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Bacterial degradation of aromatic pollutants: a paradigm of metabolic versatility

Summary. Although most organisms have detoxification abilities (i.e. mineralization, transformation and/or immobilization of pollutants), microorganisms, particularly bacteria, play a crucial role in biogeochemical cycles and in sustainable development of the biosphere. Next to glucosyl residues, the benzene ring is the most widely distributed unit of chemical structure in nature, and many of the aromatic compounds are major environmental pollutants. Bacteria have developed strategies for obtaining energy from virtually every compound under oxic or anoxic conditions (using alternative final electron acceptors such as nitrate, sulfate, and ferric ions). Clusters of genes coding for the catabolism of aromatic compounds are usually found in mobile genetic elements, such as transposons and plasmids, which facilitate their horizontal gene transfer and, therefore, the rapid adaptation of microorganisms to new pollutants. A successful strategy for *in situ* bioremediation has been the combination, in a single bacterial strain or in a syntrophic bacterial consortium, of different degrading abilities with genetic traits that provide selective advantages in a given environment. The advent of high-throughput methods for DNA sequencing and analysis of gene expression (genomics) and function (proteomics), as well as advances in modelling microbial metabolism *in silico*, provide a global, rational approach to unravel the largely unexplored potentials of microorganisms in biotechnological processes thereby facilitating sustainable development. [Int Microbiol 2004; 7(3):173–180]

Key words: aromatic compounds · catabolism · transcriptional regulation · metabolic engineering

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Introduction

Environmental pollutants are compounds that are toxic to living organisms; they are released into the ecosystem at high concentrations, usually as a consequence of human activities. Contaminants are either compounds of industrial origin that

present chemical structures alien to the biosphere (xenobiotics), e.g. polychlorobiphenyls (PCBs), polychlorodioxins, trinitrotoluene (TNT) and azo dyes, or natural compounds that have been mobilized to a bioavailable form that is toxic to organisms, e.g. hydrocarbons present in fossil fuels and heavy metals present in minerals (Fig. 1). Major sources of pollution are: (i) chemical and pharmaceutical industries that produce a wide array of xenobiotics and synthetic polymers; (ii) pulp and paper bleaching, which are the main sources of chlorinated organic compounds in the environment; (iii) mining, which releases heavy metals into biogeochemical cycles; (iv) fossil fuels (coal and petroleum), which may be acciden-

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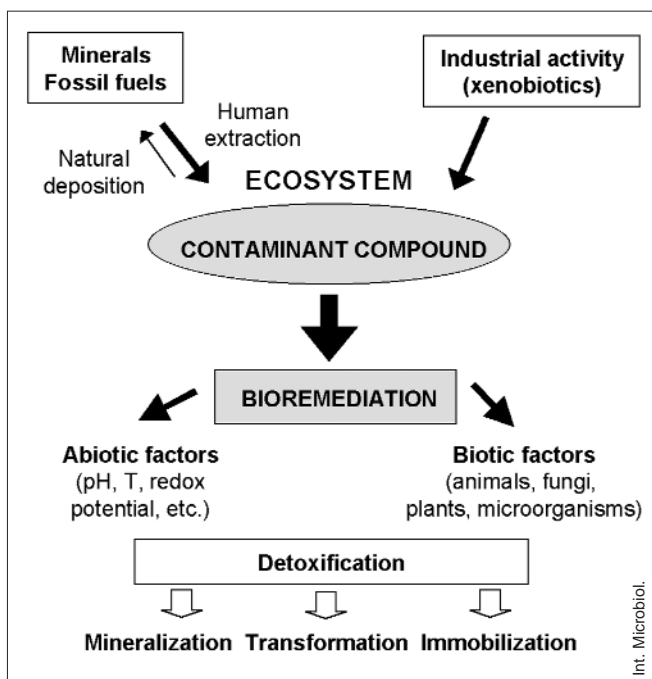


Fig. 1. Main sources of pollution in the ecosystem and the factors that influence bioremediation processes.

tally released in large amounts into the ecosystem (oil spills) and whose combustion increases significantly CO_2 atmospheric levels (green-house effect) and causes deposition of nitric and sulfuric acids (acid rain and smog); and (v) intensive agriculture, which releases massive amounts of fertilizers, pesticides, and herbicides [8,24].

The removal of pollutants from the environment via natural physico-chemical and biological processes (natural attenuation) is, in general, a slow and unpredictable way of counteracting anthropogenic pollution and irreversible damage to the biosphere. Therefore, the main, if not the only, successful strategy to fight pollution is the use and manipulation of the detoxification abilities of living organisms (bioremediation) (Fig. 1) [8,16,31,33,34]. Although most organisms are endowed with detoxification abilities, i.e. mineralization, transformation and/or immobilization of pollutants, microorganisms, particularly bacteria, have been the most well-studied and the most frequently used for bioremediation strategies.

Bacteria, which evolved more than three billion years ago, have developed strategies for obtaining energy from virtually every compound. They play a crucial role in sustainable development of the biosphere and in biogeochemical cycles. The abundance of microorganisms, together with their great ability for horizontal gene transfer and their high growth rates, allows them to evolve quickly and to adapt to environmentally changing conditions, even to extreme envi-

ronments that do not allow proliferation of other living organisms. The great genetic diversity of microorganisms accounts for their great metabolic versatility [6,16,27].

Microbial utilization of aromatic compounds

Next to glucosyl residues, the benzene ring is the unit of chemical structure most widely spread in nature. Moreover, the thermodynamic stability of the benzene ring increases its persistence in the environment; therefore, many aromatic compounds are major environmental pollutants [4]. By expressing different catabolic (biodegradative) pathways, microorganisms can use a wide array of aromatic compounds as sole carbon and energy sources [14]. The general ability of bacteria to use such compounds is related to the fact that most of these compounds are commonly present in the environment as a result of the recycling of plant-derived material [15]. Human-made xenobiotic compounds, by contrast, have been in contact with the microbiota only for about 100 years; therefore, some of them are still poorly degraded, if at all. Oxygen is the most common final electron acceptor for microbial respiration, and aerobic processes provide the highest amount of energy to cells (Fig. 2) [10]. In chemotrophic reactions, a portion of the substrate is oxidized to obtain energy and another part is assimilated into cell mass. In aerobic respiration, oxygen not only is the electron acceptor but also participates in activation of the substrate via oxygenation reactions.

Although a wide phylogenetic diversity of microorganisms is capable of aerobic degradation of contaminants, *Pseudomonas* species and closely related organisms have been the most extensively studied owing to their ability to degrade so many different contaminants [32]. However, many polluted environments are often anoxic, e.g., aquifers, aquatic sediments and submerged soils. In such environments, biodegradation is carried out by either strict anaerobes or facultative microorganisms using alternative electron acceptors, such as nitrate (denitrifying organisms), sulfate (sulfate reducers), Fe(III) (ferric-ion reducers), CO_2 (methanogens), or other acceptors (chlorate, Mn, Cr, U, etc.) (Fig. 2) [13,16,35].

The use of electron acceptors other than oxygen is based on: (i) the electron-acceptor availability and (ii) the competition of different respiratory types of microorganisms for electron donors. For example, reduction of Fe(III) is the most frequent mechanism for oxidation of organic matter in subsurface environments. Sulfate is a major electron acceptor for the anaerobic degradation of contaminants in marine environments due to the high concentrations of sulfate in seawater.

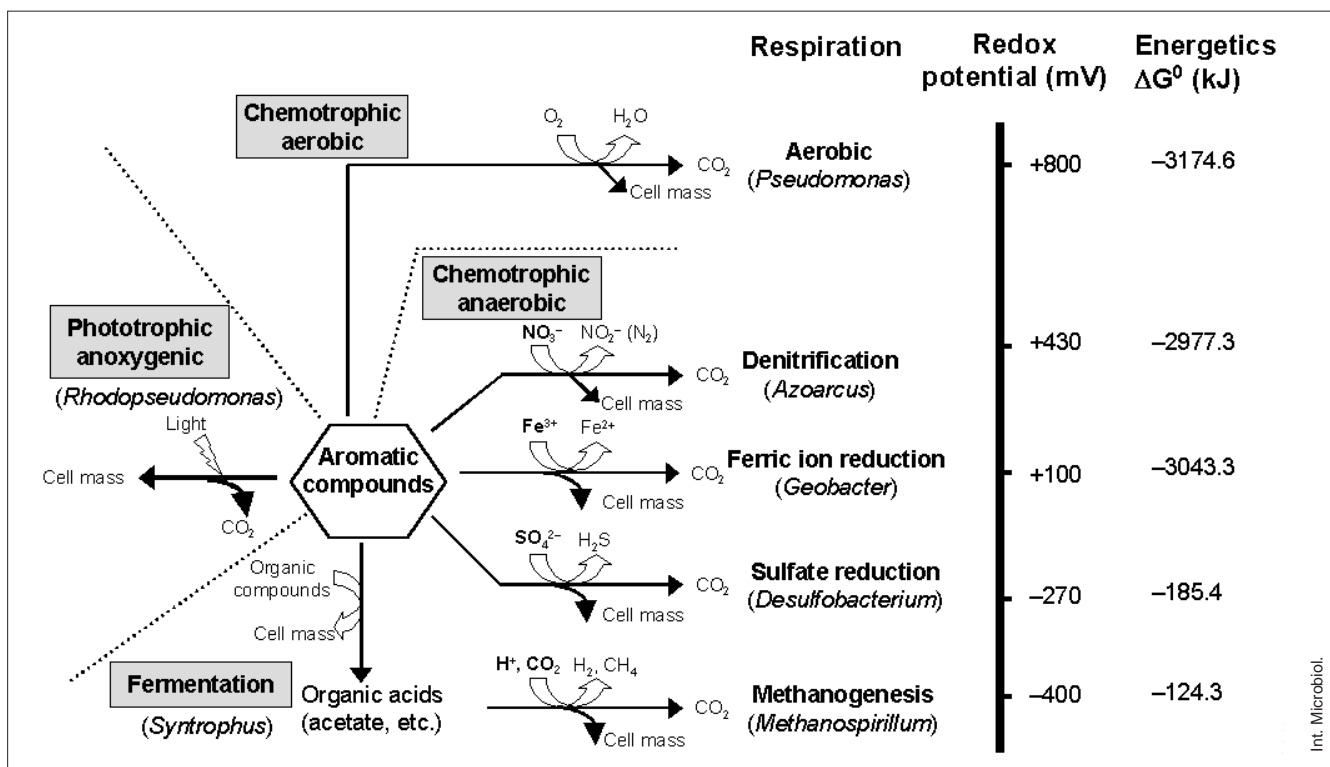


Fig. 2. Microbial utilization of aromatic compounds. The different terminal electron acceptors in respiration are indicated in bold and they are aligned with the redox potential bar. The energetics (free-energy changes) of the aerobic and anaerobic degradation of a model aromatic compound, benzoate, are indicated on the right. Methanogenesis needs to be coupled to fermentation reactions. Bacterial genera representative of each type of metabolism are shown in parentheses. Modified from [35].

ter [16]. In terms of energy, whereas degradation of aromatics using nitrate and Fe(III) as terminal electron acceptors is almost as efficient as that using oxygen, sulfate reducers and methanogenic conditions generate comparatively much less energy (Fig. 2) [10]. Consequently, the molar cell yields under methanogenic and sulfidogenic conditions are rather low. Fermentative strains tend to be restricted to a syntrophic existence because complete biodegradation becomes energetically favorable only when accompanying methanogens or sulfate-reducing bacteria promptly use the metabolic end-products generated during aromatic compound breakdown by fermenters (Fig. 2) [13]. Photosynthetic bacteria obtain energy from light and they degrade aromatic compounds anaerobically to form intermediary metabolites, such as acetyl-CoA, which are subsequently used in biosynthetic reactions (Fig. 2) [13]. Some aromatic compounds serve as electron acceptors rather than electron donors in bioremediation reactions. Thus, an important type of bioremediation is reductive dechlorination, in which bacteria remove chlorines from contaminants, such as chlorinated solvents and PCBs, by using these compounds as electron acceptors in dehalorespiration [9,13].

Aerobic and anaerobic biodegradation of aromatic compounds have several common features. Structurally diverse compounds are degraded through many different peripheral pathways to a few intermediates that are further channeled via a few central pathways to the central metabolism of the cell. In the aerobic catabolic funnel, most peripheral pathways involve oxygenation reactions carried out by monooxygenases and/or hydroxylating dioxygenases that generate dihydroxy aromatic compounds (catechol, protocatechuate, gentisate, homoprotocatechuate, homogentisate, hydroquinone, hydroxyquinol). These intermediate compounds are the substrates of ring-cleavage enzymes that use molecular oxygen to open the aromatic ring between the two hydroxyl groups (ortho cleavage, catalyzed by intradiol dioxygenases) or proximal to one of the two hydroxyl groups (meta cleavage, catalyzed by extradiol dioxygenases) (Fig. 3) [14].

Central pathways involve a series of reactions leading to the formation of Krebs cycle intermediates (central metabolism). In the anaerobic catabolism of aromatic compounds, the peripheral pathways converge to benzoyl-CoA (occasionally to resorcinol and phloroglucinol), which becomes dearomatized by a specific multicomponent reductase that requires

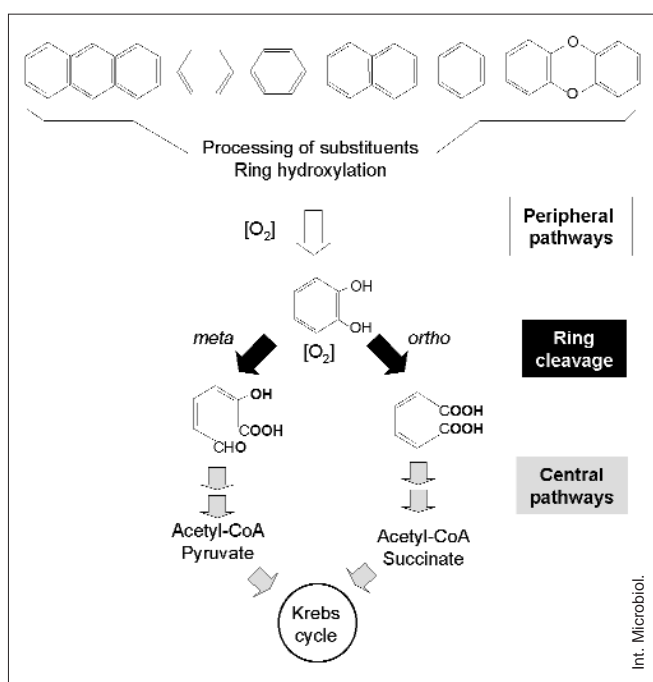


Fig. 3. The catabolic funnel for the aerobic degradation of aromatics. **White arrows**, peripheral pathways, **black arrows**, cleavage of the ring; **gray arrows**, central pathways.

energy in the form of ATP (Fig. 4A) [13]. Finally, aerobic hybrid pathways, such as that for phenylacetic acid degradation, combine anaerobic features (initial formation of CoA derivatives) with typical aerobic reactions such as aromatic-ring oxygenation (Fig. 4B) [17]. Whereas pathways involved in degradation of xenobiotic compounds, such as those carrying halogen atoms or nitro groups, are only present in certain strains, those involved in the catabolism of common aromatic compounds, such as benzoate or aromatic amino acids, are widespread [23].

Genetics and evolution of biodegradation pathways

The genes responsible for biodegradation pathways are usually arranged in clusters that comprise: (i) catabolic genes encoding the enzymatic steps of the catabolic pathway; (ii) transport genes responsible for active uptake of the compound; and (iii) regulatory genes that adjust expression of the catabolic and transport genes to the presence of the compound to be degraded [7]. Bacteria thriving in the environment are exposed to a range of physical and chemical signals that need to be processed to achieve a positive or negative physiological response. For instance, bacteria are usually

confronted with alternative carbon sources and they must “decide” which of them will be preferentially consumed before metabolizing less preferred substrates, such as pollutants, to guarantee, therefore, a satisfactory metabolic return. In order to achieve this goal, bacteria have developed a physiological response (superimposed regulation) that controls and adjusts the specific regulation of catabolic operons to the physiological and metabolic state of the cells [2]. The catabolic clusters are usually present in mobile genetic elements, such as transposons and plasmids, which facilitate their horizontal transfer of the respective genes and, therefore, rapid adaptation of microorganisms to the presence of new pollutants in a particular ecosystem [26,30].

Although microorganisms have acquired the ability to use pollutants as carbon and energy sources, their efficiency at removing such pollutants might not be optimal for cleaning up present-day pollution. In fact, microorganisms have evolved towards ecological fitness rather than biotechnological efficiency; thus, it would take a long time for bacteria capable of cleaning up anthropogenic pollution to evolve by natural selection. Hence, studying the physiology, biochemistry and genetics of the catabolic pathways becomes crucial to recreate and accelerate natural processes in the test tube as well as to accomplish their rational manipulation to design more efficient biocatalysts for different biotechnological applications. These include: (i) bioremediation of polluted sites, (ii) biotransformation of toxic compounds into fine chemicals and other high added-value products (green chemistry), and (iii) development of *in situ* biomonitoring devices and biosensors to monitor pollutant bioavailability [6,25,27]. The main limitations for the use of microorganisms in cleaning-up pollutants are summarized in Fig. 5, and some strategies to overcome these restrictions are presented below.

Designing recombinant bacteria for bioremediation

To enhance the metabolic efficiency of a microorganism for a particular environmental application, engineering should be carried out at two different levels: (i) manipulation of the specific catabolic pathway, and (ii) manipulation of the host cell. In order to improve the rate of pollutant removal and broaden the range of substrates of a catabolic pathway, manipulation of the key enzymes of both the pathway and the regulatory mechanisms that control the expression of the catabolic genes will be required [6,27]. Protein stability and protein activity can be altered and/or improved by protein engineering and rationally directed molecular evolution techniques (DNA shuffling and other *in vitro* recombination methods)

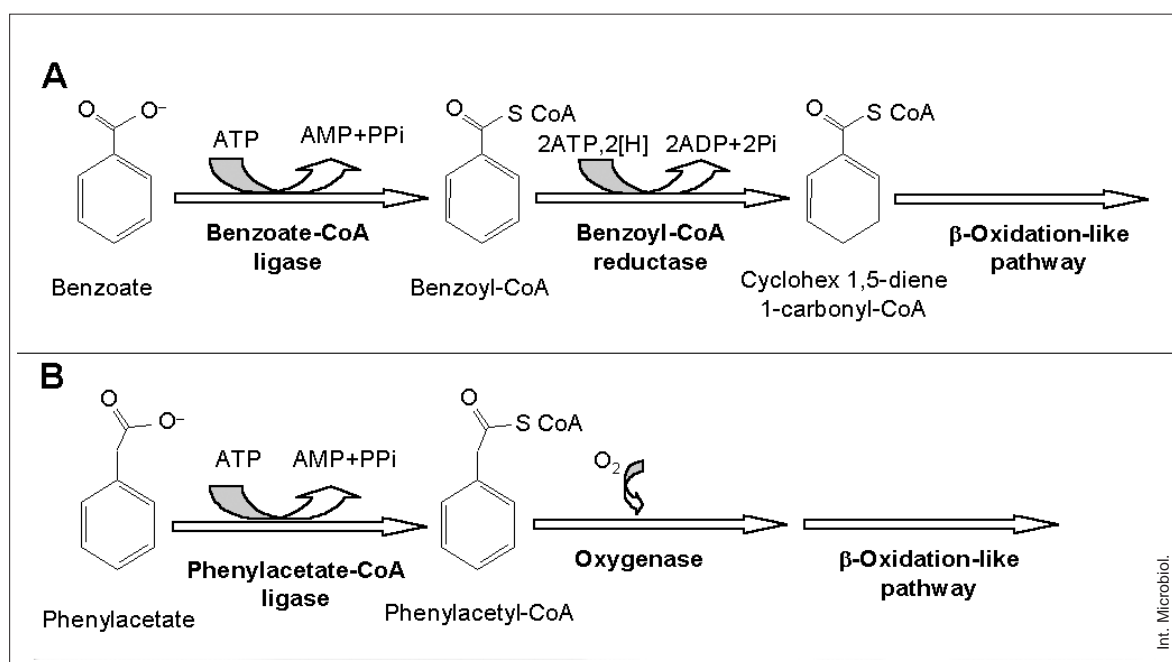


Fig. 4. (A) Anaerobic degradation of benzoate. (B) Aerobic hybrid pathway for the catabolism of phenylacetate.

[11,27]. Moreover, metabolic engineering allows the generation of novel hybrid pathways by assembling catabolic modules from different origins in the same host cell, thus leading to pathway expansion to new substrates, completion of incomplete pathways, the creation of new routes, and construction of bacteria with multiple pathways [20,23,24,27]. The rational combination of catabolic pathways may allow the complete metabolism of xenobiotics, as has been shown with the development of bacteria capable of mineralizing PCBs, and can prevent the formation of dead-end products and toxic metabolites by misrouting of the pollutants [20,27].

Bacteria used to remediate pollutants probably undergo environmental stress due to high concentrations of toxic contaminants, toxic solvents, extreme pH, temperature, ionic strength, etc. [27]. The combination in a single bacterial strain of different degradative abilities with genetic traits that provide selective advantages in the target site is a successful strategy for *in situ* bioremediation [20]. For instance, solvent-resistant strains may be ideal hosts to construct genetically engineered microorganisms for the removal of wastes with high solvent contents [20,22]. Heavy metals, including Hg, Cd and As, are currently major sources of pollution and cannot be destroyed or biodegraded. Recombinant microorganisms have been developed to accumulate and/or immobilize heavy metals present in soil and water [18,29]. As some metals can serve as terminal electron acceptors in microbial respiration, anaerobes that use them have been applied to reduce

the soluble oxidized form of the metal to the insoluble form, thereby preventing its further spread in the environment [16]. Some polluted environments contain a mixture of organic wastes, heavy metals and high-energy radionuclides. In this context, radiation-resistant bacteria are being genetically engineered with biodegradation genes to render them suitable for the treatment of such mixed wastes [5,20,31].

One of the main reasons for the persistence of some aromatic compounds in the environment is their limited bioavailability. This is the case of hydrocarbons present in fossil fuels, which are frequently attached to soil particles. The host cell can be manipulated to enhance bioavailability of the pollutant by engineering the production of biosurfactants or by promoting chemotaxis of the biodegrader to the toxic compound [8,23]. Surfactant production has been combined with the ability to selectively cleave carbon-sulfur bonds in the sulfur-containing compounds present in oil (biodesulfurization) and, hence, efficient recombinant biodesulfurizers have been obtained [12]. Some anaerobes release Fe(III) chelators, which solubilize Fe(III) from Fe(III) oxides, and electron-shuttling compounds, which accept electrons from the cell surface and then reduce Fe(III) oxides. It has been shown that enhancing the availability of some electron acceptors, such as the insoluble Fe(III) oxides, by adding suitable ligands can greatly stimulate anaerobic degradation of contaminants in subsurface environments [16].

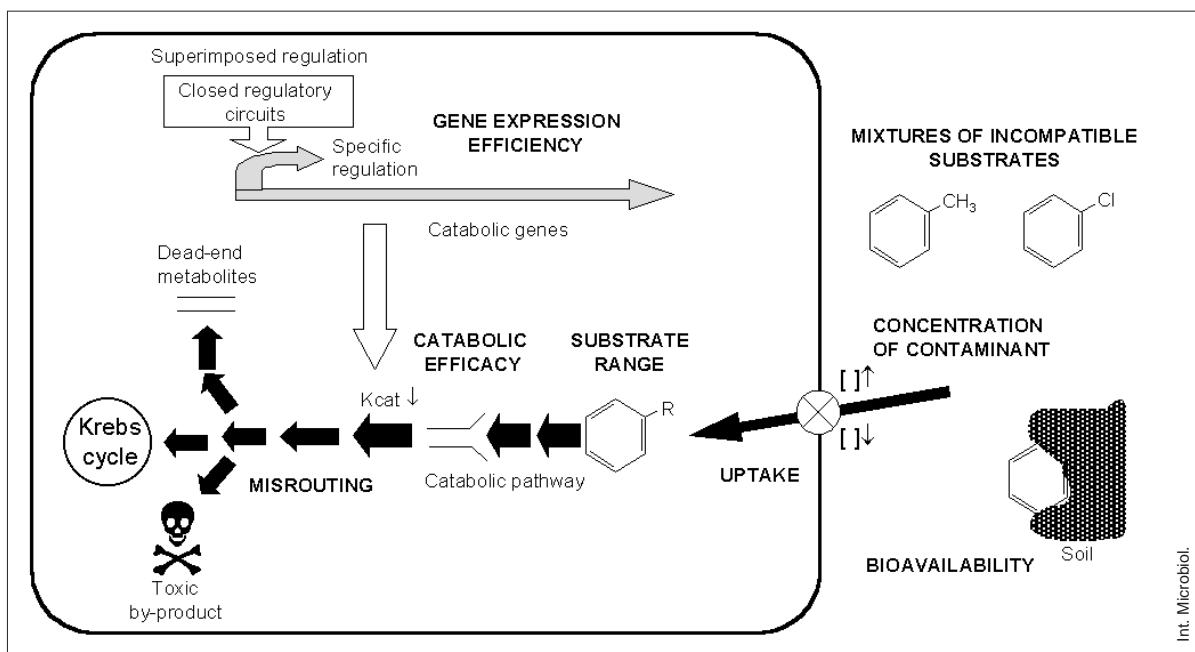


Fig. 5. Potential limitations of biological treatment approaches. The major problems that challenge biocatalyst performance are indicated by capital letters. **Gray arrows**, genes; **black arrows**, proteins.

Biosafety is a major issue when releasing recombinant microorganisms into any open environment. In order to address this concern, several genetic circuits have been developed to allow survival of the recombinant microorganism only when present in the polluted site and during the time required for removal of the pollutant (biological containment). To avoid dispersal of the recombinant trait from the recombinant bacteria to the native microbial population, different gene-containment circuits based on a toxin and its cognate antidote have also been developed. Such active containment systems reduce significantly the potential risks that release of recombinant bacteria might cause in the ecosystem [21,28].

Developing syntrophic bacterial consortia for bioremediation

It is not always possible to combine in one only organism all the required features to solve a given environmental problem, as is the case for the removal of complex mixtures in sewage plants. Under these circumstances, a suitable strategy is the generation of syntrophic bacterial consortia whose members are specialized in certain biodegradative steps or in the degradation of certain pollutants [24,27]. Plant-microbe interactions are also a feasible alternative to remove toxic compounds from

polluted environments (rhizoremediation). Bioremediation strategies involving transgenic plants that express bacterial genes for the immobilization of heavy metals or TNT removal (phytoremediation) are currently cost-effective green technologies of great public and scientific interest [20,34].

Ideally, bioremediation strategies would be designed based on knowledge of the microorganisms present in the polluted environments, their metabolic abilities, and how they respond to changes in environmental conditions. The advent of high-throughput methods for DNA sequencing and analysis of gene expression (whole-genome DNA microarrays) and function (proteomic techniques), as well as advances in the modeling of microbial metabolism (*in silico* biology), are providing new insights into environmental microbiology [16]. Biodegradation network models have been created that provide the basis for both predicting the abilities of existing or not-yet synthesized chemicals to undergo biodegradation and quantifying the evolutionary rate for their elimination in the future [19]. However, in practice, much of the required information is not yet available, and the use of microorganisms in bioremediation is highly empirical rather than knowledge-based. An alternative approach that has been shown to be successful for the treatment of some environmental disasters, including marine oil spills, is the addition of limiting nutrients (nitrogen, phosphorous, etc.) to the polluted site to enhance growth of the native microbiota able to degrade hydrocarbons (biostimulation) [34]. The

addition of terminal electron acceptors, such as sulfates, has been shown to accelerate contaminant degradation by sulfate-reducer bacteria in aquifers [1].

Conclusion

The great versatility of microorganisms offers a simpler, inexpensive and more environmentally friendly strategy to reduce environmental pollution than non-biological options. Although microorganisms represent half of the biomass of our planet, we know as little as 5% of the microbial diversity of the biosphere [3], which reveals the largely unexplored genetic pool of the microbial world. Hence, the huge potential of environmental microbiology will become crucial for promoting the welfare and sustainable growth of our society.

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Degradación bacteriana de contaminantes aromáticos: un paradigma de variabilidad metabólica

Resumen. Aunque la mayoría de los organismos pueden detoxificar el ambiente (mediante procesos de mineralización, transformación y/o inmovilización de los contaminantes), los microorganismos, especialmente las bacterias, desempeñan un papel esencial en los ciclos biogeoquímicos y en el desarrollo sostenible de la biosfera. Después de los residuos glucosilados, el anillo de benceno es la unidad química estructural más frecuente en la naturaleza, y muchos compuestos aromáticos son contaminantes importantes. Las bacterias han desarrollado estrategias para obtener energía de todo tipo de compuestos mediante procesos aeróbicos o anaeróbicos (utilizando aceptores finales de electrones alternativos como los iones nitrato, sulfato y férrico). Los grupos de genes que intervienen en el catabolismo de compuestos aromáticos suelen localizarse en elementos genéticos móviles, tales como transposones y plásmidos. Dicha localización facilita su transferencia a otros organismos y, por tanto, la rápida adaptación de los microorganismos a nuevos contaminantes. Una estrategia que se ha empleado con éxito en procesos de biorremediación *in situ* es la combinación, en una única cepa bacteriana o en un consorcio microbiano, de diferentes capacidades degradadoras con otras características genéticas que aporten alguna ventaja selectiva en un ambiente determinado. Los métodos de alto rendimiento de secuenciación de DNA y de análisis global de la expresión génica (genómica) y funcional (proteómica), junto con los avances en los modelos *in silico* del metabolismo microbiano, proporcionan un enfoque global y racional para conocer las enormes posibilidades, aún inexploradas en su mayor parte, de la utilización de los microorganismos en procesos de biotecnología ambiental que faciliten el desarrollo sostenible. [Int Microbiol 2004; 7(3):173–180]

Palabras clave: compuestos aromáticos · catabolismo · regulación transcripcional · ingeniería metabólica

Degradação bacteriana de contaminantes aromáticos: um paradigma de variabilidade metabólica

Resumo. Muito embora a maioria dos organismos tenham a capacidade de detoxificar o ambiente (mediante processos de mineralização, transformação e/ou imobilização dos contaminantes), os microorganismos, especialmente as bactérias, desempenham um papel essencial nos ciclos biogeoquímicos e no desenvolvimento sustentável da biosfera. Depois dos resíduos glicosilados, o anel benzênico é a unidade química estrutural mais frequente na natureza, e muitos compostos aromáticos são contaminantes importantes. As bactérias desenvolveram estratégias para obter energia, de todo tipo de compostos, mediante processos aeróbicos ou anaeróbicos (utilizando aceptores finais de elétrons alternativos como os íons nitrato, sulfato e férrico). Os grupos de genes que participam no catabolismo de compostos aromáticos estão localizados somente em elementos genéticos móveis, tais como os transposons e os plasmídeos. Esta localização facilita sua transferência para outros organismos e, portanto, a rápida adaptação aos novos contaminantes. Uma estratégia empregada com êxito nos processos de biorremediação *in situ* é a combinação, em uma única estirpe bacteriana ou em um consórcio microbiano, de diferentes capacidades de degradação com outras características genéticas que tragam alguma vantagem seletiva em um ambiente determinado. Os métodos de alto rendimento de sequenciamento de DNA e de análise global da expressão gênica (genômica) e funcional (proteômica), junto com os avanços nos modelos *in silico* do metabolismo microbiano, proporcionam um enfoque global e racional para conhecer as enormes possibilidades, ainda inexploradas em grande parte, da utilização dos microorganismos nos processos de biotecnologia ambiental que facilitem o desenvolvimento sustentável. [Int Microbiol 2004; 7(3):173–180]

Palavras chave: compostos aromáticos · catabolismo · regulação transcripcional · engenharia metabólica