Dissipation, dehalogenation, and denitration of chloroaromatic compounds by *Nocardioides* sp. strain PD653: Characterization of the substrate specificity

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The substrate range of *Nocardioides* sp. strain PD653, capable of mineralizing hexachlorobenzene, was investigated based on the dissipation of substrates and the liberation of halogen ions. Strain PD653 dehalogenated 10 out of 18 halophenol congeners; however, it could dehalogenate only hexachlorobenzene out of seven halobenzene congeners tested. Moreover, dehalogenation activities were shown for chloronitrobenzenes, along with an increase in the number of substituted chlorine atoms except for 2,3,4,5-tetrachloro-1-nitrobenzene. These results suggested that this strain might be applicable to remediate soil contaminated with these persistent chloroaromatic compounds.

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**Keywords:** aerobic biodegradation, dehalogenation, *Nocardioides* sp. strain PD653, substrate specificity.

**Electronic supplementary material:** The online version of this article contains supplementary material (Supplemental Fig. S1), which is available at [http://www.jstage.jst.go.jp/browse/jpestics/](http://www.jstage.jst.go.jp/browse/jpestics/)

**Introduction**

Bacteria that are capable of degrading anthropogenic chemicals, including chlorinated and recalcitrant organic compounds, have been of interest both for their applications in bioremediation and for evolutionary studies. Thus far, several *Nocardioides* species have been isolated based on their potential for bioremediation; *Nocardioides* sp. strain JS614 could assimilate vinyl chloride for its growth; *N. simplex* strain 3E used the ortho-cleavage pathway to utilize phenoxyalkanoic herbicides, 2,4-dichlorophenoxyacetate and 2,4,5-trichlorophenoxyacetate, by means of hydroxyquinol 1,2-dioxygenase; *Nocardioides* sp. strain CB22-2 and *N. simplex* strain FJ2-1A were able to grow using 2,4,6-trinitrophenol (picric acid) and 2,4-dinitrophenol as sole carbon and/or nitrogen sources; *N. aromaticivorans* strain IC177 utilized a car gene cluster to assimilate carbazole; *Nocardioides* sp. strains AN3, MTD22, and DN36 were isolated based on their ability to degrade s-triazine. *Nocardioides* sp. strain C190 was one of the most prominent *Nocardioides* strains capable of dechlorinating the triazine compounds by means of triazine hydrolase (TrzN). Notably, dehalogenation and denitration, which are rate-limiting steps under the aerobic degradation of xenobiotics substituted by nitro and halogen group(s), respectively, lead to the dissipation of subsequent metabolites. Therefore, the biological reactions accomplished by the *Nocardioides* species mentioned above are crucial for bioremediation.

*Nocardioides* sp. strain PD653, which is an aerobic actinobacterium isolated from an agricultural field contaminated with pentachloronitrobenzene (C₆Cl₅NO₂; PCNB), has been shown to degrade not only PCNB but also persistent organic pollutants (POPs), including hexachlorobenzene (C₆Cl₆; HCB) and pentachlorophenol (C₆HCl₅O; PCP). In our previous reports, *hcbA* and *hcbB* genes, which were postulated to be necessary for the HCB metabolism, have been discovered in strain PD653. The *hcbA* genes encode putative flavoproteins that catalyze the oxidative dehalogenation of HCB to PCP. The *hcbB* genes encode putative flavoproteins that catalyze the two-step dehalogenation of PCP to 3,5,6-trichloro-2-hydroxy-1,4-benzoquinone (C₆H₂Cl₄O₂; TCHQ) via 2,3,5,6-tetrachlorohydroquinone (C₆H₃Cl₄O₂; TeCH).

Strain PD653 appears to have interesting mechanisms to degrade halogenated aromatic compounds, as mentioned above; however, the substrate range of this strain remains unknown. Thus, in this study, we aimed to reveal the substrate range of a strain PD653 pure culture based on the dissipation of substrates and the liberation of halogen ions. In addition to several chloroaromatic compounds, the substrate specificity of this strain...
against α-, β-, γ-, and δ-hexachlorocyclohexanes (C₆H₆Cl₆; HCHs), the ingredients of technical HCH (t-HCH) used worldwide as an insecticide, was investigated.

**Materials and Methods**

1. **Bacterial strain and culture conditions**
   The preculture medium used for strain PD653 was prepared as described previously. A mineral-salt medium (MM) was prepared as described previously.10

2. **Chemicals**
   HCB; 1,2,4- and 1,2,3-trichlorobenzene; and 2,3-di-, 2,4-di-, 3,4-di-, 3,5-di-, 2-, 3-, and 4-chlorophenol and tetrachlorosiphtalonic acid were purchased from TCI Tokyo Kasei (Tokyo, Japan). 1,2,3,5-Tetrachlorobenzene was purchased from AccuStandard, Inc. (New Haven, CT, USA). Pentabromo- and 2,3,4,3,5,4,5-tetrachloro-phenol, hexabromobenzene (HBB), and hexafluorobenzene (HFB) were purchased from Sigma-Aldrich (Tokyo, Japan). 1,3,5-Trichlorobenzene; PCTA; pentachloroaniline (PCA) were purchased from FUJIFILM Wako Pure Chemical Corporation (Osaka, Japan).

3. **Analytical methods**
   Fluoride, chloride, bromide, and nitrate ions were analyzed via ion chromatography (IC) (761 Compact IC; Metrohm, Herisau, Switzerland). A Dionex IonPac AS23 column (Thermo Fisher Scientific, Waltham, MA, USA) was used with an aqueous solution of 4.5/0.8 mmol L⁻¹ Na₂CO₃/NaHCO₃ at a flow rate of 1.5 mL min⁻¹. The detection limit of Cl⁻, Br⁻, F⁻, and NO₂⁻ was 1.4, 1.25, 5, and 4.3 μmol L⁻¹, respectively. HFB and HCHs were analyzed via gas chromatography (GC) (HP6890 GC system; Hewlett-Packard, Palo Alto, CA, USA) with a 63Ni electron capture detector (ECD). Helium was used as a carrier gas at a flow rate of 1.5 mL min⁻¹. Chromatographic separation was performed in a capillary column DB-1MS (30 m×0.25 mm ID with 0.25 μm film thickness; J&W Scientific, Folson, CA, USA). For the detection of HFB, the oven temperature was isothermally operated at 100°C, and the inlet and detector temperatures were held at 120°C and 150°C, respectively. For the detection of HCHs, the oven temperature was isothermally operated at 190°C, and the inlet and detector temperatures were held at 220°C and 250°C, respectively. N₂ served as a make-up gas at a flow-rate of 60 mL min⁻¹. Other aromatic compounds were analyzed via high-performance liquid chromatography (HPLC) (HP1100; Hewlett-Packard) equipped with a UV detector. A ZORBAX Eclipse XDB-C18 column (150 mm × 4 mm ID with a 5 μm particle size; Agilent Technologies, Tokyo, Japan) was used, and the temperature used was 40°C. The pump was set to run in isocratic mode, with a flow rate of 1.0 mL min⁻¹. The mobile-phase composition was 90:10 acetonitrile/0.1% phosphoric acid for HCB and PCTA and 70:30 acetonitrile/0.1% phosphoric acid for pentachlorophenol and TNT. Other aromatic compounds were analyzed with a mobile-phase composition of 80:20 acetonitrile/0.1% phosphoric acid.

4. **Biodegradation of aromatic compounds by strain PD653 resting cells**
   Strain PD653 cells grown on a pre-culture medium (OD₆₀₀=0.5) were harvested at 3,000×g, 4°C, 10 min; they were then washed with MM and resuspended in the same medium. A 2 mL aliquot of the cell suspension (OD₆₀₀=1.0) was added to each of a series of 10 mL glass-stoppered test tubes. Twenty microliters of the stock solution of aromatic compounds was supplemented to the suspensions at an initial concentration of 10 μmol L⁻¹. Triplicate test tubes were shaken at 180 rpm and 30°C for 48 hr and then mixed with 2 mL of acetonitrile. After centrifugation at 15,500×g for 10 min, the concentrations of aromatic compounds and liberated ions in the supernatant were analyzed via HPLC and IC, respectively. The cells supplemented with HFB or HCHs were extracted with 8 mL of ethyl acetate, and the organic and aqueous layers were analyzed via GC-ECD and IC, respectively. As a control, resting cells autoclaved at 121°C for 20 min were prepared.

**Results and Discussion**

The ability of strain PD653 to degrade and dehalogenate various aromatic compounds is summarized in Table 1. Prior to calculating the percentage remaining of substrates, we confirmed via HPLC (or GC-ECD) the areas of each substrate in blank samples and heat-killed controls to preclude the possible dissipation by adsorption to the cell. The recovery percentages of the heat-killed controls ranged from 74.7 to 123.2%. The percentages of remaining substrates were obtained by dividing the chromatogram peak area of the heat-killed control by that of the treatment. In halogenated benzenes, strain PD653 dehalogenated only HCB but not HFB, HBB, or less-chlorinated congeners, suggesting that the substrate specificity for halobenzenes could be narrow.

In contrast to the halogenated benzenes, strain PD653 dehalogenated 10 out of 18 halophenols tested. Notably, pentachlorophenol and PCTA were successfully dehalogenated, but pentabromophenol was not. Microbial dehalogenation of pentachlorophenol by *Burkholderia cepacia* strain AC1100 (formerly classified as genus *Pseudomonas*),20 *Trichosporon cutaneum* strain CBS2466,21 and *Mycobacterium fortuitum* strain CG-222 has been reported; however, to date, no other organism from the genus *Nocardioidea* is known to dehalogenate pentachlorophenol. In other halophenols, this strain could not degrade 2,3,4,5-tetra-, 3,4,5-tri-, or 3,4-dichlorophenols and differed from the degradation patterns observed with strain AC1100, which successfully degraded each congener.20 Moreover, three
Table 1. Dissipation, dehalogenation and denitration of aromatic compounds by PD653 resting cells

| Substrate$^a$ | Chemical structure | Remaining (%)$^b$ | Dehalogenation (µmol L$^{-1}$)$^c$ | Denitration (µmol L$^{-1}$)$^d$ |
|---------------|--------------------|------------------|-----------------------------------|-------------------------------|
| Halogenated benzenes | | | | |
| HCB | ![HCB structure](image) | 0.0±4.2$^e$ | 32.5±2.1 | — |
| hexafluoro- | ![Hexafluoro structure](image) | 118.5±26.5$^e$ | 0 | — |
| hexabromo- | ![Hexabromo structure](image) | 85±8.5$^e$ | 0 | — |
| 1,2,3,5-tetrachloro- | ![Tetrachloro structure](image) | 71.9±6.3$^e$ | 0 | — |
| 1,2,4-trichloro- | ![Tetrachloro structure](image) | 81.8±26.4$^e$ | 0 | — |
| 1,3,5-trichloro- | ![Tetrachloro structure](image) | 88.7±32.6$^e$ | 0 | — |
| 1,2,3-trichloro- | ![Tetrachloro structure](image) | 87.7±11.2$^e$ | 0 | — |
| Halogenated phenols | | | | |
| PCP | ![PCP structure](image) | 0.0±1.0$^e$ | 26.0±0.8 | — |
| pentafluoro- | ![Pentafluoro structure](image) | 0.0±1.9$^e$ | 41.1±3.5 | — |
| pentabromo- | ![Pentafluoro structure](image) | 98.8±5.4$^e$ | 0 | — |
| 2,3,4,5-tetrachloro- | ![Tetrachloro structure](image) | 119.2±8.6$^e$ | 0 | — |
| 2,3,5,6-tetrachloro- | ![Tetrachloro structure](image) | 0.0±2.6$^e$ | 28.3±0.3 | — |
| 2,3,5-trichloro- | ![Tetrachloro structure](image) | 0.0±8.6$^e$ | 7.3±1.0 | — |
| 2,3,6-trichloro- | ![Tetrachloro structure](image) | 0.0±4.9$^e$ | 5.9±0.6 | — |
| 2,3,4-trichloro- | ![Tetrachloro structure](image) | 0.0±1.5$^e$ | 4.1±0.6 | — |
| 3,4,5-trichloro- | ![Tetrachloro structure](image) | 102.6±5.4$^e$ | 0 | — |
| 2,4,6-trichloro- | ![Tetrachloro structure](image) | 0.0±13.0$^e$ | 15.8±0.4 | — |
| 2,4,5-trichloro- | ![Tetrachloro structure](image) | 0.0±5.3$^e$ | 20.8±5.4 | — |
| 2,3-dichloro- | ![Dichloro structure](image) | 0.0±4.7$^e$ | 2.0±0.2 | — |
Table 1. Dissipation, dehalogenation and denitrination of aromatic compounds by PD653 resting cells

| Substrate \(^a\) | Chemical structure | Remaining (% \(^b\)) | Dehalogenation (µmol L\(^{-1}\)) \(^c\) | Denitrination (µmol L\(^{-1}\)) \(^c\) |
|------------------|--------------------|----------------------|--------------------------------------|--------------------------------------|
| 2,4-dichloro-    | ![2,4-dichloro-](image) | 64.2 ± 3.1\(^i\)     | 0                                    | —                                    |
| 3,4-dichloro-    | ![3,4-dichloro-](image) | 98.2 ± 6.0\(^i\)     | 0                                    | —                                    |
| 3,5-dichloro-    | ![3,5-dichloro-](image) | 4.0 ± 3.3\(^i\)      | 2.0 ± 0.4                            | —                                    |
| 2-chloro-        | ![2-chloro-](image)   | 91.8 ± 6.0\(^i\)     | 0                                    | —                                    |
| 3-chloro-        | ![3-chloro-](image)   | 114.5 ± 10.6\(^i\)   | 0                                    | —                                    |
| 4-chloro-        | ![4-chloro-](image)   | 96.3 ± 6.7\(^i\)     | 0                                    | —                                    |
| Halogenated nitrobenzenes | | | | |
| PCNB             | ![PCNB](image)       | 0.0 ± 9.8\(^i\)      | 23.1 ± 0.9                           | 6.5 ± 0.1                            |
| 2,3,4,5-tetrachloro-1-nitro- | ![2,3,4,5-tetrachloro-1-nitro](image) | 0.0 ± 2.2\(^i\) | 0.0 ± 0.6 | 7.0 ± 0.4 |
| 2,3,5,6-tetrachloro-1-nitro- | ![2,3,5,6-tetrachloro-1-nitro](image) | 0.0 ± 3.3\(^i\) | 13.3 ± 2.4 | 5.2 ± 0.2 |
| 2,3,4-trichloro-1-nitro- | ![2,3,4-trichloro-1-nitro](image) | 39.3 ± 3.1\(^i\) | 2.9 ± 0.3 | 0 |
| 3,5-dichloro-1-nitro- | ![3,5-dichloro-1-nitro](image) | 59.3 ± 3.9\(^i\) | 0 | 0 |
| 3,4-dichloro-1-nitro- | ![3,4-dichloro-1-nitro](image) | 52.4 ± 3.2\(^i\) | 0 | 0 |
| 2,3-dichloro-1-nitro- | ![2,3-dichloro-1-nitro](image) | 4.5 ± 0.4\(^i\) | 0 | 0 |
| 2,5-dichloro-1-nitro- | ![2,5-dichloro-1-nitro](image) | 42.1 ± 1.7\(^i\) | 0 | 0 |
| 3-chloro-1-nitro- | ![3-chloro-1-nitro](image) | 70.4 ± 6.0\(^i\) | 0 | 0 |
| 4-chloro-1-nitro- | ![4-chloro-1-nitro](image) | 110.5 ± 9.7\(^i\) | 0 | 0 |
| Others           | | | | |
| pentachlorothioanisole (PCTA) | ![pentachlorothioanisole](image) | 0.0 ± 6.0\(^i\) | 26.3 ± 2.3 | — |
| tetrachloroisophthalonitrile | ![tetrachloroisophthalonitrile](image) | 30.0 ± 4.6\(^i\) | 4.0 ± 0.3 | — |
| 2,4,6-trinitrotoluene (TNT) | ![2,4,6-trinitrotoluene](image) | 13.9 ± 2.1\(^i\) | 5.8 ± 0.6 | — |
isomeric mono-chlorinated phenols were not degraded at all. The reason for the lower recovery of Cl\(^-\) seems to be that strain PD653 could not completely dehalogenate all of the halogen ions. For example, although 50 µmol L\(^{-1}\) fluoride ions were expected to be released against pentafluorophenol, only 41.1 ± 3.5 µmol L\(^{-1}\) fluoride ions were detected, corresponding to approximately 4 fluoride ions per pentafluorophenol molecule, in the supernatant. Additionally, 40.0 µmol L\(^{-1}\) chloride ions were theoretically expected to be released against 2,3,5,6-tetrachlorophenol, whereas only 28.3 ± 0.3 µmol L\(^{-1}\) chloride ions, corresponding to approximately 3 chloride ions per 2,3,5,6-tetrachlorophenol molecule, were liberated. Furthermore, Takagi et al. reported that 34.0 µmol L\(^{-1}\) chloride ions were liberated by strain PD653 against the dissipation of 6.5 µmol L\(^{-1}\) HCB in the biodegrading test,\(^{17}\) corresponding to 5 chloride ions per HCB molecule. In this study, strain PD653 did not show a dehalogenation spectrum against monochlorinated aromatics, supporting this reason.

A selectivity of strain PD653 for highly chlorinated nitrobenzenes was shown in this experiment. On the other hand, lower dehalogenation activities were shown against chloronitrobenzenes as to decrease in halo substituents, particularly, strain PD653 poorly dehalogenated mono- and di-chlorinated nitrobenzenes. Despite the apparent dissipation of substrates, no chloride release was observed for 3,5-, 3,4-, 2,3-, and 2,5-dichloro-1-nitrobenzenes. This result indicates that an enzyme(s) other than dehalogenase attacks low chlorinated substrates. No chloride release was observed for 2,3,4,5-tetrachloro-1-nitrobenzene, despite the 7.0 ± 0.4 µmol L\(^{-1}\) nitrate ion being liberated. A plausible reason for this might be the generation of a dead-end product, 2,3,4,5-tetrachlorophenol, via denitration. This hypothesis is supported by Fig. S1, showing the accumulation of putative 2,3,4,5-tetrachlorophenol in the sample supplemented with 2,3,4,5-tetrachloro-1-nitrobenzene. Compared to PCNB, HCB, and PCTA, PCA was degraded to a lesser extent, 53.1 ± 9.8%. If an electron donating a –NH\(_2\) group on the benzene ring affects the degradation rate, from our data, one could hypothesize that strain PD653 cannot degrade substrates whose aromatic ring is activated by the electron-donating group. The inductive effects by substituents could be considered a key factor in determining whether strain PD653 recognizes aromatic compounds as substrates. Given that PCTA, PCA, and the impurity ingredient HCB have been detected in agricultural soil to which technical PCNB has been applied,\(^{23–25}\) it is of interest that strain PD653, which was isolated from PCNB-contaminated soil,\(^{17}\) exhibited substrate specificity toward each of those compounds.

Among the four HCH stereoisomers, strain PD653 could dehalogenate only β-HCH. It was completely dissipated, and 18.94 ± 1.4 µmol L\(^{-1}\) of Cl\(^-\) ions, corresponding to approximately 2 chloride ions per β-HCH molecule, was liberated. This result clearly showed that strain PD653 prefers to dehalogenate β-HCH, whose six chlorine atoms are all in equatorial positions. Among the four isomers, β-HCH seems to be a planar structure such as chlorobenzenes or chlorophenols. Considering this, the capability of HCH metabolism of this strain might be restricted by the steric hindrance of chloride atoms. Among the t-HCH isomers, β-HCH has the most recalcitrant nature and the highest stability.\(^{26,27}\) Bacterial dehalogenation of β-HCH has been well characterized in halo-alkane dehalogenase (LinB) from Sphingomonas paucimobilis strain UT26.\(^{28}\) In addition, thus far, various bacteria have been found to degrade β-HCH\(^{29,30}\); however, this is the first report of a Nocardioides strain that can degrade this compound.

In conclusion, our results indicate that strain PD653 has a narrow substrate specificity toward chlorobenzenes, whereas it has a broad substrate specificity toward nitrochlorobenzenes and chlorophenols, in which highly chlorinated congeners are preferably recognized by this strain. Moreover, the novel aspect that strain PD653 has degradation capability for compounds associated with a PCNB-contaminated environment was shown, indicating that this strain might be applicable to bioremediation contaminated by these compounds. Our ongoing work, including the purification of HcbA1, HcbA2, and HcbA3 enzymes, would provide further insights into the conclusion reached in this study.

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**Table 1.** Continued

| Substrate\(^a\) | Chemical structure | Remaining (%)\(^b\) | Dehalogenation (µmol L\(^{-1}\))\(^c\) | Denitration (µmol L\(^{-1}\))\(^d\) |
|-----------------|-------------------|-------------------|---------------------------------|-----------------|
| pentachloroaniline (PCA) | ![Chemical Structure](image1) | 53.1 ± 9.8\(^e\) | 7.5 ± 1.8 | — |
| α-hexachlorocyclohexane (HCH) | ![Chemical Structure](image2) | 93.8 ± 9.3\(^f\) | 0 | — |
| β-HCH | ![Chemical Structure](image3) | 0 ± 5.3\(^g\) | 18.94 ± 1.4 | — |
| γ-HCH | ![Chemical Structure](image4) | 102.8 ± 19.1\(^h\) | 0 | — |
| δ-HCH | ![Chemical Structure](image5) | 99.0 ± 17.9\(^i\) | 0 | — |

\(^a\) Each substrate was used at a concentration of 10 µmol L\(^{-1}\). \(^b\) Percentages of remaining substrates were obtained by dividing chromatogram peak area of the heat-killed control by that of the treatment. \(^c\) The substrate analyzed by HPLC. \(^d\) The substrate analyzed by GC-ECD. \(^e\) The concentration of ion generated in the supernatant.
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References

1) K. Furukawa and F. Matsumura: J. Agric. Food Chem. 42, 543–548 (1976).
2) D. H. Pieper and W. Reinke: Curr. Opin. Biotechnol. 11, 262–270 (2000).
3) R. Imai, Y. Nagata, K. Senoo, H. Wada, M. Fukuda, M. Takagi and K. Yano: Agric. Biol. Chem. 53, 2015–2017 (1989).
4) R. T. Mandelbaum, D. L. Allan and L. P. Wackett: Appl. Environ. Microbiol. 61, 1451–1457 (1995).
5) N. V. Coleman, T. M. Mattes, J. M. Gossett and J. C. Spain: Appl. Environ. Microbiol. 68, 6162–6171 (2002).
6) V. M. Travkin, A. P. Jadan, F. Briganti, A. Scozzafava and L. A. Golovleva: FEBS Lett. 407, 66–72 (1997).
7) C. Behrend and K. Heesche-Wagner: Appl. Environ. Microbiol. 65, 1312–1377 (1999).
8) J. Rajan, K. Valli, R. E. Perkins, F. S. Sariaslani, S. M. Barns, A.-L. Reysenbanch, S. Rehm, M. Ehringer and N. R. Pace: J. Ind. Microbiol. Biotechnol. 16, 319–324 (1996).
9) K. Inoue, H. Habe, H. Yamane and H. Nojiri: Appl. Environ. Microbiol. 72, 3321–3329 (2006).
10) K. Yamazaki, K. Fuji, A. Iwasaki, K. Takagi, K. Satsuma, N. Harada and T. Uchimura: FEMS Microbiol. Lett. 286, 171–177 (2008).
11) K. Satsuma: Appl. Microbiol. Biotechnol. 86, 1585–1592 (2010).
12) E. Topp, W. M. Mulbry, H. Zhu, S. M. Nour and D. Cuppels: Appl. Environ. Microbiol. 66, 3134–3141 (2000).
13) P. K. Arora and H. Bae: Microb. Cell Fact. 13, 31–47 (2014).
14) P. K. Arora, A. Srivastava and V. P. Singh: J. Hazard. Mater. 266, 42–59 (2014).
15) C. S. Harwood and R. E. C. S. Parales: Annu. Rev. Microbiol. 50, 553–590 (1996).
16) K. Takagi, Y. Yoshioka, A. Iwasaki, I. Kamei and N. Harada: Organohalog. Compd. 69, 2576–2579 (2007).
17) K. Takagi, A. Iwasaki, I. Kamei, K. Satsuma, Y. Yoshioka and N. Harada: Appl. Environ. Microbiol. 75, 4452–4458 (2009).
18) K. Ito, K. Takagi, A. Iwasaki, N. Tanaka, Y. Kanesaki, F. Martin-Laurent and S. Igimi: Appl. Environ. Microbiol. 83, e00824–17 (2017).
19) K. Ito, K. Takagi, Y. Matsushima, A. Iwasaki, N. Tanaka, Y. Kanesaki, F. Martin-Laurent and S. Igimi: J. Pestic. Sci. 43, 124–131 (2018).
20) J. S. Karns, J. J. Kilbane, S. Duttagupta and A. M. Chakraborty: Appl. Environ. Microbiol. 46, 1176–1181 (1983).
21) S. Peelen, I. M. C. M. Rietjens, M. G. Boersma and J. Vervoort: Eur. J. Biochem. 227, 284–291 (1995).
22) J. S. Uttila, V. H. Kitunen, T. Saastamoinen, T. Coote, M. M. Häggblom and M. S. Salkinoja-Salonen: J. Bacteriol. 174, 5669–5675 (1992).
23) Y. Fushiwaki, N. Tase, A. Saeki and K. Urano: Sci. Total Environ. 92, 55–67 (1990).
24) K. Osawa, T. Miyamoto and I. Yamamoto: J. Pestic. Sci. 9, 339–344 (1984) (in Japanese).
25) R. H. de Vos, M. C. ten Noever de Brauw and P. D. A. Olthof: Bull. Environ. Contam. Toxicol. 11, 567–571 (1974).
26) J. E. M. Beurskens, A. J. M. Stams, A. J. B. Zehnder and A. Bachmann: Ecotoxicol. Environ. Saf. 21, 128–136 (1991).
27) K. L. Willett, E. M. Ulrich and R. A. Hites: Environ. Sci. Technol. 32, 2197–2207 (1998).
28) Y. Nagata, Z. Prokop, Y. Sato, P. Jerabeck, A. Kumar, Y. Ohtsubo, M. Tsuda and J. Damborský: Appl. Environ. Microbiol. 71, 2183–2185 (2005).
29) T. M. Phillips, A. G. Seech, H. Lee and J. T. Trevors: Biodegradation 16, 363–392 (2005).
30) R. Lal, G. Pandey, P. Sharma, K. Kumari, S. Malhotra, R. Pandey, V. Raina, H.-P. E. Kohler, C. Holliger, C. Jackson and J. G. Oakeshott: Microbiol. Mol. Biol. Rev. 74, 58–80 (2010).