d	[41]
Imidazolinone: imazaquin and imazamethabenzmethyl	50 mg L ⁻¹	Laboratory scale, shake flask cultures	Enrichment consortium	54.2% for imazaquin, 61.9% for imazamethabenzmethyl in 7 d	[63]

Table 1 Examples of bioremediation involving mechanisms other than chemotaxis (*continued*)

Contaminant	Initial concentration of contaminant and matrix used if any	Methods used for remediation study	Organisms involved	Efficiency	Reference
Other compounds					
p-nitrophenol in soil	70 ppm in soil	Tray assay using soil	<i>Burkholderia cepacia</i> RKJ200 non-chemotactic to p-nitrophenol	No degradation after 36 h (sampling from 8 cm of inoculation zone)	[64]
Sulfolane	100 mg L ⁻¹	0.293 L continuous column, with 5.88 mM H ₂ O ₂ , 7 mg L ⁻¹ dissolved oxygen	Microbial community	99.6% in 7.9 h	[65]

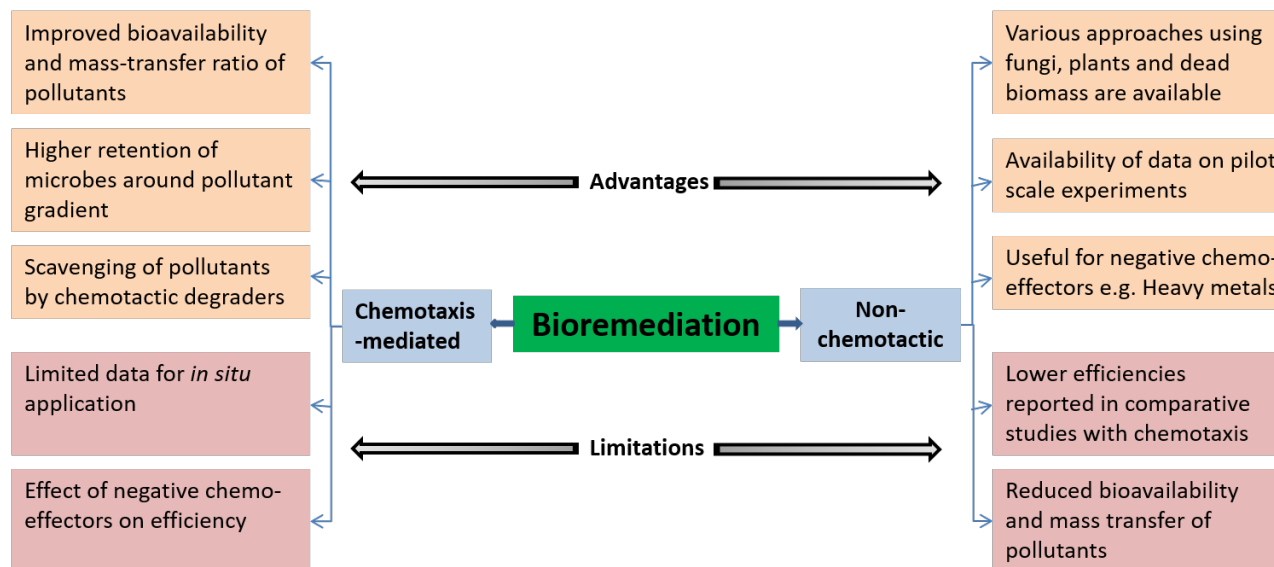


Figure 2 Advantages and limitations of chemotaxis-mediated and non-chemotactic bioremediation.

Chemotaxis-mediated bioremediation

Chemotaxis is classically defined as movement of motile organisms in response to chemical gradients, which helps them to find optimum conditions for growth (Figure 3). Motile organisms respond to the chemical cues and move towards or away from them. This phenomenon has been particularly useful in bioremediation. Several limitations of non-chemotactic bioremediation were discussed in the preceding text and chemotactic bioremediation can be useful in overcoming some these limitations. Growing amount of literature is suggestive of co-evolution of the process of toxic compound degradation and chemotaxis to those compound leading to increased bio-availability [70–71]. Moreover the genes encoding chemoreceptors have been located on degradation or resistance plasmids thus far [70], making them a suitable target for transferring to other organisms. Some experiments could tell us the speed of chemotactic movement of bacteria isolated from soil to be around 1 mm min^{-1} and this could be controlled by choice of chemo-effectors [72]. Chemotactic

response allows bacteria to move towards a suitable substrate such as hydrocarbons and away from harmful chemicals resulting in most advantageous conditions for growth in given environment [73], thus, chemotactic bioremediation has great potential of *in situ* applications [71, 74].

The hydrophobic organic contaminants tend to get adsorbed on particulate matter in water and thus have reduced accessibility. Chemotactic biofilm forming bacteria attach to such non aqueous phases, form a biofilm and use the adsorbed contaminants as nutrients [75–76]. This behavior improves the bioavailability as well as mass transfer of contaminants making biodegradation efficient [77–78]. Biofilms have another advantage that mixed populations of bacteria can survive together by mutualism. Chemotactic organisms play a significant role in such a heterogeneous association by sensing the advantageous and disadvantageous gradients. Different categories of pollutants and their chemotaxis mediated degradation is discussed in subsequent sections.

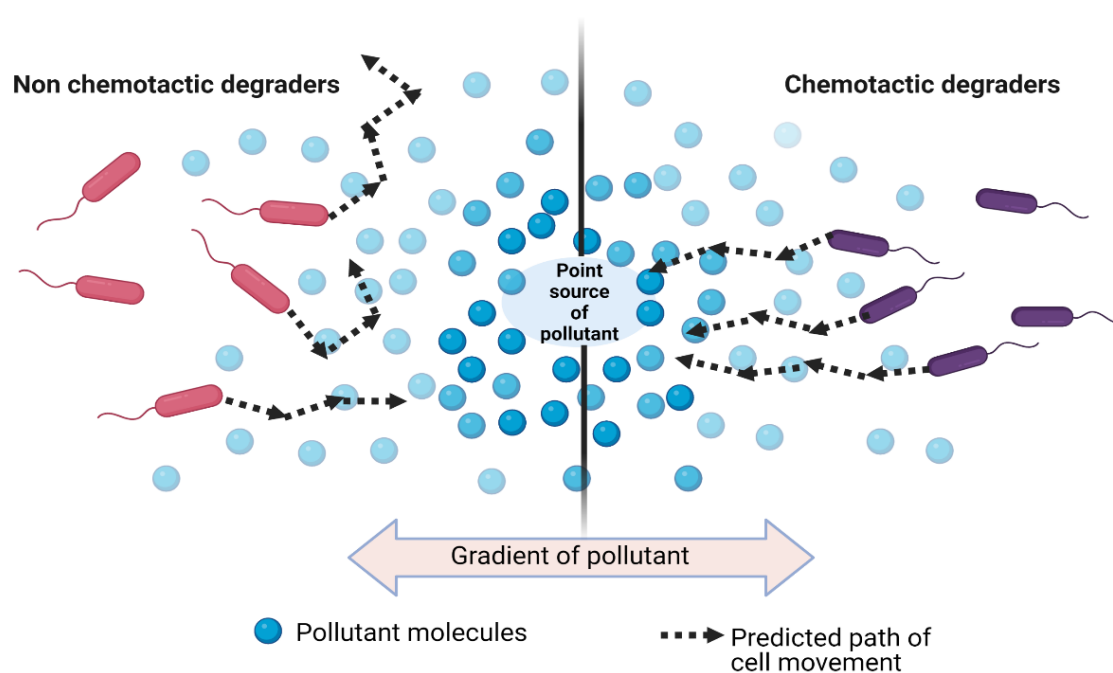


Figure 3 A schematic representing cell movement response to the diffusible chemical gradient from a point source.

1) Hydrocarbons

A well-known study in the field of chemotactic bioremediation was by Mason et al. (2012) on the Deep-water Horizon oil spill in the Gulf of Mexico [79]. The members of Oceanospirillales dominantly present in the plume samples were shown to be enriched in motility and chemotaxis genes using shotgun metagenomic and metatranscriptomic sequencing approach. Authors concluded that the chemotactic genes may have played a significant role in aggregation of cells towards oil spill resulting in efficient degradation. Meng et al. (2019) discussed a novel approach of chemotactic adsorption of *Pseudomonas synxantha* LSH-71 for bioremediation of oil contaminated seawater in vitro mimicking environmental conditions. Researchers found a significant correlation between chemotaxis and adsorption of hydrocarbons on *P. synxantha* LSH-71 which in turn correlated with biodegradation rates. The rate of sorption was observed to increase with increasing biosurfactant concentration [60]. *Serratia* sp. isolated from oil spillage site was found to exhibit chemotaxis towards hydrocarbons and had high *in vitro* degradation efficiency of 87.54% and 85.48% of diesel and kerosene respectively [80]. Similarly, in another study, the organism most efficient in degrading refined petroleum oil was found to be chemotactic, could form biofilm and was identified to be *Pseudomonas aeruginosa* [81]. Desai et al. (2018) used rising oil droplets with dissolved chemoeffector to study the nutrient uptake efficiency of bacteria chemotactic to the compound. They reported that chemotactic organisms consume the chemoeffector at least 45% faster than the non-motile organisms [82]. There are several reports on linear n-alkane chemotaxis and degradation. Examples include *Flavimonas oryzi-habitans* for hexadecane and hydrocarbons in gas oil, *P. aeruginosa* PAO1 for hexadecane, *Pseudomonas* sp. strain H for n-hexadecane, 1-dodecene, 1-undecene, and kerosene, *P.*

aeruginosa, *Paenibacillus jamilae*, *Brevibacillus brevis*, *Bacillus sonorensis*, *Providencia rettgeri* for chain alkanes (C12–C28) [83].

Increased mass transfer and rate of biodegradation was demonstrated for naphthalene degradation by chemotactic *P. putida* G7 which showed 90% removal of naphthalene in 6 h whereas the non-chemotactic mutant of the same organism took 30 h [61]. In another study on non-aqueous phase liquid (NAPL) contaminants of aquifer, a sand column containing naphthalene dissolved in a model NAPL 2, 2, 4, 4, 6, 8, 8-heptamethylnonane was used to show that the migratory chemotactic response of *P. putida* G7 to chemical gradient of naphthalene. Chemotaxis led to 45% decrease in recovery of cells in the column effluent at superficial velocity of 0.05–0.25 cm min⁻¹ and threefold increase in longitudinal dispersion of cells. This indicated that chemotactic cells were retained around the contaminant gradient in column more than non-chemotactic bacteria, hence increasing the efficiency of bioremediation [84, 124]. In a similar study using *P. putida* G7, it was found that chemotactic cells aggregate around the source of contaminants by sensing the gradient, increasing the mass transfer rate and biodegradation of NAPL-associated hydrophobic pollutants [85]. Bisht et al. (2010) isolated bacteria that could degrade naphthalene and anthracene from the rhizosphere of *Populus deltoids* grown in non-contaminated sites. Furthermore, they found that among the isolates, *Kurthia* sp. and *B. circulans* were chemotactic to both naphthalene and anthracene and could degrade these chemicals with the efficiency in the range of 85–95% [62]. *P. putida* RKJ1 was found to chemotactically degrade naphthalene and salicylate, where, both chemotaxis and degradation were plasmid encoded [86]. A biofilm forming marine isolate *P. aeruginosa* N6P6 was reported to be chemotactic for naphthalene and the quorum sensing regulatory genes were found to control the *ndo* gene expression responsible for naph-

thalene degradation [87]. A halophile *Halomonas anticariensis* FP35 was found to be very useful in chemotactic bioremediation of phenol and naphthalene under saline conditions [88]. Ibrar and Zhang (2020) reported chemotaxis of *Lysinibacillus* strains to glyceryl tributyrate for the first time. In their study, authors constructed an artificial consortium of *Lysinibacillus*, *Paenibacillus*, *Gordonia* and *Cupriavidus* spp. which were enriched using glyceryl tributyrate and could degrade several compounds and PAHs with biosurfactant production [89]. Ahmad et al. (2020), in their review have extensively discussed about chemotaxis signaling and bioremediation of polycyclic aromatic hydrocarbons and concluded that chemotaxis increases the bioavailability of these hydrophobic compounds [90].

2) Heavy metals

Chemotaxis has been found to be beneficial in remediation of heavy metals and dyes as well [77]. Borrok et al. (2005) tried to establish a link between adsorption of Ni^{2+} on *E. coli* cell surface and chemotactic response to Ni^{2+} by the cells [91]. Interestingly, some arsenite oxidizing bacteria, such as, *Rhizobium* sp. NT-26, *Agrobacterium tumefaciens* GW4 and *Herminiimonas arsenicoxydans* ULPAs1 are reported to show positive chemotaxis towards the arsenite at low concentrations. Moreover, arsenite oxidation was essential for chemotaxis as deletion of oxidation genes stopped chemotaxis in some of these organisms [92]. *Enterobacter ludwigii* LY6, reported in biosorbing cadmium, showed over-expression of bacterial chemotaxis genes with increasing cadmium concentration ($> 10 \text{ mg L}^{-1}$ to 100 mg L^{-1}) when analyzed using KOBAS software in Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways [93]. Mohapatra et al. (2020) have given extensive review on use of biofilms and chemotaxis in bioremediation of heavy metals [70]. *P. aeruginosa* and *P. fluorescens* are

reported to exhibit chemotaxis towards cadmium and lead with bioremediation of these heavy metals [94]. Cadmium works as a chemottractant for *Escherichia coli* as well [95]. Anaerobic thermophilic bacterium *Anoxybacillus* was reported to be chemotactic towards Fe (III) and showed over 50% reduction of Fe (III) in studies with co-contamination with hydrocarbons [96]. In another study, *Bacillus altitudinis* MT422188 was found to be chemotactic towards zinc [97] and nickel [98] which aided in efficient biosorption of these heavy metals.

3) Pesticides and herbicides

2,4-Dichlorophenoxyacetate (2, 4-D) is quite often used in agricultural applications and has become a recalcitrant contaminant. Hawkins and Harwood reported chemotaxis of *Ralstonia eutropha* JMP134 (pJP4) to 2,4-D and could degrade it. The authors also concluded that chemotaxis might be an essential feature of 2,4-D biodegradation [99]. Liu and Parales (2009) found that *Pseudomonas* sp. strain ADP was not only chemotactic to atrazine but also to the intermediates of atrazine metabolism. The same organism was also chemotactic to related s-triazines. On genetic analysis of the organism, authors concluded that the chemotaxis and metabolism of atrazine were not linked. Imidazolinone are widely used group of herbicides now emerged as contaminants due to accumulation in soil and water [100]. Recently, Chen et al. (2019) have discussed a microfluidic SlipChip method for screening of bacteria chemotactic to imazethapyr herbicide belonging to imidazolinone group. In their work, they compared efficiencies of degradation of herbicide by two bacterial consortia, an enrichment consortium obtained at the end of enrichment culture and a chemotactic consortium prepared only using imazethapyr chemotactic bacteria. They found that the chemotactic consortium dominated by *Ochrobactrum* had 10% higher efficiency of degradation as compared to en-

richment consortium [63]. Organophosphates are one of the major contaminants around the globe due to their wide-spread use as pesticides and nematocides. Compounds belonging to this class, such as parathion and chlorpyrifos, are known recalcitrants. Pailan and Saha (2015) reported a novel *Pseudomonas* sp. strain BUR11, moderately thermo-halo tolerant, was chemotactic to parathion and chlorpyrifos as well as degraded both pesticides [101]. Metabolism independent chemotaxis was observed for parathion by *Pseudomonas* sp. strain WBC-3. The strain was able to degrade parathion but retained chemotaxis towards the compound even after disruption of degradation genes [102]. Mu et al. (2020) found that the *nic* gene cluster and methyl accepting chemotaxis protein gene cluster (*mcp*) to be associated in nicotine degraders indicating a possibility of chemotaxis to nicotine or its metabolites by these organisms [103].

4) Nitrophenols, nitrobenzoates and their derivatives

Chloronitrophenols (CNP) are toxic compounds known to have mutagenic activity and thus are potential carcinogens. Different bacterial species have been shown to exhibit chemotaxis to CNPs with further degradation or biotransformation [104]. 4-chloro-2-nitrophenol (4C2N) is a CNP compound detected in various contaminated sites worldwide. Arora and Bae (2014) reported biotransformation and chemotaxis of 4C2N by *Pseudomonas* sp. JHN in presence of additional carbon source for the first time [105]. *Ralstonia* sp. SJ98 was shown to exhibit sole carbon source metabolism dependent chemotaxis towards *p*-nitrophenol, 4-nitrocatechol, *o*-nitrobenzoic acid, and *p*-nitrobenzoic acid [106]. *Burkholderia* sp. strain SJ98 exhibited metabolism dependent chemotaxis towards nitroaromatic compounds. The organism could mineralize 2-chloro-4-nitrophenol, 4-chloro-2-nitrobenzoate and 5-chloro-2-nitrobenzoate and the chemotaxis to these compounds was in-

dependent of presence of classical chemoattractants such as succinate and aspartate [107]. Chlorophenols were able to attract *P. aeruginosa* and *Achromobacter marplatensis* in swarm plate assays. The authors used a new method of video processing to calculate chemotaxis index and concluded that this behavior must be helpful in degradation of chlorophenols [108]. Chemotaxis of *E. coli* to phenol has been reported where the organism was found to exhibit both attractant and repellent mechanisms to phenol [109]. Wang et al. (2019) have given a broad review on chemotaxis and degradation of aromatic compounds by *Comamonas testosteroni* and other species [110]. *P. putida* PRS2000 and two other strains of *Pseudomonas* were chemotactic to nitrobenzoates and aminobenzoates and could degrade it through β -ketoacid pathway [111].

Polychlorinated biphenyls (PCBs) are compounds used for variety of industrial applications have now become recalcitrant contaminants. The bioremediation of these compounds is not easy owing to low bioavailability and high toxicity [112]. Bacteria such as *Pseudomonas* sp. B4 [112], *P. putida* P106 and *Rhodococcus erythropolis* NY05 have been reported to show metabolic chemotaxis to PCBs which increased the bioavailability of these compounds. A comparative study for degradation of PCBs and chlorobenzoate using chemotactic *Pseudomonas* sp. B4 and its non-chemotactic transformant showed that the chemotactic organism had clear advantage in access and consequent degradation of contaminants [113]. Wang et al. (2018) studied chemotaxis and degradation of biphenyls, polychlorinated biphenyls and their metabolites by non-flagellated *Rhodococcus* spp. The two *Rhodococcus* sp. studies showed significant degradation of these pollutants up to 83.2% under laboratory conditions which indicated their potential for *in situ* application [114]. It is interesting to note that, some reports suggest gliding motility in few *Rhodococcus*

species as well as chemotactic response by these organisms. Gliding motility may be the underlying reason behind chemotactic behavior of these organisms. However, the exact mechanisms of flagella-independent chemotaxis are still unclear [115–116].

Nitroaromatic compounds and 2, 4, 6-trinitrotoluene (TNT) have also been reported to be chemoattractants for *Burkholderia cepacia* R34 and *Burkholderia* sp. strain DNT. Furthermore, these strains could degrade 2,4-dinitrotoluene (2,4-DNT) [117]. Cyclic nitramine explosives such as RDX, HMX and CL-20 are hydrophobic chemicals which remain adsorbed on solid surfaces and hence less bioavailable for degradation by microorganisms. These chemicals were reported to be degraded in simulated sedimentation microcosm by strict anaerobe *Clostridium* sp. strain EDB2 isolated from marine sediments. Nitrite released during degradation was believed to elicit chemotactic response in these organisms and hence better degradation efficiency [118]. Sodium dodecyl sulfate (SDS) is an anionic detergent used in many detergent and disinfection formulations has been found to be a contaminant of emerging concern due to its toxicity to microorganisms, aquatic life and difficulty to treat using known methods. In a study, *P. aeruginosa* N1 isolated from detergent contaminated pond was found to exhibit chemotaxis to SDS and could metabolize it as a sole source of carbon [119].

5) Other compounds

Chemotaxis towards polysaccharides such as pectin has also been reported. Konishi et al.

(2020) studied the characteristics of protein involved in triggering the chemotactic response to pectin and its assimilation for the first time. According to their report, the chemotactic organism *Sphingomonas* sp. strain A1 was more efficient at degrading pectin than the non-chemotactic mutant of the same organism, and the same protein was involved in binding to pectin and signaling chemotaxis [120]. In a novel approach to degrade plasticizer dibutyl phthalate by *Enterobacter* sp. DNB-S2, anthraquinone-2 and 6-disulfonate was found to enhance the degradation capacity by enhancing the chemotaxis of bacterium towards di-butyl phthalate and protecting it from membrane damage as well. The chemotaxis proteins and membrane components were found to be up-regulated [121]. Recent reports are showing contamination of different types of waters with microplastic [122]. Mangrove rhizosphere isolates were found to colonize microplastic. This colonization was chemotaxis-selective [123]. According to previous reports, biofilm formation and chemotaxis are attributed to be significant factors to enhance removal of dyes from environmental matrices and bioremediation efficiency for acidic, basic, sulfur containing and reactive dyes can be enhanced by optimization of these factors. 100% removal of Amarnath dye has been reported by biofilms of *Bacillus* sp. AK1, *Lysinibacillus* sp. AK2, and *Kersteasia* sp. VKY1 at initial concentrations as high as 600 mg L⁻¹ [70]. Table 2 includes examples of chemotactic bioremediation with the process efficiency.

Table 2 Examples of chemotaxis-mediated bioremediation^a

Contaminant	Initial concentration of contaminant and matrix used if any	Chemotactic organisms involved	Method used to confirm chemotaxis	Efficiency	Reference
Heavy metals					
Zinc ^b	100 mg L ⁻¹	<i>Bacillus altitudinis</i> MT422188 (Chemotactic biosorption)	Swarm plate assay	81 and 87 mg L ⁻¹ removal after 4 and 8 d	[97]
Nickel ^b	1.5 g L ⁻¹	<i>B. altitudinis</i> MT422188 (Chemotactic biosorption)	Swarm plate assay	70 and 85 mg L ⁻¹ removal after 4 and 8 d	[98]
Hydrocarbons					
Hexadecane, tetradecane, phenanthrene, pyrene Diesel and kerosene	0.5% to 2% v/v for alkane; 5 to 200 mg L ⁻¹ for PAHs 2% (v/v)	<i>Pseudomonas synxantha</i> LSH-7 ¹	Chemotactic biosorption assay	80–95% (Chemotactic adsorption and biodegradation)	[60]
		<i>Serratia sp.</i>	Agar plug assay	87.54%: diesel 85.48%: kerosene after 28 d	[80]
Glyceryltributyrate	2% (v/v)	<i>Lysinibacillus</i>	Swarm plate and capillary assay	80% in 10 d	[89]
Naphthalene	Saturated naphthalene solution 100 ppm	<i>P. putida</i> G7	Capillary assay	90% degradation efficiency in 6 h	[61]
Naphthalene dissolved in NAPL ganglia	15.4 mg L ⁻¹ aqueous concentration in equilibrium	<i>P. aeruginosa</i> N6P6 <i>P. putida</i> G7	Swim assay Drop plate assay	99.4% in 20 h Increased recovery of cells in column	[87] [124]
Sodium dodecyl sulfate	1 g L ⁻¹	<i>P. aeruginosa</i> N1	Swarm and drop plate assay	100% in 12 h	[119]
Nitrophenols, nitrobenzoates and its derivatives					
4-chloro-2-nitrophenol	0.6mM	<i>Pseudomonas sp.</i> JHN	Drop plate and capillary assay	100% biotransformation in 16 h	[105]
p-nitrophenol in soil	70 ppm	<i>Ralstonia sp.</i> SJ98	Swarm plate, drop plate and capillary assay	82% in 36 h in soil (sampling from 8 cm of inoculation zone)	[64]

Table 2 Examples of chemotaxis-mediated bioremediation^a (*continued*)

Contaminant	Initial concentration of contaminant and matrix used if any	Chemotactic organisms involved	Method used to confirm chemotaxis	Efficiency	Reference
Nitrophenols, nitrobenzoates and its derivatives (<i>continued</i>)					
Biphenyls, polychlorinated biphenyls and their metabolites	1300 mg L ⁻¹	<i>Rhodococcus</i> sp.	Modified drop plate assay	83.2% at 86 h	[114]
Cyclic nitramine explosives: RDX, HMX and CL-20	20 µM	<i>Clostridium</i> sp. Strain EDB2	Agarose plug assay and capillary assay	Biotransformation efficiency in nmol h ⁻¹ mg ⁻¹ biomass RDX: 4.5±0.5 HMX: 2.5±0.5 CL-20: 7.2±0.6	[118]
Pesticides and Herbicides					
Imidazolinone	50 mg L ⁻¹	<i>Ochrobactrum</i> dominated chemotactic consortium	Microfluidic SlipChip device	65–72 % in 7 d	[63]
Parathion	200 ppm	<i>Pseudomonas</i> sp. strain BUR11	Swarm plate, drop plate and capillary assay	62% in 96 h	[101]
Atrazine	2 mg L ⁻¹	<i>Pseudomonas</i> sp. ADP	Capillary assay	100% in 2.5 h	[125]

Remark: ^a All studies were carried out using varied volumes but at laboratory scale only.

^b 11 L volume used for pilot scale studies.

A study by Adadevoh et al. (2016) showed that chemotaxis may help in enhancing the retention of degrading bacteria in contaminated groundwater sites with typical interstitial velocity around 1.8 m d^{-1} [84]. Since the genes for chemoreceptors are found to be present on plasmids, genetic engineering can be of help to make other bacteria with better growth and degradation characters in given environment competent for chemotaxis [70]. In a novel approach, Roggo et al. (2018) transformed *E. coli* with chemoreceptor genes for toluene and benzoate from *P. putida*. The resultant *E. coli* cells could exhibit chemotaxis to these contaminants over a range of concentrations [126]. Such successful strategies indicate that organisms suitable to grow in particular environmental habitats can be genetically modified to exhibit chemotaxis and thus degrade the contaminants efficiently. This approach can be used to overcome the disadvantage of introducing non-native organisms in ecosystem. Since most of the studies are confined to laboratory conditions, Wang et al. (2018) tried to develop an equation to predict the *in situ* efficiency of chemotactic bioremediation based on the data generated in laboratories. They formulated a dimensionless equation based on previous researches which gives a chemotaxis number for the process, if the number is greater than one, the chemotactic degradation may be expected to be efficient [127]. However, the study of outcomes of this equation is at preliminary stages. Measurement of chemotaxis index has become more accurate with advancement in microfluidic technology and its use in chemotaxis assays [128]. Such technologies will be helpful in efficient designing of chemotactic bioremediation.

Heavy metals are known to exhibit oligodynamic effect and are toxic to microorganisms above a threshold level. Thus, many organisms are reported to show negative chemotaxis towards heavy metals and thus mechanisms other than involving chemotaxis can give efficient bio-

remediation. Although, as discussed in preceding text, some organisms exhibiting positive chemotaxis showed efficiency of 87% in zinc remediation and 85% in nickel remediation. However, these efficiencies are less as compared to those reported in non-chemotactic bioremediation. Chemotaxis has been proved to enhance bioremediation of hydrocarbons in terms of process efficiency or time taken to achieve desired removal. A similar trend is reported for pesticides as well. 100% removal of atrazine in 2.5 hours was reported by chemotactic *Pseudomonas* sp. ADP as compared to around 90% reduction by non-chemotactic mechanisms that took 15 days of incubation. Majority of reports indicated great correlation between chemotaxis and bioavailability of pollutant as well as process efficiency in laboratory conditions, however, field studies are required to validate this correlation *in situ*.

Conclusions

Bioremediation remains to be a highly attractive option with maximum likelihood of *in situ* application for removing or reducing harmful contaminants from the environment. Chemotaxis mediated bioremediation seems to overcome some of the disadvantages of non-chemotactic bioremediation due to better mass transfer rates, bioavailability and improved efficiency at lower concentrations. Nevertheless, further research is inevitable to get insights of *in situ* applications of chemotaxis mediated bioremediation as motility of organisms will be affected by attractants as well as repellents. Literature suggests that, most of the researches so far are focused on laboratory scale studies and more research is needed on field in order to achieve competing rates of *in situ* remediation. Research to develop consortia surviving in contaminated environmental matrices and ecological implications of adding non-native flora to contaminated sites is needed. Designing of bioreactors to handle *ex situ* remediation rates that meet or exceed the rate of generation of waste would be necessary.

Conflict of interest

The authors declare no conflicts of interest.

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