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MINI-REVIEW

Bacteria-mediated bisphenol A degradation

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Abstract Bisphenol A (BPA) is an important monomer in the manufacture of polycarbonate plastics, food cans, and other daily used chemicals. Daily and worldwide usage of BPA and BPA-contained products led to its ubiquitous distribution in water, sediment/soil, and atmosphere. Moreover, BPA has been identified as an environmental endocrine disruptor for its estrogenic and genotoxic activity. Thus, BPA contamination in the environment is an increasingly worldwide concern, and methods to efficiently remove BPA from the environment are urgently recommended. Although many factors affect the fate of BPA in the environment, BPA degradation is mainly depended on the metabolism of bacteria. Many BPA-degrading bacteria have been identified from water, sediment/soil, and wastewater treatment plants. Metabolic pathways of BPA degradation in specific bacterial strains were proposed, based on the metabolic intermediates detected during the degradation process. In this review, the BPA-degrading bacteria were summarized, and the (proposed) BPA degradation pathway mediated by bacteria were referred.

Keywords Bisphenol A · Bacteria · Degradation · Degradation pathway

Introduction

Bisphenol A [2,2-bis(4-hydroxyphenyl)propane, BPA, CAS # 80-05-7; made by combining acetone and phenol] is an organic compound with two phenol functional groups connected by a bridge attaching two methyl functional groups. BPA is widely used as a monomer in the synthesis of polycarbonate plastics, epoxy resins, flame retardants, food–drink packaging coating, and other specialty chemicals (Staples et al. 1998). The production of BPA is among the highest-production-volume chemicals, with a quantity of three million tons each year all over the world. Meanwhile, the worldwide demand and annual consumption of BPA is also increasing. BPA enters the environment mainly from the permitted discharges of industrial wastewater treatment plants (WWTPs), leachates of waste plastic in landfills, processing of BPA in manufacture, combustion of computer printed circuit boards in electronic waste, and spraying of paint (Peltonen and Pukkila 1988; Staples et al. 1998; Furhacker et al. 2000; Yamamoto et al. 2001; Cousins et al. 2002; Owens Jr. et al. 2007; Fu and Kawamura 2010; Huang et al. 2012). BPA discharged into water system counted for about 92 % of its total emissions (European Commission 2003). Levels of BPA in different environments, including leachates from hazardous waste disposal sites, industrial wastewaters, influents and effluents of WWTPs, river water, seawater, sediment, and atmosphere were extensively assessed previously. The highest levels of BPA in the aquatic environment were detected in China mainland and Taiwan whereas the atmospheric levels of BPA in Indian megacities were roughly one order of magnitude higher than those in China, New Zealand, Japan, and the United States (Fu and Kawamura 2010; Huang et al. 2012).

The worldwide distribution of BPA in various environments was considered as the sources of BPA exposure to human beings (Kang et al. 2006b; Ulutao et al. 2011). Another way of exposure to BPA occurred through ingestion followed by accumulation in the fatty tissues (Oehlmann et al. 2008; Sanchez-Avila et al. 2009). In addition, BPA possesses estrogenic and genotoxic effects on both human beings and other organisms. BPA could interact with the estrogen receptor and affect the reproductive behavior (Staples et al. 1998; Snyder et al. 2001; Bonefeld-Jørgensen et al. 2007; Matsushima et al. 2007). BPA concentrations within

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the range of 0.1–10 μM showed the estrogenic and mutagenic effects on human beings (Takahashi et al. 2001; Saiyood et al. 2010), while BPA concentrations within the range of 0.04–0.4 μM showed acute toxicity towards algae, invertebrates, and fish (Alexander et al. 1988). Therefore, BPA has been identified as one of the endocrine disrupting chemicals (EDCs) by the US Environmental Protection Agency, World Wide Fund For Nature. Due to its retention and harmful effects, the fate of BPA in the environments has become a social issue concerned by the public (Li et al. 2007). Thus, development of effective techniques to remove BPA from various environments are urgently recommended (Suzuki et al. 2004; Ying et al. 2008; Liu et al. 2011).

Methods to remove environmental pollutants, especially BPA, included photodegradation (Neamtu and Frimmel 2006), oxidation (Deborde et al. 2008), photoelectrocatalytic oxidation (Brugnera et al. 2010), and biodegradation (Kang et al. 2006a). Among all these methods, biodegradation has been proved to be an advanced technique to remove various pollutants from the environment. In our lab, efforts were made to investigate the biotransformation of heavy metals, and biodegradation of sulfonamide drugs, nitrofurans drugs, and EDCs by bacterial strains and their potential application in bioremediation (Zhang et al. 2012a, 2012b, 2012c, 2013). Bacterial community is readily catabolized to BPA, and BPA-degrading bacterial strains were isolated and identified from various environments (Kang et al. 2006a). BPA degradation by bacterial strains played a major role in the decomposition of BPA in the environment (Dorn et al. 1987; Staples et al. 1998), and biodegradation has also been proved to be an effective way to remove BPA from water, sediment, and soil. The information about BPA degradation by bacteria can, not only supply new techniques to remove BPA from the environment, but also improve our understanding of the fate of BPA in the environment. Detailed and general themes arising from BPA degradation by bacteria are described below.

Bacteria-mediated BPA degradation

BPA in the environment is mainly decomposed by a variety of microorganisms (Dorn et al. 1987; Staples et al. 1998). More and more BPA-degrading bacteria were isolated, identified, characterized, and used to treat BPA in WWTPs (Kang et al. 2006a; Melcer and Klecka 2011). BPA-degrading bacterial strains were isolated from soils, sludge, river, seawater, and even food sample (Table 1). These bacterial strains capable of growing on BPA as a sole source of carbon and energy included gram-negative strains *Sphingomonas* sp., *Pseudomonas* sp., *Achromobacter* sp., *Novosphingobium* sp., *Nitrosomonas* sp., *Serratia* sp., *Bordetella* sp., *Alcaligenes* sp., *Pandoraea* sp., *Klebsiella* sp., and *Cupriavidus* sp. and gram-positive strains *Streptomyces* sp., and *Bacillus* sp. Although there are many BPA-degrading bacteria in the environment, their BPA degradation ability are strongly different with strain specificity. Bacteria with high BPA biodegradability are limited. Many environmental factors such as biomass amount, temperature, pH, metal ions, biological compounds, and oxygen affect their degradation efficiency. Based on the degrading metabolites of BPA generated by bacterial degradation, three dominant BPA degradation pathways in bacteria have already been proposed.

BPA degradation by gram-negative bacteria

Sphingomonas sp. strains were the most frequently isolated BPA-degrading bacteria, and all the isolated BPA-degrading *Sphingomonas* sp. strains could use BPA as the sole source of carbon and energy. The first BPA-degrading bacterial strain was isolated from the sludge of WWTP and was identified to be *Sphingomonas* sp. strain MV1 (Lobos et al. 1992; Spivack et al. 1994). *Sphingomonas* sp. strain MV1 could completely consumed 10 g/l BPA within 4 days. Later, a *Sphingomonas* sp. strain TTNP3 was isolated from activated sludge sample obtained from laboratory-scale semi-continuous activated sludge unit, which was fed with nonylphenol for a period of approximately 4 months (Tanghe et al. 1999). However, its BPA degradation ability was firstly proposed by Kolvenbach et al. (2007). *Sphingomonas* sp. strain AO1 (or named *Sphingomonas bisphenolicum* strain AO1), with high BPA degradation efficiency, was isolated from the soil of a vegetable-growing field in Japan (Sasaki et al. 2005b). It completely degraded 115 mg/l BPA at the sixth hour and showed a little higher degradation efficiency than that of the three *Sphingomonas* sp. strains SO11, SO1a, and SO4a isolated by Matsumura et al. (2009) that completely degraded 115 mg/l BPA within 15 h. Sakai et al. (2007) reported the first seawater BPA-degrading isolate of *Sphingomonas* sp. strain BP-7. Its degradation efficiency could be enhanced by another non BPA-degrading bacterium *Pseudomonas* sp. strain BP-14. A mixture of *Sphingomonas* sp. strain BP-7 and *Pseudomonas* sp. strain BP-14 completely degraded 100 mg/l BPA within 7 days, while *Sphingomonas* sp. BP-7 alone needed about 40 days for complete consumption of BPA. Although *Sphingomonas* sp. strain BP-7 could use BPA as the sole source of carbon and energy, it could not degrade BPA on the mineral salt media. BPA degradation by *Sphingomonas* sp. strain BP-7 needed a nutrient supplement, such as peptone. Both *Sphingomonas* sp. strain BP-7 and *Sphingomonas yanoikuyae* strain BP-11R isolated by Yamanaka et al. (2008) efficiently degraded 300 mg/l BPA in the presence of activated carbon (AC), suggesting that an efficient system for BPA removal can be constructed by introducing BPA-degrading bacteria into an AC treatment system.

Table 1 Bacterial strains capable of degrading BPA

Sources	Bacterial strains	References
Sediment/soil		
	Unidentified strain WH1	Ronen and Abeliovich 2000
	Sphingomonas sp. strain AO1(or *S. bisphenolicum* strain AO1)	Sasaki et al. 2005a and 2005b; Oshiman et al. 2007
	Pseudomonas sp. strain LBC1	Telke et al. 2009
	Alcaligenes sp. strain OIT7	Matsumura et al. 2009
	Bacillus sp. strains NO13, NO15 and YA27	Matsumura et al. 2009
	Bordetella sp. strain OS17	Matsumura et al. 2009
	Enterobacter sp. strains HI9 and HA18	Matsumura et al. 2009
	Klebsiella sp. strains NE2, SU3 and SU5	Matsumura et al. 2009
	Pandoraea sp. strain HYO6	Matsumura et al. 2009
	Pseudomonas sp. strains SU1, SU4, NAR11, FU12, NO14, KA16, SU19, FU20, HUK21 and HUK22	Matsumura et al. 2009
	Serratia sp. strain HI10	Matsumura et al. 2009
	Sphingomonas sp. strains SO11,SO1a and SO4a	Matsumura et al. 2009
	Bacillus sp. strain GZB	Li et al. 2012
Water		
	Pseudomonas sp. strain KA4	Kang and Kondo 2002a and b
	P. putida strain KA5	Kang and Kondo 2002a and b
	Streptomyces sp.	Kang et al. 2004
	Sphingomonas sp. strain BP-7	Sakai et al. 2007; Yamanaka et al. 2008
	S. yanoikuyae strain BP-11R	Yamanaka et al. 2008
Bed reactor/sludge		
	Sphingomonas sp. strain MV1	Lobos et al. 1992; Spivack et al. 1994
	P. paucimobilis strain FJ-4	Ike et al. 1995; Ike et al. 2000; Ike et al. 2002
	Sphingomonas sp. strain TTNP3	Tanghe et al. 1999;Kolvenbach et al. 2007
	C. basilensis strain JF1	Fischer et al. 2010
Leachate of waste		
	A. xylosoxidans strain B-16	Zhang et al. 2007
Rhizosphere of plant		
	Novosphingobium sp. strain TYA-1	Toyama et al. 2009
	Bacillus cereus strain BPW4	Saiyood et al. 2010
	Enterobacter sp. strains BPR1 and BPW5	Saiyood et al. 2010
Food of kimchi		
	B. pumilus strains BP-2CK, BP-21DK and BP-22DK	Yamanaka et al. 2007
Unidentified place		
	P. monteilii strain N-502	Masuda et al. 2007
	N. europaea	Roh et al. 2009

BPA degradation pathways proposed in the above *Sphingomonas* sp. strains were described in Fig. 1. (1) The first BPA degradation pathway was described in *Sphingomonas* sp. strain MV1. BPA degradation by *Sphingomonas* sp. strain MV1 occurred via several rearrangements involving phenonium ion intermediates. Through the solvolysis of the first phenonium ion intermediate (compound IV), BPA was catabolized into two metabolites, 2,2-bis(4-hydroxyphenyl)-l-propanol (compound I, a minor metabolite) formed by the hydroxylation of methyl group, and 1,2-bis(4-hydroxyphenyl)-2-propanol (compound II, a major metabolite), formed by the hydroxylation of the quaternary carbon (Spivack et al. 1994). (2) Both compounds I and II were detected in *Sphingomonas* sp. strain AO1, but it was proposed that the formation of compound II was through another intermediate (compound V). Because the study of Sasaki et al. (2005a) was focused on the function of cytochrome P450 monooxygenase system in BPA degradation, further degradation of compounds I and II was not investigated. (3) BPA

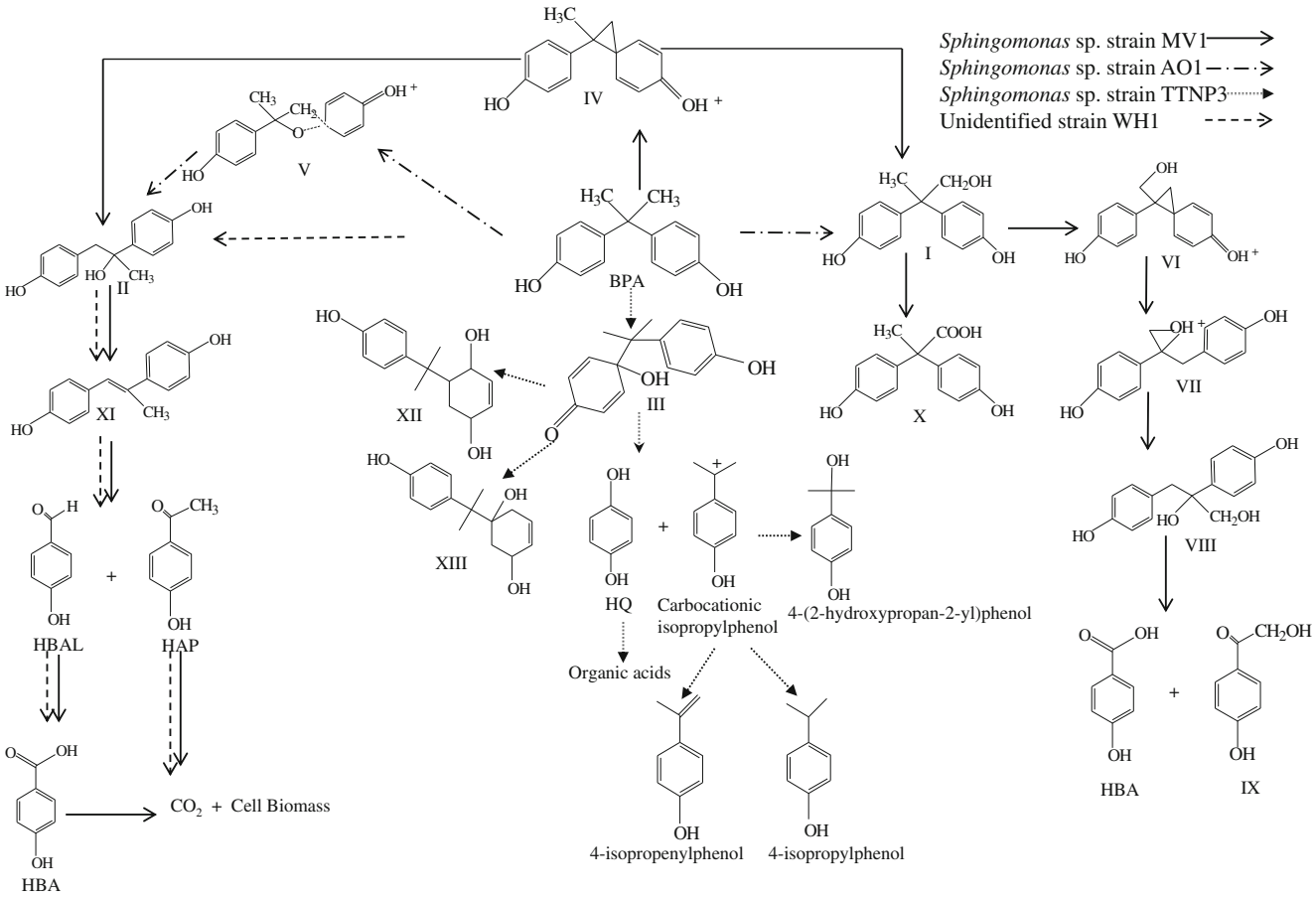

Fig. 1 The proposed BPA degradation pathways in *Sphingomonas* sp. strains MV1, AO1 and TTNP3 and the unidentified strain WH1

degradation via a type II *ipso* substitution mechanism occurred in *Sphingomonas* sp. strain TTNP3. Different from the BPA degradation through the formation of phenoniumion intermediates, the first step of BPA degradation in *Sphingomonas* sp. strain TTNP3 was to introduce one atom of molecular oxygen into the BPA by the NADPH and FAD-aided monooxygenase to form a quinol intermediate (compound III). Then, the breakage of C–C bond between the phenolic moiety and the isopropyl group of BPA occurred (Kolvenbach et al. 2007).

Compound I was further metabolized in *Sphingomonas* sp. strain MV1 (Lobos et al. 1992; Spivack et al. 1994). Oxidation and rearrangement were simultaneously taking place in compound I to form another intermediate (compound VI), which has the C1 hydroxyl positioned for internal displacement to form the oxirane (compound VII). Subsequent hydrolysis of the oxirane mainly led to the production of the 2,3-bis (4-hydroxyphenyl)-1,2-propanediol (compound VIII). 2,3-bis(4-Hydroxyphenyl)-1,2-propanediol was then degraded very slowly into 4-hydroxybenzoic acid (HBA) and 4-hydroxyphenacyl alcohol (compound IX). A minor pathway to further oxidize compound I was the formation of 2,2-bis(4-hydroxyphenyl)propanoic acid (compound X). Further oxidation of compound II was also proposed in *Sphingomonas* sp. strain MV1 (Lobos et al. 1992; Spivack et al. 1994). Compound II was dehydrated to 4,4'-dihydroxy-α-methylstilbene (compound XI), and then the oxidative cleavage took place, leading to the formation of 4-hydroxybenzaldehyde (HBAL) and 4-hydroxyacetophenone (HAP). HBAL was then subsequently oxidized to HBA. Finally, both HAP and HBA were completely metabolized by *Sphingomonas* sp. strains MV1 without the production of any HPLC-UV detectable products. Compound III was mainly further metabolized by *Sphingomonas* sp. strain TTNP3 through the cleavage of the C–C bond between the phenolic moiety and the isopropyl group of BPA to form p-hydroquinone (HQ) and a carbocationic isopropylphenol. HQ was further degraded into organic acids. The carbocationic isopropylphenol was metabolized in two pathways: One way was the formation of 4-(2-hydroxypropan-2-yl)phenol through the reaction with water. Another way was the formation of 4-isopropenylphenol and 4-isopropylphenol by the way of the loss of H^+ and the addition of H^-, respectively, as the side reactions. Metabolism of compound III was also occurred to form two other possible degrading metabolites 2-[2-(4-hydroxyphenyl)propan-2-

yl]cyclohex-2-ene-1,4-diol (compound XII) or 1-[2-(4-hydroxyphenyl)propan-2-yl]cyclohex-2-ene-1,4-diol (compound XIII), by a NIH shift with subsequent hydrogenations of the hydroxylated ring or direct successive hydrogenations of the ring of the quinol intermediate (Kolvenbach et al. 2007).

Pseudomonas sp. strain was another kind of BPA-degrading bacteria that were frequently isolated from the environment and grown on BPA as the sole carbon and energy source. *Psudomonas paucimobilis* strain FJ-4 was isolated from sludge taken from a WWTP at an epoxy resin-manufacturing facility by Ike et al. (1995). It could efficiently degrade 100 mg/l BPA to a concentration below the limit of detection within 12 h. Later, a *Pseudomonas* sp. strain KA4 and a *Pseudomonas putida* strain KA5 were isolated by Kang and Kondo (2002a and b). Both of the *Pseudomonas* sp. strains degraded about 90 % of BPA when the initial BPA concentration was 1 mg/l. A *Pseudomonas monteilii* strain N-502 with high BPA degradation ability was isolated by Masuda et al. (2007). It completely degraded 500 mg/l BPA within 10 days, and its degradation efficiency could be accelerated by 1 and 10 mM Ca^{2+}, Mg^{2+}, and folic acid to different degrees. Matsumura et al. (2009) reported other ten *Pseudomonas* sp. strains SU1, SU4, NAR11, FU12, NO14, KA16, SU19, FU20, HUK21, and HUK22 that could completely degrade 115 mg/l BPA. Moreover, BPA degradation by *Pseudomonas* sp. strains SU1 and SU4 introduced some degrading metabolites that were different from the metabolites produced by *Sphingomonas* sp. strain AO1. Thus, it was postulated that *Pseudomonas* sp. strains SU1 and SU4 may exhibit novel BPA degradation pattern which was distinctly different from those of *Sphingomonas* sp. strain AO1 (Matsumura et al. 2009).

BPA degradation by *Achromobacter xylosoxidans* strain B-16 and *Cupriavidus basilensis* strain JF1 was also reported (Zhang et al. 2007; Fischer et al. 2010). BPA-degrading *A. xylosoxidans* strain B-16 was isolated from the compost leachate of the municipal solid waste. It could grow using BPA as the sole carbon source and degrade 86.83 % of 5 mg/l BPA at the seventh day. Like other bacterial strains, the optimal temperature and pH for BPA degradation by *A. xylosoxidans* were found to be 35–37 °C and 7.0, respectively. Higher temperature promoted BPA degradation within the range of temperature lower than 37 °C. Temperature higher than 37 °C inhibited bacterial growth and subsequently affected the BPA biodegradation activity (Kang and Kondo 2002a, b; Zhang et al. 2007; Li et al. 2012). The optimal pH and temperature for BPA degradation may due to the greatest biomass and BPA-degrading enzymatic activity under the optimal conditions (Zhang et al. 2007). According to the metabolic intermediates HBAL, HBA and HQ, the BPA degradation by *A. xylosoxidans* strain B-16 was in the following pathways: BPA was firstly decomposed to form three intermediates HAP (not detected), HBAL and 4-isopropenylphenol (not detected). Subsequently, HBAL was converted to CO_2 and biomass directly. HAP was oxidized to form HBA, followed by the conversion to CO_2 and biomass. 4-Isopropenylphenol was converted to HQ by ·OH radicals attack, which was different from the way of HQ formation in *Sphingomonas* sp. strain TTNP3 via *ipso*-hydroxylation after the alkyl substituent left the quinol intermediate and mineralized later (Ohko et al. 2001; Kaneco et al. 2004; Zhang et al. 2007). However, detailed degradation pathway from BPA to HAP (a proposed metabolite), HBAL, and 4-isopropenylphenol (a proposed metabolites) was not further investigated by Zhang et al. (2007). *C. basilensis* strain JF1 isolated from a planted fixed-bed reactor continuously running with BPA was also able to use BPA as sole carbon and energy source; however, its BPA degradation efficiency was lower. *C. basilensis* strain JF1 could use phenol as a co-substrate during BPA degradation. It completely consumed 1.7 mM phenol at the first 2 h and then degraded 90 % of 38.8 mg/l BPA after 225 days. Based on the detected metabolites 4-isopropenylphenol, 4-(2-propanol)-phenol, HAP, HBAL, HBA, and HQ, BPA degradation pathway in *C. basilensis* strain JF1 was proposed by Fischer et al. (2010) in the light of previous BPA degradation pathways. *C. basilensis* strain JF1 seemed to mineralize BPA in a pathway different from the degradation pathway in *Sphingomonas* sp. strain MV1 proposed by Lobos et al. (1992) and Spivack et al. (1994) but in a pathway similar to that in *Sphingomonas* sp. strain TTNP3 proposed by Kolvenbach et al. (2007), with minor difference. 4-(2-Propanol)-phenol and HQ were the products of cleavage of the ring of BPA. HQ was then completely mineralized by *C. basilensis* strain JF1. 4-(2-Propanol)-phenol was further metabolized in the following two pathways: The main product 4-isopopenylphenol was formed by the elimination of H_2O at the phenol residue and another product HAP was formed by the splitting of a C1-body. Both 4-isopropenylphenol and HAP were oxidized to HBAL and HBA via *ortho*-degradation pathway sequentially. Finally, HBA was mineralized by *C. basilensis* strain JF1 (Fig. 2) (Fischer et al. 2010).

Other novel species of BPA-degrading bacteria were also isolated. An unidentified bacterial strain WH1, closely resembling *Sphingomonas* sp., was isolated from sediment obtained from the vicinity of an industrial complex in the northern Negev in Israel. WH1 could use BPA as a sole source of carbon and energy and completely degrade 205 mg/l BPA at the eighth day. BPA degradation by WH1 was proposed to be via the main degradation pathway occurred in *Sphingomonas* sp. strain MV1, based on the detectable metabolites of HBA and HAP (Ronen and Abeliovich 2000) (Fig. 1). Matsumura et al. (2009) reported that three *Klebsiella* sp. strains NE2, SU3, and SU5; two *Enterobacter* sp. strains HI9 and HA18; one *Alcaligenes* sp. strain OIT7; one *Bordetella* sp. strain OS17; one *Pandoraea* sp. strain HYO6; and one *Serratia* sp. strain HI10 could completely degrade 115 mg/l BPA, respectively. Three

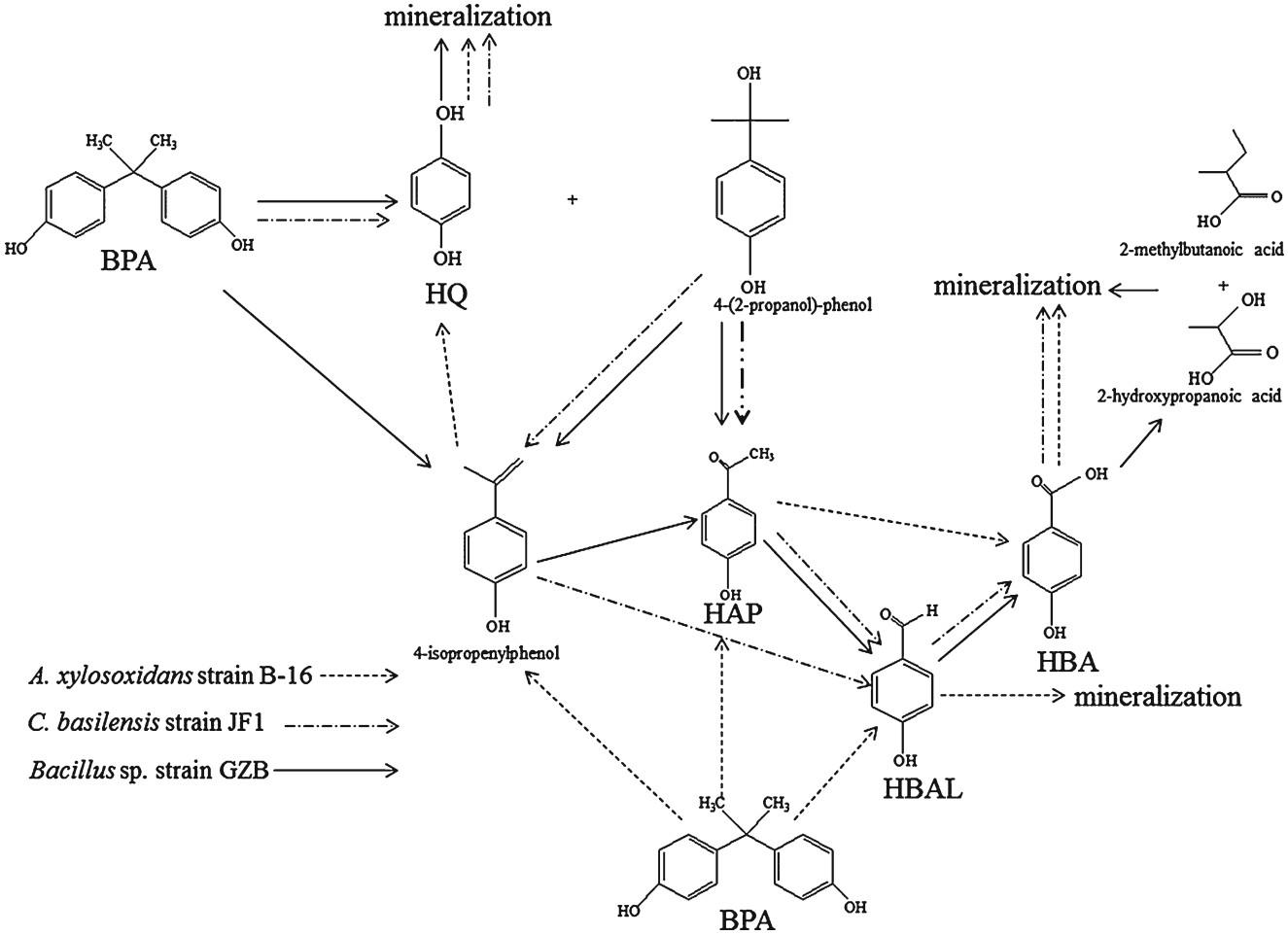

Fig. 2 The proposed BPA degradation pathways in *A. xylosoxidans* strain B-16, *C. basilensis* strain JF1 and *Bacillus* sp. strain GZB

gram-negative bacterial strains, *Novosphingobium* sp. strain TYA-1, and *Enterobacter* sp. strains BPR1 and BPW5, were isolated from the rhizosphere of plants with BPA removal capacity. *Novosphingobium* sp. strain TYA-1 was isolated from the rhizosphere of *Phragmites australis*. It could grow on BPA as the sole carbon source and completely degrade 22.8–228.3 mg/l BPA within 24 h (Toyama et al. 2009). *Enterobacter* sp. strains BPR1 and BPW5 were found to be associated with the plant *Dracaena sanderiana* and adhered at the root surface to play a significant role in BPA biodegradation. All the identified strains could enhance BPA dissipation in the plant hydroponic system (Saiyood et al. 2010).

Three enzymes had been reported to be involved in BPA degradation. The presence of metyrapone, an inhibitor of cytochrome P450, contributed to the reduction in the cell growth and BPA degradation efficiency of *Sphingomonas* sp. strain AO1. In the presence of NADH, the purified components of P450 monooxygenase degraded BPA into 2,2-bis(4-hydroxyphenyl)-1-propanol and 1,2-bis(4-hydroxyphenyl)-2-propanol via hydroxylation of the methyl group and the quaternary carbon, respectively. The $P450_{bisd}$ monooxygenase system was predicted to catalyze the hydroxylation of either a C atom of a methyl group (C-8 or C-9) or the quaternary carbon (C-7) attacked by H_2O (Sasaki et al. 2005a, 2005b; Oshiman et al. 2007). P450 monooxygenase was also the initial enzyme that led to *ipso* substitution in other xenobiotics containing phenol with a quaternary-carbon (Kolvenbach et al. 2007). Ammonia monooxygenase (AMO) was another enzyme that was involved in BPA degradation. Degradation efficiency of a *Nitrosomonas europaea* strain was inhibited by the presence of allylthiourea, an inhibitor of AMO (Roh et al. 2009). The decreased removal efficiency of nitrifier-enriched activated sludge in the presence of allylthiourea or Hg_2SO_4 was also observed by Kim et al. (2007). An extracellular laccase from a *Pseudomonas* sp. strain LBC1 completely degraded 36.5 mg/l BPA within 5 h. Compared with eukaryotic laccases and peroxidases, this extracellular laccase is a more efficient biocatalyst for the complete removal of BPA without the requirement of other redox mediators (Telke et al. 2009).

BPA degradation by gram-positive bacteria

The first gram-positive BPA-degrading bacterium was a *Streptomyces* sp. strain isolated from river water by Kang et al. (2004). The *Streptomyces* sp. strain degraded 90 % of 1 mg/l BPA in the river water at the fourth day and then showed little degradation activity. The most prevalent gram-positive BPA-degrading bacteria were *Bacillus* sp. Three *Bacillus pumilus* strains BP-2CK, BP-21DK, and BP-22DK were isolated from kimchi, a traditionally fermented food, by Yamanaka et al. (2007). The three *B. pumilus* strains efficiently degraded 10 mg/l BPA within 20–40 h, in media supplemented with nutrients. The 12.5 % NaCl and 100 mg/l BPA showed complete inhibitory effects on both cell growth and degradation activity. *B. pumilus* strains BP-2CK, BP-21DK, and BP-22DK were unable to grow using BPA as the sole carbon source. Similarly, other two *Bacillus* sp. strains NO13 and NO15 isolated from soil samples by Matsumura et al. (2009) were also unable to grow and degrade BPA in mineral salt media with BPA as the sole carbon source whereas both strains completely degraded 115 mg/l BPA in media supplied with tryptone and yeast extract. This phenomenon was consisted with the fact that many strains belonging to *Bacillus* sp. require growth factors, and *B. pumilus* strains require biotin and amino acids according to Bergey's Manual of Systematic Bacteriology (Sneath et al. 1986). Thus, addition of nutrients was effective for the growth and BPA degradation ability of the three *Bacillus* sp. strains. This should also interpret why the genus *Bacillus* sp. capable of degrading BPA had not been isolated with the conventional enrichment techniques using mineral salt media containing BPA as the sole carbon source (Yamanaka et al. 2007). A *Bacillus* sp. strain YA27 isolated from soil samples by Matsumura et al. (2009) and *Bacillus* sp. strain GZB isolated by Li et al. (2012) were able to grow using BPA as the sole carbon source. *Bacillus* sp. strain YA27 degraded 50 mg/l BPA in media supplied with tryptone and yeast extract. *Bacillus* sp. strain GZB was isolated from sediment of a creek in an electronic-waste recycling site and removed 100 % of 5 mg/l BPA under optimal aerobic conditions (Li et al. 2012). Similar to the synergistic effect of the biomass amount and BPA degradation observed by Zhang et al. (2007), more bacterial cells could increase not only the degradation efficiency but also the degradation rate of *Bacillus* sp. strain GZB. However, no such positive relationship between the biomass amount and BPA degradation was observed in seawater. The difference may be due to the size of bacterial cell counts that can perform the fast and complete BPA degradation, or due to the existence of other chemical degradation of BPA, such as degradation by reactive oxygen species, in seawater (Klecka et al. 2001; Sajiki and Yonokubo 2002, 2003; Kang and Kondo 2005; Zhang et al. 2007). The substrate concentration was another factor that affected BPA degradation. The degradation efficiency of *Bacillus* sp. GZB decreased from 92.9 to 66.3 % as BPA concentration rose from 5 to 30 mg/l. Under anaerobic condition, *Bacillus* sp. strain GZB could use Fe^{3+} as an alternative electron acceptor to degrade BPA, although its degradation efficiency was slightly lower than that of using O_2. Under both anaerobic and aerobic conditions, 10 mg/l BPA was completely degraded by *Bacillus* sp. strain GZB within 100 h. Thus, *Bacillus* sp. GZB provided a promising alternative for treatment of BPA contamination when bioremediation had to be taken under anaerobic condition (Li et al. 2012).

BPA degradation pathway in *Bacillus* sp. strain GZB under aerobic conditions was similar to that proposed in *C. basilensis* strain JF1 with minor difference (Li et al. 2012). 4-(2-Propanol)-phenol and HQ were also identified as the first two metabolites. HQ could be completely mineralized by *Bacillus* sp. strain GZB. 4-(2-Propanol)-phenol was oxidized to HAP and then demethylated to form HBAL followed by the conversion to HBA through the same pathway described in *C. basilensis* strain JF1. Another metabolite 4-isopropenylphenol was formed from direct cleavage of BPA and also from the dehydration of 4-(2-propanol)-phenol, which was also frequently found in photocatalytic degradation of BPA pathway (Nomiyama et al. 2007). 4-Isopropenylphenol was then further oxidized to HAP, HBAL, and HBA subsequently. Two small molecular products 2-hydroxypropanoic acid and 2-methylbutanoic acid were derived from the breakage of benzene ring and were completely mineralized to CO_2 and H_2O (Fig. 2). However, different BPA degradation pathways may exist in other gram-positive BPA-degrading bacterial strains. HAP produced by other BPA-degrading bacterial strains was not detected in the metabolites of BPA generated by *B. pumilus* strains BP-2CK, BP-21DK, and BP-22DK (Yamanaka et al. 2007). Metyrapone could not inhibit BPA degradation ability of *Bacillus* sp. strain YA27 (Matsumura et al. 2009), which also indicated that *Bacillus* sp. strain YA27 might possess a unique BPA degradation pathway.

Challenge in the study of BPA degradation by bacterial strains

Degrading metabolites of BPA under aerobic conditions were exhaustively studied, and several BPA degradation pathways were proposed. However, only a few reports focused on the enzymes and genes that were involved in BPA degradation. Sasaki et al. (2005a) demonstrated that cytochrome P450 monooxygenase of *Sphingomonas* sp. strain AO1 was involved in BPA degradation for the first time. Enzymatic reaction of the P450 monooxygenase system in the presence of NADH was predicted to catalyze the attack on either a C atom of a methyl group or the quaternary

carbon of BPA by H_2O. Hydroxylation of the methyl group converted BPA to the minor metabolite 2,2-bis(4-hydroxyphenyl)-l-propanol, and hydroxylation of the quaternary carbon led to the formation of the major metabolite 1,2-bis(4-hydroxyphenyl)-2-propanol. In the simultaneous presence of NADPH and FAD, P450 monooxygenase was also reported to catalyze the *ipso* substitution in the BPA degradation by *Sphingomonas* sp. strain TTNP3. Various inhibitors of cytochrome P450 monooxygenase had identically inhibitory effects on the conversion of BPA (Kolvenbach et al. 2007). Beside P450 monooxygenase, an AMO from *N. europaea* and an extracellular laccase from *Pseudomonas* sp. strain were also involved in BPA degradation (Roh et al. 2009; Telke et al. 2009). However, the catalytic mechanism of the known enzymes still needs further investigation. For example, it is still necessary to detect the intermediates for the study of the reaction mechanism of the P450 monooxygenase system in BPA degradation. It is highly postulated that the relevant amounts and activities of the enzymes involved in the BPA degradation pathway are significantly varied in different bacterial strains. Thus, the new genes and enzymes involved in the BPA degradation also need to be explored.

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