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The Branched-Chain Dodecylbenzene Sulfonate Degradation Pathway of *Pseudomonas aeruginosa* W51D Involves a Novel Route for Degradation of the Surfactant Lateral Alkyl Chain

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***Pseudomonas aeruginosa* W51D is able to grow by using branched-chain dodecylbenzene sulfonates (B-DBS) or the terpenic alcohol citronellol as a sole source of carbon. A mutant derived from this strain (W51M1) is unable to degrade citronellol but still grows on B-DBS, showing that the citronellol degradation route is not the main pathway involved in the degradation of the surfactant alkyl moiety. The structures of the main B-DBS isomers and of some intermediates were identified by gas chromatography-mass spectrometric analysis, and a possible catabolic route is proposed.**

Alkylbenzene sulfonates are the most commonly used surfactants in domestic detergent formulations (8). In the United States and Europe, linear alkylbenzene sulfonates (LAS) have been used since the early 1960s, when the low rate of biodegradation of branched-chain alkylbenzene sulfonates (BAS) was recognized (2, 4, 5, 8). In some Latin American countries, BAS are currently used in different detergent formulations due to their low costs. Water pollution by BAS is a significant environmental problem in these countries.

A *Pseudomonas aeruginosa* strain (W51D) which is able to mineralize at least 70% of a BAS commercial mixture and completely degrade LAS has been isolated (17). This strain is resistant to high concentrations of these surfactants (17). *P. aeruginosa* W51D is the only reported bacterium able to mineralize BAS at a significant rate. LAS-degrading *Pseudomonas* strain C12B barely degrades BAS (4, 11, 19).

LAS are completely degraded in wastewater treatment plants, and different organisms participate in their mineralization, each degrading a part of the molecule. A four-member consortium was identified as responsible for LAS mineralization (9), and a larger consortium was found to be involved in mineralization in a marine environment (15). In these consortia, some members attacked the side chain, while others degraded the aromatic moiety. So far, no consortium that is able to efficiently degrade BAS has been described. The low rate of BAS biodegradation is due to the presence of highly branched alkyl groups (2, 18). Branched alkanes are generally less susceptible to biodegradation than n-alkanes and certain methyl-branched alkanes. Special 3-methyl-branched and quaternary-substituted alkyl chains can result in environmental recalcitrance (2, 7, 12–14, 18).

Some *Pseudomonas* strains degrade branched alkanes and alkenes. Citronellol (3,7-dimethyl-6-octen-1-ol) has been used as a model compound to study the route of degradation of branched alkenes (7, 13, 14). It has previously been reported that *P. aeruginosa* W51D is able to use citronellol as a sole carbon source (17). The characterization of a *ctrA* mutant derived from strain W51D, which has a low citronellal dehydrogenase activity (6), has also been previously reported.

The aim of this work was to contribute to the elucidation of the branched-chain dodecylbenzene sulfonate (B-DBS) degradation pathway of *P. aeruginosa* W51D and to evaluate the contribution of the reported route to citronellol degradation. We present evidence showing that the citronellol pathway is not the only route involved in the degradation of the surfactant alkyl lateral chain. Identification of the main B-DBS isomer structures and the direct identification of some of their degradation intermediates suggest that strain W51D completely assimilates the surfactant lateral chain prior to the aromatic ring cleavage.

Identification of the isomers present in the B-DBS mixture. The substrate used for *P. aeruginosa* W51D degradation studies, B-DBS, was purified by high-performance liquid chromatography (HPLC) from a commercial BAS preparation as a single peak on a semipreparative (250- by 22-mm) Econosil C_{18} column (Alltech Associates Inc.) by treatment with 60:40 H_2O-acetonitrile (ACN) for 10 min, followed by a linear gradient reaching pure ACN in 5 min; this solvent was kept for an additional 2 min. The flow rate used was 5 ml/min, and the elution profile was monitored as described above. The B-DBS mixture obtained from HPLC was desulfonated by reflux treatment in the presence of phosphoric acid as previously described (18) and was injected onto a gas chromatograph coupled with mass spectrometry (MS). The desulfonated B-DBS mixture showed the existence of multiple isomers. The gas chromatography-MS (GC-MS) analysis of 11 of the branched-chain isomers showed that all of them had a molecular weight (M^+, molecular ion) of 246 *m*/*z* (Table 1). The mass spectrum analysis showed an important ion peak of 91 *m*/*z*, indicating the $C_6H_5CH_2^+$ ion. The electron impact fractionation also showed a branched nature of the alkyl moiety. Upon electron impact, saturated hydrocarbons fragment preferentially at the branching points; the positive charge remains on the more highly substituted carbon atom, and elimination of the longest carbon chain is favored. The absence of an $(M-15)^+$ ion in the mass spectrum of the alkylbenzenes is not surprising, although there are many methyl groups present. The methyl radical is the least

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TABLE 1. GC-MS data for a purified and desulfonated B-DBS mixture

Compound	Area (%)[a]	RT (min)[b]	*m/z* of major ion peaks (%)[c]
1	13.6	15.0	246(M^+) (5), 204 (1), 203 (10), 190 (1), 189 (10), 175 (3), 162 (2), 161 (17), 159 (1), 148 (2), 147 (20), 133 (5), 131 (2), 120 (1), 119 (15), 114 (5), 113 (6), 112 (1), 106 (12), 105 (100), 103 (2), 92 (3), 91 (35), 79 (2), 78 (1), 77 (2), 71 (3)
2	2.48	15.4	246(M^+) (17), 175 (19), 161 (22), 147 (16), 133 (9), 119 (15), 117 (7), 106 (2), 105 (36), 104 (9), 92 (9), 91 (100), 71 (10)
3	1.34	15.7	246(M^+) (9), 133 (15), 120 (15), 119 (100), 118 (6), 106 (5), 105 (7), 91 (21), 71 (2)
4	13.92	16.5	246(M^+) (5), 217 (4), 175 (1), 147 (3), 134 (1), 133 (15), 120 (12), 119 (100), 118 (7), 117 (3), 115 (2), 106 (3), 105 (20), 104 (1), 103 (2), 92 (2), 91 (13), 79 (2), 77 (2), 71 (1)
5	12.34	16.9	246(M^+) (5), 133 (2), 120 (11), 119 (100), 118 (6), 117 (1), 105 (3), 103 (2), 92 (1), 91 (13), 79 (2), 77 (2), 71 (1)
6	7.93	17.4	246(M^+) (4), 147 (4), 133 (5), 120 (10), 119 (100), 118 (6), 117 (1), 106 (2), 105 (12), 103 (2), 92 (2), 91 (17), 79 (3), 77 (2), 71 (1)
7	17.87	18.1	246(M^+) (5), 217 (3), 189 (2), 175 (3), 161 (4), 147 (1), 134 (1), 133 (8), 120 (10), 119 (100), 118 (6), 117 (2), 115 (2), 106 (2), 105 (23), 103 (2), 92 (2), 91 (24), 79 (3), 78 (1), 77 (2), 71 (2
8	1.75	18.4	246(M^+) (9), 203 (12), 187 (15), 174 (8), 173 (48), 159 (12), 147 (28), 133 (17), 131 (27), 129 (8), 128 (8), 120 (6), 119 (39), 118 (8), 117 (14), 115 (10), 106 (22), 105 (100), 91 (47), 85 (10), 79 (7), 71 (14)
9	2.21	18.7	246(M^+) (4), 217 (6), 134 (3), 133 (26), 131 (2), 120 (11), 119 (100), 118 (4), 117 (5), 106 (4), 105 (35), 92 (3), 91 (28), 79 (4), 71 (3)
10	16.97	19.5	246(M^+) (5), 173 (1), 161 (3), 159 (4), 147 (1), 131 (1), 120 (11), 119 (100), 118 (7), 117 (3), 115 (1), 106 (3), 105 (22), 103 (2), 92 (1), 91 (18), 79 (3), 77 (2), 71 (4)
11	2.96	19.9	246(M^+) (4), 174 (2), 173 (15), 161 (2), 133 (2), 131 (4), 120 (12), 119 (100), 118 (5), 117 (4), 115 (2), 106 (2), 105 (11), 103 (2), 91 (20), 79 (2), 77 (2)

[a] Based on the total ion current response of the MS detector.
[b] RT, retention time.
[c] Ions with more than 1% abundance are shown. The ion abundance percentages are shown in parentheses.

stable of the alkyl radicals and will not be eliminated readily if other fragmentations are facile. The analytical techniques used in this work do not allow the determination of the positions of both the methyl groups and phenyl moiety. The suggested structures of the alkyl chains of the five most abundant B-DBS isomers are shown in Fig. 1.

Participation of the citronellol pathway in B-DBS degradation. *Pseudomonas* degradation of citronellol (12) is the only enzymatic pathway characterized in bacteria for the assimilation of methyl-ramified alkanes so far. The isolation and characterization of a *P. aeruginosa* W51D mutant (W51M1) unable to degrade citronellol due to the reduced activity of the enzyme citronellal dehydrogenase have previously been described (6). To determine whether the citronellol pathway was used by strain W51D to degrade the B-DBS alkyl chain, we studied the ability of mutant W51M1 to assimilate the surfactants. We found that even though mutant W51M1 is unable to use citronellol as a carbon source, it is still able to grow on M9 plus B-DBS (0.2% [wt/vol]). Quantitative determination of B-DBS degradation by strain W51M1 was obtained from HPLC analysis of culture supernatants, in which the extent of B-DBS consumed by this mutant on M9 plus glucose (0.2% [wt/vol]) plus B-DBS was estimated after 48 h of growth. The consumption by strain W51M1 was reduced by 40% compared to that by the wild-type strain W51D. Even though the total amount of surfactant consumed on this medium was reduced, we could not detect differences in the relative proportion of the accumulated intermediates. These results show that the enzymes involved in citronellol degradation could also be involved in B-DBS degradation, presumably at the first steps of the catabolism, but it is apparent that this pathway is not the main route of B-DBS degradation by strain W51D.

It has been reported that the wild-type strain PAO1 (supplied by Bruce Holloway) is able to grow with citronellol as the sole source of carbon (6); however, this strain is unable to use B-DBS as a carbon source. These results suggest that the capability of strain W51D to degrade B-DBS is mainly due to the presence of a degradation route of the B-DBS lateral chain that is different from the citronellol pathway, which is not present in strain PAO1.

Analysis of the W51D pathway for B-DBS degradation. To obtain information on the main W51D route for B-DBS degradation, we determined the structure of the degradation intermediates by analyzing the 72-h culture supernatants of W51D cells grown on M9 plus B-DBS by GC-MS. These supernatants were acidified with HCl to pH 3 to eliminate the extracellular matrix of the biofilm formed in this medium. The acidified supernatant was centrifuged, the supernatant was extracted three times with ethylacetate, the organic fraction was concentrated by evaporation, and the extracted product was dried with N_2. The dried product was resuspended in methanol at a final concentration of 1 mg/ml. Samples were silylated prior to GC-MS analysis with $ClSi(CH_3)_3$ (Sigma) according to the manufacturer's instructions. One microliter of the com-

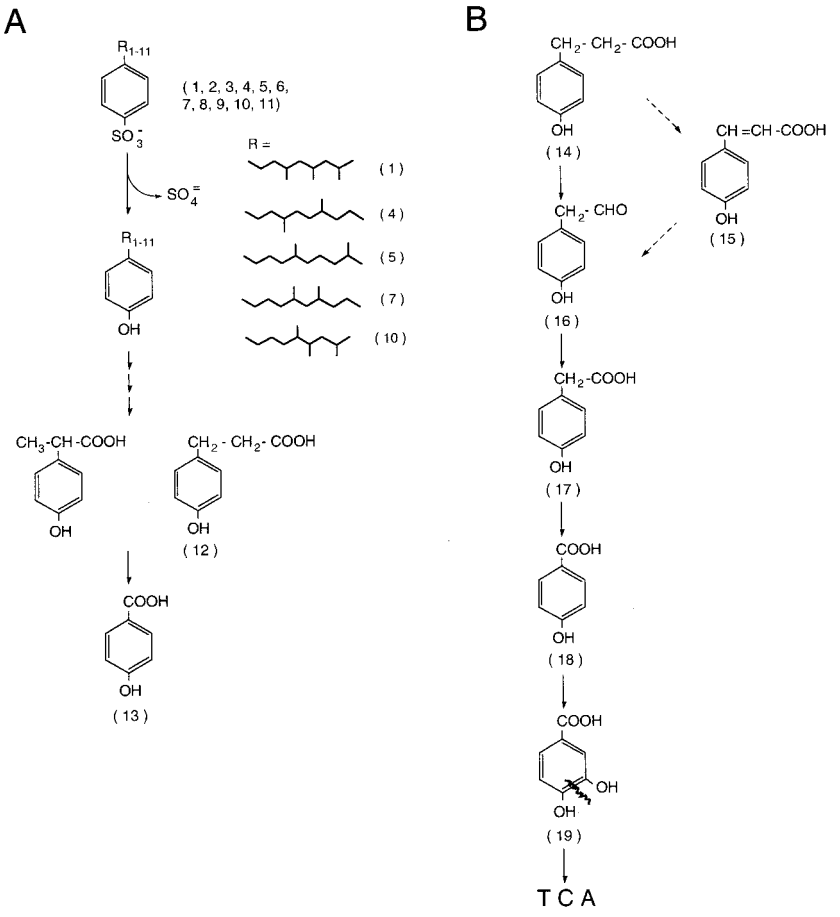

FIG. 1. Schematic representation of the proposed degradation route of B-DBS (A) and 4-hydroxyphenylpropionate (B) by *P. aeruginosa* W51D. The numbers in parentheses correspond to the compound numbers in Tables 1 and 2, where the MS results are given. The structures of the alkyl lateral chains of the most abundant B-DBS isomers are shown as R groups. TCA, tricarboxylic acid cycle.

pound solutions separated by HPLC or directly silylated after being concentrated was injected onto a gas chromatograph coupled with an MS detector (Hewlett-Packard HP6890 GC-MS system). Table 2 shows the MS data of these identified metabolites.

Considering the structure of the identified compounds, it is possible to suggest the partial pathway for B-DBS degradation shown in Fig. 1. The first step in B-DBS degradation seems to be the desulfonation of the benzene ring and its concomitant hydroxylation. This proposition was initially made based on the finding that all the degradation intermediates detected were hydroxylated derivatives (Table 2) and no sulfonated molecules were found. To further confirm this result, we treated the ethylacetate extract from the cell-free culture supernatant with diazomethane to form the methylsulfonate derivatives and then analyzed the products by GC-MS. In accordance with our original observation, only the sulfonated B-DBS substrate was detected and no other sulfonated intermediate was found. Desulfonation with the concomitant hydroxylation of the aromatic ring has been reported as the first step in LAS degradation by *Pseudomonas putida* strains (9, 21).

The GC-MS analysis of the culture supernatants of W51D cells grown on M9 plus B-DBS showed the production of 4-hydroxypropionate and 4-hydroxybenzoate (Table 2). These aromatic compounds, as well as phenylacetate, are readily degraded by strain W51D (all supplied as a carbon source to M9 medium at a concentration of 5 mM), suggesting that they could be B-DBS degradation intermediates. The identification of 4-hydroxybenzoate as a possible B-DBS degradation intermediate suggests that strain W51D completely oxidizes the B-DBS lateral chain prior to the aromatic ring cleavage.

The oxidation of the branched lateral B-DBS chain could proceed by the removal of C-1 units through α-oxidation, as reported for LAS degradation (3, 18), in conjunction with classical β-oxidation, or by a modified β-oxidation in which two carbons are cleaved from the main hydrocarbon chain together with a methyl ramification, as has been reported to occur in the degradation of methyl-branched alkanes by an unclassified gram-positive bacterium (12).

W51D pathway for the degradation of 4-hydroxyphenylpropionate. Considering that 4-hydroxyphenylpropionate is a B-DBS catabolic intermediate, we studied the W51D route for the degradation of this compound as a way to analyze further B-DBS catabolism by strain W51D. The proposed route of W51D degradation of 4-hydroxyphenylpropionate (Fig. 1) was elucidated by using this compound as a carbon source and by identifying the intermediates (Table 2) by GC-MS analysis, as described above. The degradation intermediates were purified by HPLC as follows: 50 μl of the concentrated supernatant or of the supernatant of strain W51D grown for 48 h on 4-hydroxyphenylpropionate was injected on a Nova-Pak C_{18} 3.9- by 150-mm reverse-phase column (Waters), and the elution sol-

TABLE 2. GC-MS data for products formed by *P. aeruginosa* W51D grown in the compound indicated

Compound source and no.	*m/z* of major ion peaks (%)[a]	Suggested structure (% identity)[b]
B-DBS		
12	310(M^+) (8), 295 (4), 281 (10), 267 (4), 208 (6), 207 (24), 193 (12), 192 (40), 191 (4), 181 (4), 180 (11), 179 (64), 177 (12), 163 (5), 149 (5), 147 (12), 136 (4), 133 (8), 131 (5), 129 (4), 117 (6), 116 (4), 105 (8), 95 (15), 93 (32), 79 (16), 77 (15), 76 (5), 75 (42), 74 (10), 73 (100)	Hydrocinnamic acid, *p*-[(TMS)oxy]-, TMS estere (97)
13	282(M^+) (8), 268 (9), 267 (36), 224 (7), 223 (36), 217 (6), 207 (5), 204 (5), 195 (4), 194 (7), 193 (38), 190 (6), 179 (4), 151 (4), 149 (6), 147 (8), 135 (6), 133 (5), 126 (14), 105 (4), 95 (8), 94 (4), 93 (8), 91 (6), 76 (4), 75 (16), 74 (10), 73 (100)	Benzoic acid, 4-[(TMS)oxy]-, TMS ester (97)
3(4-hydroxyphenyl-propionic) acid		
14	310(M^+) (20), 311 (4), 295 (5), 194 (4), 193 (12), 192 (70), 181 (5), 180 (18), 179 (100), 177 (22), 163 (6), 149 (4), 140 (4), 75 (24), 74 (6), 73 (58)	Hydrocinnamic acid, *p*-[(TMS)oxy]-, TMS ester (99)
15	308(M^+) (40), 309 (9), 310 (4), 295 (5), 194 (12), 293 (52), 250 (8), 249 (36), 233 (4), 221 (4), 220 (16), 219 (72), 203 (8), 192 (5), 191 (5), 179 (16), 175 (8), 147 (8), 135 (5), 115 (10), 102 (4), 89 (4), 76 (4), 75 (34), 74 (10), 73 (100)	Cinnamic acid, *p*-[(TMS)oxy], TMS ester (99)
16	208(M^+) (24), 195 (5), 194 (18), 193 (100), 151 (14), 149 (4), 147 (4), 135 (6), 133 (5), 123 (4), 93 (8), 91 (9), 89 (14), 77 (6), 75 (13), 74 (6), 73 (33)	Benzene acetaldehyde, 4-[(TMS)oxy][c]
17	252(M^+) (28), 207 (4), 193 (7), 192 (8), 180 (15), 179 (100), 177 (12), 164 (11), 163 (18), 149 (8), 135 (7), 133 (9), 131 (11), 107 (8), 91 (9), 89 (22), 78 (8), 75 (15), 74 (7), 73 (88)	4-Hydroxypehnylacetic acid ethyl ester TMS (92)
18	282(M^+) (14), 269 (5), 268 (12), 267 (56), 263 (6), 262 (28), 225 (4), 224 (8), 223 (45), 207 (6), 194 (8), 193 (4), 179 (4), 151 (4), 149 (5), 147 (8), 135 (6), 133 (5), 130 (5), 126 (14), 117 (4), 103 (4), 95 (8), 93 (24), 91 (5), 89 (5), 77 (4), 75 (17), 74 (8), 73 (100)	Benzoic acid, 4-[(TMS)oxy]-, TMS ester (97)
19	370(M^+) (8), 355 (16), 343 (10), 342 (12), 341 (38), 327 (6), 325 (8), 302 (6), 297 (12), 283 (8), 267 (17), 255 (6), 254 (8), 253 (27), 239 (14), 238 (24), 237 (100), 221 (7), 208 (6), 191 (10), 179 (9), 165 (8), 164 (14), 163 (70), 149 (7), 147 (10), 135 (7), 133 (10), 119 (6), 117 (6), 105 (6), 93 (6), 89 (30), 73 (62)	Benzoic acid 3,4-[(TMS)-dioxy]-, TMS ester[c]

[a] Ions with more than 4% abundance are shown. The ion abundance percentages are shown in parentheses.
[b] Identification was based on an instrument library match. TMS, trimethylsilyl.
[c] Tentative assignment of structure.

vent was H_2O-ACN-acetic acid 75/4/1, vol/vol/vol for 3 min, followed by a linear gradient to reach 100% ACN in 6 min. The flux used was 1 ml/min, and the elution was monitored at 254 nm with a Hewlett-Packard 1050 diode array UV detector. We found, in accordance with the results obtained by studying B-DBS degradation, that the propionate moiety of this molecule was completely oxidized and degraded to 4-hydroxybenzoate prior to the aromatic ring cleavage. This is unusual, since most bacteria cleave the aromatic ring of short-chain alkylbenzenes without previous oxidation of the alkyl chain (16).

It has been reported that cinnamic acid is accumulated as a nonmetabolized by-product of the degradation of long-chain alkylbenzenes (16). We detected the production of 4-hydroxycinnamic acid when strain W51D was grown on M9 plus 4-hydroxyphenylpropionate (Table 2). Our data are insufficient to conclude whether this compound is an intermediate or a by-product of this catabolic route. However, the oxidation of the cinnamic acid lateral chain by W51D, as judged by the detected degradation intermediates of cells grown on M9 plus glucose plus cinnamic acid (5 mM) for 48 h, is consistent with 4-hydroxycinnamic acid being a 4-hydroxyphenylpropionate degradation intermediate, since the same degradation products were detected in both cases (Fig. 1). The oxidation of the cinnamic acid lateral chain by W51D is similar to styrene lateral chain oxidation by *Pseudomonas* sp. strain Y2 (20).

Quantitative data were obtained from the GC analysis by using the flame ionization detection response. After 48 h of W51D growth on M9 plus 4-hydroxyphenylpropionate, the product/substrate ratios (according to the areas of the peaks in the chromatograms) for the different compounds detected were as follows: for 4-hydroxycinnamic acid (isomer A), 0.442; for 4-hydroxycinnamic acid (isomer B), 0.218; for 4-hydroxybenzene acetaldehyde, 0.007; for 4-hydroxyphenylacetate, 0.003; for 4-hydroxybenzoate, 0.035; and for 3,4-dihydroxybenzoate, 0.004.

In conclusion, our studies show, so far, that *P. aeruginosa* W51D degrades the surfactant B-DBS by using in part the citronellol pathway but that most of the surfactant degradation seems to be carried out by a new catabolic pathway. The data obtained suggest that strain W51D desulfonates B-DBS prior to alkyl chain oxidation. Desulfonation is followed by a complete oxidation of the alkyl moiety before the aromatic ring is

cleaved. To our knowledge, there has been no report of a similar pathway involved in the degradation of alkylbenzenes. Therefore, whatever route strain W51D uses for B-DBS degradation, its characterization will reveal a novel catabolic pathway, and its complete elucidation is a matter of great importance which remains to be further analyzed.

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