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Simultaneously Discrete Biomineralization of Magnetite and Tellurium Nanocrystals in Magnetotactic Bacteria[▽]

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Magnetotactic bacteria synthesize intracellular magnetosomes comprising membrane-enveloped magnetite crystals within the cell which can be manipulated by a magnetic field. Here, we report the first example of tellurium uptake and crystallization within a magnetotactic bacterial strain, *Magnetospirillum magneticum* AMB-1. These bacteria independently crystallize tellurium and magnetite within the cell. This is also highly significant as tellurite (TeO_3^{2-}), an oxyanion of tellurium, is harmful to both prokaryotes and eukaryotes. Additionally, due to its increasing use in high-technology products, tellurium is very precious and commercially desirable. The use of microorganisms to recover such molecules from polluted water has been considered as a promising bioremediation technique. However, cell recovery is a bottleneck in the development of this approach. Recently, using the magnetic property of magnetotactic bacteria and a cell surface modification technology, the magnetic recovery of Cd^{2+} adsorbed onto the cell surface was reported. Crystallization within the cell enables approximately 70 times more bioaccumulation of the pollutant per cell than cell surface adsorption, while utilizing successful recovery with a magnetic field. This fascinating dual crystallization of magnetite and tellurium by magnetotactic bacteria presents an ideal system for both bioremediation and magnetic recovery of tellurite.

Magnetotactic bacteria are known to synthesize magnetosomes that comprise membrane-enveloped magnetic crystals (e.g., Fe_3O_4 and Fe_3S_4) (4, 6, 23). These crystals allow them to be directly manipulated with magnetic force (35, 40). This biomineralization process is highly regulated by the cell, rendering the crystals highly chemically pure. However, there have been reports of magnetite and iron sulfide magnetosome crystals containing manganese and copper, respectively, found in environmental magnetotactic bacteria, but the nonferrous metal quantities within the crystals were not consistent or controlled (5, 15, 30). Recently, the controlled cobalt doping of magnetite magnetosome crystals was also reported in magnetotactic bacteria (37). Until now, however, there has been no report of other toxic metal or metalloid (e.g., tellurium) being taken up by magnetotactic bacteria. Additionally, all reports so far show metal incorporated into the magnetosome. There has been no report of separate crystallization independent from the magnetite within magnetotactic bacteria. In this study, we investigate the tellurium uptake and crystallization in a magnetotactic bacterial strain, *Magnetospirillum magneticum* AMB-1.

The rare metalloid tellurium is used as an alloy component in a wide range of high-technology products, including optical discs, solar cell materials, and thermoelectric elements (27, 42). Although it is naturally rare, due to its use in the technologies described, it is becoming more and more in demand and is therefore highly commercially desirable. This chalcogen is rarely found in the nontoxic elemental state Te(0), but is more commonly present in the environment in its highly toxic soluble oxyanion form, tellurite(IV) (9). The increasing use of tellurium has indirectly led to the increased contamination of water with tellurite, which raises serious concerns for both ecological systems and mammalian health (12, 17). There is thus a growing need to recover tellurium from the environment to both (i) remove a toxic chemical and (ii) recycle a valuable element.

The recovery of metals and metalloids using microorganisms has emerged as a potentially attractive (33, 34, 47) and environment-friendly alternative to conventional techniques such as reclamation treatments (46). The crystallization of target molecules within the microorganisms has the potential to provide some advantages over other bioremediation technology, such as increased accumulation efficiency over cell surface adsorption or nonprecipitous uptake within the cell, decreasing the toxicity of the pollutant by reductive (or oxidative) precipitation/crystallization, and additional potential to utilize the pollutant product for further material applications. The uptake and crystallization of Pb(II), Ag(I), Au(III), U(VI), Se(IV), and other metals by many species has been well documented previously (11, 14, 16, 19, 24). Some bacteria in particular have been the subject of increased study due to the reduction and crystallization of tellurite within or onto the cell (2, 16, 25, 45). However, although these bacteria have been adapted and utilized for the accumulation of various metals and metalloids, cell recovery remains a bottleneck in this approach. Therefore, modification of the system is needed to improve this step.

Recently, the potential of combining a cell surface modification technology with magnetic recovery of heavy metals using magnetotactic bacteria was proposed (40). Here, we present the serendipitous discovery of the simultaneous biomineralization of tellurium and magnetite as discrete nanoparticles within magnetotactic bacteria during cell growth. This

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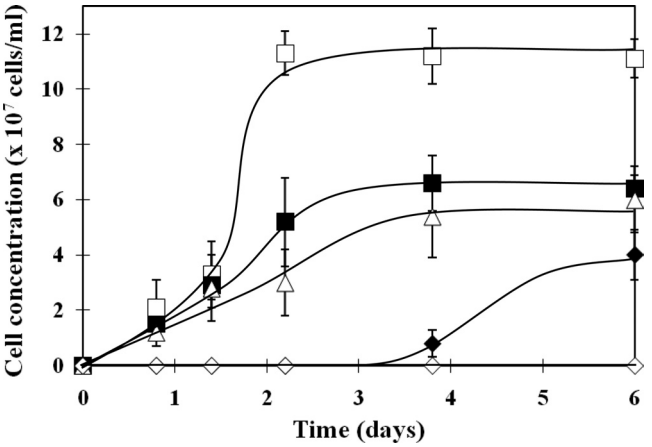

FIG. 1. Tolerance of *M. magneticum* AMB-1 to tellurite. Cells grown in different concentrations of tellurite were directly counted (□, 0 μM; ■, 10 μM; △, 20 μM; ◆, 40 μM; and ◇, 60 μM). The average values from three independent experiments were obtained. Error bars show standard deviations.

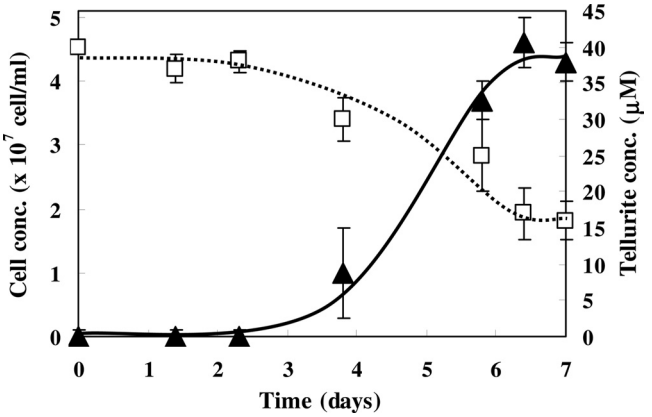

FIG. 2. Tellurite removal during magnetotactic bacterial cell growth. Tellurite removal using magnetotactic bacteria (□, dashed line) and cell growth (▲, black line) was evaluated in the presence of 40 μM tellurite for 7 days. The average values from three independent experiments were obtained. Error bars show standard deviations.

has great potential for development of a bioremediation system that incorporates tellurite removal from polluted water with magnetic recovery.

MATERIALS AND METHODS

Determination of the MIC of tellurite for *M. magneticum* AMB-1 growth. *M. magneticum* AMB-1 was microaerobically cultured in magnetic spirillum growth medium (MSGM) at 28°C as previously described (39, 41). Microaerobic conditions were established by purging the cultures (250 ml) with argon gas for 5 min. The MIC of tellurite for *M. magneticum* AMB-1 in MSGM was determined by growing the cells in various concentrations of tellurite: 0 (control), 10, 20, 40, 60, 80, and 100 μg/ml. The cells were directly counted with a hemocytometer and an optical microscope (Olympus BH-2) for 6 days.

Tellurite removal using magnetotactic bacteria. For tellurite removal, *M. magneticum* AMB-1 was inoculated into the medium containing tellurite and grown until the stationary phase. The medium was filtered (pore size, 0.45 μm), dried, and dissolved with a nitric acid solution (0.1 N) at 180°C. These samples were analyzed with an atomic absorption spectrophotometer (AA-6700; Shimadzu, Japan) (214.3 nm). All assays were performed in triplicate.

TEM and EDX analyses of *M. magneticum* AMB-1 grown in different tellurite concentrations. *M. magneticum* AMB-1 cells grown in the presence of tellurite were observed by transmission electron microscopy (TEM) (H7100; Hitachi, Japan). Cells harvested from MSGM containing tellurite (0 and 40 μM) were washed with phosphate-buffered saline (PBS) buffer (pH 7.4) and spotted onto 150-mesh copper grids (Nisshin EM). The samples were analyzed by TEM operated at an accelerating voltage of 100 kV. To measure the number of magnetite and tellurium crystals, over 30 cells were manually counted.

To verify the biomineralization of tellurium within the cell, ultrathin-section TEM analysis was also conducted. Magnetotactic bacteria in the stationary phase cultured in the presence of 20 μM tellurite were washed and fixed overnight with 2% glutaraldehyde in a 0.05 M sodium cacodylate buffer. After being washed overnight with 0.05 M sodium cacodylate buffer, the material was postfixed with 2% osmium tetroxide for 2 h at 4°C, washed with Milli-Q at 4°C, dehydrated with ethanol, and embedded in Epon 812. Ultrathin sections were obtained from several blocks, stained with lead citrate and uranyl acetate, and observed in a JEOL JEM1200EX electron microscope operated at 80 kV. Scanning TEM (STEM)–energy-dispersive X-ray spectrometry (EDX) analysis was performed with a JEOL JEM-2500SE electron microscope operating at 200 kV and was performed with a beam current of 10 nA for 20 s (live time). Selected-area electron diffraction SAED analysis was conducted with TEM (H-9000NAR; Hitachi, Japan) at 200 kV.

Magnetic recovery assay of tellurium crystal-containing *M. magneticum* AMB-1. A magnetic recovery assay was conducted to verify the ability to recover *M. magneticum* AMB-1. Cells cultured in the presence of tellurite were harvested and adjusted to 1.0×10^8 cells/ml MSGM. Six milliliters of each sample was transferred to separate glass test tubes (10 mm in diameter and 7.6 cm in height), and each test tube was sealed with a rubber bung. A cylindrical neodymium-boron magnet (3,710 G) was used to recover the cells by attracting them to one side of the tube. At the designated times (1, 2, 3, 4, 5, 7, 8, 13, 15, and 20 h), culture medium from each test tube was collected by inserting a syringe through the rubber bung and by extracting the culture medium (20 μl) near the surface. A cell count was performed against the extracted culture medium samples. In addition, the removed cells and tellurium concentration were also measured at the endpoint for further verification.

RESULTS

Tellurite tolerance and uptake in *M. magneticum* AMB-1. The toxic effect of tellurite on the growth of *M. magneticum* AMB-1 was investigated at various concentrations of tellurite (Fig. 1). Cells cultured in MSGM containing 10 and 20 μM tellurite showed similar growth rates, with stationary-phase cell densities of approximately 6.0×10^7 cells/ml, which was approximately half the number of cells grown in the absence of tellurite. However, when the cells were cultured in higher tellurite concentrations, a slow growth rate (40 μM) or complete growth inhibition (60 μM) was observed (data for 80 and 100 μM not shown). Based on these observations, it was concluded that the MIC of tellurite for *M. magneticum* AMB-1 was 60 μM.

The time course of tellurite concentrations in the cell and in the medium was measured (Fig. 2). For cells grown in 40 μM tellurite, the cell growth and tellurite uptake were saturated at 7 days. The final cell density gradually decreased with increasing concentrations of tellurite in the medium (Table 1). The most effective condition for tellurite removal with respect to proportion of initial concentration was 20 μM tellurite, where 58.8% of the initial tellurite and 1.8×10^8 tellurite molecules were accumulated by the cells. On the other hand, in the medium containing 40 μM tellurite, 38.6% of the initial tellurite was accumulated by the cells, which accounts for 2.7×10^8 tellurite molecules per cell, which is the maximum tellurite concentration accumulated.

In order to compare this method with the cell surface adsorption of tellurium, tellurium adsorption onto a magnetotactic bacteria cell membrane modified with hexahistidine-tagged

TABLE 1. Tellurium recovery using magnetotactic bacteria

Initial tellurite concn in MSGM (μM)	Final cell density ($\times 10^7$ cells/ml)	Recovery of tellurium from MSGM (%)	No. of recovered tellurium molecules/cell	Avg no. of particles/cell[a]	
				Magnetite	Tellurium
0	12.4			23.6 ± 4.1	
10	6.5	45.2	4.2×10^7	15.1 ± 3.3	8.2 ± 4.8
20	4.0	58.8	1.8×10^8	11.7 ± 3.5	14.8 ± 7.6
40	3.5	38.6	2.7×10^8	9.4 ± 4.2	32.2 ± 9.6

[a] The data are shown as means ± standard deviations.

outer membrane protein (MspI) in 40 μM tellurite was also evaluated based on the previously described EDTA wash method (40). Approximately 3.6×10^6 tellurium atoms per cell were adsorbed. This value is similar to that of Cd^{2+} adsorption onto the modified cell surface (3.8×10^6) (40), which is 2 orders of magnitude less than the accumulation achieved by crystallization within the cell presented in this study.

Analysis of simultaneous biomineralization of discrete tellurium and magnetite nanoparticles within *M. magneticum* AMB-1. To verify the accumulation of tellurium within *M. magneticum* AMB-1, TEM analysis was conducted on unstained samples. Rod-shaped nanostructures (~15 nm in diameter by ~200 nm in length) in addition to the magnetite magnetosome crystals were observed (Fig. 3A and B). The

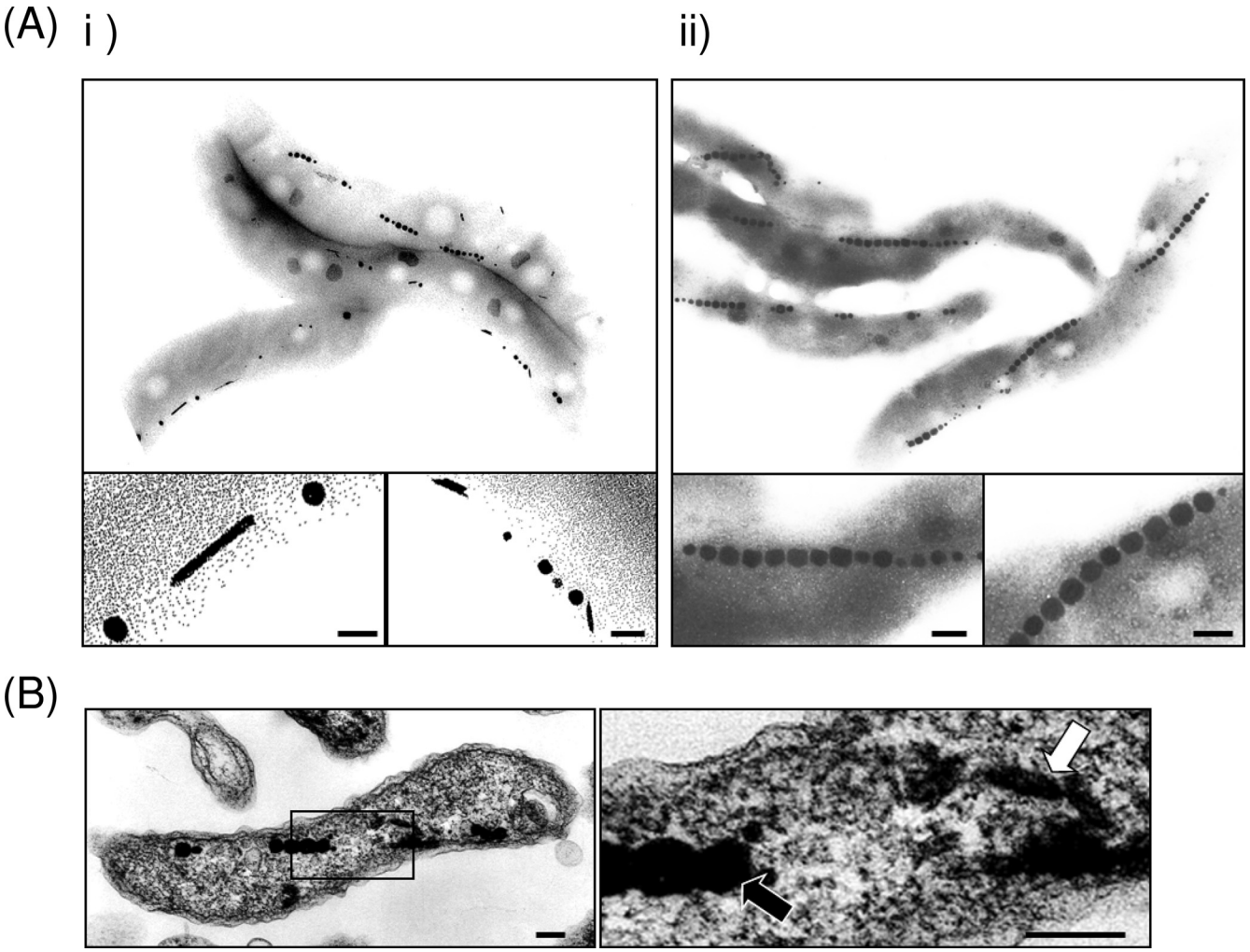

FIG. 3. Transmission electron micrographs of magnetotactic bacteria grown in the presence of tellurite. (A) Magnetotactic bacteria grown (i) in the presence of tellurite (40 μM) and (ii) in its absence. The scale bar indicates 100 nm. (B) Ultrathin-sectioned micrograph of magnetotactic bacteria grown in the presence of tellurite. The image on the right is a magnification of the square area from the left image. Black and white arrows indicate magnetite and tellurium, respectively. The scale bar indicates 100 nm.

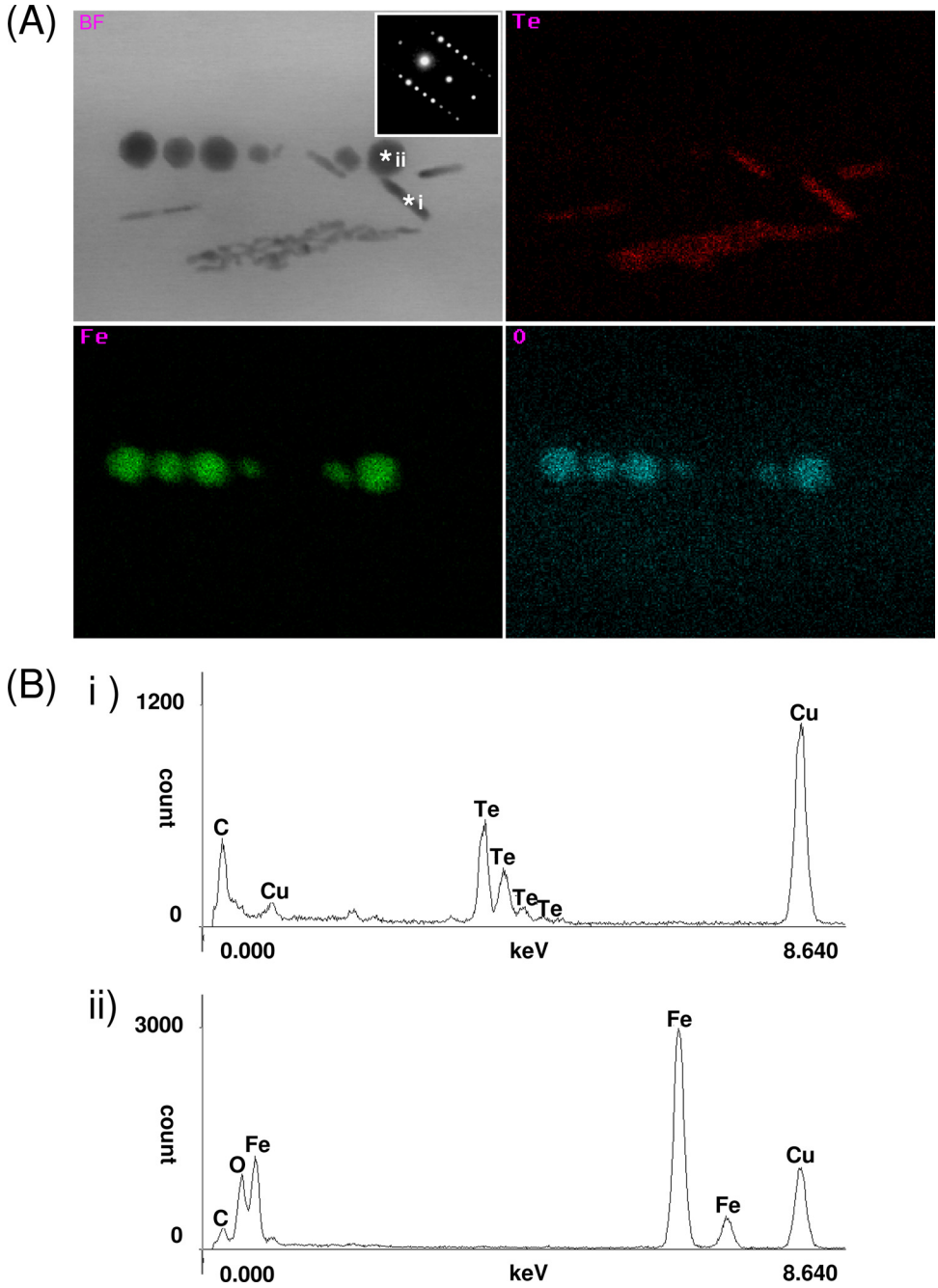

FIG. 4. STEM-EDX and SAED analyses for magnetite and tellurium within magnetotactic bacteria. (A) Bright-field (BF) STEM image with SAED patterns of a rod-shaped crystal and STEM-EDX maps of Te, Fe, and O taken using a probe size of approximately 2 nm; (B) spot scans of *i and *ii as representations of tellurium and magnetite, respectively.

number and the size of these crystals within the cell increased with increasing initial concentration of tellurite in the medium (Table 1). Additionally, the morphological change of magnetite crystals within the magnetotactic bacteria grown in the presence of tellurite was not observed. Elemental analysis using STEM-EDX on these samples reveals that the magnetosomes are composed of magnetite (black arrow) and the nanorods contain tellurium (white arrow), and both are present within the same cell. It should also be noted that tellurium nanorods were not observed in either the periplasmic space or on the cell surface (Fig. 3B). Results from representative *M. magneticum* strain AMB-1 with biominerals containing tellurium are presented in Fig. 4A. Te, Fe, and O element mapping of magnetotactic bacteria clearly shows crystals containing either Te or Fe and O. The spot scan shows that C, O, Fe, and Te were the only elements present (the Cu and C were from the copper TEM grid and carbon coating, respectively) (Fig. 4B). Tellurium in the rod-shaped crystals (*i) and Fe and O in

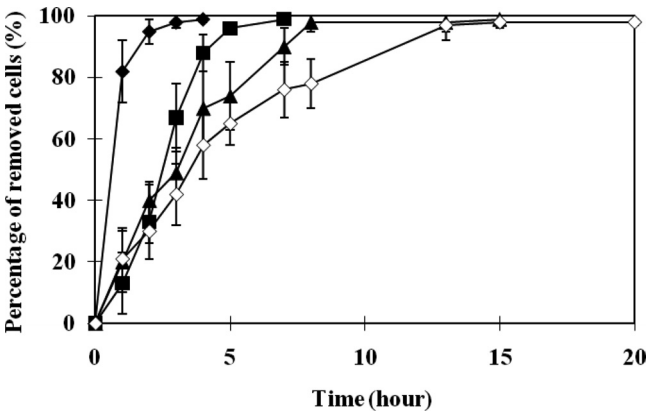

FIG. 5. Magnetic recovery assay of tellurium crystal-containing *M. magneticum* AMB-1. The percentage of recovered cells is calculated from the initial cell numbers (1.0×10^8/ml) by counting the number of dispersed cells left within the culture medium. In addition, the number of cells recovered by magnetic force was also verified by counting the cells recovered at the endpoints. *M. magneticum* AMB-1 (0 μM (◆), 10 μM (■), 20 μM (▲), and 40 μM (◇)) was cultured and assayed with the respective concentrations of tellurite. The average values from three independent experiments were obtained. Error bars show standard deviations.

magnetite (*ii) were concentrated within the magnetotactic bacteria. In addition, the linear electron diffraction pattern of spots, which is identical to the tellurium single crystalline form (the Joint Committee on Powder Diffraction Standards no. 36-1452), was observed from the rod-shaped crystal by SAED analysis. Therefore, these analyses show that there is no tellurium doping of the magnetite and suggest the rod-shaped crystals are composed of pure elemental crystalline tellurium(0), which seems to be reduced from tellurite(IV) in the medium.

Magnetic recovery of magnetotactic bacteria cultured in the presence of tellurite. The fact that magnetotactic bacteria can be recovered using a magnetic field significantly increases the potential to utilize them for bioremediation. The magnetic recovery assay shows that approximately 100% of the bacteria grown in 10 μM tellurite were successfully recovered within 7 h (Fig. 5). However, the time for magnetic cell recovery gradually increased with increasing concentrations of tellurite. For cells grown in 40 μM tellurite, total cell recovery required 15 h. The amount of tellurium depleted from the medium containing 40 μM tellurite was also determined, and a total of approximately 33.6% of the tellurium was accumulated in the cells. Thus, in addition to the finding that magnetotactic bacteria can be utilized for bioremediation, in the presence of tellurite, we have demonstrated that the cells can be efficiently recovered.

DISCUSSION

Tellurite is known to be toxic to most microorganisms at concentrations as low as 10 μM (38, 45). The model Gram-negative bacterium *Escherichia coli* O157 (wild type) has a MIC of 4.5 μM for tellurite. However, a specific resistant isolate has shown a MIC of 4.6 mM (44). The MIC of tellurite for *M. magneticum* AMB-1 was determined to be 60 μM, which shows *M. magneticum* AMB-1 to be 13 times more resistant to tellurite than *E coli* (wild type). Although *M. magneticum* AMB-1 does not display resistance as high as that of some tellurite-resistant organism, the cells are capable of tellurite reduction and crystallization mechanisms within the cell (Fig. 4).

A number of genetic tellurite resistance determinants that can be found in the bacterial chromosome have been identified in different bacteria (9). Although these determinants mediate tellurite resistance by an as-yet-unknown mechanism, several genes such as those coding for nitrate reductase (*narGHIJ*; *E. coli*) (1) and dihydrolipoamide dehydrogenase (*lpdA*; *Aeromonas hydrophila*) (8), the tellurite resistance gene *trgAB* (*Rhodobactor sphaeroides*) (28), and the toxic anion resistance gene *telA* (*R. sphaeroides*) (28) were suggested to be linked to the reduction of tellurite. Within the whole-genomic information on *M. magneticum* AMB-1 (22), *lpdA* (Amb3963, 4e−88; Amb2321, 1e−63; and Amb1666, 1e−41), *trgB* (Amb1307, 5e−26), *narH* (Amb3289, 3e−21; Amb3542, 2e−18; Amb1649, 4e−17; and Amb3377, 4e−13) were found and presumed to be the respective homologous gene. Although further study is necessary, these genes may play a role in the reduction of tellurite within the magnetotactic bacteria. Recently, tellurite was suggested to serve as an electron acceptor for anaerobic growth of some prokaryotes during production of the tellurium(0) crystal, while no dissimilatory electron transport to tellurium compounds is known to date (10). To understand the tellurium precipitation mechanism within the magnetotactic bacteria, further biochemical and genetic studies are required.

Tellurium is an interesting element. A metalloid, it has properties likening it to metals such as iron, as well as its fellow chalcogens such as oxygen and sulfur, having various oxidation states and a similar ionic radius. A gradual decrease of magnetite crystal formation was seen for cells grown in higher tellurite concentrations (Table 1). This was also verified by the magnetic recovery assay, as cells recovered from a higher tellurite concentration contained more tellurium crystals and fewer magnetite crystals, rendering them less magnetic, thus demanding a longer recovery time (Fig. 5). These observations suggest tellurium inhibits magnetosome formation or that the tellurium crystallization system competes to some extent with the magnetosome synthesis system.

Interestingly, many (not all) rod-shaped tellurium nanocrystals were observed along the magnetite crystal chain within magnetotactic bacteria (Fig. 3). Within other microorganisms, internal tellurium crystals are formed close to the cell's periphery, conform to the contour of the cell envelope, and randomly form in the cytoplasmic space (7, 29, 32, 44). This leads to questions of how these nanorods interact with magnetosome components such as the actin-like protein MamK (18, 43) and thus questions about the possibility of whether or not these nanorods are forming within magnetosome-like vesicles. However, tellurium crystals surrounded by membranous structure were not observed by TEM analysis of thin-sectioned samples in this study.

In addition to tellurium affecting magnetosome synthesis and tellurium crystal localization, the fact that tellurium crystals form independently of magnetite crystals is also very curious. There have been reports of nonferrous metal incorporation (e.g., manganese and cobalt) into magnetite crystals in magnetosomes (15, 37). In this research, tellurite has been reduced and crystallized independently of magnetite crystals,

contrary to the partial oxidation and incorporation into magnetosomes that occur for ferrous ions. Perhaps then tellurium should be considered to be behaving like the other chalcogens. Thiosulfate ($S_2O_3^{2-}$) is frequently taken up by bacteria and reduced to elemental sulfur (S^0) to form sulfur globules (20). Indeed there have been reports of sulfur globule formation occurring in several magnetotactic bacteria, although the mechanism is still unknown (3, 36). There are literature reports of tellurium substitution of sulfur in amino acids such as cysteine in tellurium-resistant fungi (26, 31). Therefore, as tellurium can be considered to be an analogue to sulfur, we tentatively suggest that the tellurium nanorods described in this report are analogues to sulfur globules.

Recent research in material sciences has focused on preparing nanorods of either TeO_2 or Te using expensive and hazardous organic coordinating solvents, as well as some complexing agents (13, 21). Crystallization within magnetotactic bacteria may also yield diverse tellurium nanomaterials that can be generated under mild conditions using tellurite from the environment and without requiring the use of either harsh chemical or physical methods.

Conclusion. We have reported the first account of tellurite uptake by magnetic bacteria and demonstrated successful biomineralization of discrete crystals of tellurium and magnetite within the same cell, and thus efficient magnetic recovery was verified. This discovery could lead to development of a novel tellurium recovery system. Therefore, we believed that magnetotactic bacteria provide new advantages for the development of various biorecovery technologies, the bioremediation of polluted water, and also new methods of tellurium nanomaterial synthesis.

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REFERENCES

1. **Avazéri, C., R. Turner, J. Pommier, J. Weiner, G. Giordano, and A. Vermeglio.** 1997. Tellurite reductase activity of nitrate reductase is responsible for the basal resistance of Escherichia coli to tellurite. Microbiology **143:** 1181–1189.
2. **Baesman, S. M., T. D. Bullen, J. Dewald, D. Zhang, S. Curran, F. S. Islam, T. J. Beveridge, and R. S. Oremland.** 2007. Formation of tellurium nanocrystals during anaerobic growth of bacteria that use Te oxyanions as respiratory electron acceptors. Appl. Environ. Microbiol. **73:**2135–2143.
3. **Bazylinski, D., A. Dean, T. Williams, L. Long, S. Middleton, and B. Dubbels.** 2004. Chemolithoautotrophy in the marine, magnetotactic bacterial strains MV-1 and MV-2. Arch. Microbiol. **182:**373–387.
4. **Bazylinski, D. A., R. B. Frankel, B. R. Heywood, S. Mann, J. W. King, P. L. Donaghay, and A. K. Hanson.** 1995. Controlled biomineralization of magnetite Fe_3O_4 and Greigite Fe_3S_4 in a magnetotactic bacterium. Appl. Environ. Microbiol. **61:**3232–3239.
5. **Bazylinski, D. A., A. J. Garratt-Reed, A. Abedi, and R. B. Frankel.** 1993. Copper association with iron sulfide magnetosomes in a magnetotactic bacterium. Arch. Microbiol. **160:**35–42.
6. **Blakemore, R. P., D. Maratea, and R. S. Wolfe.** 1979. Isolation and pure culture of a freshwater magnetic spirillum in chemically defined medium. J. Bacteriol. **140:**720–729.
7. **Borghese, R., F. Borsetti, P. Foladori, G. Ziglio, and D. Zannoni.** 2004. Effects of the metalloid oxyanion tellurite (TeO_3^{2-}) on growth characteristics of the phototrophic bacterium *Rhodobacter capsulatus*. Appl. Environ. Microbiol. **70:**6595–6602.
8. **Castro, M., R. Molina, W. Díaz, S. Pichuantes, and C. Vásquez.** 2008. The dihydrolipoamide dehydrogenase of Aeromonas caviae ST exhibits NADH-dependent tellurite reductase activity. Biochem. Biophys. Res. Commun. **375:**91–94.
9. **Chasteen, T., D. Fuentes, J. Tantaleán, and C. Vásquez.** 2009. Tellurite: history, oxidative stress, and molecular mechanisms of resistance. FEMS Microbiol. Rev. **33:**820–832.
10. **Csotonyi, J., E. Stackebrandt, and V. Yurkov.** 2006. Anaerobic respiration on tellurate and other metalloids in bacteria from hydrothermal vent fields in the eastern Pacific Ocean. Appl. Environ. Microbiol. **72:**4950–4956.
11. **Deplanche, K., and L. E. Macaskie.** 2008. Biorecovery of gold by Escherichia coli and Desulfovibrio desulfuricans. Biotechnol. Bioeng. **99:**1055–1064.
12. **Dopp, E., L. M. Hartmann, A. M. Florea, A. W. Rettenmeier, and A. V. Hirner.** 2004. Environmental distribution, analysis, and toxicity of organometal(loid) compounds. Crit. Rev. Toxicol. **34:**301–333.
13. **Gautam, K. U., and C. N. R. Rao.** 2004. Controlled synthesis of crystalline tellurium nanorods, nanowires, nanobelts and related structures by a self-seeding solution process. J. Mater. Chem. **14:**2530–2535.
14. **Junier, P., M. Frutschi, N. Wigginton, E. Schofield, J. Bargar, and R. Bernier-Latmani.** 2009. Metal reduction by spores of Desulfotomaculum reducens. Environ. Microbiol. **11:**3007–3017.
15. **Keim, C., U. Lins, and M. Farina.** 2009. Manganese in biogenic magnetite crystals from magnetotactic bacteria. FEMS Microbiol. Lett. **292:**250–253.
16. **Klonowska, A., T. Heulin, and A. Vermeglio.** 2005. Selenite and tellurite reduction by *Shewanella oneidensis*. Appl. Environ. Microbiol. **71:**5607–5609.
17. **Kobayashi, A., and Y. Ogra.** 2009. Metabolism of tellurium, antimony and germanium simultaneously administered to rats. J. Toxicol. Sci. **34:**295–303.
18. **Komeili, A., Z. Li, D. K. Newman, and G. J. Jensen.** 2006. Magnetosomes are cell membrane invaginations organized by the actin-like protein MamK. Science **311:**242–245.
19. **Law, N., S. Ansari, F. Livens, J. Renshaw, and J. Lloyd.** 2008. Formation of nanoscale elemental silver particles via enzymatic reduction by *Geobacter sulfurreducens*. Appl. Environ. Microbiol. **74:**7090–7093.
20. **Lee, Y., M. Dashti, A. Prange, F. Rainey, M. Rohde, W. Whitman, and J. Wiegel.** 2007. Thermoanaerobacter sulfurigignens sp. nov., an anaerobic thermophilic bacterium that reduces 1 M thiosulfate to elemental sulfur and tolerates 90 mM sulfite. Int. J. Syst. Evol. Microbiol. **57:**1429–1434.
21. **Liu, Z., Z. Hu, J. Liang, S. Li, Y. Yang, S. Peng, and Y. Qian.** 2004. Size-controlled synthesis and growth mechanism of monodisperse tellurium nanorods by a surfactant-assisted method. Langmuir **20:**214–218.
22. **Matsunaga, T., Y. Okamura, Y. Fukuda, A. T. Wahyudi, Y. Murase, and H. Takeyama.** 2005. Complete genome sequence of the facultative anaerobic magnetotactic bacterium Magnetospirillum sp. strain AMB-1. DNA Res. **12:**157–166.
23. **Matsunaga, T., T. Suzuki, M. Tanaka, and A. Arakaki.** 2007. Molecular analysis of magnetotactic bacteria and development of functional bacterial magnetic particles for nano-biotechnology. Trends Biotechnol. **25:** 182–188.
24. **Mikheenko, I., M. Rousset, S. Dementin, and L. Macaskie.** 2008. Bioaccumulation of palladium by *Desulfovibrio fructosivorans* wild-type and hydrogenase-deficient strains. Appl. Environ. Microbiol. **74:**6144–6146.
25. **Moore, M., and S. Kaplan.** 1992. Identification of intrinsic high-level resistance to rare-earth oxides and oxyanions in members of the class *Proteobacteria*: characterization of tellurite, selenite, and rhodium sesquioxide reduction in *Rhodobacter sphaeroides*. J. Bacteriol. **174:**1505–1514.
26. **Moroder, L.** 2005. Isosteric replacement of sulfur with other chalcogens in peptides and proteins. J. Pept. Sci. **11:**187–214.
27. **Nilges, T., S. Lange, M. Bawohl, J. M. Deckwart, M. Janssen, H. D. Wiemhofer, R. Decourt, B. Chevalier, J. Vannahme, H. Eckert, and R. Weihrich.** 2009. Reversible switching between p- and n-type conduction in the semiconductor $Ag_{10}Te_4Br_3$. Nat. Mater. **8:**101–108.
28. **O'Gara, J., M. Gomelsky, and S. Kaplan.** 1997. Identification and molecular genetic analysis of multiple loci contributing to high-level tellurite resistance in *Rhodobacter sphaeroides* 2.4.1. Appl. Environ. Microbiol. **63:**4713–4720.
29. **Ollivier, P., A. Bahrou, S. Marcus, T. Cox, T. Church, and T. Hanson.** 2008. Volatilization and precipitation of tellurium by aerobic, tellurite-resistant marine microbes. Appl. Environ. Microbiol. **74:**7163–7173.
30. **Pósfai, M., P. Buseck, D. Bazylinski, and R. Frankel.** 1998. Iron sulfides from magnetotactic bacteria: structure, composition, and phase transitions. Am. Mineral. **83:**1469–1481.
31. **Ramadan, S., A. Razak, A. Ragab, and M. Elemeleigy.** 1989. Incorporation of tellurium into amino-acids and proteins in a tellurium-tolerant fungi. Biol. Trace Elem. Res. **20:**225–232.
32. **Rathgeber, C., N. Yurkova, E. Stackebrandt, J. T. Beatty, and V. Yurkov.** 2002. Isolation of tellurite- and selenite-resistant bacteria from hydrothermal vents of the Juan de Fuca Ridge in the Pacific Ocean. Appl. Environ. Microbiol. **68:**4613–4622.
33. **Ruta, L., C. Paraschivescu, M. Matache, S. Avramescu, and I. Farcasanu.** 2010. Removing heavy metals from synthetic effluents using "kamikaze" Saccharomyces cerevisiae cells. Appl. Microbiol. Biotechnol. **85:**763–771.
34. **Shibasaki, S., H. Maeda, and M. Ueda.** 2009. Molecular display technology using yeast—arming technology. Anal. Sci. **25:**41–49.
35. **Simmons, S. L., D. A. Bazylinski, and K. J. Edwards.** 2006. South-seeking magnetotactic bacteria in the Northern Hemisphere. Science **311:**371–374.
36. **Spring, S., R. Amann, W. Ludwig, K. Schleifer, H. van Gemerden, and N.**

Petersen. 1993. Dominating role of an unusual magnetotactic bacterium in the microaerobic zone of a freshwater sediment. Appl. Environ. Microbiol. **59:**2397–2403.
37. **Staniland, S., W. Williams, N. Telling, G. Van Der Laan, A. Harrison, and B. Ward.** 2008. Controlled cobalt doping of magnetosomes in vivo. Nat. Nanotechnol. **3:**158–162.
38. **Summers, A. O., and G. A. Jacoby.** 1977. Plasmid-determined resistance to tellurium compounds. J. Bacteriol. **129:**276–281.
39. **Tanaka, M., A. Arakaki, and T. Matsunaga.** 2010. Identification and functional characterization of liposome tubulation protein from magnetotactic bacteria. Mol. Microbiol. **76:**480–488.
40. **Tanaka, M., Y. Nakata, T. Mori, Y. Okamura, H. Miyasaka, H. Takeyama, and T. Matsunaga.** 2008. Development of a cell surface display system in a magnetotactic bacterium, *Magnetospirillum magneticum* AMB-1. Appl. Environ. Microbiol. **74:**3342–3348.
41. **Tanaka, M., Y. Okamura, A. Arakaki, T. Tanaka, H. Takeyama, and T. Matsunaga.** 2006. Origin of magnetosome membrane: proteomic analysis of magnetosome membrane and comparison with cytoplasmic membrane. Proteomics **6:**5234–5247.
42. **Tang, Z., Z. Zhang, Y. Wang, S. C. Glotzer, and N. A. Kotov.** 2006. Self-assembly of CdTe nanocrystals into free-floating sheets. Science **314:**274–278.
43. **Taoka, A., R. Asada, L. F. Wu, and Y. Fukumori.** 2007. Polymerization of the actin-like protein MamK, which is associated with magnetosomes. J. Bacteriol. **189:**8737–8740.
44. **Taylor, D.** 1999. Bacterial tellurite resistance. Trends Microbiol. **7:**111–115.
45. **Taylor, D. E., M. Rooker, M. Keelan, L. K. Ng, I. Martin, N. T. Perna, N. T. Burland, and F. R. Blattner.** 2002. Genomic variability of O islands encoding tellurite resistance in enterohemorrhagic *Escherichia coli* O157:H7 isolates. J. Bacteriol. **184:**4690–4698.
46. **Tordoff, G. M., A. J. Baker, and A. J. Willis.** 2000. Current approaches to the revegetation and reclamation of metalliferous mine wastes. Chemosphere **41:**219–228.
47. **Yamada, A., N. Miyagishima, and T. Matsunaga.** 1997. Tellurite removal by marine photosynthetic bacteria. J. Mar. Biotechnol. **1:**46–49.