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MINI REVIEW

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Bacterial degradation of pyridine, indole, quinoline, and their derivatives under different redox conditions

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Abstract Bacteria have evolved a diverse potential to transform and even mineralize numerous organic compounds of both natural and xenobiotic origin. This article describes the occurrence of N-heteroaromatic compounds and presents a review of the bacterial degradation of pyridine and its derivatives, indole, isoquinoline, and quinoline and its derivatives. The bacterial metabolism of these compounds under different redox conditions – by aerobic, nitrate-reducing, sulfate-reducing and methanogenic bacteria – is discussed. However, in natural habitats, various environmental factors, such as sorption phenomena, also influence bacterial conversion processes. Thus, both laboratory and field studies are necessary to aid our understanding of biodegradation in natural ecosystems and assist the development of strategies for bioremediation of polluted sites. Occurring predominantly near (former) wood-treatment facilities, creosote is a frequent contaminant of soil, subsoil, groundwater, and aquifer sediments. In situ as well as withdrawal-and-treatment techniques have been designed to remediate such sites, which are polluted with complex mixtures of aromatic and heterocyclic compounds.

Occurrence of N-heteroaromatic compounds

In nature, N-heterocyclic compounds perform a variety of biological functions. They exist as electron carriers [NAD(P)H, flavine nucleotides] and as constituents of the nucleotides in RNA, DNA and in energy-storage molecules (ATP, GTP). Other naturally occurring N-heterocycles include pyridoxine (vitamin B_6), various porphyrines, melamine, and also mycotoxins and alkaloids. Quinoline derivatives have been isolated from sea-dwelling sponges (Alvarez et al. 1991), myxobacteria (Böhlendorf et al. 1996), the cyanobacterium *Lyngbya majuscula* (Orjala and Gerwick 1997), pseudomonads, fungi, and – most abundantly – from higher plants (Sainsbury et al. 1978, 1987). Quinine alkaloids produced by subtropical *Cinchona* and *Remija* sp. are used as schizontocides against the erythrocytic stage of the malaria parasite (and also as beverage bitters).

Numerous man-made compounds – pharmaceuticals, dyes, industrial solvents, and pesticides (such as *s*-triazines, paraquat, diquat, and picloram) – are also based on N-heterocyclic compounds. N-heteroaromatics are produced mainly from coal tar. Tars are produced by low-temperature carbonization, coking, or gasification of fossil raw material or biomass (coal, lignite, peat, wood, oil shale). Shale oil contains especially high concentrations of nitrogen compounds (Bett et al. 1983). Approximately 15×10^6 t year^{-1} coal tars are produced worldwide, mainly high-temperature coal tars from coking plants. These are the basic material for industrial carbon products (approx. 4×10^6 t year^{-1}), technically pure condensed aromatic hydrocarbons (approx. 1×10^6 t year^{-1}), technically pure heteroaromatics such as carbazole, quinoline, pyridine, and indole (several thousand t year^{-1}), phenols (several hundred thousand t year^{-1}), thermoplastic indenecoumarone resins (approx. 100×10^3 t year^{-1}), and aromatic oils used as wood preservatives, solvents, and gas-washing oils ($> 2 \times 10^6$ t year^{-1}) (Collin and Höke 1995). The approximate contents of N-heteroaromatic compounds in high-temperature coal tar are 0.9% carbazole, 0.2%–0.3% quinoline, 0.2% indole, 0.1%–0.2% isoquinoline, 0.1%–0.2% 2-methylquinoline, 0.1% acridine, 0.03% pyridine, and 0.02% 2-methylpyridine (Collin and Höke 1989, 1993, 1995). Quinoline (world production >2000 t year^{-1}; Collin and Höke 1993) and carbazole are obtained exclusively from coal tar. In contrast, pyridine bases, although constituents of tars, are produced by synthesis. The amounts of pyridine bases produced

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worldwide (in 1989) were estimated as follows: pyridine, 26000 t $year^{-1}$, 2-methylpyridine 8000 t $year^{-1}$, 3-methylpyridine 9000 t $year^{-1}$, 4-methylpyridine 1500 t $year^{-1}$, 5-ethyl-2-methylpyridine 8000 t $year^{-1}$ (Shimizu et al. 1993).

In situ processes of shale oil production generate approximately equal volumes of retort waste water highly contaminated with organic solutes (Sims and O'Loughlin 1989; Leenheer et al. 1982). Pyridine and quinoline (including isoquinoline) derivatives, for instance, are major components in the basic fraction of shale oil process waters with concentrations in the range 20–100 mg l^{-1} and 2–50 mg l^{-1} respectively (roughly estimated from several reports: Richard and Junk 1984; Dobson et al. 1985; Zhu et al. 1988; Leenheer et al. 1982).

Although azaarenes may enter the environment through a variety of sources, coal gasification sites, oil processing facilities, coal-tar wastes, and creosote are the major ones (Table 1). Creosote is a distillate of coal tar. It contains more than 200 individual compounds and consists of up to 75%–85% (by weight) polynuclear aromatic hydrocarbons, 5%–15% monoaromatic hydrocarbons, 1%–12% phenolic, and 3%–13% N-, S-, and O-heterocyclic compounds (Mueller et al. 1989; Godsy et al. 1994, Dyreborg et al. 1997). Quinoline, isoquinoline, carbazole, 2,4-dimethylpyridine (each in concentrations of about 10 mg l^{-1}), acridine, 2- and 4-methylquinoline, pyrrole, and pyrrolidine (5 mg l^{-1} each) are the major N-heterocyclic compounds in creosote (Mueller et al. 1989). Many of the more than 700 wood-preserving plants in the U.S. use creosote as the primary wood-preserving chemical. Creosoting operations within the U.S. were reported to consume approximately 4.5×10^7 kg creosote annually (Mattraw and Franks 1986).

Heteroaromatic compounds generally are more polar than their homocyclic analogs and possess lower octanol/water partition coefficients (K_{ow}) (for log K_{ow} values, see Hansch and Leo 1979; Sims and O'Loughlin 1989; Ondrus and Steinheimer 1990). Owing to their relatively high water solubilities and weak sorption to soil and aquifer organic material, many heteroaromatic pollutants are readily transported to subsurface environments, resulting in contamination of subsoil and groundwater (for reviews on groundwater pollution, and analysis, see Canter and Sabatini 1994; Hale and Aneiro 1997; Mayer et al. 1997). Table 1 lists some cases of groundwater pollution by N-heterocyclic compounds. These contaminated ecosystems generally contain complex mixtures of coal tar compounds (polynuclear aromatic hydrocarbons, phenolics, and heterocycles). At the American Creosote Works Superfund site near Pensacola, Florida, an abandoned wood-treatment facility, groundwater samples contained up to several milligrams per liter each of quinoline, isoquinoline, and their oxo derivatives, depending on the distance of the sampling

Table 1 Detection of pyridine, indole, isoquinoline, quinoline and their derivatives and some other N-heteroaromatic compounds in polluted groundwaters

N-heterocyclic pollutants	Origin of groundwater pollution	References
Methylpyridine	Coal distillation, synthesis of pesticides, rubber, vinyl pyridine, solvent	Dunlap et al. 1976
Pyridine, alkyl(C-1 to C-5)pyridines, dialkyl(C-1,C-2)pyridines, quinoline, isoquinoline, methylquinolines, dimethylquinolines, (methyl)tetrahydroquinolines	Coal gasification site	Stuermer et al. 1982
Alkylpyridines	Oil shale facility	Riley et al. 1981
3-Methylindole	Leachate from municipal refuse	Harmsen 1983
Quinoline, 2(1*H*)quinolinone, isoquinoline, 1(2*H*)isoquinolinone, 2- and 4-methylquinoline, (di)methylquinolinones, 2-methylisoquinolinone, benzoquinolines, carbazole, acridine, 9(10*H*)acridinone	Former wood-treatment plant (American Creosote Works Superfund site, Pensacola, Fla.)	Pereira et al. 1987a;b; Ondrus and Steinheimer 1990; Godsy et al. 1992, 1994
Alkyl(C-1,C-2)pyridines, phenylpyridines, quinoline, (di)methylquinolines, isoquinoline, (iso)quinolinones, methylquinolinones, benzoquinolines, 1,2,3,4-tetrahydro(methyl)quinolines, acridine, 9(10*H*)acridinone	Former coal-tar distillation and wood-preserving facility	Pereira et al. 1983; Ondrus and Steinheimer 1990
Pyridine, (mono-/di-/tri-) methylpyridines, 2-ethyl-6-methylpyridine, (mono-/di-) methylquinolines, isoquinoline, (iso) quinolinones, carbazole	Coal and oil gasification site with nonaqueous phase liquids	Turney and Goerlitz 1990
1(2*H*)Isoquinolinone, methyl and dimethyl derivatives of 2(1*H*)quinolinone, 6(5*H*)phenanthridinone	Former gas plant	Edler et al. 1997
About 50 organic tar compounds; among 17 N-/S-/O-heteroaromatic compounds: carbazole, 2(1*H*)quinolinone, 1(2*H*) isoguinolinone, basic N-compounds	Three different creosote sites	Johansen et al. 1997a
Coal-tar compounds	Subsurface nonaqueous-phase liquids at coke ovens site (steel production)	Baechler and MacFarlane 1992
Creosote compounds	Subsurface nonaqueous-phase liquids at former wood-treating facility	Mueller et al. 1997

wells from the source of contamination (Pereira et al. 1987a, b; Godsy et al. 1992, 1994; Ondrus and Steinheimer 1990). A literature survey of the maximum concentrations of N–heteroaromatic compounds in creosote-contaminated groundwater was reported by Johansen et al. (1997a).

The contamination of groundwater by transport of N-heteroaromatic compounds through soil and subsoils is a major environmental concern, since many of these compounds are considered toxic and/or mutagenic and cancerogenic (Hirao et al. 1976; Nagao et al. 1977; Santodonato and Howard 1981; LaVoie et al. 1988; Willems et al. 1992). Apart from groundwater and aquifers, N-heteroaromatic compounds have also been identified in aquatic sediments, industrial and urban air, tobacco smoke, sea water, and the tissue of fish (Santodonato and Howard 1981; Adams et al. 1983; Barrick et al. 1984; Warshawsky 1992).

There are a number of review articles on the microbial metabolism of both natural and xenobiotic N-heteroaromatic compounds. This mini-review describes the pathways of bacterial degradation of pyridine and its derivatives, indole, isoquinoline, and quinoline and its derivatives. The biodegradation of these coal tar compounds under different redox conditions is compared, environmental factors that influence bacterial degradation processes are discussed briefly, and some biotechnological applications are indicated. For literature on the degradation of purines, pyrimidines, tryptophan, pyridoxine, acridine, and *s*-triazines, see, for example, the reviews of Vogels and van der Drift 1976; Scazzocchio 1994; Callely 1978; Berry et al. 1987a; Bollag and Kaiser 1991; Koenig and Andreesen 1992; Kaiser et al. 1996; Cook 1987.

Bacterial degradation under aerobic conditions

Degradation of N-heteroaromatic compounds very often is initiated by a hydroxylation adjacent to the N-heteroatom. This feature applies to pyridine (Fig. 1) and derivatives such as nicotinate (Fig. 2), picolinate, isonicotinate (Fig. 3) as well as to isoquinoline (Fig. 4), quinoline and various quinoline derivatives (Fig. 5), and xanthine. The incorporated oxygen typically is derived from water, and a number of molybdenum-containing hydroxylases catalyzing these hydroxylation reactions have been characterized thoroughly (for reviews on the enzymology and genetics of this type of hydroxylation, see Hille 1996; Romão and Huber 1998; Fetzner et al. 1998). The utilization of pyrrole-2-carboxylate by *Arthrobacter* sp. strain Py1 and *Rhodococcus* sp. strain Sedi2, however, is initiated by an oxygenation reaction, catalyzed by distinct NADH-dependent pyrrole-2-carboxylate monooxygenases (Hormann and Andreesen 1991, 1994; Becker et al. 1997).

Aerobic degradation in many cases involves several hydroxylation steps, followed by dioxygenolytic cleavage of the (hetero)aromatic ring. However, there are also aerobic pathways involving reductive steps prior to ring cleavage.

Pyridine and derivatives

Chemically, the pyridine ring is susceptible to reduction and to attack by nucleophilic agents (preferably at C-2 and C-4). These characteristic properties have been exploited by microorganisms for evolving mechanisms for pyridine ring degradation. Two general strategies of bacterial pyridine degradation involve (i) hydroxylation reactions, followed by reduction, and (ii) (aerobic) reductive pathway(s) not initiated by hydroxylations (for detailed reviews on the biodegradation of pyridine and its derivatives, see Shukla 1984; Sims and O'Loughlin 1989; Kaiser et al. 1996). Biodegradability of pyridine derivatives was found generally to follow the order pyridinecarboxylic acids > pyridine ≡ monohydroxypyridines > methylpyridines > aminopyridines ≡ chloropyridines (Naik et al. 1972; Sims and Sommers 1985, 1986; Sims and O'Loughlin 1989).

Pyridine

The ability to degrade pyridine is widespread in microorganisms. Hypothetical pathways for the aerobic microbial degradation of pyridine are summarized in Fig. 1. From a number of organisms (Fig. 1A–F), only aliphatic intermediates of pyridine degradation have been identified, and some (pyridine-induced) enzymes converting (proposed) aliphatic intermediates detected. However, the mechanism(s) of cleavage of the pyridine ring remain(s) unknown (Fig. 1A– F). In earlier studies, hydroxylated pyridine derivatives were not observed during the transformation of pyridine. In contrast, UV and IR spectroscopy and gas chromatography/mass spectrometry analyses of extracts of the culture broth of *Rhodococcus opacus* and *Arthrobacter crystallopoietes* strains revealed the formation of a number of hydroxylated metabolites during pyridine utilization. Products of pyridine ring cleavage were also detected, but studies on the enzymes that would be involved in the proposed pathways were not performed (Fig. 1G, H; Zefirov et al. 1994).

Alkylpyridines

For 2-methylpyridine utilization by an *Arthrobacter* strain, a reductive pathway involving succinic semialdehyde (cf. Fig. 1) as intermediate was suggested (Shukla 1974, 1984). Degradation of 2- and 4-ethylpyridine by a mixed culture from soil was found to involve ring hydroxylation and reduction prior to ring cleavage (Feng et al. 1994).

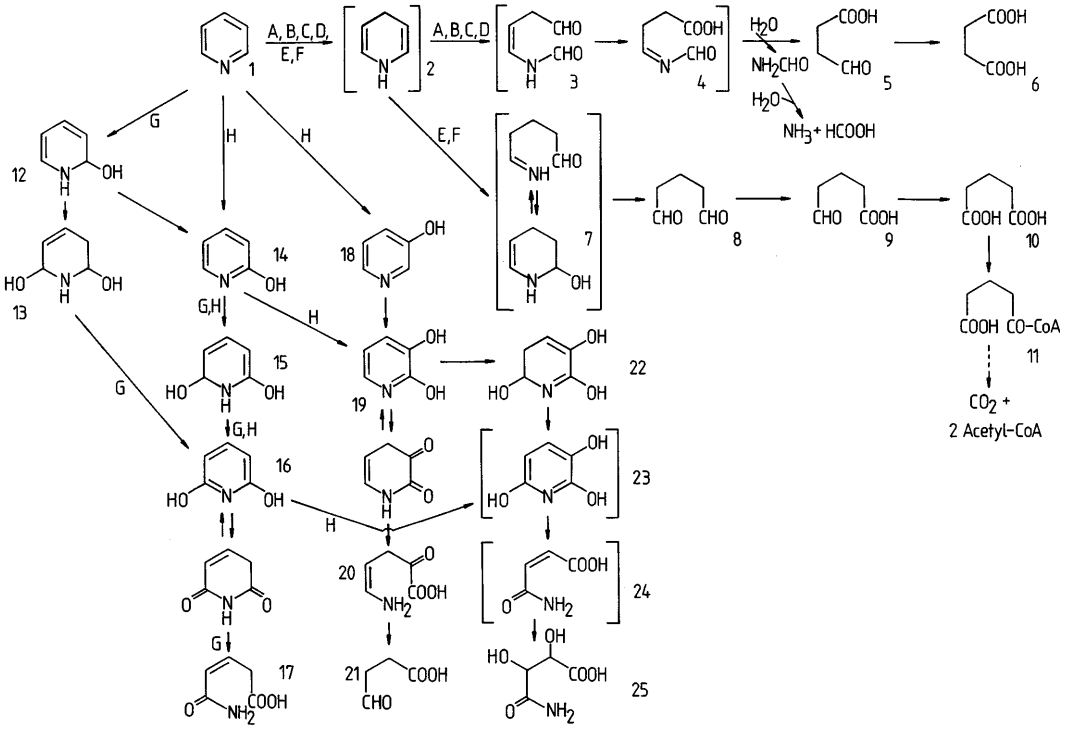


Fig. 1 Pathways of aerobic bacterial degradation of pyridine. *A Corynebacterium* sp. (Shukla and Kaul 1974; Shukla 1984), *B Bacillus* sp. (Watson and Cain 1975; Shukla 1984), *C Micrococcus luteus* (Sims et al. 1986), *D Nocardia* sp. PNO (Shukla and Kaul 1986), *E Nocardia* sp. Z1 (Watson and Cain 1975), *F Azoarcus evansii* pF6 (Rhee et al. 1997), *G Rhodococcus opacus*, and *H Arthrobacter crystallopoietes* (Zefirov et al. 1994). Pyridine *1*; 1,4-dihydropyridine *2*; *N*-formylaminovinylacetaldehyde *3*; *N*-formylaminovinylacetic acid *4*; succinic semialdehyde *5*; succinic acid *6*; 2-hydroxy-1,2,3,4-tetrahydropyridine *7*; glutaric dialdehyde *8*; glutaric semialdehyde *9*; glutaric acid *10*; glutaryl-coenzyme A *11*; 2-hydroxy-1,2-dihydropyridine *12*; 2,6-dihydroxy-1,2,3,6-tetrahydropyridine *13*; 2-hydroxypyridine *14*; 2,6-dihydroxy-1,2-dihydropyridine *15*; 2,6-dihydroxypyridine *16*; 3-pentenoic acid monoamide *17*; 3-hydroxypyridine *18*; 2,3-dihydroxypyridine *19*; 5-amino-2-oxo-4-pentenoic acid *20*; succinic semialdehyde *21*; 2,3-dihydro-2,5,6-trihydroxypyridine *22*; 2,3,6-trihydroxypyridine *23*; maleamic acid *24*; tartaric acid monoamide *25*. (Compounds depicted in brackets were not detected)

Hydroxypyridines

Degradation of hydroxypyridines occurs via hydroxylation of the ring yielding a di- or trihydroxypyridine intermediate, followed by ring cleavage (cf. Fig. 1; Houghton and Cain 1972; Shukla 1984; Kaiser et al. 1996). 3,4-Dihydroxypyridine undergoes *meta* cleavage (2,3-dioxygenolysis) in an *Agrobacterium* sp. (Watson et al. 1974). In *Nocardia* sp. strain PNO, 2-hydroxypyridine is hydroxylated to 2,5-dihydroxypyridine (and presumably to 2,3,6-trihydroxypyridine) prior to ring cleavage and formation of maleamate (Shukla and Kaul 1986). 2,5-Dihydroxypyridine was found to undergo 5,6-dioxygenolytic ring cleavage and subsequent hydrolysis to maleamate and formate in *Achromobacter* sp. (cf. Fig. 2; Cain et al. 1974).

Pyridine carboxylic acids

Nicotinic acid may undergo degradation via the maleamate pathway, as outlined in Fig. 2A, B. Surprisingly, *Azorhizobium caulinodans*, as does *Clostridium barkeri*, reduces 6-hydroxynicotinate to 6-oxo-1,4,5,6-tetrahydronicotinate, which subsequently undergoes hydrolytic degradation (Fig. 2C). In contrast to the fermentative pathway (Fig. 7), the *Azorhizobium* pathway involves glutaric acid as intermediate (Fig. 2C; Kitts et al. 1992). Succinic semialdehyde (see Fig. 1) was characterized as a key intermediate of isonicotinic acid degradation by *Bacillus brevis*, and a pathway involving oxygenative cleavage of the partially reduced pyridine ring was proposed (Singh and Shukla 1986). In contrast, *Mycobacterium* sp. INA1 (Kretzer et al. 1993), *Pseudomonas* sp. (Ensign and Rittenberg 1965) and *Micrococcus* (formerly, *Sarcina*) sp. (Gupta and Shukla 1979) degrade isonicotinic acid via 2-hydroxy- and 2,6-dihydroxyisonicotinic acid. Further degradation by *Mycobacterium* sp. strain INA1 involves coenzyme A activation and ring reduction prior to ring cleavage and 2-oxoglutarate formation (Fig. 3; Kretzer et al. 1993). Picolinic acid, which may occur as degradation product of the herbicide diquat, is initially hydroxylated at C-6, and there is a second hydroxylation at C-3. Decarboxylation produces 2,5-dihydroxypyridine, which is further metabolized via the maleamate pathway (cf. Fig. 2) in a *Bacillus* sp. and in a gram-negative isolate (Shukla and Kaul 1973; Shukla et al. 1977). Dipicolinic acid, a typical constituent of the core of the bacterial endospore, is degraded by *Achromobacter* via hydroxylation at C-3 and ring cleavage between C-2 and C-3. Subsequent hydrolysis

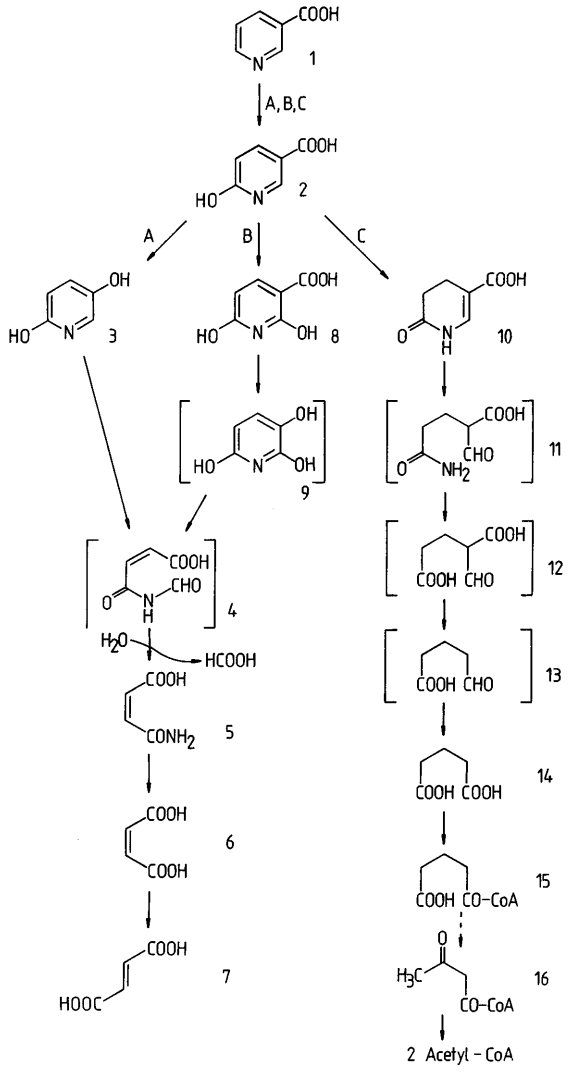


Fig. 2 Pathways of aerobic bacterial degradation of nicotinic acid. *A Pseudomonas* sp. (Behrman and Stanier 1957), *B Bacillus* sp. (Ensign and Rittenberg 1964; Hirschberg and Ensign 1971; Nagel and Andreesen 1989, 1990, 1991), *C Azorhizobium caulinodans* (Kitts et al. 1992). Nicotinic acid *1*; 6-hydroxynicotinic acid *2*; 2,5-dihydroxypyridine *3*; *N*-formylmaleamic acid *4*; maleamic acid *5*; maleic acid *6*; fumaric acid *7*; 2,6-dihydroxynicotinic acid *8*; 2,3,6-trihydroxypyridine *9*; 6-oxo-1,4,5,6-tetrahydronicotinic acid *10*; 2-formylglutaryl-5-amide *11*; 2-formylglutaric acid *12*; glutaric semialdehyde *13*; glutaric acid *14*; glutaryl-coenzyme A *15*; acetoacetyl-coenzyme A *16*. (Compounds depicted in brackets were not detected)

and rearrangement reactions generate oxalate, ammonia, and 2-oxoglutarate (Kobayashi and Arima 1962).

Indole

Claus and Kutzner (1983) investigated indole catabolism by *Alcaligenes* sp. strain IN3. Indole was metabolized via isatin and anthranilate (cf. Fig. 8) to gentisate, which was subsequently cleaved to maleylpyruvate.

Isoquinoline

Several bacterial strains utilizing isoquinoline have been isolated. All isolates metabolized isoquinoline via 1(2*H*)isoquinolinone (Aislabie et al. 1989, 1994; Röger et al. 1990). For *Brevundimonas diminuta* strain 7, a putative degradation pathway via phthalate, 4,5-dihydroxyphthalate, and protocatechuate was suggested by Röger et al. (1995) (Fig. 4).

Quinoline and derivatives

Currently, four pathways of aerobic degradation of quinoline (derivatives) are known, namely, the 5,6-dihydroxy-2(1*H*)quinolinone pathway, the 7,8-dihydroxy-2(1*H*)quinolinone pathway, the anthranilate pathway, and the 8-hydroxycoumarin pathway (Fig. 5; for reviews on the pathways and on the enzymes involved, see Schwarz and Lingens 1994; Fetzner et al. 1998). In both the 5,6- and the 7,8-dihydroxy-2(1*H*)quinolinone pathway, after initial hydroxylation adjacent to the N-heteroatom, the benzene moiety of the quinoline ring is transformed to a dihydroxy derivative (5,6- or 7,8- respectively), which subsequently undergoes ring cleavage (Fig. 5a, b). Formation and dioxygenolytic cleavage of dihydroxy compounds is a common strategy of aerobic bacteria to degrade aromatic compounds. In contrast, in both the anthranilate pathway (Fig. 5c; Hund et al. 1990; Bott et al. 1990) and the 8-hydroxycoumarin pathway (Fig. 5d; Shukla 1986, 1989; Schwarz et al. 1989), the pyridine ring is degraded prior to benzene ring cleavage. In the anthranilate pathway of quinaldine (Fig. 5c) and 4(1*H*)quinolinone degradation, 2,4-dioxygenases catalyze the cleavage of the pyridine

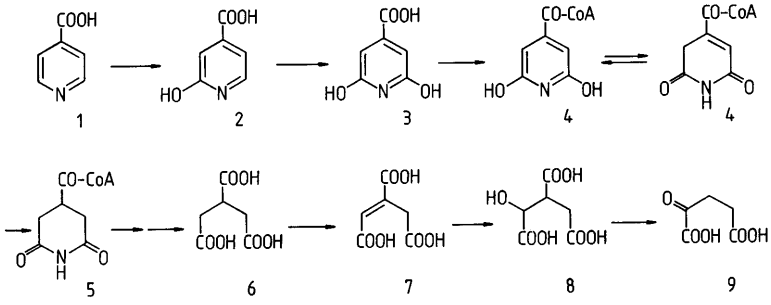


Fig. 3 Aerobic degradation of isonicotinic acid by *Mycobacterium* sp. INA1 (Kretzer et al. 1993). Isonicotinic acid *1*; 2-hydroxyisonicotinic acid *2*; citrazinic acid *3*; citrazyl-coenzyme A *4*; 2,6-dioxopiperidine-4-carboxyl-coenzyme A *5*; propane-1,2,3-tricarboxylic acid *6*; *cis*-aconitic acid *7*; isocitric acid *8*; 2-oxoglutaric acid *9*

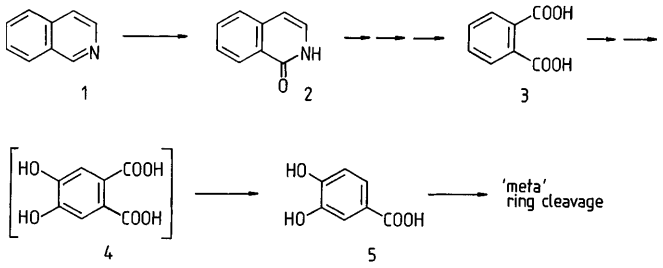
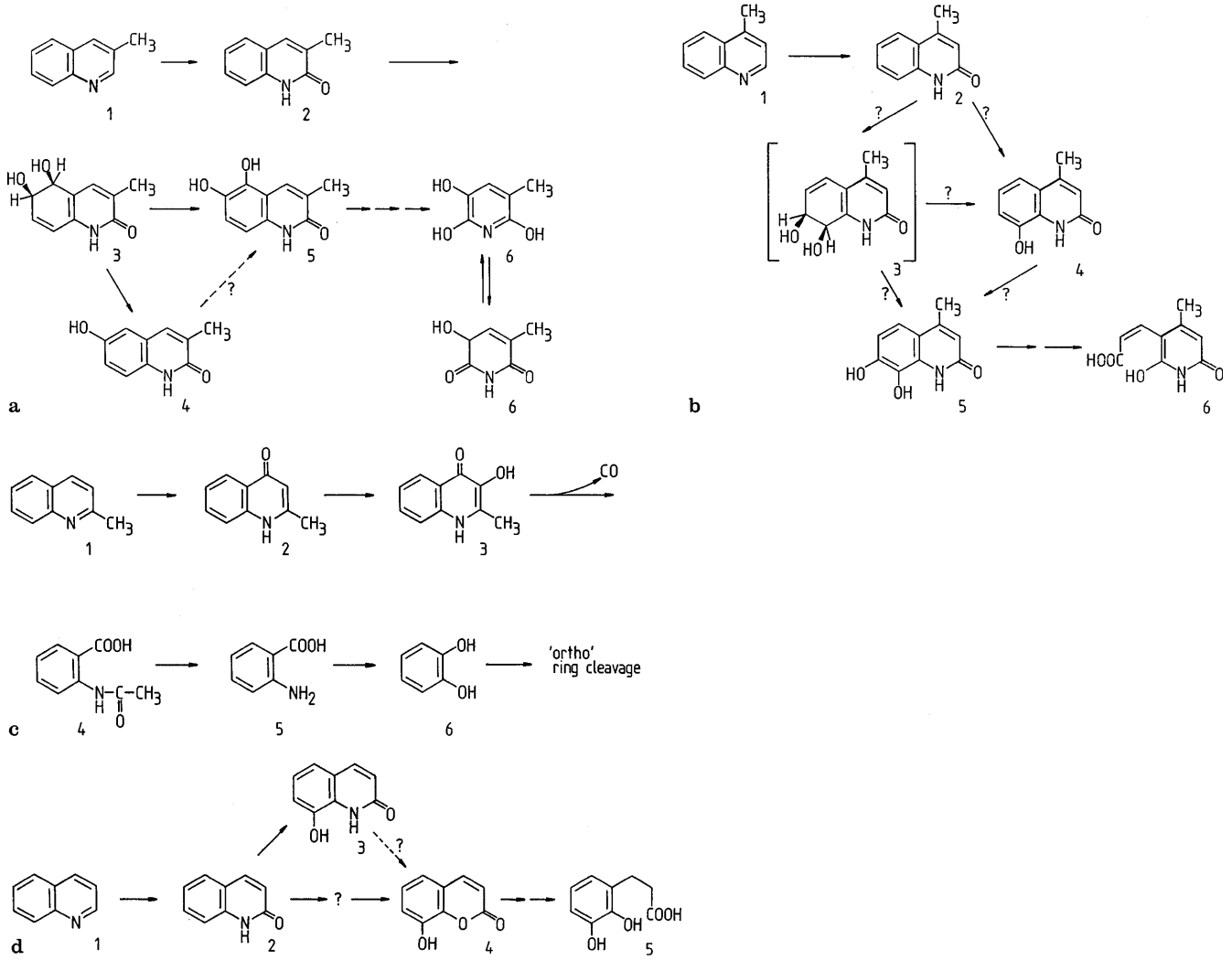


Fig. 4 Hypothetical pathway of aerobic degradation of isoquinoline by *Brevundimonas diminuta* 7 (Röger et al. 1995). Isoquinoline *1*; 1(2*H*)isoquinolinone *2*; phthalic acid *3*; 4,5-dihydroxyphthalic acid *4*; protocatechuic acid *5*. (Compound in brackets: not detected)

moiety of 2-methyl-3-hydroxy-4(1*H*)quinolinone and 3-hydroxy-4(1*H*)-quinolinone respectively. These dioxygenases are rather exceptional, since they catalyze the cleavage of two carbon-carbon bonds of the respective substrate with concomitant release of carbon monoxide (Fig. 6; Bauer et al. 1994, 1996).

Fig. 5a–d Degradation of quinoline and its derivatives by aerobic bacteria. **a** 5,6-Dihydroxy-2(1*H*)quinolinone pathway: early steps of the degradation pathway of 3-methylquinoline by *Comamonas testosteroni* 63 (Schach et al. 1993, 1995). 3-Methylquinoline *1*; 3-methyl-2(1*H*)quinolinone *2*; 5,6-dihydro-5,6-dihydroxy-3-methyl-2(1*H*)quinolinone *3*; 6-hydroxy-3-methyl-2(1*H*)quinolinone *4*; 5,6-dihydroxy-3-methyl-2(1*H*)quinolinone *5*; 3-methyl-2,4,6-trihydroxypyridine *6*. **b** 7,8-Dihydroxy-2(1*H*)quinolinone pathway: proposed early steps of degradation of 4-methylquinoline by *Pseudomonas putida* K1 (Rüger et al. 1993). 4-Methylquinoline *1*; 4-methyl-2(1*H*)quinolinone *2*; 7,8-dihydro-7,8-dihydroxy-4-methyl-2(1*H*) quinolinone *3*; 8-hydroxy-4-methyl-2(1*H*)quinolinone *4*; 7,8-dihydroxy-4-methyl-2(1*H*)quinolinone *5*; 6-hydroxy-5-(2-carboxyethenyl)-4-methyl-2(1*H*)pyridone *6*. (Compound in brackets: not detected). **c** Anthranilate pathway: degradation of quinaldine (2-methylquinoline) by *Arthrobacter* sp. Rü61a (Hund et al. 1990; Bauer et al. 1994). Quinaldine (2-methylquinoline) *1*; 2-methyl-4(1*H*)-quinolinone *2*; 3-hydroxy-2-methyl-4(1*H*)quinolinone *3*; *N*-acetylanthranilic acid *4*; anthranilic acid *5*; catechol *6*. An analogous pathway, via 3-hydroxy-4(1*H*)quinolinone, *N*-formylanthranilate, and anthranilate, was found for the utilization of 4(1*H*)quinolinone by *Pseudomonas putida* 33/1 (Bott et al. 1990; Bauer et al. 1994). **d** Early steps of the 8-hydroxycoumarin pathway of aerobic quinoline degradation (Shukla 1986, 1989; Schwarz et al. 1989). Quinoline *1*; 2(1*H*)quinolinone *2*; 8-hydroxy-2(1*H*)quinolinone *3*; 8-hydroxycoumarin *4*; 2,3-dihydroxyphenylpropionic acid *5*



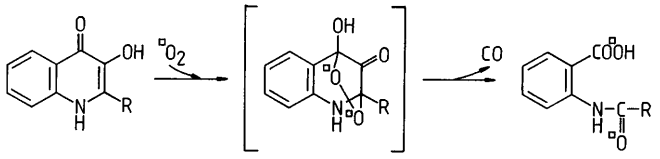


Fig. 6 2,4-Dioxygenolysis. Reactions catalyzed by (1*H*)-3-hydroxy-4-oxoquinoline 2,4-dioxygenase (R = H) (*Pseudomonas putida* 33/1) and by (1*H*)-3-hydroxy-4-oxoquinaldine 2,4-dioxygenase (R = CH_3) (*Arthrobacter* sp. Rü61a). The 2,4-dioxygenolytic (□) mode of ring cleavage was proven by dioxygen incorporation studies, allowing the enzyme-catalyzed reaction to proceed in a 50% ($^{16}O)O_2$ /50% ($^{18}O)O_2$ atmosphere (Bauer et al. 1996). (In brackets: proposed catalytic intermediate)

Bacterial transformation or degradation under anoxic conditions

Anaerobiosis occurs in any habitat in which oxygen consumption exceeds its supply. Examples include compacted or flooded soils, sediments from eutrophic lakes, landfills, lagoons, and some groundwater. One of the most important anoxic habitats is the saturated subsurface soil. Heteroaromatic compounds showing relatively good water solubility, low sorption and thus high aqueous mobility have often been found in subsurface environments (Table 1).

Comparison of the bacterial conversion under nitrate-reducing, sulfate-reducing and methanogenic conditions

In order to predict the fate of heterocyclic aromatic compounds in a habitat, it is important to evaluate the physical, chemical and physiological factors of the environment that affect the bioavailability and the metabolism of bioconversion or biodegradation, such as temperature, pH, moisture, salinity, oxygen concentration, availability of electron donors and electron acceptors, sorption of chemicals to particulate material, and concentration of chemicals. The availability of a specific electron acceptor, for instance, may govern biotransformation (Bollag and Kaiser 1991; Kaiser and Bollag 1991, 1992). Under certain redox conditions, complete mineralization of a compound may be observed, while under others transformation may be incomplete or may not occur at all.

Kuhn and Suflita (1989) compared the anaerobic biodegradation of some pyridine derivatives (0.2 mM initial concentration) by anoxic aquifer slurries incubated under sulfate-reducing or methanogenic conditions. Nicotinic acid was the most readily depleted compound under both redox conditions, having disappeared after 1 month. Pyridine was removed after 8 months under both redox conditions, whereas 2- and 4-methylpyridine disappeared only under sulfate-reducing and methanogenic conditions, respectively. 3-Methylpyridine was partially transformed in 8 months only under sulfate-reducing conditions. Liu et al. (1994a) evaluated the influence of redox conditions on the anaerobic biotransformation of pyridine, quinoline, indole and carbazole in anoxic freshwater sediment slurries. Pyridine (10 mg l^{-1}) was rapidly lost from the sediment slurries within 4 weeks under denitrifying conditions but persisted for up to 3 months under sulfate-reducing and methanogenic conditions. Quinoline (10 mg l^{-1}) was completely transformed to 2(1*H*)quinolinone under methanogenic and sulfate-reducing conditions after incubation for 23 and 45 days respectively. The hydroxylated product accumulated and was not further transformed. (In contrast, quinoline has been shown to be biodegraded under methanogenic conditions by Godsy et al. 1992, 1994) Under denitrifying conditions, less than 23% of the initial concentration of quinoline was transformed after 83 days. Indole (10 mg l^{-1}) was completely removed from the sediment slurries under methanogenic, nitrate-reducing, and sulfate-reducing conditions after 17, 18, and 27 days respectively. Stoichiometric amounts of oxindole accumulated under sulfate-reducing conditions, whereas under methanogenic and denitrifying conditions it was further degraded via unknown compounds. No evidence for anaerobic biotransformation of carbazole was noted. Carbazole strongly sorbed to the sediments and was the least bioavailable of the N-heterocyclic compounds investigated (Liu et al. 1994a). In another comparative study, soil samples from a creosote-contaminated site in Denmark were used as inoculum to examine the degradation of indole and quinoline under nitrate-reducing, sulfate-reducing, and methanogenic conditions. Indole and quinoline were transformed under all three redox conditions, with highest degradation rates observed under sulfate-reducing conditions. Maximum conversion rates were as follows: denitrifying conditions, indole 1.9 μmol l^{-1} day^{-1}, quinoline 0.5 μmol l^{-1} day^{-1}; methanogenic conditions, indole 6.6 μmol l^{-1} day^{-1}, quinoline 1.8 μmol l^{-1} day^{-1}; sulfate-reducing conditions, indole 16.0 μmol l^{-1} day^{-1}, quinoline 13.1 μmol l^{-1} day^{-1} (Licht et al. 1996). Similarly, Dyreborg et al. (1997), investigating the potential of groundwater microorganisms to degrade some N-, S-, and O-heteroaromatic compounds, reported that quinoline was degraded by anaerobic microcosms with degradation rates that were slightly higher under sulfate-reducing conditions than under denitrifying and methanogenic conditions.

Pyridine and derivatives

Pyridine

Degradation of pyridine has been observed to occur under nitrate-reducing, sulfate-reducing and methanogenic conditions (Kaiser and Bollag 1991, 1992; Kuhn and Suflita 1989; Bak and Widdel 1986; Ronen

and Bollag 1991, 1992; Battersby and Wilson 1989). *Azoarcus evansii* strain pF6 degrades pyridine under both aerobic and nitrate-reducing conditions through the same pathway (Fig. 1F; Rhee et al. 1997). Hydroxy intermediates were not involved in this pathway. In contrast, Kaiser and Bollag (1991) suggested that 3-hydroxypyridine might be an intermediate in pyridine degradation by mixed cultures obtained from sewage sludge under nitrate- and sulfate-reducing conditions.

Alkylpyridines

2-, 3-, and 4-methylpyridine were utilized by various sulfate-reducing mixed cultures (Kuhn and Suflita 1989; Kaiser and Bollag 1992; Kaiser et al. 1993). 4-Methyl-2(1*H*)pyridone was identified as intermediate of 4-methylpyridine degradation (Kaiser et al. 1993). Complete mineralization of 4-methylpyridine by aquifer slurries also occurred under methanogenic conditions (Kuhn and Suflita 1989).

Hydroxypyridines

2-, 3-, and 4-hydroxypyridine disappeared completely from a sulfate-reducing mixed culture obtained from polluted subsurface soil (Kaiser and Bollag 1992). Mixed cultures from sewage sludge completely degraded 3-hydroxypyridine under sulfate- and nitrate-reducing conditions (Kaiser and Bollag 1991).

Pyridine carboxylic acids

Nicotinic acid was degraded in anoxic aquifer slurries under methanogenic conditions, whereas, in this study, pyridine was not mineralized (Adrian and Suflita 1994). Nicotinic acid was degraded by sulfate-reducing and methanogenic aquifer slurries (Kuhn and Suflita 1989). The sulfate-reducing bacterium *Desulfococcus niacini* completely mineralizes nicotinic acid via unknown intermediates (Imhoff-Stuckle and Pfennig 1983). In the fermentative pathway of nicotinic acid degradation by *Clostridium barkeri*, the initial step is ring hydroxylation, followed by a ring reduction – ring cleavage sequence as shown in Fig. 7 (Stadtman et al. 1972). A fermentative bacterium in a defined two-membered coculture from marine sediment degraded dipicolinate to propionate, acetate, NH_3 and CO_2 (Seyfried and Schink 1990).

Indole

Complete microbial degradation of indole has frequently been observed under nitrate-reducing as well as under sulfate-reducing and methanogenic conditions (Wang et al. 1984; Berry et al. 1987b; Madsen et al. 1988; Shanker and Bollag 1990; Liu et al. 1994a; Licht et al. 1996). The transformation pathway of indole by

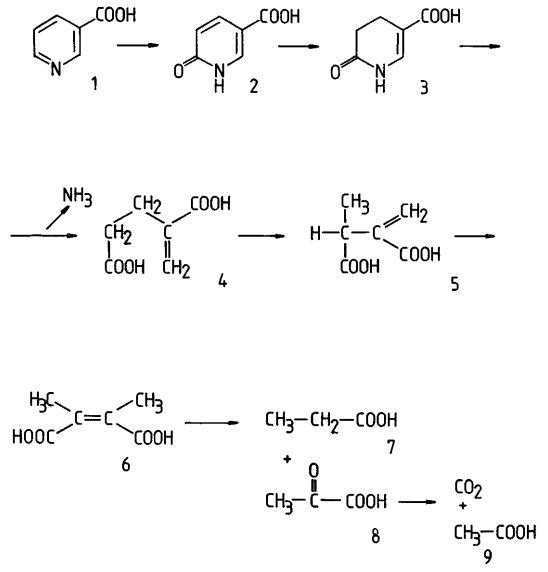


Fig. 7 Pathway of nicotinic acid fermentation by *Clostridium barkeri* (Stadtman et al. 1972). Nicotinic acid *1*; 1,6-dihydro-6-oxonicotinic acid *2*; 6-oxo-1,4,5,6-tetrahydronicotinic acid *3*; 2-methyleneglutaric acid *4*; methylitaconic acid *5*; dimethylmaleic acid *6*; propionic acid *7*; pyruvic acid *8*; acetic acid *9*

Desulfobacterium indolicum preceeds via oxindole, isatin, and anthranilate (Fig. 8; Johansen et al. 1997b). The same catabolic steps were suggested for indole mineralization by a denitrifying microbial community obtained from sewage sludge (Madsen and Bollag 1989). This anaerobic pathway shows similarities to the early steps of the aerobic indole catabolism described above (Claus and Kutzner 1983).

Isoquinoline, quinoline and its derivatives

Isoquinoline and quinoline can be degraded anaerobically. Isoquinoline has been removed from municipal sludge in a primary digester (Parker et al. 1994) and from creosote-contaminated aquifer material and groundwater (Godsy et al. 1992, 1994) under methanogenic conditions. Anoxic sediment slurries from both a freshwater and an oceanic (3.7% salinity) environment showed a complete loss of quinoline (approximately 0.2 mM) within 3 months (Liu and Kuo 1996). Quinoline completely disappeared from a mixed culture from creosote-polluted soil under nitrate-reducing, sulfate-reducing and methanogenic conditions (Licht et al. 1996). Whereas, in some studies, 2(1*H*)quinolinone accumulated from quinoline under sulfate-reducing and methanogenic conditions (Pereira et al. 1988; Liu et al. 1994a), complete degradation under methanogenic conditions was also observed (Battersby and Wilson 1989; Godsy et al. 1992, 1994; Liu et al. 1994b). Licht et al. (1997) proposed that the sulfate-reducing bacterium *D. indolicum*, which is able to grow on indole and quinoline (Bak and Widdel 1986), uses the same inducible enzyme to hydroxylate both indole and quinoline,

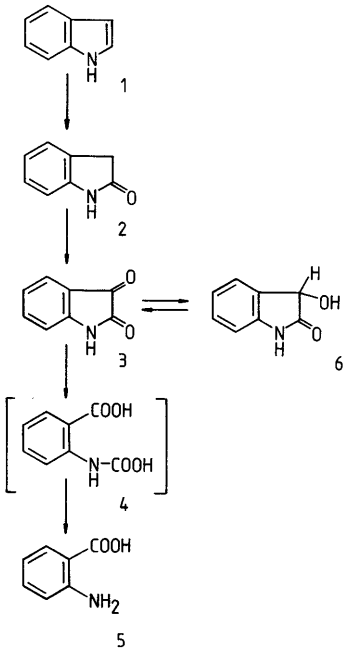


Fig. 8 Early steps of anaerobic degradation of indole by *Desulfobacterium indolicum* (Johansen et al. 1997b) and hypothetical metabolic steps of indole degradation by a denitrifying microbial community enriched from sewage sludge (Madsen and Bollag 1989). Indole *1*; oxindole *2*; isatin *3*; isatoic acid *4*; anthranilic acid *5*; dioxindole *6*. (Compound in brackets: not detected)

forming oxindole and 2(1*H*)quinolinone respectively. *D. indolicum*, after this initial hydroxylation at position 2, forms 3,4-dihydro-2(1*H*)quinolinone (Fig. 9), which is further transformed into unidentified products. 6- and 8-methylquinoline were converted to 6- and 8-methyl-3,4-dihydro-2(1*H*)quinolinone in stoichiometric amounts, whereas 3- and 4-methyl-2(1*H*)quinolinone were not reduced by *D. indolicum* (Johansen et al. 1997b). The degradation of quinoline in a biofilm system under denitrifying conditions likewise proceeded via 2(1*H*)quinolinone and 3,4-dihydro-2(1*H*)-quinolinone, which subsequently was converted to unidentified compounds. 3-, 4-, 6-, and 8-methylquinoline also were hydroxylated at C-2. The hydroxylated metabolites of the quinolines methylated at the heterocyclic ring were not transformed further, whereas the 6- and 8-methyl-2(1*H*)quinolinones were hydrogenated at position 3 and 4. The resulting methylated 3,4-dihydro-2(1*H*)quinolinones accumulated (Johansen et al. 1997c).

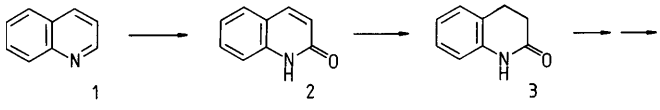


Fig. 9 Early steps of anaerobic degradation of quinoline by *Desulfobacterium indolicum* (Johansen et al. 1997b) and anaerobic transformation of quinoline by a denitrifying mixed culture (Johansen et al. 1997c). Quinoline *1*; 2(1*H*)quinolinone *2*; 3,4-dihydro-2(1*H*) quinolinone *3*

Sorption of N-heteroaromatic compounds to soil and other solids

As a rule, sorption phenomena play an important role in the transport of organic contaminants in sediment and soil/water systems, and influence biotic processes. Catallo (1996) examined the transformation of N-, O-, and S-heterocyclic compounds in estuarine sediment water microcosms. Under continuously stirred conditions in the microcosms, degradation processes were limited by increased particle surface area and reduced electrochemical conditions (i.e., degradation was fastest in oxidized sediments of large particle size). In quiescent systems, transformation rates were also faster with increasing particle size, but were promoted by reducing electrochemical conditions. Most biochemical and chemical transformations appeared to occur in the aqueous phases of the sediment slurries, rather than at the surface sites on particles. Hence, reducing redox conditions in the unstirred systems promoted liberation of heteroaromatic compounds from iron colloids and particles into the aqueous phase where chemical and microbial processes proceed at more rapid rates. Other processes that liberate the heteroaromatics from sediment surfaces to the aqueous phase, such as protonation to soluble ion pairs, were also expected to increase the degradation rates of some heterocyclic compounds in the sediment microcosms (Catallo 1996).

Sorption tends to decrease the degradation rate of organic chemicals by reducing their bioavailability. On the other hand, pollutants showing low sorption to soil are readily leached into subsoil and groundwater. For quinoline ($pK_a = 4.9$), a dominant role of cation exchange in partitioning between water and low-organic-carbon materials (subsoils, clay, amorphous silica) has been suggested in several reports (Zachara et al. 1986, 1990; McBride et al. 1992; Szecsody and Streile 1992). In the presence of clays (montmorillonite, hectorite), Smith et al. (1992) found that microbial utilization of quinoline was desorption-rate-limited and suggested that sorption of the quinolinium ion (QH^+) reduces its bioavailability. However, Helmy et al. (1983) discussed the possibility that the neutral species of quinoline in a chemisorption mechanism replaces the surface hydroxyls bonded to structural atoms (Al, Fe) of the clay.

In contrast to low-organic-carbon clay, where sorption is thought to occur mainly by cation exchange (and chemisorption), the partitioning of azaarenes, such as quinoline and acridine, between organic-rich wastewater sludge and water appeared to be dominated by the mechanism of hydrophobic interaction. The cationic species (acidic pH) were less readily sorbed by the sludge than the neutral azaarenes (Southworth and Keller 1984). Thus, the adsorption/desorption balance of azaarenes depends on the nature of the sorbent as well as on physicochemical conditions such as salinity and pH.

In situ transformations and bioremediation strategies; trends and prospects

Because of the complexity of natural ecosystems, extrapolations of laboratory studies to in situ environments are very difficult, if not impossible (Mandelbaum et al. 1997). For a compound to be degraded biologically under field conditions, some basic criteria must be met. Bioavailability of the substrate must be considered, especially with respect to sorption phenomena and concentration of the compound, an appropriate microbial community possessing the requisite catabolic ability must be present, and environmental parameters must be conducive to growth of the degrading microorganisms. Investigating the biotransformation of pyridine derivatives under different redox conditions by slurries of unpolluted as well as polluted surface and subsurface soils, Kaiser and Bollag (1992) showed that long-term adaptation of the indigenous microflora may well be a crucial factor for biodegradation. Concerning the presence of appropriate microbial communities, diverse and abundant microbial populations have been found even in deep subsurface samples (Shanker et al. 1991; Thomas et al. 1997). Aerobic microbial mineralization of indole and pyridine occurred in sediment samples taken from different depths (up to 526 m), and sulfate-reducing bacteria capable of indole transformation were also present in several samples taken from the deep (several hundred meters) subsurface (Shanker et al. 1991).

However, polluted ecosystems generally contain complex mixtures of compounds, which differ in their toxicity to microorganisms. When toxic pollutants are present together with contaminants that, as sole substrates, are easily biodegradable, degradation of the latter may be affected or even prevented. Typical creosote compounds, such as pyrrole, thiophene, and benzofuran, for instance, were found to inhibit the aerobic degradation of toluene (Dyreborg et al. 1996).

Field studies by in situ monitoring of organic contaminants provide insight into the transport and fate of the respective compound(s) in the habitat. In a long-term field experiment to evaluate the mobility, persistence and fate in groundwater of compounds present in coal tar creosote, creosote was placed into a well-characterized sand aquifer that showed mostly aerobic conditions. With increasing distance from the source of contamination, the concentration of naphthalene was reduced while that of quinoline increased, reflecting the relative aqueous solubilities and mobilities of the two compounds. Also observed, after 471 days at sampling sites most distant from the source, was the presence of quinolinone (Fowler et al. 1994).

The transport and fate of the water-soluble fraction of creosote in a contaminated aquifer were studied thoroughly at the American Creosote Works Superfund site at Pensacola, Florida (see Table 1). Whereas wells located near the source of contamination contained, for instance, quinoline and isoquinoline as well as 2(1*H*)quinolinone and 1(2*H*)isoquinolinone, samples from wells at more distant sites only contained the oxo compounds. This finding was attributed to microbial transformation (Pereira et al. 1987a, b). Under the predominantly anoxic conditions of the Pensacola aquifer, removal of N-heteroaromatics appeared to occur: 25 mg l^{-1} quinoline and 2 mg l^{-1} isoquinoline were reported to disappear on a 47-m stretch between two sampling wells downhill from the contamination source (Grbic-Galic 1989). Godsy et al. (1992, 1994) also reported field evidence for methanogenic degradation of quinoline and isoquinoline to CH_4 and CO_2 in the anoxic groundwater ecosystem near Pensacola. In situ observations like these suggest that transformations of N-heteroaromatic compounds are indeed occurring in subsurface environments.

Bioremediation techniques exploit the ability of microorganisms to degrade organic substances. In situ stimulation of the indigenous microflora, in situ inoculation of specialized microbial strains, or withdrawal-and-treatment techniques such as land farming, trickling filters or bioreactors are a few means to treat contaminated soils and aquifers. Most studies, however, have concentrated on the removal of gasoline, polycyclic aromatic hydrocarbons, phenolic wastes, or chlorinated hydrocarbons (Lee et al. 1988; Mueller et al. 1989; Grbic-Galic 1989).

For the treatment of groundwater polluted with alkylpyridines, a two-stage fixed-film reactor, using an aerobic mixed culture enriched from subsurface sediment as inoculum, was developed. It removed alkylpyridines with an efficiency of 98%–100% from a synthetic groundwater (Ronen et al. 1996).

An integrated bioreclamation approach, including land farming with added water and nutrients, bioreactors for heavily contaminated groundwater, irrigation of contaminated rocks with bioreactor effluent, and in situ aquifer treatment by addition of nutrients and H_2O_2, was used to remediate soil, groundwater, and aquifer sediments contaminated with the wood preservatives creosote and pentachlorophenol (Fredrickson et al. 1993). For bioremediation of the American Creosote Works Superfund site at Pensacola and other creosote-contaminated sites, which all contain complex mixtures of pollutants, multiphasic treatment strategies were developed. Soil washing technology with dewatering and chemical fractionation of substances through a filtration process, and biodegradation of targeted compounds using patented bacteria capable of utilizing distinct compounds as carbon and energy sources for growth were used to treat creosote-contaminated soils and subsoil materials (Mueller et al. 1991, 1993). To treat the creosote-contaminated groundwater of the Pensacola site, Mueller et al. (1993) developed a (pilot-scale) two-stage, sequential inoculation, continuous-flow bioreactor system. A mixture of 15 selected bacterial strains that had been isolated from creosote-contaminated soil were used as inocula for the bioreactor. This type of biore-

actor system on the field scale was shown to degrade about 70% of the polycyclic aromatic hydrocarbons and heterocycles present in the groundwater (Middaugh et al. 1994).

Since there may be specific problems associated with aerobic in situ treatment, such as biofouling or – quite frequently – the impossibility of introducing sufficient oxygen (especially in aquifers with low permeabilities), it seems important to evaluate the applicability of anaerobic transformations. Ronen and Bollag (1992) inoculated subsurface sediment from a polluted site with a pyridine-degrading *Alcaligenes* sp. At high inoculum size, pyridine was rapidly mineralized under nitrate-reducing conditions. Amending the sediment with nitrate and phosphate improved pyridine mineralization.

It is obvious that different microbial communities have different capabilities to convert the same substrates, and that the physicochemical properties of the environment considerably influence biotransformation processes. Thus, for each specific site, both laboratory and field studies will be necessary to predict the fate of a compound in this habitat. A thorough understanding of microbial catabolic pathways and of the environmental factors that influence biodegradation is prerequisite for the development of bioremediation techniques.

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