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Survival of *Escherichia coli* O157:H7 in various soil particles: importance of the attached bacterial phenotype

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Abstract The risk of enteropathogens to food and water is highly dependent on their survival in soil environments. Here, the effects of soil type, particle size, the presence of natural organic matter (NOM) or Fe/Al (hydro)oxides on pathogenic *Escherichia coli* O157:H7 survival in sterilized soil particles were assessed through survival, attachment, metabolic activity, and qRT-PCR analyses. The abundance of inoculated *E. coli* O157:H7 in Brown soil (Alfisol) particles increased 0.6–1.4 $\log_{10}$ CFU/g within 3 days (except for NOM-stripped clay), while that in Red soil (Ultisol) particles decreased rapidly in 8 days post-inoculation. Additionally, survival of bacteria was significantly enhanced when Fe/Al (hydro)oxides had been removed from Red soil particles. For the two soils, *E. coli* O157:H7 survived the longest in NOM-present clays and the bacterial adenosine 5′-triphosphate (ATP) levels were 0.7–2.0 times greater in clays than in sands and silts on day 8. Moreover, clays were more effective than silts and sands in binding cells and changing the expressions of acetate pathway-associated genes (*pta* and *ackA*). For silts and sands, *E. coli* O157:H7 decayed more rapidly in the presence of NOM and similar trends of bacterial ATP levels were observed between NOM-stripped and NOM-present soil particles, indicating that the primary role of NOM was not as a nutrient supply. These findings indicate that soil particles function mainly through attachment to change the metabolic pathway of *E. coli* O157:H7 and ultimately impact the survival of bacterial pathogens in soils.

Keywords *Escherichia coli* O157:H7 · Survival · Attachment · ATP · Gene expression · Fe/Al (hydro)oxides

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Introduction

Escherichia coli O157:H7, the most prevalent manure-borne zoonotic pathogen, poses significant threats to public health because of its severity of complications (hemolytic uremic syndrome and thrombotic thrombocytopenic purpura) and low infective dosage (as few as ten cells) (Jones 1999; Pennington 2010). Ruminants, especially cattle, are the major reservoir of *E. coli* O157:H7 and this manure-borne pathogen can invade the soil through sewage irrigation, runoff from stored manure, or manure application to fields, or other related processes (Chase-Topping et al. 2008). *E. coli* O157:H7 has been reported to survive in soil or manure environments for more than a year (Jiang et al. 2002), affording the opportunity for reinfection by animals. Furthermore, *E. coli* O157:H7 present in agricultural soils has the potential to be transported to both surface and ground water (Gagliardi and Karns 2000), or attach to plant surfaces and become internalized into plant tissues (Ongeng et al. 2015), which represents a serious risk to public health. Therefore, soil is a particularly important repository for *E. coli* O157:H7 and plays an important role in the circulation of pathogens in the environment.

A critical issue is the actual survival of bacterial pathogens in agricultural settings (van Elsas et al. 2011). A growing body of research has yielded considerable information about *E. coli* O157:H7 survival in soils (Jiang

et al. 2002; Semenov et al. 2007; van Elsas et al. 2007, 2011; Franz et al. 2008; Moynihan et al. 2013; Zhang et al. 2013; Brennan et al. 2014; Wang et al. 2014a, b; Yao et al. 2014, 2015; Naganandhini et al. 2015). As a general observation, the abundance of this organism in soil habitats declines over time due to a wide range of biotic and abiotic factors, including indigenous microbial diversity, nutrient levels, temperature, moisture status, pH, salinity, soil type, etc. (van Elsas et al. 2011). For example, Jiang et al. (2002) observed a more rapid decline of *E. coli* O157:H7 as a function of temperature in a manure-amended unautoclaved soil (greater rate of death at 21 °C than at 5 °C). Likewise, *E. coli* O157:H7 survival in manure under fluctuating temperatures was generally lower than that under constant temperature (Semenov et al. 2007). van Elsas et al. (2007) found that *E. coli* O157:H7 showed a progressive decline of abundance by at least six orders of magnitude over 60 days in unfumigated soil, while the survival of this pathogen in all chloroform-fumigated soils was significantly enhanced. The highest survival rate was recorded in the soil that had been subjected to the highest fumigation level (24 h), and the abundance decrease recorded amounted to just about two orders of magnitude. Survival time of *E. coli* O157:H7 was found to decrease with greater sand content in manure-amended loam soils (Franz et al. 2008). However, Moynihan et al. (2013) found that *E. coli* O157:H7 was inactivated more rapidly in clay loam than in sand loam, which is contrary to the result observed by Franz et al. (2008). Moynihan et al. (2013) attributed this discrepancy to the differences in microbial community composition and soil organic matter between soil types. Zhang et al. (2013) found that *E. coli* O157:H7 survived for up to 8 days in strongly acidic soils (pH 4.57 to 5.14), and in more neutral soils (pH 6.51 to 7.39), bacteria could last up to 34 days. The survival of *E. coli* O157:H7 in 14 soils collected from eastern China was strongly enhanced by microbial biomass C and total N, but decreased by amorphous Al_2O_3 and Chloroflexi (Wang et al. 2014a). Yao et al. (2015) found longer survival of *E. coli* O157:H7 in agricultural soils with lower free Fe_2O_3 and higher pH, but electrical conductivity played a more important role than free Fe_2O_3 and pH in regulating pathogen survival in fertilizer-amended soils.

Notably, previous studies on *E. coli* O157:H7 survival did not pay attention to the effects of soil particle characteristics such as size and mineral composition. Indeed, soils consist of different-sized clay, silt, and sand particles. The variable size of clays (μm) to sands (mm), distinct mineral components and natural organic matter (NOM) presence, dramatically affect the surface chemistry of soils (Stotzky 1986). Therefore, hypothesis developed was as follows, different soil particles have specific physiochemical properties that would impact differentially the survival of bacterial pathogens. Cai et al. (2013) found that attached *E. coli* O157:H7 cells on kaolinite or montmorillonite were mostly viable (viability >90%), whereas the viability of attached cells on goethite dropped dramatically to ~6% after 6 h. Asadishad et al. (2013) also observed a consistent increase in *E. coli* O157:H7 inactivation rate with the type of minerals in the order: alumina > iron oxide > silica, suggesting that alumina exhibited a greater antimicrobial effect on adhered bacteria. Recently, Brennan et al. (2014) found that addition of clay minerals (montmorillonite, kaolinite, or illite) altered some physicochemical parameters (cation-exchange capacity and surface area) of the soil, leading to increased survival of *E. coli* O157:H7. Although these studies have reported the impacts of pure minerals on *E. coli* O157:H7 survival behavior, no work has been done to date for natural soil particles with heterogeneous clay minerals, NOM, and Fe/Al (hydro)oxides.

The survival pattern of *E. coli* O157:H7 in sterilized soil particles of different sizes (sand, silt, and clay) from Red soil (Ultisol) and Brown soil (Alfisol) with NOM either present or stripped was conducted to determine the effects of soil type, particle size, and NOM on the survival of bacteria. Subsequently, the antimicrobial role of Fe/Al (hydro)oxides was evaluated through survival experiments using Fe/Al (hydro)oxides-stripped Red soil particles. In the bulk soil, 80–90% of the microbes commonly live on the surfaces of soil particles (Nannipieri et al. 2003). Rather than simply measuring the microbial biomass, adenosine 5′-triphosphate (ATP) content can also be used as an index of microbiological activity in soil (Brookes et al. 1983; Wen et al. 2005). Additional bacterial attachment and the variation of ATP in various soil particles were examined in batch systems. Acetyl phosphate, a global signal, could transmit environmental conditions to central metabolism, and contributed to biofilm biomass and structure of *E. coli* (Wolfe 2005; Klein et al. 2007; Prüß et al. 2010). For acetate metabolism, *pta* is related to acetyl phosphate synthesis and *ackA* is responsible for acetate kinase that converts acetyl phosphate to acetate (Prüß et al. 2010). Therefore, the expression of genes *pta* and *ackA* were explored using quantitative reverse transcription polymerase chain reaction (qRT-PCR) with bacterial cells after exposure to soil particles.

Materials and methods

Bacterial preparation

The pathogenic *E. coli* O157:H7 was provided by the State Key Laboratory of Agricultural Microbiology, Huazhong Agricultural University, Wuhan, Hubei Province, China. Bacterial preparation methods are provided in the Supplementary data.

Characterization of soil particles

Red soil with clay loam texture was sampled from the 0–20 cm layer of a farmland in Changsha County, Changsha City, Hunan Province, China (28° 15′ N, 113° 4′ E). The Red soil has an organic matter content of 10.1 g kg^{-1}, pH of 4.01, and primary clay mineral compositions of Red soil were kaolinite and hydromica. Brown soil with silt loam texture was collected from a depth of 0–20 cm of a farmland in Tianwai Village, Taishan City, Shandong Province, China (36° 10′ N, 117° 7′ E). The soil has an organic matter content of 12.0 g kg^{-1}, pH of 6.02, and clay mineral composition was mostly 2:1 minerals such as montmorillonite and vermiculite. After removal of large rocks and debris, the soil was rinsed in sterilized-deionized water (dH_2O) and dispersed with sonication. The soil suspension was separated into three fractions of different particle sizes (Xiong 1985). The fine sand fraction (48–250 μm) was obtained by wet sieving to get through a 250-μm aperture sieve and left on 48-μm aperture sieve. The silt fraction (2–48 μm) and the clay fraction (<2 μm) were separated by repeated sedimentation. A portion of each soil was treated with 30% H_2O_2 to remove organic matter to obtain NOM-stripped fractions (Pronk et al. 2011). Soil particles were autoclaved twice at 121 °C for 30 min. Soil particles, as confirmed by plate counting, were effectively sterile as no bacteria detection during the incubation period. All soil particles were washed three times with dH_2O and ethanol to remove residual reagents. Finally, soil particles were dried at 60 °C and kept for analysis. NOM content and specific surface area of various soil particles were analyzed by $K_2Cr_2O_7$ digestion and the N_2 sorption method (Beijing Analytical Instrument Company, Beijing, P.R. China) (Xiong 1985), respectively. Zeta potentials of soil particles in dH_2O were determined by the zeta potential analyzer (Nano ZS90, Malvern Instruments Ltd., UK). The operationally defined crystalline Fe/Al (DC-Fe/Al) (hydro) oxides of the soil particles were extracted with a dithionite citrate solution buffered with $NaHCO_3$. The amorphous Fe/Al (AO-Fe/Al) (hydro)oxides of the soil particles were extracted with acidified ammonium oxalate (pH 3.0) in the dark (Pronk et al. 2011). After extraction of Fe/Al (hydro)oxides, soil particles were centrifuged (8000×*g*) and washed with dH_2O until the conductivity was <50 μS cm^{-1}. Samples were then autoclaved and kept for further experiment. Aqueous leachates were prepared using sterilized soil particles and dH_2O (100 mg mL^{-1}) to determine the soluble Fe^{2+}/Al^{3+} followed a protocol previously described by Williams et al. (2011). The iron and aluminum concentrations of aqueous leachates were measured with an atomic absorption spectrophotometer (AAS, Varian AA240FS, USA). Measured properties of the soil particles are listed in Table 1.

Survival of *E. coli* O157:H7 in soil particles

The *E. coli* O157:H7 cells were inoculated into 500 mg autoclaved soil particles at a final density of ~10^7 CFU g^{-1} of dry soil in 10-mL sterilized plastic tubes. Then, the mixtures were well dispersed by vortex for 1 min. Next, microcosms of soil-pathogen mixtures were supplemented with dH_2O until oversaturation (~40% *w*/*w* water content) to exclude the influences of water. Tubes were partially sealed and placed in the dark at 25 °C. Moisture loss was compensated by adding dH_2O through weighing every 3 days to maintain the saturation of microcosms. The inoculated soil-pathogen mixtures were destructively sampled in triplicate on days 0, 0.25, 1, 2, 3, 4, 5, 6, 7, and 8 to determine the survival of bacteria by colony-forming unit counts on MAC agar plates. Based on the preliminary experiments, additionally inoculated soil-pathogen samples on days 11, 15, 25, 40, and 60 were conducted for Brown soil particles with slow decline of *E. coli* O157:H7. For extraction of bacteria from soil, 5 mL dH_2O was added to 500 mg of soil. This mixture was well dispersed by vortex, and then, 0.5 mL soil-bacteria mixture was pipetted from the bottom of the tube. Viable cell counts were performed in triplicate by serial dilution in dH_2O and spread-plate cultured 0.1 mL onto MAC agar, followed by incubation at 37 °C for 18 h. For the uninoculated control soil samples, no *E. coli* O157:H7 was detected by plating analysis during the entire incubation period. Prior to incubation, the initial abundance was determined and the mean extraction efficiency was about 131 ± 18, 111 ± 10, and 109 ± 6% for sands, silts, and clays of two soils, respectively. It should be noted that bacterial cells could enter into viable but nonculturable (VBNC) state and plate-counting technique could not detect them. For presentation in Fig. 1, microbiological data were converted to log number of CFU g^{-1} and detection limit of the plating technique was approximately 100 CFU per gram dry weight of soil particles.

Attachment experiments

Attachment experiments were conducted by mixing 40 mg autoclaved soil particles with 10 mL bacterial solutions containing (0–1.50) × 10^{10} cells of *E. coli* O157:H7 in plastic tubes. Distilled H_2O was used and the mixture was orbitally shaken at 150 rpm and 25 °C for 1 h. An initial experiment indicated that 1 h was sufficient for attachment to reach a plateau (Liu et al. 2015). Then, 5 mL sucrose solution (60% by mass) was injected into the bottom of the tube to create a density gradient (Zhao et al. 2014), and suspension was centrifuged at 4000×*g* for 15 min. After the centrifugation, the unattached cells were at the top in the least dense region of the sucrose. In order to exclude the effects of soil particles, the unattached cells were measured by total protein analysis (Zhao et al. 2014). Briefly, the unattached cells (10 mL) were

Table 1 Measured properties of particles separated from Red soil (Ultisol) and Brown soil (Alfisol)

Soil type	Soil particles	Size (mm)	NOM (g kg^{-1})	OM removal (%)	SSA (m^2 g^{-1})	ZP (mV)	DC-Fe (g kg^{-1})	AO-Fe (g kg^{-1})	WS-Fe (μg kg^{-1})	DC-Al (g kg^{-1})	AO-Al (g kg^{-1})	WS-Al (μg kg^{-1})
Red soil (Ultisol)	NOM-present sand	0.05–2	3.64	–	2.739	–35.4 ± 1.2	13.95 ± 1.00	1.74 ± 0.08	67 ± 22	23.62 ± 0.45	8.45 ± 0.93	1054 ± 164
	NOM-stripped sand	0.05–2	0.37	89.8%	1.902	–32.6 ± 1.4	14.09 ± 2.29	1.74 ± 0.09	70 ± 17	27.05 ± 1.25	8.90 ± 0.24	1278 ± 237
	NOM-present silt	0.002–0.05	4.72	–	10.07	–35.2 ± 1.2	24.21 ± 3.74	1.96 ± 0.16	264 ± 19	19.14 ± 2.66	8.73 ± 0.65	1047 ± 129
	NOM-stripped silt	0.002–0.05	0.91	80.7%	11.58	–32.1 ± 0.8	23.73 ± 4.51	1.87 ± 0.02	287 ± 24	20.37 ± 3.68	11.82 ± 0.75	1174 ± 165
	NOM-present clay	<0.002	11.45	–	58.99	–21.4 ± 1.1	119.69 ± 5.00	10.97 ± 0.24	2528 ± 294	68.57 ± 6.21	38.77 ± 7.37	3769 ± 64
	NOM-stripped clay	<0.002	1.76	84.6%	72.25	–18.6 ± 1.8	119.18 ± 0.71	10.81 ± 0.20	2599 ± 345	69.78 ± 2.95	46.62 ± 1.01	4154 ± 267
Brown soil (Alfisol)	NOM-present sand	0.05–2	3.70	–	2.091	–39.8 ± 0.7	5.66 ± 0.44	0.60 ± 0.07	25 ± 10	3.13 ± 0.21	1.64 ± 0.16	296 ± 140
	NOM-stripped sand	0.05–2	0.70	81.1%	3.935	–37.1 ± 1.1	7.40 ± 0.19	0.64 ± 0.01	22 ± 11	3.07 ± 0.15	1.15 ± 0.17	369 ± 51
	NOM-present silt	0.002–0.05	2.76	–	4.188	–39.3 ± 1.3	10.90 ± 1.47	1.67 ± 0.12	63 ± 2	4.57 ± 0.36	1.99 ± 0.29	294 ± 4
	NOM-stripped silt	0.002–0.05	0.71	74.3%	6.028	–36.7 ± 0.7	11.96 ± 1.46	1.63 ± 0.07	64 ± 15	5.89 ± 0.37	2.06 ± 0.14	358 ± 66
	NOM-present clay	<0.002	10.62	–	83.84	–28.7 ± 1.1	32.00 ± 0.19	6.39 ± 0.09	1200 ± 142	16.09 ± 1.64	10.67 ± 1.24	2078 ± 299
	NOM-stripped clay	<0.002	2.00	75.3%	101.6	–23.4 ± 1.4	34.18 ± 1.87	6.41 ± 0.41	1535 ± 222	18.58 ± 2.70	11.15 ± 0.31	2813 ± 189

NOM natural organic matter, *SSA* specific surface area, *ZP* zeta potential, *DC-Fe* dithionite-citrate extractable free Fe_2O_3, *AO-Fe* ammonium-oxalate extractable amorphous Fe_2O_3, *WS-Fe* water-soluble Fe^{2+}, *DC-Al* dithionite-citrate extractable free Al_2O_3, *AO-Al* ammonium-oxalate extractable amorphous Al_2O_3, *WS-Al* water-soluble Al^{3+}

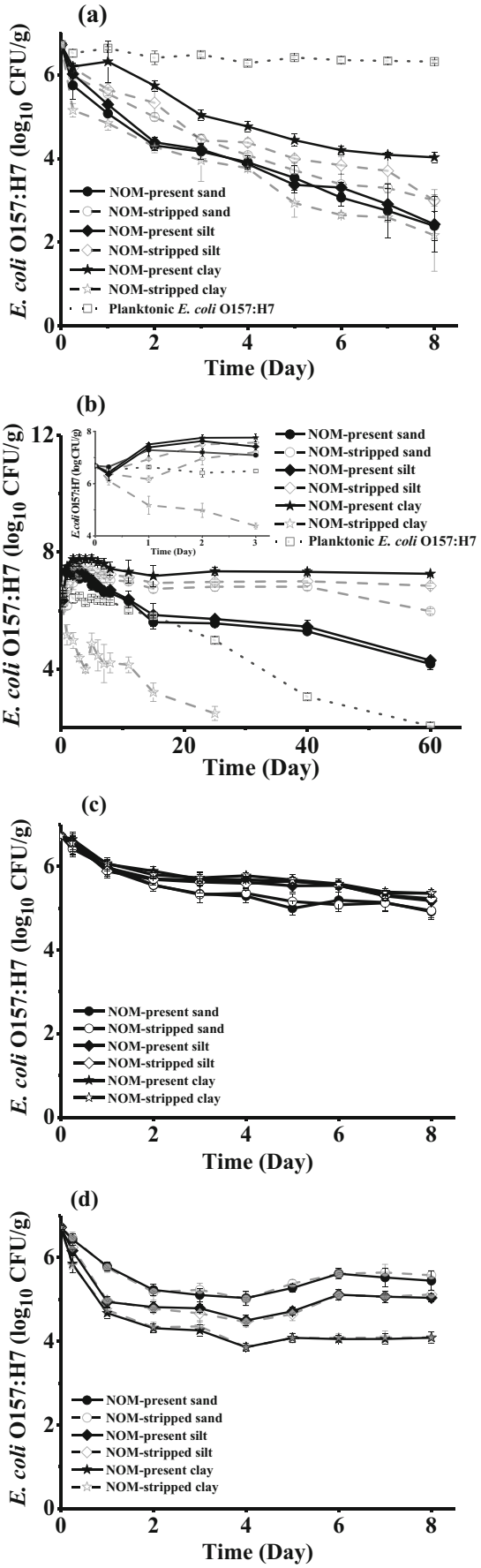

Fig. 1 Survival of *E. coli* O157:H7 at 25 °C in **a** Red soil particles, **b** Brown soil particles, **c** DC-Fe/Al (hydro)oxides-stripped Red soil particles, and **d** AO-Fe/Al (hydro)oxides-stripped Red soil particles. The *figure insert* highlights the regrowth of *E. coli* O157:H7 in Brown soil particles of different sizes within 3 days. The *solid lines* and *dashed lines* represent NOM-present and NOM-stripped particles, respectively. The *dot line* is blank control within dH_2O

carefully transferred to another plastic tube, mixed with 3 mL of NaOH (2 mol L^{-1}), and placed in a water bath at 100 °C for 30 min to lyze the cells. After cooling at room temperature, the bacterial proteins were filtered, dyed with 5 mL of Coomassie brilliant blue for 3 min, and valuated by a spectrophotometer at 595 nm. The content of bacterial protein was used to represent the abundance of bacteria.

Bioluminescence assay for metabolic activity via ATP determination

ATP experiments were conducted by mixing 40 mg autoclaved soil particles with 10-mL bacterial solution containing 1.0×10^{10} cells of *E. coli* O157:H7 in plastic tubes. All tubes were partially sealed and placed vertically on a shaker (40 rpm) to keep cells suspended at 25 °C. On days 0, 0.17, 0.33, 1, 2, 3, 4, 5, 6, 7, and 8, three vials were sampled from each experimental series. ATP generation was detected using BacTiter-Glo™ (Promega), and bioluminescence was monitored with a Multimode Plate Reader (EnVision, PerkinElmer, USA) in dark opaque 96-well microtiter plates. The procedure was carried out according to the manufacturer's protocol. Each well contained 50 μL of bacteria-soil suspension and 50 μL BacTiter-Glo™ reagent. Measurements were performed in triplicate for each sample and soil particles without bacteria as the negative control.

qRT-PCR experiments for assessing cell response

The expression of genes such as *pta* and *ackA* were explored using qRT-PCR with bacterial cells after 1 h of exposure to soil particles. Forty milligrams of soil particle were mixed with 10-mL bacterial solutions (1.0×10^{10} cells of *E. coli* O157:H7) in tubes, and the mixture was shaken at 150 rpm and 25 °C for 1 h. Total RNA was isolated using the FastRNA Pro Soil-Direct Kit (Obiogene, Inc., CA) with minor modifications by Duffitt et al. (2010). The RNA quality was determined by 0.8% (*w*/*v*) agarose gel electrophoresis and by spectrophotometric analysis (OD_{260}/OD_{280}) using a NanoDropTM ND-2000. The primers were designed by using online software tools Primer 3 and Beacon Designer 7 and listed in Table S1. Total RNA samples were synthesized to first-strand cDNA using HiScript II Q RT SuperMix from Vazyme Biotech Co., Ltd (China). Quantitative PCR was performed on the ABI ViiA™ 7 (USA) using 3 μL of cDNA in triplicate. The reaction mix was prepared with 5 μL iTaq™ Universal SYBR green supermix (Bio-Rad), 1 μL each of forward and reverse primers, 1 μL cDNA, and 2 μL of nuclease-free water. Three microliters of cocktail were added to 3 μL aliquots of cDNA samples and amplified by the following parameters: q-PCR program for the reaction was 95 °C for 30 s, 40 cycles at 95 °C for 10 s, and 55 °C for 20 s, with a final temperature of 60 °C for 35 s. Data analysis was performed using the threshold cycle method ($2^{-\Delta\Delta CT}$) with the amount of the target gene normalized to a reference gene, *gapA*, and compared to control samples (Pfaffl 2001).

Statistical analysis

All experiments were performed in triplicate. The data are presented as the mean ± standard deviation of three independent experiments. Statistical differences between mean values were analyzed using a Student's *t* test. Probability (*P*) values greater than or equal to 0.05 were considered not significant at a 95% confidence interval.

Results

Characterization of soil particles

Physicochemical properties of various soil particles are presented in Table 1. Overall, when compared to Brown soil particles, Red soil particles have a higher amount of Fe/Al (hydro)oxides for the same size. Specifically, the amount of DC-Fe oxides ranged from 13.95 to 119.69 g kg^{-1} in Red soil particles, substantially higher than that in Brown soil particles (5.66 to 34.18 g kg^{-1}) ($P < 0.05$). The percentage of DC-Al (hydro)oxides in Red soil particles was also 3.46–8.81 times higher than that in Brown soil particles. Moreover, the concentrations of AO-Fe/Al (hydro)oxides and water-soluble Fe^{2+} and Al^{3+} were also consistently higher in Red soil particles than those in Brown soil particles ($P < 0.05$). Additionally, the zeta potentials of soil particles were in the range of −18.6 to −35.4 mV and −23.4 to −39.8 mV for Red soil and Brown soil, respectively. For both soils, clays with the largest specific surface area varied from 58.99 to 101.6 m^2 g^{-1}, which was significantly higher than that of silts and sands (1.902 to 11.58 g kg^{-1}) ($P < 0.05$). The amounts of DC- and AO-Fe/Al (hydro)oxides in both soils followed the order of clays > silts > sands. Additionally, the content of NOM was also the greatest on clays and decreased with increasing particle size. In the same size range of soils, surface charges were less negative on NOM-stripped particles than on NOM-present particles. After the treatment of H_2O_2, ~20% of NOM still remained in the NOM-stripped soil particles. Therefore, the comparison of *E. coli* O157:H7 survival, attachment, metabolic activity, and gene expression in NOM-present soil with those in NOM-stripped soil may only reflect

the influence of most NOM in soil particles on bacterial behaviors.

Dynamics of *E. coli* O157:H7 survival in soil particles

Figure 1 shows the number of inoculated *E. coli* O157:H7 colonies changing with time, as a function of particle size for both Red soil and Brown soil. In the control *E. coli* O157:H7-dH_2O system, bacterial abundances remained stable over 8 days. However, *E. coli* O157:H7 abundance in Red soil particles significantly decreased 0.52 to 0.97 $\log_{10}$ CFU/g in the initial 6 h, and then continued to die off rapidly in the following 8 days. Except for the NOM-stripped clay, other Brown soil particles' bacterial abundances decreased 0.04 to 0.33 $\log_{10}$ CFU/g in the initial 6 h, followed by regrowth of cells and reached a maximum abundance within 3 days. *E. coli* O157:H7 survived well after 60 days in Brown soil sands and silts, with 0.7 to 2.5 $\log_{10}$ CFU/g reduction in cell abundance. In Brown soil NOM-present clay, the bacterial abundance was observed to increase 0.58 $\log_{10}$ CFU/g compared with the initial inoculation over the 60 days (from 6.68 to 7.26 $\log_{10}$ CFU/g). Conversely, the abundance of *E. coli* O157:H7 in the Brown NOM-stripped clay decreased to an undetectable level (<2 $\log_{10}$ CFU/g) at day 24.

E. coli O157:H7 survived substantially more in the Red soil particles stripped of the oxides than those with the native oxides present. Specifically, during the experimental period (8 days), *E. coli* O157:H7 abundance declined less in the DC-Fe/Al (hydro)oxides-stripped Red soil particles (1.34 to 1.67 $\log_{10}$ CFU/g) than in Fe/Al (hydro)oxides-present Red soil particles (2.69 to 4.56 $\log_{10}$ CFU/g) (Fig. 1c) ($P < 0.05$). The survival capacity of the former followed the order of clays = silts > sands. However, the abundance of the pathogen remained the highest in sand fractions among AO-Fe/Al (hydro)oxides-stripped Red soil particles, and the regrowth of pathogen occurred after 4 days in AO-Fe/Al (hydro)oxides-stripped silts and sands (Fig. 1d), as well as in Brown soil particles (Fig. 1b).

Quantification of attachment of *E. coli* O157:H7 to soil particles

Figure 2 shows the attachment isotherms for *E. coli* O157:H7 to soil particles of different sizes in batch systems. The attachment data followed a linear equation $C_s = K_d \times C_{eq}$, where C_s is the equilibrium abundance of bacteria attached per gram of soil particles, C_{eq} is the equilibrium abundance of cells in solution, and K_d is the partition coefficient. The K_d value is directly proportional to the attachment of bacteria to soil particles. The values of K_d for *E. coli* O157:H7 attachment to Brown soil particles (154.3 to 596.7 mL g^{-1}) were lower than those for Red soil particles (216.8 to 895.8 mL g^{-1}), which may be due to the dissimilar surface charges of soil particles

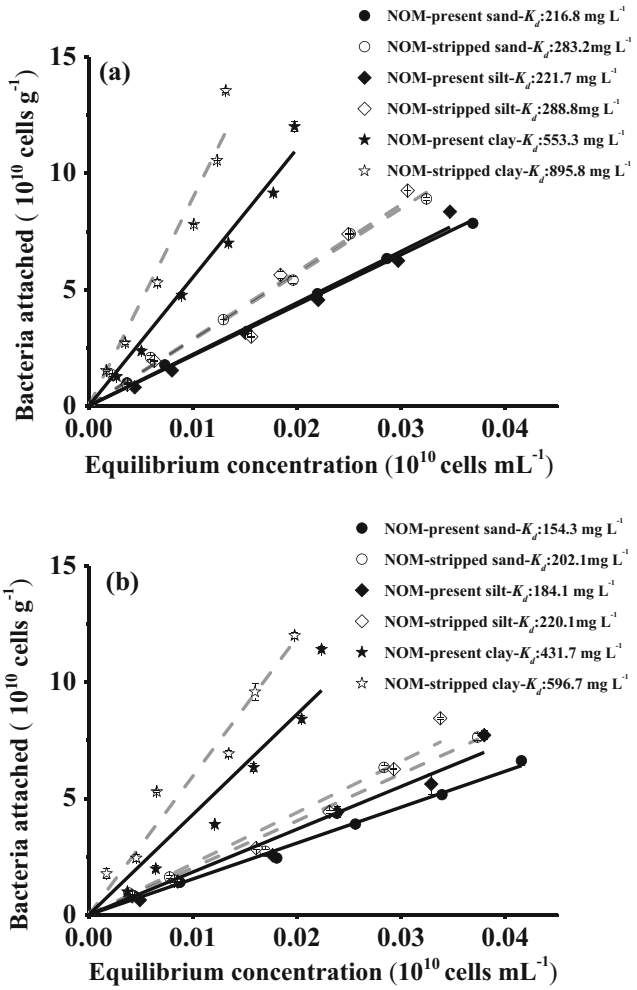

Fig. 2 Attachment isotherms of *E. coli* O157:H7 at 25 °C to **a** Red soil and **b** Brown soil particles of different sizes. The *solid lines* and *dashed lines* represent NOM-present and NOM-stripped particles, respectively

originated from mineral compositions (Stotzky 1986), especially for the high content of Fe/Al (hydro)oxides in Red soil (Table 1). Clays were more effective than silts and sands in binding cells regardless of soil type. Specifically, attachment to clays resulted in 2.3- to 3.2-fold increase of mass transfer (K_d = 431.7 to 895.8 mL g^{-1}) over that to silts and sands (K_d = 154.3 to 288.8 mL g^{-1}). In the same size of soil particles, the extent of *E. coli* O157:H7 attachment to NOM-present particles was significantly less than that to NOM-stripped particles ($P < 0.05$), and this trend is most obvious for Red soil clays, with the K_d value of the latter being 62% higher than that of the former.

Evaluation of ATP levels for *E. coli* O157:H7 in soil particles

To detect that metabolic activity of the cells as a function of time and their exposure to the different soil types and size fractions, an extensive analysis of ATP levels was conducted.

Figure 3 shows the ATP level per *E. coli* O157:H7 in soil particle suspensions as a function of time. During the initial 5 days, ATP levels per *E. coli* O157:H7 decreased quickly in soil suspension, but gradually exhibited higher level than that in dH_2O during the later period of experiment, indicating soil particles may allow bacteria to maintain a relatively high stable ATP level for extended periods. ATP levels per cell were observed to be lower in Red soil particles than in the same size range of Brown soil particles. For the *E. coli* O157:H7-clay system, about 39–70% loss was detected in the ATP level, substantially higher than the 9–32% loss in sands and silts during the first day ($P < 0.05$) and then the ATP level remained relatively constant. At the end of experiment (day 8), ATP levels were observed to be significantly higher in clays (0.36×10^{-18} to 0.39×10^{-18} mol ATP/CFU) than in sands and silts (0.13×10^{-18} to 0.21×10^{-18} mol ATP/CFU) ($P < 0.05$), suggesting attached bacteria maintained a relatively high activity than free cells for extended periods (Stotzky 1986; van Loosdrecht et al. 1990). For both soils, similar trends of bacterial ATP levels were observed between NOM-present and NOM-stripped particles (silts and sands) during the experiment period (8 days), which slowly decreased from 1.18×10^{-18} to 0.13×10^{-18} mol ATP/CFU. The bacterial ATP level in NOM-present clays was 1.4–1.9 times higher than that in NOM-stripped clays at the first 8 h ($P < 0.05$), but showed no significantly differences at day 8 ($P > 0.05$).

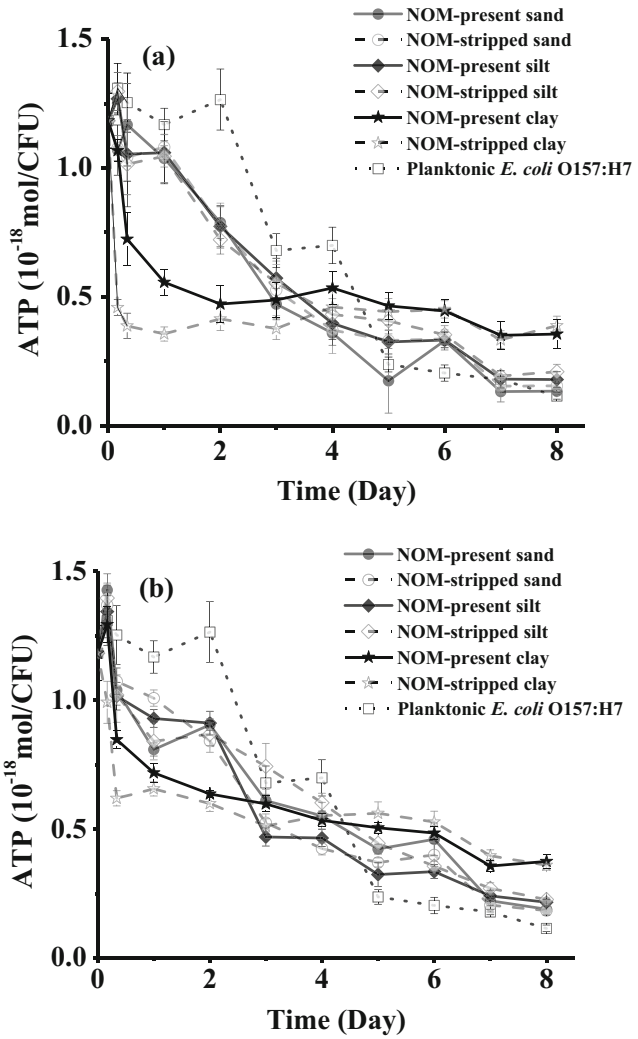

Fig. 3 Dynamics of ATP level per *E. coli* O157:H7 at 25 °C in **a** Red soil particles and **b** Brown soil particles as a function of time. The *solid lines* and *dashed lines* represent NOM-present and NOM-stripped particles, respectively. The *dot line* is blank control within dH_2O

Determination of gene expression

Figure 4 shows the changing the expression of acetate pathway associated genes (*pta* and *ackA*) after 1 h of bacterial attachment to various soil particles. Generally, *pta* showed a significant increase in gene expression after exposure to soil particles, while *ackA* displayed an obviously decreasing trend ($P < 0.05$). Compared to expression in cells within sands and silts, *pta* was more highly induced in clays, with 6.1–9.3-fold increase following exposure to clays ($P < 0.05$). Clays significantly repressed the expression of *ackA*, having an average decrease of 75% in expression. After exposure to sands, the relative expression of *ackA* was reduced by 8, 34, 32, and 23% for Red soil NOM-present sand, Red soil NOM-stripped sand, Brown soil NOM-present sand, and Brown soil NOM-stripped sand, respectively, when compared to the control. For Red soil particles, *pta* was upregulated and *ackA* was downregulated by the NOM stripping (Fig. 4a). However, *pta* showed no significant change when NOM was either present in or removed from Brown soil particles ($P > 0.05$).

Discussion

Since the indigenous soil microbial community was removed by autoclaving, the bacterial attachment, metabolic activity, gene expression, and survival in our study could differ from natural conditions. Additionally, the oversaturation will shift cellular metabolism to anaerobic processes, which could also affect *E. coli* O157:H7 survival (Fremaux et al. 2007). Despite these the goal of this study was to assess the effects of soil particle characteristics, such as particle size, Fe/Al (hydro)oxides, NOM, and soil types, on the survival of *E. coli* O157:H7 in sterilized soil particles from Red soil and Brown soil. The results of this study highlight the importance of surface-attached bacterial phenotype and associated metabolic pathways in generating strong natural selection for bacterial pathogens in soil environments. Moreover, this finding may be helpful in the prediction of bacterial fate in saturated soil (i.e., following heavy rains, snow melt, flooding, or irrigation).

Clay content has long been known to enhance enteropathogen survival in soil (Santamaria and Toranzos 2003; Franz et al. 2008; Brennan et al. 2014), which is in

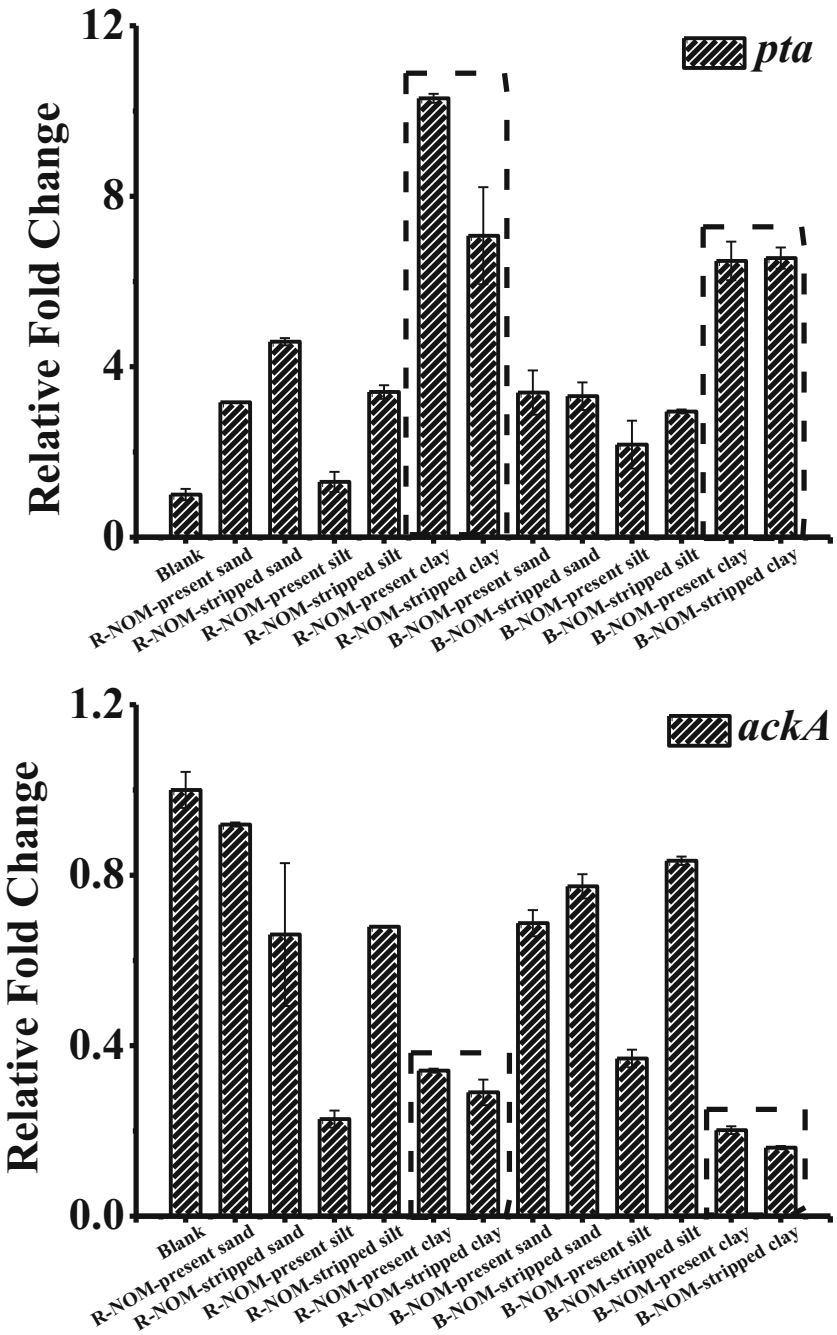

Fig. 4 Relative fold change of genes versus a housekeeping gene in relation to acetate pathway (*pta*, *ackA*) after 1 h of exposure to varying soil particles of different sizes (sand, silt, and clay), with the NOM either present or stripped. *Blank* represents the *E. coli* O157:H7 without soil particles under same operation (150 rpm and 25 °C for 1 h). The *dotted box insert* highlights the most remarkable variations of *pta* and *ackA* genes when exposed to clays in the *dotted box*. *R* Red soil, *B* Brown soil

agreement with this current study that *E. coli* O157:H7 survived best in NOM-present clays for both Red soil and Brown soil (Fig. 1a, b). The smallest particle size fraction, clay, is composed mainly of clay minerals, and the larger fractions (silts and sands) are composed principally of primary minerals at various stages of weathering (Stotzky 1986). Clay minerals are the most active inorganic colloid components in soils and influence bacterial attachment, metabolic activity, colonization, or biofilm formation (Stotzky 1986; Courvoisier and Dukan 2009; Cai et al. 2013; Huang et al. 2015). Clays with the largest surface areas and specific surface electrical properties were more effective than silts and sands in binding *E. coli* O157:H7. Bacterial adhesion, the first step in biofilm formation, stimulates the organism to produce extracellular polymeric substances, such as polysaccharides, protein, lipids, and nucleic acids, forming a protective matrix around the bacterial surface and protecting cells from harsh environmental conditions (Busscher and van der Mei 2012). As expected, higher attachment was shown to result in progressively longer survival of *E. coli* O157:H7 (except in the case of the clay stripped of NOM). Surface-attached bacteria could exhibit an altered physiological or metabolic state with respect to gene transcription

for growth and metabolism (Donlan and Costerton 2002), which enhances opportunities for microbial species to establish and persist in adverse environments. Monds and O'Toole (2009) proposed a biofilm model and attributed the change in biofilm structure and amount to central metabolic changes. In this study, the expressions of the acetate pathway-associated genes showed a significant increase for *pta*, but a decreasing trend for *ackA* after exposure to soil particles. This phenomenon caused acetyl phosphate levels to rise, which increases expression of genes involved in type 1 fimbriae assembly and biosynthesis of colanic acid and decreases expression of genes involved in flagella biogenesis and ultimately possibly promotes the bacterial transformation from a planktonic to biofilm phenotype (Wolfe 2005; Fredericks et al. 2006; Prüß et al. 2010). Acetyl phosphate could also act as a phospho-donor for response regulators like RcsB, FimZ, and OmpR, which are known to control biofilm-related genes (Wolfe 2005; Prüß et al. 2010). Duffitt et al. (2010) also observed *E. coli* O157:H7 grown in sterile soil microcosms expressed genes for colanic acid at significantly higher levels than cells incubated in LB and sterile stream water, which suggested that the biofilm formation was likely in soil. Therefore, the ability of *E. coli* O157:H7 to attach surfaces constitutes a successful trait for survival and generates strong natural selection for pathogens in soil environments.

It was noteworthy that the highest inactivation rate was observed in NOM-stripped clays (Fig. 1a, b). The higher content of Fe/Al (hydro)oxides in the clay fraction may be responsible for bactericidal ability. Figure 1c also shows that survival of bacteria was significantly enhanced when Fe/Al (hydro)oxides had been removed from Red soil particles, which demonstrated the antibacterial role of Fe/Al (hydro)oxides. A variety of physical, chemical, or biological processes can make oxides antibacterial. Bactericide can occur either by surface attraction between oxides and bacteria through hampering uptake of essential nutrients, disrupting cell envelopes, or by exchange of soluble oxide constituents toxic to the bacteria (Rong et al. 2007; Williams et al. 2011). Due to the washing processes, Fe^{2+} and Al^{3+} leached from the soil particles were below the minimum inhibitory abundances for *E. coli* (Williams et al. 2011). This was supported by the fact that the abundance of *E. coli* O157:H7 remained stable over the experimental period (60 days) in the clay fraction of Brown soil in the presence of NOM, in which there were relatively high concentrations of Fe^{2+} and Al^{3+}. Therefore, the die-off of *E. coli* O157:H7 may rest upon the direct interactions between pathogen and Fe/Al (hydro)oxides. These direct interactions are facilitated by the electrostatic interactions occurring between the oxides and bacterial cells. Notably, Fe/Al (hydro)oxides have an isoelectric point of about 8.5 and carry net positive charges in acidic and neutral soils (Mills 2003; Asadishad et al. 2013), which could effectively increase the attachment of negatively charged *E. coli* O157:H7. NOM-stripped clays displayed exposed additionally Fe/Al (hydro)oxides, which could provide new sites for *E. coli* O157:H7 binding. The strong and close association between bacterial pathogens and Fe/Al (hydro)oxides may yield stress on the cellular membrane (Glasauer et al. 2001; Rong et al. 2007; Asadishad et al. 2013) or produce reactive oxygen species (Taylor et al. 2014), both of which would be expected to promote bacterial die-off. In the presence of the NOM coating, the charge of the soil particles was more negative and led to an increased electrostatic repulsion forces between bacteria and clays. Furthermore, the presence of NOM also changed the roughness of surfaces and may have enhanced the extent of repulsive steric interactions (Liu et al. 2015), thereby inhibiting the direct contact between positive Fe/Al (hydro)oxides and negative bacteria.

Lethal effects upon adhesion require a minimum positive charge density of the substratum surface (Kügler et al. 2005). Additionally, the damaged or dead surface-attached cells could be a source of nutrients to remaining bacterial pathogens or act as a scaffold to initiate and promote cell accumulation, providing survival fitness against a hostile environment (Terada et al. 2012). These may explain the regrowth of *E. coli* O157:H7 occurred in AO-Fe/Al (hydro)oxides-stripped Red soil particles (Fig. 1d), as well as in Brown soil particles (except for NOM-stripped clay) (Fig. 1b). Compared with AO-Fe/Al (hydro)oxides-stripped soil particles (silts and sands), *E. coli* O157:H7 survival in DC-Fe/Al (hydro)oxides-stripped soil particles was not significantly enhanced (Fig. 1c, d), which suggested that relative low content of DC-Fe/Al (hydro)oxides could not effectively kill bacterial pathogens. However, clays with high content of DC-Fe/Al (hydro)oxides were detrimental to pathogen (Fig. 1a, d). Additionally, Fig. 1a, c shows that distinct survival of *E. coli* O157:H7 when AO-Fe/Al (hydro)oxides had been removed from Red soil particles after 2 days, which suggested that despite low content, AO-Fe/Al (hydro)oxides played a strong antimicrobial.

The availability of resources such as NOM may be the primarily factor for the viability and growth of chemoheterotrophic *E. coli* O157:H7 in soil and water environments (van Elsas et al. 2011). Moreover, the sterilization process eliminated the microorganisms and relative microbial residues could be used by *E. coli* O157:H7 as energy and nutrient sources, as Moynihan et al. (2013) observed a significant increase in the abundance of *E. coli* O157:H7 in sterile soil. However, in this study, the soil particles may contain low concentrations of available nutrients including organic C, N, and P after washing processes with dH_2O and ethanol. Figure 3 also shows no obvious difference in the bacterial activity between NOM-present and NOM-stripped particles (silts and sands). After the treatment of H_2O_2, ~20% of NOM still remained in the NOM-stripped soil particles, suggesting that the effect of NOM on survival of *E. coli* O157:H7 may not have been excluded completely from NOM-stripped

soil particles. *E. coli* O157:H7 has been reported to survive even in oligotrophic environments with low concentrations of 0.1–0.7 mg L^{-1} organic C (Chekabab et al. 2013). Additionally, oligotrophic conditions have often been routinely linked to a reduction in cell size and cellular processes (e.g., protein synthesis, ATP formation, respiratory activity) (Thomas et al. 2002; Cook and Bolster 2007), which were consistent with results that the abundance of *E. coli* O157:H7 was not decreased (Fig. 1), but the content of ATP was declined with time in the control (Fig. 3). A microcalorimetry study showed that organic C tightly bound to soil particles after washing may not easily utilized by *Pseudomonas putida* (Wu et al. 2014). Prolonged bacterial persistence was also observed in NOM-stripped particles in Fig. 1a, b, implying that the primary role of NOM was not as an effective nutrient supply in this study. The removal of negatively charged NOM could significantly impact the soil particle charge, creating a less negative surface (Table 1) and additional sites for bacterial attachment (Zhao et al. 2014). Therefore, interfacial interaction, such as attachment, may be critical for metabolic activity and survival of *E. coli* O157:H7, which is in agreement with the positive correlation between attachment and the survival time of the bacterial pathogens.

The Red soil was predominantly of kaolinitic mineralogy, while the clay mineral of Brown soil was mostly 2:1 minerals such as montmorillonite and vermiculite (Carson et al. 1982). Compared to 1:1 clay (kaolinite), 2:1 clay has higher specific surface area and cation exchange capacity, which could enhance bacterial metabolism in part by buffering the pH of suspension or adsorbing toxic metabolites within the optimal range for growth (Stotzky 1986; Brennan et al. 2014; Wu et al. 2014). In oligotrophic environments, *E. coli* would activate enzymes to catabolize poorly available nutrients (Tao et al. 1999). Kaolinite and goethite notably decreased the catabolic activity of *P. putida*, whereas montmorillonite significantly stimulated the bacterial activity (Wu et al. 2014). Addition of clay minerals reduced the decay rate of *E. coli* O157:H7 (montmorillonite, 0.06 day^{-1} < illite, 0.15 day^{-1} < kaolinite, 0.23 day^{-1}) (Brennan et al. 2014). Wang et al. (2014b) also found acidic soils containing Fe/Al (hydro)oxides and kaolinite were unfavorable for *E. coli* O157:H7 survival, as the average survival time of pathogen ranged 2.1 to 3.6 days. Therefore, the Brown soil with 2:1 clay component was likely a more favorable environment for *E. coli* O157:H7 survival, while the bacterial abundances decreased in Red soil particles.

Conclusions

The results of this study highlight that the clay mineralogical status of a soil has a profound effect on the survival of *E. coli* O157:H7 in the soil and NOM functions mainly through interfacial interaction rather than serving as an effective nutrient supply. The bacterial pathogens may adopt a survival strategy through attaching to soil particles and activating acetate metabolism for biofilm formation. However, the direct contact of the positively charged Fe/Al (hydro)oxides with bacterial pathogens resulted in the cell die-off after the initial attachment stage. Therefore, soils (Ultisols) with a large amount of Fe/Al (hydro)oxides are detrimental to pathogens, but other types of soils (Alfisols) with a small quantity of Fe/Al (hydro)oxides may be a favorable environment for pathogen survival. In addition, more studies are required to comprehend the selective effect of clay minerals on the fate of bacterial pathogen in soil. Especially, how the clay minerals trigger the pathogen transformation from planktonic to sessile growth, and subsequently form biofilms under natural conditions.

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