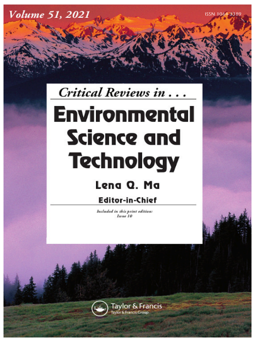

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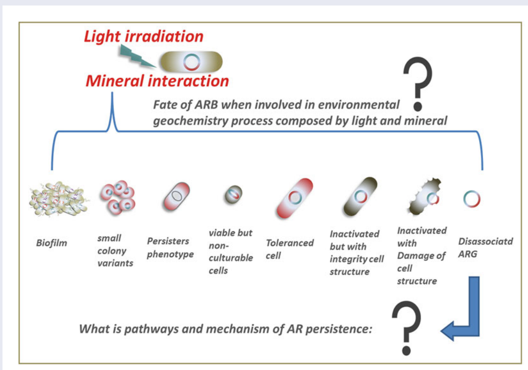
ABSTRACT



The antibiotic resistance (AR) is a threatening risk for human health at a global scale. The propagation, dissemination and evolution of AR have been well-studied these years. With development of AR, the antibiotic-resistance bacteria (ARB) and antibiotic-resistance genes (ARGs) have been detected in almost all environmental systems and matrices. Herein, we attempted to summarize how ARB/ARGs become persist when they enter water environments and further be involved in geochemical processes especially at the interface of natural mineral with light irradiation. During the processes, bacteria have different form of transformation and come into stressed or non-stressed states. Their existed forms will be varied including being inactivated, transient tolerance and persistence phenotypes, which make AR problem become stubborn and complicated. Besides, separation of ARB and ARGs further intensified complexity of AR problem after naked ARGs diffusing into water, which acted as reservoir of ARGs and set stage for their transfer between bacteria. Furthermore, acquisition of ARGs mediated plasmid could even bring some advantages or disadvantage to bacteria, making problem more complex and uncontrollable. To enable AR under control, it is critical to understand the mechanism how ARB/ARGs participate in environmental geochemical transformation and in what condition that AR persistence happen. Understanding ponderance of AR persistence is not only key to properly assess its risk, but also to seriously prevent the continued development of AR.

KEYWORDS Antibiotic-resistance bacteria; persistence; environmental mineral interface

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1. Introduction

Antibiotic resistance (AR) has becoming a challenging problem to global public health by making antibiotics less effective (Amarasiri et al., 2020; Laxminarayan et al., 2013; Pruden et al., 2006; Toprak et al., 2011). The primary factors that drive the development of AR problem is the overuse of antibiotics in veterinary and human medicine (Shah et al., 2012). Many studies have focused on the evolution and dissemination of antibiotic-resistance bacteria (ARB) and antibiotic-resistance genes (ARGs) as well as elimination techniques so that attempt to control the development of AR problem (Hall, 2004; Hershberg, 2017; Jia et al., 2015; Lehtinen et al., 2017; Martinez, 2011; Singh et al., 2012; Toprak et al., 2011; Yoshida et al., 2017). However, due to the stubbornness of ARB and ARGs in various environmental systems, many researchers began to realize the problem of AR persistence (Eckert et al., 2018; Enne et al., 2001; Lopatkin et al., 2017; Mao et al., 2014; Zhao et al., 2020).

Based on highly detected frequency as well as concentrations, ARB and ARGs have been defined as persistent pollutants in different environmental systems including rivers (Proia et al., 2016; Storteboom et al., 2010), air (Li et al., 2018), soil (Knapp et al., 2011), sediment (Dong et al., 2019), lagoons (Chee-Sanford et al., 2001) and lakes (Eckert et al., 2018). Furthermore, in recent years, many studies have reported that the ARGs could be also detected in airborne particulate matters (Liang et al., 2020), which provide a new pathway of ARG transmission. For example, the ARGs and mobile genetic elements (MGEs) have been highly detected in airborne particulate matters in cattle feed yards, hospitals, wastewater treatment plants and urban environments (Gao et al., 2017; Hu et al., 2018; Ling et al., 2013; Pal et al., 2016; Xie et al., 2018). Besides, tetracycline resistance genes are also available in human-occupied indoor environments (Ling et al., 2013). It has also been reported that airborne *blaSHA* to β-lactams and *sul1* could be detected in urban parks (Echeverria-Palencia et al., 2017).

Reports indicate that even after reducing usage of antibiotics for almost 10 years (Enne et al., 2001; Hajdúch et al., 1997; Heinemann et al., 2000; Sundqvist, 2014; Zhang et al., 2019), the related ARB and ARGs still persist in clinic treatment. These indicate that once the ARB and ARGs emerged, they will diffuse and participate in complicated environmental processes, which could largely affect their longevity. It has been reported that in river sediment, the ARGs located on plasmid could persist for over 20 weeks (Mao et al., 2014). Actually, some studies have already revealed the phenomenon that natural or anthropogenic factors play an important role in bacterial persistence in water environment (Durao et al., 2018; Eckert et al., 2018; Lu et al., 2015; Pruden & Arabi, 2011; Williams-Nguyen et al., 2016). Besides, some researchers supposed that on highly polluted days, the airborne particles might provide extra adhesion sites for microorganisms so that help them suspend more stably and persistent in air (Hu et al., 2018).

In various environmental systems, natural minerals and light irradiation are ubiquitously exists in individually or simultaneously. Sunlight mainly contains ultraviolet-light, visible-light, infrared-light, all of which are involved in many environmental processes and have intensively interacted with bacteria inevitably (Baliga et al., 2004; Dantur & Pizarro, 2004; Gustavson, 2000; Herndl et al., 1993; Kumar et al., 2016; Ruiz-Gonzalez et al., 2013; Santos et al., 2013). As for natural minerals, it is a basic constitution of geochemical characteristics that exist in various environmental interfaces, where bacteria or extracellular genes could attach and interact (Cai et al., 2009; Cao et al., 2011; Chen et al., 2016; Morrison et al., 2014; Stotzky, 1986; Stotzky & Rem, 1966; Williams et al., 2011). Some part of naturally-occurred minerals such as montmorillonite, kaolinite could exhibit obvious antibacterial activity directly to bacteria (Rong et al., 2007; Stotzky & Rem, 1967), while some could influence bacterial metabolic process as well as the growth process (Ferris et al., 1987). It has also been reported that mineral interaction could facilitate transfer of ARGs (Li et al., 2020). Besides, the adhesion of bacteria and DNA on minerals could also play a crucial role in biological activity and diversity, as well as in the transfer of genetic information among bacteria (Cai et al., 2009; Chen et al., 2016).

During real environmental geochemistry processes, the natural mineral and sunlight are usually coexisted. Among these minerals, some have semiconductor properties, leading to a typical naturally photocatalytic process occur when irradiated by sunlight, where reactive oxygen species (ROSs) such as $^{\bullet}OH$, $O_2^{\bullet}-$, H_2O_2 could be generated. It has been reviewed that many kinds of metal oxides and metal sulfide minerals have semiconductor characteristics and participate in the natural geochemistry process (Table 1) (Huang et al., 2003; Xia et al., 2017). It has been found that the maximal adsorption wavelength of most of natural semiconductor minerals is located within the range of visible light and infrared light. This phenomenon suggests that most minerals could be excited by sunlight and form a naturally photocatalytic interface. The photocatalytic function in minerals can play a unique role in environmental self-cleaning on the Earth's surface, where complex pollutants will be oxidized and degraded. When bacteria transport through shallow surface water, it could encounter such interfaces and subjected to a certain degree of oxidative stimulation. Here, this special natural mineral interface, that irradiated by light was defined as light and semiconductor mineral (LSM) interface. All these studies suggest that ARB and ARGs could participate in the environmental self-cleaning processes and interact with each other in various pathways, which might

Table 1. Natural existed semiconducting metal oxides and metal sulfide minerals (Xia et al., 2017).

Name	Formula	Name	Formula	Name	Formula
Baddeleyite	ZrO_2	Massicot	PbO	Pyrolusite	MnO_2
Romarchite	SnO	Bismite	Bi_2O_3	Magnetite	Fe_3O_4
Geikielite	$MgTiO_3$	Shcherbinaite	V_2O_5	Sphalerite	ZnS
Manganosite	MnO	Ilmenite	$FeTiO_3$	Alabandite	MnS
Bunsenite	NiO	Goethite	FeOOH	Orpiment	As_2S_3
Cassiterite	SnO_2	Wuestite	FeO	Greenockite	CdS
Eskolaite	Cr_2O_3	Monteponite	CdO	Berndtite	SnS_2
Zincite	ZnO	Hematite	Fe_2O_3	Cinnabar	HgS
Anatase	TiO_2	Cuprite	Cu2O	Lorandite	$TlAsS_2$
Pyrophanite	$MnTiO_3$	Montroydite	HgO	Stibnite	Sb_2S_3
Rutile	TiO_2	Tenorite	CuO	Livingstonite	$HgSb_4S_8$
Senarmontite	Sb_2O_3	Avicennite	Tl_2O_3	Tungstenite	WS_2
Enargite	Cu_3AsS_4	Molybdenite	MoS_2	Chalcocite	Cu_2S
Herzenbergite	SnS	Bornite	Cu_5FeS_4	Pyrite	FeS_2
Argentite	Ag_2S	Cobaltite	CoAsS	Hauerite	MnS_2
Polydymite	NiS	Galena	PbS	Chalcopyrite	$CuFeS_2$
Vaesite	NiS_2	Arsenopyrite	FeAsS		
Pyrrhotite	FeS	Covellite	CuS		

largely affect their environmental behavior and fate. However, the existing forms and evolution trend of ARB and ARGs are unpredictable, which will impose a big obstacle to the understanding of how AR problem exist and persist in the natural environments.

Therefore, the main objective of this review is to advance the knowledge of how does ARB/ARGs transform in the LSM interface as well as their association with AR persistence. In addition, the mechanisms that mediate persistence of ARB/ARGs were further illustrated.

2. Damage effects of ARB/ARGs at interface of natural minerals with light irradiation

Sunlight provides the energy necessary for the functioning of some bacterioplankton communities by supporting the action of biologically usable photons such as photosynthesize or some other indirectly pathways. Nevertheless, part of sunlight energy occurs at different wavelengths which could harm bacteria at various environmental interface; this is mainly the case of ultraviolet (UV) region of spectrum which categorized into three wavelength ranges, UVA (320–400 nm), UVB (280–320 nm) (Ruiz-Gonzalez et al., 2013) and UVC (185–280 nm), which is often used as a direct sterilizing lamp. The UVC is usually considered as the most biologically harmful to bacteria, while it is absorbed in the air and cannot reach the surface of the earth. Artificial light sources are also utilized to study the antibacterial effects of specific spectrum of light (Hockberger, 2002). Most of studies focused on the UV irradiation, which could be absorbed by DNA structure directly and lead to the inactivation of bacteria through inducing the formation of cyclobutane dimer and breakage of DNA (Pfeifer, 1997; Ravanat et al., 2001). It has been reported that under the exposure of UV irradiation, the damage of plasmid encoding ampicillin resistance gene bla_{TEM-1} would occur (Pang et al., 2016). Furthermore, the UV irradiation could also inactivate ampicillin-resistance and trimethoprim-resistance *Escherichia coli* (*E. coli*) (Templeton et al., 2009). In contrast, some studies reported that UV irradiation showed no significant decrease in the levels of *tert*(Q) and *tert*(W) genes (Auerbach et al., 2007). Except the damage of ARGs, other components of bacteria were also affected by natural or artificial light irradiation. For example, UVB could cause the alternation of whole cell protein profile (Kumar et al., 2016). The UVC and mid-infrared irradiation could also inhibit the synthesis of bacterial proteins as well as the damage to lipid structure (Chamberlain & Moss, 1987; Frols et al., 2007; Santos et al., 2012). The C-glucose leakage, lipid peroxidation, and microviscosity of liposomal membrane increased linearly with the increase of UVA intensity, which could subsequently alter the permeability of bacterial cell membrane (Bose & Chatterjee, 1995). Extracellular polymeric substances (EPS) as an important active component of bacteria could also be suppressed by UVB irradiation (Herndl et al., 1993). Furthermore, the morphology and flora structure of bacteria could also be changed under UV light irradiation (Margaryan et al., 2016). Based on above description, it could be inferred that the injury pathways of light irradiation are multifarious, which constitute the uncertainty of bacterial stress responses and follow-up existence form of lucky escaped bacterial individuals. Compared with UV irradiation, the visible light cannot cause a strong damage on ARB and ARGs. It is suggested that visible light irradiation could provide some advantage to bacterial growth (Li et al., 2017). Also, it has been reported that the emergence of gentamicin resistance could be induced by visible light (Harris et al., 1981). Visible light could also help bacteria to eliminate intracellular ROSs so that improve their survival capability (Li et al., 2017). Besides, certain dose of visible light irradiation could trigger various bacterial stress responses to improve their survival as well as increase conjugative transfer of ARGs (Chen et al., 2019).

Three decades of experimental work evaluating the effects of sunlight on natural bacterial activity suggest the responses ranging from high stimulation to total inhibition. Many researches related to the inhibition or stimulation of bacterial activities under the exposure of sunlight has been noted (Pakulski et al., 2007; 2008; Santos et al., 2012). Additionally, some environmental factors, including nutrient impairment and temperature, significant modulate the interactions between bacteria and sunlight (Ruiz-Gonzalez et al., 2013). It has been reported that the simulated sunlight irradiation could triggered SOS stress response and oxidative stress of antibiotic resistance of *E. coli* (Chen et al., 2019). Based on the above description that related to the stimulation of sunlight irradiation, it could be inferred that with the exposure of sunlight, bacteria might be damaged with various extends and arouse different stress responses.

The natural mineral is widespread in environmental system and closely related to bacteria. During the life process of bacteria, a lot of physical-chemistry interactions happened at the interface of environmental minerals. Among these processes, bacteria usually undergo an antibacterial effect posed by some mineral materials, which can hamper passive and active uptake of essential nutrient, disrupt cell envelope or impair efflux of metabolites (Ferris et al., 1987). Some specific minerals such as allophane and imogolite could make antibacterial by chemical sorption of known bacterial element (Ag, Cu, Co, Zn) onto certain crystallographic sites of mineral surface (Malachová et al., 2011; Onodera et al., 2001). It has been reported that the effects of antibacterial are mineralogically different, but they have in common in the presence of Fe-rich phases (e.g., biotite, Fe-smectite, jarosite, magnetite, pyrite, hematite, amphibole, and goethite) (Williams et al., 2011). Besides, nano-minerals may enhance the solubility of toxic element (Williams et al., 2011). When the antibacterial of natural mineral has been revealed, some studies start to synthesize the artificial mineral media or mineral complexes to inhibit the growth ability of bacteria (Lachowicz et al., 1996; Wu et al., 2009).

Except for single stimulation posed by mineral interface, in nature environment, more often than not, minerals are co-existing with light irradiation, which composed the LSM interface as described above. However, in most of time, the intensity of oxidative pressure that bacteria received in LSM interface are indistinct, which creates a variety of scenarios for the subsequent state of bacteria. However, based on its potential photocatalysis effects, which are superior method to inactivate wide range of microorganisms especially ARB in natural water environments (Cho et al., 2004, 2005), the natural minerals applied as photocatalyst in water disinfection has been greatly developed in recent decade. It has been reported that the photocatalytic interface could inactivate ARB as well as its associated ARGs totally due to the oxidative pressure of continuously produced ROSs at the interface (Guo et al., 2017; Jiang et al., 2017). In another word, the environmental effects of LSM interface posed by sunlight and natural minerals have been magnified significantly. Among these studies, the widespread natural minerals which could be used for direct photocatalytic bacterial inactivation include natural magnetic sphalerite, natural sphalerite, as well as natural pyrrhotite (Chen et al., 2011; 2013; Xia et al., 2013; 2018; Yang et al., 2011). Some other semiconductors collected from mineral deposits are also incorporated with several exogenous metal elements (e.g. Fe^{2+} and Cd^{2+}), which help to shift their adsorption edge to visible light region (Wang et al., 2017). Besides, some studies try to artificially build a more efficiently catalyst to acquire higher photocatalytic activity. For example, titanium and titanium-iron species has been incorporated inside a smectite-type mineral for photocatalytic bacterial inactivation (Carriazo et al., 2010). Due to its strong oxidative pressure, the bacterium not only lose its vitality but also be further oxidatively degraded and then released the intracellular substances including protein and DNA (Sun et al., 2014). Based on the above description, it is indicated that bacteria can receive different adverse effects from pure light irradiation, mineral contact and LSM oxidative interface when they participate in the environmental geochemistry process. However, the extent of bacterial damage varies widely from mild stimulation to severe oxidative damage, which can affect different forms of bacterial transformation.

3. Geochemistry transformation and their persistence of ARB/ARGs

Herein, various transformation pathways of bacteria were summarized systematically when they were involved in the geochemistry processes of light irradiation with mineral interaction (Figure 1). Based on the different types and degrees of stimulation processes, bacteria tend to appear in many different states, where some individuals emerge stress response to resist external stimuli, while some were inactivated. Corresponding to different states, there will be different development trend for each bacterium.

3.1. Bacteria transformation with stress responses

3.1.1. Improved tolerance

Different from dead cells, large part of bacteria could escape from the fate of death through various stress responses to improve their tolerance to

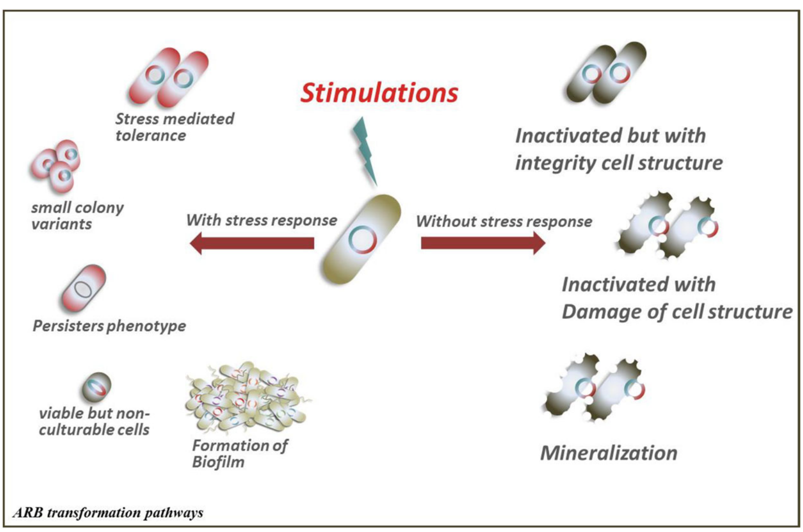

Figure 1. The transformation of ARB after stimulation: with or without stress responses.

adverse environmental factors. Some stress responses were directly help bacteria to survive. For example, after the bacteria being exposed to UVA stimulation, the damage of their DNA could be reversed by three mechanisms: photo-enzymatic repair (PER), nucleotide excision repair and post-replication repair (so-called "dark repair system") (Sancar & Sancar, 1988; Schultz et al., 1985). It is well known that the increased mutation rates could be induced under the UVA irradiation, which accelerate the occurrence of more fitted mutants to UVA stimulation (Runger & Kappes, 2008). It has also been reported that some special individuals could arouse their global regulation system which can mediate oxidation stress response, SOS stress responses as well as envelope stress responses to protect bacteria from directly or secondary-action of UVA attack (Chen et al., 2019). Further, different light irradiation such as visible light and simulated sunlight could also elicit bacterial stress responses related to oxidative stress and SOS stress responses (Chen et al., 2019).

Some natural mineral could also cause adverse effects on bacteria, as expected, bacteria could arouse their stress response to survive when they interact with natural sphalerite nanoparticles (G. Li et al., 2020). With the oxidation pressure posed by LSM interface, the bacteria could arouse their oxidative stress response to help themselves to get rid of the attack of ROSs (Sun et al., 2017). During this process, the antioxidative enzymes such as catalase activity (CAT) and superoxide dismutase (SOD) could overexpress to counteract with increased ROSs so that maintain the redox equilibrium in bacterial intracellular (Sun et al., 2017). Furthermore, under the stimulation of LSM interface, various bacterial stress responses including nutrient impairment, oxidative stress, envelope stress and SOS stress could both be elicited in ARB (Yin et al., 2020). Besides, under the state of stress responses, the ARB transiently exhibit high tolerance to the attack of antibiotics through higher mutation rate and more efficient efflux pump (Yin et al., 2020). However, all above mentioned stress responses related to the improved tolerance are mediated by temporary change in the bacterial state, which is un-inheritable and non-genetic when stimulation was removed.

In addition, it is worth mentioning that in some cases, the ARB exhibited different stress response from the bacteria without carrying ARGs. Usually, the exogenous ARGs were defined as an unnecessary element for ASB when there is no antibiotic selection existed (Enne et al., 2005). The expression of ARGs might increase the growth burden of bacteria so that impair their proliferation. However, some studies reported that acquirement of ARGs could endow bacteria with growth advantage as well as better tolerance to some specific stimulations. For example, by comparative study, the bacteria carrying with cefotaxime and colistin resistance genes could exhibit stronger stress responses and with less change of intracellular enzyme activity when expose to oxidative stimulation (Yin et al., 2019; 2020). The bacteria with colistin resistance gene could build up better tolerance to photocatalytic inactivation (Tseng et al., 2016). Furthermore, ARB is much more tolerant to UV disinfection than antibiotic-susceptible bacteria (Pang et al., 2016). This finding indicated that the UV irradiation have potential selection function to help the emerge of ARB and ARGs and its further persistence. However, the current researches only found the existence of this phenomenon without exploration of the underlining mechanisms, for example, which type of ARGs or plasmids can strengthen or weaken bacteria and what kind mechanisms can explain these phenomena.

Beyond the normal stress that we usually known, the conjugation transfer of genes as an pathway of horizontal gene transfer (HGT) could also be elicited after the exposure of UVA stimulation (Ajon et al., 2011; Chen et al., 2019), which seem belong to part of bacterial stress system. It is that the bacteria could transfer some useful elements to other individuals to learn from each other. Obviously, during this process, the ARGs located in plasmids or integrons could also be transferred to other hosts. Besides, some studies showed that the conjugation transfer could also be facilitated through the external stimulation (Dunlop et al., 2015), which belong to another stress response of bacteria discussed in this paper. Furthermore, it has been reported that some ARB could exhibited more resistant to the attack of ROSs as compared with antibiotic-susceptible bacteria (Gogniat & Dukan, 2007; Tseng et al., 2016). It has been reported that both associated and disassociated ARGs can spread between bacterial individuals through the conjugation transfer (Cai et al., 2007; Overballe-Petersen et al., 2013; Sand & Jelavic, 2018). As we mentioned above, with sub-lethal dosage of UV irradiation, the bacterial efficiency of conjugation transfer could be improved so that facilitate the spread and exchange of different ARGs in bacterial community (Zhang et al., 2019). Although the conjugation transfer of ARGs cannot increase the abundance of ARGs in bacterial community, there still have some evidences that the conjugation transfer, to a large extent, is responsible for the persistence of plasmid-mediated AR (Andersson & Hughes, 2011; Lopatkin et al., 2017; Norman et al., 2009; Schluter et al., 2007; Slater et al., 2008). Based on the above description, it is obvious that the aroused stress responses and improved tolerance could increase the persistence of ARB when they are under the exposure of light irradiation together with mineral interface.

3.1.2. Formation of persistence phenotypes

Non-sporulating bacteria tend to exhibit a persistence phenotype when they are subjected to environmental stress. Persistence phenotype is a

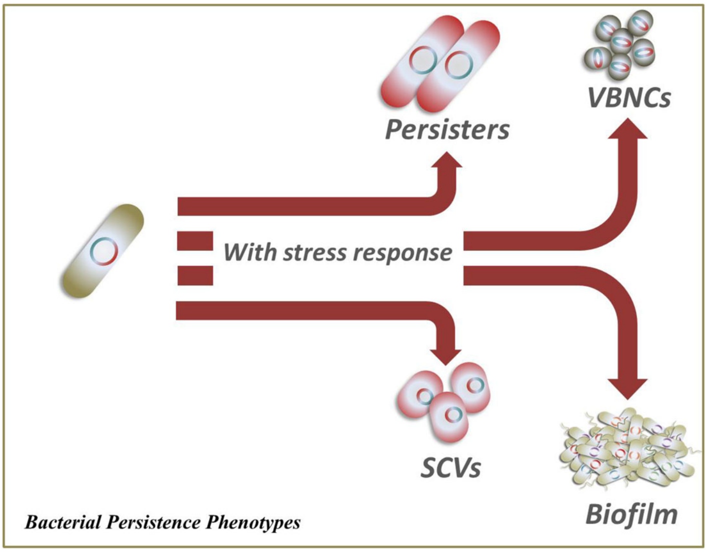

Figure 2. The persistence phenotypes of ARB with stress responses after stimulation.

phenotypic variation (non-genotypic variation) of bacteria that is tolerant or resistant to stimulus such as antibiotics and oxidative damage. This transient resistance phenotype is generally considered to be non-hereditary. That is, by removing external pressure and transferred them to a suitable growth condition, the proliferated progeny are no longer resistant to corresponding stimulus. As reported, bacterial persistence phenotype is the main cause of clinical persistent infections, which have greater impact than chronic and recurrent infections due to its important role in the evolution of genetic resistance (Windels et al., 2019). Therefore, the elimination strategy of bacterial persistence may be an important breakthrough point to solve the current AR crisis, because it can not only shorten the treatment time, but also slow down the development of AR problem. The common persistence phenotypes are persisters, small colony variants (SCVs), viable but nonculturable cells (VBNCs) and bacterial biofilm formation (Figure 2), all of which belong to the general stress responses of bacteria.

In 1942, for the first time, Hobby et al. found that in a bactericidal test by penicillin, a small portion of hemolytic *Streptococci* of the same genotype as the wild types was resistant to penicillin, forming a persistence subpopulation (Hobby et al., 1942). Subsequently, during the treatment of penicillin, it was founded that some nonresistant bacteria survived and named it as persisters (Bigger, 1944). Bacterial persisters are phenotypic variants that have high tolerance to antibiotics. Given that antibiotics are well known triggers of many types of stress, there have been broadly studied about the role of stress responses in persisters (Ayrapetyan et al., 2018; Lin et al., 2017; Pu et al., 2016; 2019). It has been reported that many stress responses are up-regulated in the transcriptome of populations enriched for persisters (Keren et al., 2004; Shah et al., 2006). Besides, some external stimulations such as acid, temperature and osmotic stress could increase the process of persister formation (Javid et al., 2014; Kuczyńska-Wiśnik et al., 2015; Leszczynska et al., 2013; Leung & Levesque, 2012; Mordukhova & Pan, 2014; Murakami et al., 2005). Although some detailed information related to stress responses have been reported to influence bacterial persistence like transtranslation (Li et al., 2013; Wilson & Nierhaus, 2007; Withey & Friedman, 2003), most of researches to date have concentrated on the well-known and broad stress responses including nutrient impairment, DNA damage, SOS stress response as well as oxidative stress responses caused by ROSs. For example, the bacterial populations with SOS stress response enriched for persisters (Keren et al., 2004; Orman & Brynildsen, 2013). Correspondingly, inactivation of the SOS response (Debbia et al., 2001; Goneau et al., 2014; Volzing & Brynildsen, 2015) or impairing DNA repair mechanisms (De Groote et al., 2009; Hansen et al., 2008; Volzing & Brynildsen, 2015) decrease persister levels. Besides, the induction of SOS regulon expression also lead to the increased persistence (Dorr et al., 2009). Pre-incubation of *E. coli* populations with ROSs-inducing compounds, such as H_2O_2 (Vega et al., 2012) paraquat (Wu et al., 2012), results in increased persister levels.

CAT and SOD are also needed in *P. aeruginosa* and *E. coli* persisters to protect them from antibiotics. The expression of these enzymes also depends on stringent response (Khakimova et al., 2013; Nguyen et al., 2011). In *Acinetobacter baumannii* (*A. baumannii*), the quorum-sensing-dependent induction of persistence also leads to the increase of enzymes activity such as CAT and SOD to protect against ROSs (Bhargava et al., 2014). Likewise, impairing SOD activity also leads to a decrease of persisters (Bink et al., 2011). Based on above description, it is obvious that bacterial oxidative stress responses are closely related to bacterial persistence. Although there is no much direct evidence that light and mineral stimuli can induce the emergence of persisters, many studies have reported that different light irradiation (Caldeira de Araujo & Favre, 1986; Chen et al., 2019; Dantur & Pizarro, 2004) and some mineral nano-particles (Li et al., 2020; Williams et al., 2011) could trigger various bacterial stress responses especially SOS stress and oxidative stress, which might play an important role in emergence of persisters. The results lead to speculation that ARB could convert into persisters so as to avoid the external damage when they are under the exposure of light and mineral stimulations. However, the research in this area is still relatively lacking. That is, how environmental geochemistry factors affect the formation of bacterial persisters, which is an important pathway for ARB to persist.

Interestingly, some bacteria will grow colonies of unusually small diameters on agar plates after being stressed. These small colonies are called SCVs (small colony variants), the colony diameter of which is usually only about one-tenth that of wild-type colonies. Due to small diameter, without pigment and non-hemolytic colonies, it is difficult to observe at the early stage of growth on agar plates (Proctor et al., 2006). The SCVs were originally discovered in 1910 by Jacobsen who observed that *Salmonella enterica* serovar Typhi (*S. typhi*) grew small colonies on the agar plate (Jacobsen, 1910). Due to the similar characteristics to the bacterial persisters, the SCVs were even classified as a subpopulation of persisters by some studies (Vulin et al., 2018). However, the SCVs are differ from the conventionally defined persisters. That is, SCVs can last longer for their phenotype when stressors were removed (Kahl et al., 2016; Sakatos et al., 2018). In addition, after the environmental stimulus is removed, the persisters can basically quickly restore to wild-type phenotype by given an appropriate nutritional environment (Balaban et al., 2019), while the SCVs were difficult to restore in a short period of time despite in the eutrophic environment. Some studies even believe that the phenotype of SCVs has genetic or semi-stable characteristics (Sakatos et al., 2018). The formation rate of these unstable SCVs is usually low in community, however, they can be induce to increase the formation of these SCVs after exposure to the host cells or external stimulus such as low-pH (Leimer et al., 2016; Wong Fok Lung et al., 2020). Besides *S. aureus* and *S. typhi*, some Gram-positive bacteria such as *Streptococcus tigurinus* (*S. tigurinus*), *Listeria monocytogenes* (*L. monocytogenes*), *Streptococcus pneumoniae* (*S. pneumoniae*) and Gram-negative bacteria such as *Burkholderia cepacian* (*B. cepacian*), *E. coli* and *Pseudomonas aeruginosa* (*P. aeruginosa*) can be induced to form SCVs (Al Ahmar et al., 2019; Nandy et al., 2020; Ochiai et al., 2017; Tikhomirova et al., 2018; Zbinden et al., 2014). Notable phenotypic characteristics of *S. aureus* SCVs include low growth rate, reduction or loss of hemolytic enzymes and coagulases, reduced sensitivity to aminoglycoside antibiotics, and nutritional requirements for heme, menadione, thiamin, or carbon dioxide. When these nutrients are added into the medium, they usually restore to wild-type phenotype (Chen et al., 2018). In addition, the activation of SOS response can also increase the frequency of SCVs formation (Vestergaard et al., 2015). It is reported that *E. coli*, *Salmonella enterica* serovar Enteritidis (*S. enteritidis*) and *P. aeruginosa* can form SCVs when exposed to UVA irradiation (Robertson et al., 2005). There seem to be no reports on the induction of SCVs by natural minerals, but some reports indicate that certain metal ions like Ru^{3+}, Ca^{2+}, Cu^{2+}, Ni^{2+}, Ag^{+}, Pb^{2+}, and SeO_3^{2-} can improve formation of SCVs (Harrison et al., 2008).

Furthermore, after being subjected to excessive stress, bacteria can easily enter a state that called VBNCs (Chen et al., 2018). These VBNCs cannot grow and proliferate under common laboratory conditions, but can survive and grow under some certain conditions (Dworkin & Shah, 2010). To date, more than 100 bacterial species have been found to be able to enter VBNCs state (Ayrapetyan et al., 2018). Once the bacteria enter VBNCs state, they can exhibit stronger resistance to stressors including antibiotics, hot shock, acid, heavy metals, starvation and even ethanol (Nowakowska & Oliver, 2013; Schrammel et al., 2018). Further, after bacteria entering VBNCs state, their defense capacity dramatically improves when face to conventional disinfection processes. It has been reported that UVC disinfection can effectively induce *E. coli*, *P. aeruginosa* and *S. aureus* enter VBNCs state (Guo et al., 2019; Zhang et al., 2015), indicating that UVC has potential ability to enhance persistence of ARB. Besides, visible light and simulated sunlight could also induce the formation of VBNCs (Idil et al., 2010; Muela et al., 2000). According to some studies, long-term interaction between bacteria and deposited minerals in water system can also trigger bacteria to enter VBNCs state (Hassard et al., 2016). Besides the single stimulation of light and mineral, LSM interface could also induce bacteria enter VBNCs state. For example, *P. aeruginosa* could be induced to enter VBNCs state by the photocatalysis of TiO_2 (Degussa P-25) with UVA (Ben Said et al., 2020).

Biofilm is microbial communities encased in a self-produced extracellular matrix. Usually, biofilm could provide protection from environmental insults and benefit of bacterial genetic exchange (Fux et al., 2005). In nature, biofilm could be found in various environments. Surviving with biofilm usually cause depletion of nutrients, oxygen, and some other resources so that it is still uncertainty whether bacteria form biofilm by sense stressors or being in biofilm trigger stress responses. However, it has been reported that some factors like iron limitation, hot shock, ethanol and salt could trigger the up-regulating of *icaADBC* operon which is response for robust biofilm formation (Mihara et al., 2005; O'Gara, 2007). The global stress responses are also important for biofilm formation in *S. epidermidis* (Mack et al., 2004). Besides, the nutrient limitation could also result in the formation of biofilm (Jiang et al., 2000). Some study further reported that, under the oxidative stress posed by LSM interface, bacteria start to growth as a form of biofilm (Yin et al., 2020). In addition, oxidative stress response has great relationship with the formation of biofilm in the interface of metal materials (Wang et al., 2020). Based on the above description, it is easy to infer that the stimulation from geochemistry processes may trigger bacterial stress responses to promote the formation of biofilms and thus enhance the persistence of ARB. However, more evidences should be support to put forward in this area that related to the behavior of ARB when they interact with environmental geochemistry factors, which is critical to understand the environmental fate of ARB and ARGs.

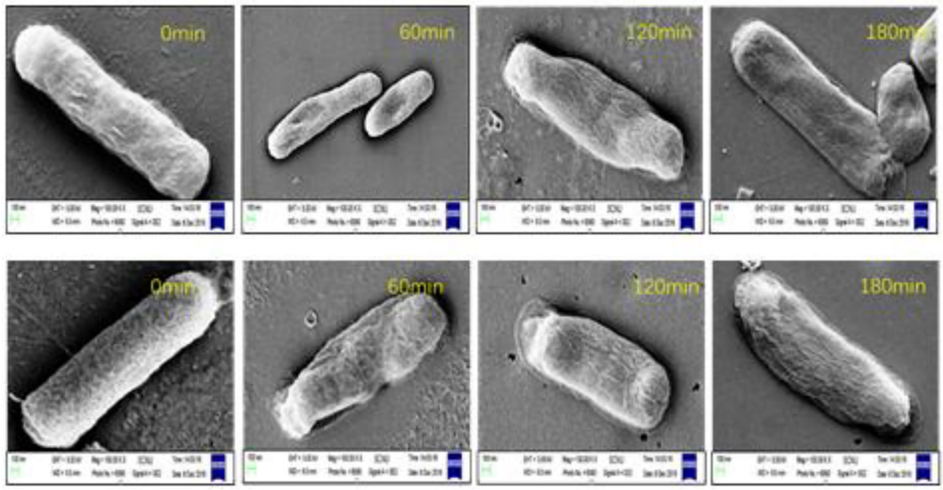

Figure 3. Bacterial inactivation process under the exposure of UV irradiation (Chen et al., 2019).

3.2. Bacteria transformation without stress responses

Different from above description that bacteria could convert into the state of stress response, some bacterial individuals were inactivated quickly in short time without induction period that did not make any response to help themselves survival. However, the inactivation of bacteria usually happened in intracellular, where their metabolism and function as well as the activities of some enzymes were blocked. That means some individuals will lose their ability of growth while with their structural integrity, which support a protective cover for ARGs even the ARB activity being eliminated. For example, the scanning electron microscopy images (Figure 3) of some inactivated ARB caused by UV irradiation and photocatalytic oxidation still maintain integrity cell structure (Chen et al., 2019; Huang et al., 2015; Jiang et al., 2017). Besides, the inactivated bacteria could further be adsorbed by natural mineral, where the genetic materials could be migrated or reserved (Cai et al., 2007; Overballe-Petersen et al., 2013; Pietramellara et al., 2009; Sand & Jelavic, 2018; Takeuchi et al., 2014; Yu et al., 2013). These results indicated that the elimination of ARB is not equal to resolve the AR problem, where ARGs could still exist and even transfer to other living bacteria so as to transfer AR. In this case, even there exist some environmental self-cleaning process, the ARB and ARGs still have strong ability to persist in the form of non-life. It could be inferred that the problem of non-life form AR is an important part of the problem for the resistance in the environment. However, the detailed researches related to proportion and duration of this form of resistance is still limited.

Based on the different mechanisms, some other inactivated individuals will lose both of their vitality and structure due to the peroxidation occurred in bacterial intracellular and cell membrane, which could cause the leakage of intracellular substances including ARGs and protein (Bose & Chatterjee, 1995; Pattison & Davies, 2006). It has been largely reported that high dose of UV irradiation and photocatalytic oxidative pressure could cause extreme damage to bacteria including their cell structure. On the one hand, some stimulation blocks the synthesis of cell membrane so that lead to the collapse of cellular structure. On the other hand, with long-term attack of ROSs generated at interface of LSM, the components of cell membrane were oxidized and degraded (Li et al., 2011; 2013; Ng et al., 2015; Nie et al., 2014; Sun et al., 2014; 2017; van Grieken et al., 2010). Obviously, the damage described here is stronger than that mentioned above, where bacteria inactivated but with integrity cell structure. However, after disrupted, the disassociated ARGs could be further attached to some other substances or interface such as clay mineral and cell debris (Shi et al., 2014), which might protect them from further degradation by ROSs so as to contribute longer persistence of ARGs (Chen et al., 2016; Takahashi et al., 1991). It has been reported that the ARG could be adsorbed by cell debris even after destroy of bacterial structure (Pietramellara et al., 2009). Besides, the EPS existed in extracellular also provide a savings pool for leaky ARG (Omoike & Chorover, 2006).

Usually, DNA released into the water or soil is subjected to the degradation by dynamic biological, chemical, and physical factors which decrease the preservation of free DNA (Levy-Booth et al., 2007). However, ARGs could also be reserved through type of the complexes of bacteria and mineral, and support a protection against to some degradation components such as DNase I (Demaneche et al., 2001; Takahashi et al., 1991). Besides, in the real environmental system, the disassociated and associated ARGs as well as bacteria are co-existed, indicating that there have three forms of complexes, that is ARGs-mineral (Chen et al., 2016; Takahashi et al., 1991), ARB-mineral (Chen et al., 2016), and ARGs-ARB-mineral (Chen et al., 2016). EPS as an important deposit of disassociated ARGs could also be adsorbed by clay mineral and iron oxide (Cao et al., 2011; Omoike & Chorover, 2006). It means that the disassociated extracellular ARGs in EPS could also be adsorbed. As above mentioned, except the antibacterial effects of mineral, the main interactions between bacteria and mineral is related to adsorption processes. Firstly, the adsorption of ARGs onto mineral could prevent the degradation of ARGs by various components (Sand & Jelavic, 2018), which supply a reservoir for both associated and disassociated ARGs. Free DNA is found in the majority of Earth's surface ecosystems such as aqueous environments, soils and sediments (Dell'Anno & Danovaro, 2005; Levy-Booth et al., 2007), up to 95% of this DNA is estimated to be in association with minerals (Gogarten et al., 2002) and the prolonged longevity provided by this association significantly contributes to ARG persistence in environmental system. Besides, it was found that DNA adsorbed onto a sediment was much more resistant to enzymatic digestion than aqueous DNA (Lorenz et al., 1981). Compared to the degradation of disassociated DNA, DNA adsorbed onto minerals was exhibited 10 times more resistant (Khanna & Stotzky, 1992) and DNA adsorbed onto sand grains needed 100 times more for DNase to be degraded (Takahashi et al., 1991). Additionally, about 14–550 thousand years old DNA retrieved from sediments confirms that the minerals could protect adsorbed DNA in a natural setting and preserve it at geologically relevant time scales (Haile et al., 2007; Slon et al., 2017). Based on the above mentioned, the reserve function of mineral through the adsorption processes is also an important mechanism for the persistence of ARGs in natural environments.

Except for physical adsorption, the HGT of ARG can happen though the transformation mechanism, where the minerals adsorbed DNA are incorporated in the genome of a recipient microorganism (Pietramellara et al., 2009; Yu et al., 2013). Besides, the facilitation of HGT by mineral was also be proposed through dynamic process of seawater transgression and regression, weathering rates as well as acting local sedimentation, which accelerate transport of DNA-mineral association across space and time (Sand & Jelavic, 2018). Herein, the mineral facilitating the HGT, which include the mechanism of conjugation transfer, might also contribute the persistence of ARGs. Based on the above description, it could be inferred that even the bacteria were destroyed, the disassociated ARGs could also contribute to problem of AR persistence.

Based on above description, prolonging the process of stimulation could further degrade disassociated ARGs and even mineralize the components of ARB. The whole process of bacterial mineralization is show in the Figure 4. This is the only one case where AR is completely eliminated. Based on some techniques, the mineralization can be achieved. The processes of mineralization begin with the oxidative destruction of cell walls, which is the first protective layer of bacteria (Sun et al., 2014; 2016; 2017). The bacterial cell wall consists of phospholipid bilayer, which can consume the exogenous ROSs firstly when bacterial exposure to ROSs. With the oxidative damage of the cell membrane, the integrity of the cell membrane decrease and the permeability begins to increase, leading to the leakage of intracellular components (Sun et al., 2014). Without protection of cell wall, the leaking protein and some small biological compounds could be further rapidly degraded and finally complete mineralization (Li et al., 2015; 2015; 2011). As a part of nucleic acid, ARGs could also be degraded and completely oxidized in the process of reaction. It has been reported that after bacteria being inactivated, 6-h prolonged photocatalysis could further degrade

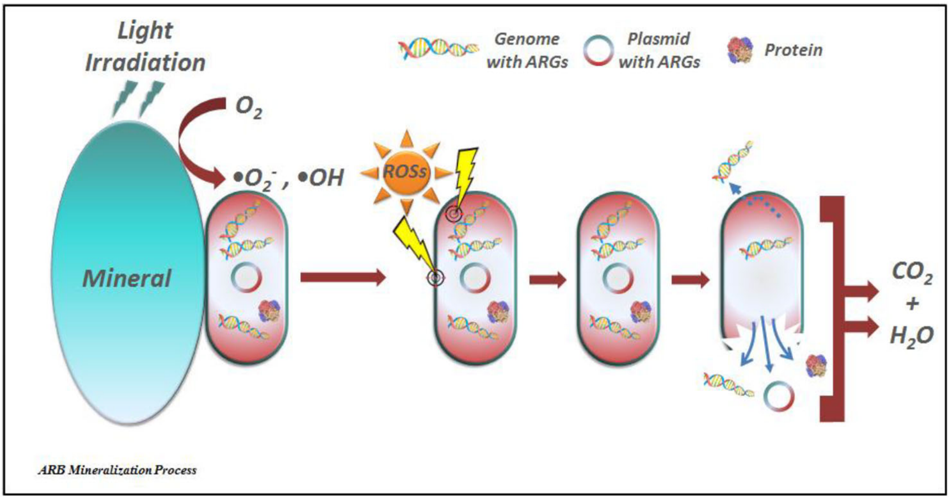

Figure 4. The whole process of ARB mineralization under LSM stimulation.

blaTEM-1 and *aac(3)-II* genes (Jiang et al., 2017). However, it is not certain that ARB and ARGs can receive such a strong and long-term stimulus in the real environment. Presumably, in short term, the bacteria will not be mineralized. Comparatively, Bacteria are more likely to fall into one of the above states rather than complete mineralization, indicating that ARB and ARG have great potential to persist in water environments when they are involved in geochemistry process. These results also provide us with the ideas about bacterial inactivation research, where totally mineral are effective to control the AR problem.

4. Conclusion and perspective

In this review, the interactions between bacteria and above three environmental stimulations were elaborated. Several different geochemistry transformations of ARB/ARGs as well as their persistence pathways are summarized in detailed. We can conclude that bacteria experience many complex and various stimulations in the natural environments, which not only affect bacterial stress responses but also their transformation. Furthermore, along with the interaction with the various environmental matrixes, the environmental fate of ARB and ARGs become complicated and persistence. As a matter of fact, these three effects on ARB and ARGs could interplay and it is extremely complex when take all these above process into consideration. We believe that, in real environmental system, the interaction should be much more complicated than what we described here. Besides, there are some key questions that still need more research to clarify: (1) How environmental factors affect stress responses of ARB, behavior as well as their fate; (2) how environmental geochemistry factors affect the formation of bacterial phenotypic variants of persisters; (3) what type of ARGs or plasmids that work as enhancement gene for bacteria and what kind mechanisms are really accounted for these phenomenon. Clarifying these issues is still very critical to understand the problem of AR persistence in environments.

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References

Ajon, M., Frols, S., van Wolferen, M., Stoecker, K., Teichmann, D., Driessen, A. J., Grogan, D. W., Albers, S. V., & Schleper, C. (2011). UV-inducible DNA exchange in hyperthermophilic archaea mediated by type IV pili. *Molecular Microbiology*, *82*(4), 807–817. https://doi.org/10.1111/j.1365-2958.2011.07861.x

Al Ahmar, R., Kirby, B. D., & Yu, H. D. (2019). Pyrimidine biosynthesis regulates the small-colony variant and mucoidy in *Pseudomonas aeruginosa* through sigma factor competition. *Journal of Bacteriology*, *201*(1), e00575-18. https://doi.org/10.1128/JB.00575-18

Amarasiri, M., Sano, D., & Suzuki, S. (2020). Understanding human health risks caused by antibiotic resistant bacteria (ARB) and antibiotic resistance genes (ARG) in water environments: Current knowledge and questions to be answered. *Critical Reviews in Environmental Science and Technology*, *50*(19), 2016–2059. https://doi.org/10.1080/10643389.2019.1692611

Andersson, D. I., & Hughes, D. (2011). Persistence of antibiotic resistance in bacterial populations. *FEMS Microbiology Reviews*, *35*(5), 901–911. https://doi.org/10.1111/j.1574-6976.2011.00289.x

Auerbach, E. A., Seyfried, E. E., & McMahon, K. D. (2007). Tetracycline resistance genes in activated sludge wastewater treatment plants. *Water Research*, *41*(5), 1143–1151. https://doi.org/10.1016/j.watres.2006.11.045

Ayrapetyan, M., Williams, T., & Oliver, J. D. (2018). Relationship between the viable but nonculturable state and antibiotic persister cells. *Journal of Bacteriology*, *200*(20), e00249-18. https://doi.org/10.1128/JB.00249-18

Balaban, N. Q., Helaine, S., Lewis, K., Ackermann, M., Aldridge, B., Andersson, D. I., Brynildsen, M. P., Bumann, D., Camilli, A., Collins, J. J., Dehio, C., Fortune, S., Ghigo, J. M., Hardt, W. D., Harms, A., Heinemann, M., Hung, D. T., Jenal, U., Levin, B. R., … Zinkernagel, A. (2019). Definitions and guidelines for research on antibiotic persistence. *Nature eviews. Microbiology*, *17*(7), 441–448. https://doi.org/10.1038/s41579-019-0196-3

Baliga, N. S., Bjork, S. J., Bonneau, R., Pan, M., Iloanusi, C., Kottemann, M. C., Hood, L., & DiRuggiero, J. (2004). Systems level insights into the stress response to UV radiation in the halophilic archaeon Halobacterium NRC-1. *Genome Research*, *14*(6), 1025–1035. https://doi.org/10.1101/gr.1993504

Ben Said, M., Ben Saad, M., Achouri, F., Bousselmi, L., & Ghrabi, A. (2020). The application of phage reactivation capacity to sens bacterial viability and activity after photocatalytic treatment. *Environmental Technology*. https://doi.org/10.1080/09593330.2020.1716078

Bhargava, N., Sharma, P., & Capalash, N. (2014). Pyocyanin stimulates quorum sensing-mediated tolerance to oxidative stress and increases persister cell populations in *Acinetobacter baumannii*. *Infection and Immunity*, *82*(8), 3417–3425. https://doi.org/10.1128/IAI.01600-14

Bigger, J. W. (1944). Staphylococcal infections with penicillin by intermittent sterilisation. *The Lancet*, *244*(6320), 497–500. https://doi.org/10.1016/S0140-6736(00)74210-3

Bink, A., Vandenbosch, D., Coenye, T., Nelis, H., Cammue, B. P., & Thevissen, K. (2011). Superoxide dismutases are involved in *Candida albicans* biofilm persistence against miconazole. *Antimicrobial Agents and Chemotherapy*, *55*(9), 4033–4037. https://doi.org/10.1128/AAC.00280-11

Bose, B., & Chatterjee, S. (1995). Correlation between UVA-induced changes in microviscosity, permeability and malondialdehyde formation in liposomal membrane. *Journal of Photochemistry and Photobiology B: Biology*, *28*(2), 149–153. https://doi.org/10.1016/1011-1344(94)07102-T

Cai, P., Huang, Q., Lu, Y., Chen, W., Jiang, D., & Liang, W. (2007). Amplification of plasmid DNA bound on soil colloidal particles and clay minerals by the polymerase chain reaction. *Journal of Environmental Sciences*, *19*(11), 1326–1329. https://doi.org/10.1016/S1001-0742(07)60216-2

Cai, P., Zhu, J., Huang, Q. Y., Fang, L. C., Liang, W., & Chen, W. L. (2009). Role of bacteria in the adsorption and binding of DNA on soil colloids and minerals. *Colloids and Surfaces. B, Biointerfaces*, *69*(1), 26–30. https://doi.org/10.1016/j.colsurfb.2008.10.008

Caldeira de Araujo, A., & Favre, A. (1986). Near ultraviolet DNA damage induces the SOS responses in *Escherichia coli*. *The EMBO Journal*, *5*(1), 175–179. https://doi.org/10.1002/j.1460-2075.1986.tb04193.x

Cao, Y. Y., Wei, X., Cai, P., Huang, Q. Y., Rong, X. M., & Liang, W. (2011). Preferential adsorption of extracellular polymeric substances from bacteria on clay minerals and iron oxide. *Colloids and Surfaces. B, Biointerfaces*, *83*(1), 122–127. https://doi.org/10.1016/j.colsurfb.2010.11.018

Carriazo, J. G., Moreno-Forero, M., Molina, R. A., & Moreno, S. (2010). Incorporation of titanium and titanium–iron species inside a smectite-type mineral for photocatalysis. *Applied Clay Science*, *50*(3), 401–408. https://doi.org/10.1016/j.clay.2010.09.007

Chamberlain, J., & Moss, S. H. (1987). Lipid peroxidation and other membrane damage produced in *Escherichia coli* K1060 by near-uv radiation and deuterium oxide. *Photochemistry and Photobiology*, *45*(5), 625–630. https://doi.org/10.1111/j.1751-1097.1987.tb07389.x

Chee-Sanford, J. C., Aminov, R. I., Krapac, I. J., Garrigues-Jeanjean, N., & Mackie, R. I. (2001). Occurrence and diversity of tetracycline resistance genes in lagoons and groundwater underlying two swine production facilities. *Applied and Environmental Microbiology*, *67*(4), 1494–1502. https://doi.org/10.1128/AEM.67.4.1494-1502.2001

Chen, H., Wang, Q., Yin, Y., Li, S., Niu, D. K., & Wang, H. (2018). Genotypic variations between wild-type and small colony variant of *Staphylococcus aureus* in prosthetic valve infectious endocarditis: a comparative genomic and transcriptomic analysis. *International*

Journal of Antimicrobial Agents, *51*(4), 655–658. https://doi.org/10.1016/j.ijantimicag.2017.12.006

Chen, S., Li, X., Wang, Y. H., Zeng, J., Ye, C. S., Li, X. P., Guo, L. Z., Zhang, S. H., & Yu, X. (2018). Induction of *Escherichia coli* into a VBNC state through chlorination/chloramination and differences in characteristics of the bacterium between states. *Water Research*, *142*, 279–288. https://doi.org/10.1016/j.watres.2018.05.055

Chen, X., Huang, Q., & Chen, W. (2016). Adsorption of DNA by bacteria and their composites with minerals. *Geomicrobiology Journal*, *33*(9), 822–831. https://doi.org/10.1080/01490451.2015.1117545

Chen, X., Yin, H. L., Li, G., Wang, W., Wong, P. K., Zhao, H. J., & An, T. (2019). Antibiotic-resistance gene transfer in antibiotic-resistance bacteria under different light irradiation: Implications from oxidative stress and gene expression. *Water Research*, *149*, 282–291. https://doi.org/10.1016/j.watres.2018.11.019

Chen, Y., Lu, A., Li, Y., Zhang, L., Yip, H., Zhao, H., An, T., & Wong, P. (2011). Naturally occurring sphalerite as a novel cost-effective photocatalyst for bacterial disinfection under visible light. *Environmental Science & Technology*, *45*(13), 5689–5695. https://doi.org/10.1021/es200778p

Chen, Y., Ng, T., Lu, A., Li, Y., Yip, H., An, T., Li, G., Zhao, H., Gao, M., & Wong, P. (2013). Comparative study of visible-light-driven photocatalytic inactivation of two different wastewater bacteria by natural sphalerite. *Chemical Engineering Journal*, *234*, 43–48. https://doi.org/10.1016/j.cej.2013.08.106

Cho, M., Chung, H. M., Choi, W. Y., & Yoon, J. Y. (2004). Linear correlation between inactivation of *E. coli* and OH radical concentration in TiO_2 photocatalytic disinfection. *Water Research*, *38*(4), 1069–1077. https://doi.org/10.1016/j.watres.2003.10.029

Cho, M., Chung, H. M., Choi, W. Y., & Yoon, J. Y. (2005). Different inactivation behaviors of MS-2 phage and *Escherichia coli* in TiO_2 photocatalytic disinfection. *Applied and Environmental Microbiology*, *71*(1), 270–275. https://doi.org/10.1128/AEM.71.1.270-275.2005

Dantur, K. I., & Pizarro, R. A. (2004). Effect of growth phase on the Escherichia coli response to ultraviolet-A radiation: influence of conditioned media, hydrogen peroxide and acetate. *Journal of Photochemistry and Photobiology. B, Biology*, *75*(1-2), 33–39. https://doi.org/10.1016/j.jphotobiol.2004.04.006

De Groote, V. N., Verstraeten, N., Fauvart, M., Kint, C. I., Verbeeck, A. M., Beullens, S., Cornelis, P., & Michiels, J. (2009). Novel persistence genes in *Pseudomonas aeruginosa* identified by high-throughput screening. *FEMS Microbiology Letters*, *297*(1), 73–79. https://doi.org/10.1111/j.1574-6968.2009.01657.x

Debbia, E. A., Roveta, S., Schito, A. M., Gualco, L., & Marchese, A. (2001). Antibiotic persistence: the role of spontaneous DNA repair response. *Microbial Drug Resistance (Larchmont, N.Y.)*, *7*(4), 335–342. https://doi.org/10.1089/10766290152773347

Dell'Anno, A., & Danovaro, R. (2005). Extracellular DNA plays a key role in deep-sea ecosystem functioning. *Science (New York, N.Y.).)*, *309*(5744), 2179. https://doi.org/10.1126/science.1117475

Demaneche, S., Jocteur-Monrozier, L., Quiquampoix, H., & Simonet, P. (2001). Evaluation of biological and physical protection against nuclease degradation of clay-bound plasmid DNA. *Applied and Environmental Microbiology*, *67*(1), 293–299. https://doi.org/10.1128/AEM.67.1.293-299.2001

Dong, P. Y., Cui, Q. J., Fang, T. T., Huang, Y., & Wang, H. (2019). Occurrence of antibiotic resistance genes and bacterial pathogens in water and sediment in urban recreational water. *Journal of Environmental Sciences*, *77*, 65–74. https://doi.org/10.1016/j.jes.2018.06.011

Dorr, T., Lewis, K., & Vulic, M. (2009). SOS response induces persistence to fluoroquinolones in *Escherichia coli*. *PLoS Genetics*, *5*(12), e1000760. https://doi.org/10.1371/journal.pgen.1000760

Dunlop, P. S. M., Ciavola, M., Rizzo, L., McDowell, D. A., & Byrne, J. A. (2015). Effect of photocatalysis on the transfer of antibiotic resistance genes in urban wastewater. *Catalysis Today*, *240*, 55–60. https://doi.org/10.1016/j.cattod.2014.03.049

Durao, P., Balbontin, R., & Gordo, I. (2018). Evolutionary mechanisms shaping the maintenance of antibiotic resistance. *Trends in Microbiology*, *26*(8), 677–691. https://doi.org/10.1016/j.tim.2018.01.005

Dworkin, J., & Shah, I. M. (2010). Exit from dormancy in microbial organisms. *Nature Reviews. Microbiology*, *8*(12), 890–896. https://doi.org/10.1038/nrmicro2453

Echeverria-Palencia, C. M., Thulsiraj, V., Tran, N., Ericksen, C. A., Melendez, I., Sanchez, M. G., Walpert, D., Yuan, T., Ficara, E., Senthilkumar, N., Sun, F., Li, R., Hernandez-Cira, M., Gamboa, D., Haro, H., Paulson, S. E., Zhu, Y., & Jay, J. A. (2017). Disparate antibiotic resistance gene quantities revealed across 4 major cities in California: A survey in drinking water, air, and soil at 24 public parks. *ACS Omega*, *2*(5), 2255–2263. https://doi.org/10.1021/acsomega.7b00118

Eckert, E. M., Di Cesare, A., Coci, M., & Corno, G. (2018). Persistence of antibiotic resistance genes in large subalpine lakes: the role of anthropogenic pollution and ecological interactions. *Hydrobiologia*, *824*(1), 93–108. https://doi.org/10.1007/s10750-017-3480-0

Enne, V. I., Delsol, A. A., Davis, G. R., Hayward, S. L., Roe, J. M., & Bennett, P. M. (2005). Assessment of the fitness impacts on Escherichia coli of acquisition of antibiotic resistance genes encoded by different types of genetic element. *The Journal of Antimicrobial Chemotherapy*, *56*(3), 544–551. https://doi.org/10.1093/jac/dki255

Enne, V. I., Livermore, D. M., Stephens, P., & Hall, L. M. C. (2001). Persistence of sulphonamide resistance in *Escherichia coli* in the UK despite national prescribing restriction. *The Lancet*, *357*(9265), 1325–1328. https://doi.org/10.1016/S0140-6736(00)04519-0

Ferris, F. G., Fyfe, W. S., & Beveridge, T. J. (1987). Bacteria as nucleation sites for authigenic minerals in a metal-contaminated lake sediment. *Chemical Geology*, *63*(3-4), 225–232. https://doi.org/10.1016/0009-2541(87)90165-3

Frols, S., Gordon, P. M., Panlilio, M. A., Duggin, I. G., Bell, S. D., Sensen, C. W., & Schleper, C. (2007). Response of the hyperthermophilic archaeon *Sulfolobus solfataricus* to UV damage. *Journal of Bacteriology*, *189*(23), 8708–8718. https://doi.org/10.1128/JB.01016-07

Fux, C. A., Costerton, J. W., Stewart, P. S., & Stoodley, P. (2005). Survival strategies of infectious biofilms. *Trends in Microbiology*, *13*(1), 34–40. https://doi.org/10.1016/j.tim.2004.11.010

Gao, M., Jia, R. Z., Qiu, T. L., Han, M. L., & Wang, X. M. (2017). Size-related bacterial diversity and tetracycline resistance gene abundance in the air of concentrated poultry feeding operations. *Environmental Pollution (Barking, Essex: 1987)*, *220*(Pt B), 1342–1348. https://doi.org/10.1016/j.envpol.2016.10.101

Gogarten, J. P., Doolittle, W. F., & Lawrence, J. G. (2002). Prokaryotic evolution in light of gene transfer. *Molecular Biology and Evolution*, *19*(12), 2226–2238. https://doi.org/10.1093/oxfordjournals.molbev.a004046

Gogniat, G., & Dukan, S. (2007). TiO_2 photocatalysis causes DNA damage via fenton reaction-generated hydroxyl radicals during the recovery period. *Applied and Environmental Microbiology*, *73*(23), 7740–7743. https://doi.org/10.1128/AEM.01079-07

Goneau, L. W., Yeoh, N. S., MacDonald, K. W., Cadieux, P. A., Burton, J. P., Razvi, H., & Reid, G. (2014). Selective target inactivation rather than global metabolic dormancy causes antibiotic tolerance in uropathogens. *Antimicrobial Agents and Chemotherapy*, *58*(4), 2089–2097. https://doi.org/10.1128/AAC.02552-13

Guo, C., Wang, K., Hou, S., Wan, L., Lv, J., Zhang, Y., Qu, X., Chen, S., & Xu, J. (2017). H2O2 and/or TiO_2 photocatalysis under UV irradiation for the removal of antibiotic resistant bacteria and their antibiotic resistance genes. *Journal of Hazardous Materials*, *323*(Pt B), 710–718. https://doi.org/10.1016/j.jhazmat.2016.10.041

Guo, L., Ye, C., Cui, L., Wan, K., Chen, S., Zhang, S., & Yu, X. (2019). Population and single cell metabolic activity of UV-induced VBNC bacteria determined by CTC-FCM and D_2O-labeled Raman spectroscopy. *Environment International*, *130*, 104883. https://doi.org/10.1016/j.envint.2019.05.077

Gustavson, K. (2000). Influence of UV-B radiation on bacterial activity in coastal waters. *Journal of Plankton Research*, *22*(8), 1501–1511. https://doi.org/10.1093/plankt/22.8.1501

Haile, J., Holdaway, R., Oliver, K., Bunce, M., Gilbert, M. T., Nielsen, R., Munch, K., Ho, S. Y., Shapiro, B., & Willerslev, E. (2007). Ancient DNA chronology within sediment deposits: are paleobiological reconstructions possible and is DNA leaching a factor? *Molecular Biology and Evolution*, *24*(4), 982–989. https://doi.org/10.1093/molbev/msm016

Hajdúch, M., Kolár, Z., Novotný, R., Hanus, J., Mihál, V., Hlobílková, A., Nosková, V., & Strnad, M. (1997). Induction of apoptosis and regression of spontaneous dog melanoma following in vivo application of synthetic cyclin-dependent kinase inhibitor olomoucine. *Anti-Cancer Drugs*, *8*(10), 1007–1013. https://doi.org/10.1097/00001813-199711000-00012

Hall, B. G. (2004). Predicting the evolution of antibiotic resistance genes. *Nature Reviews. Microbiology*, *2*(5), 430–435. https://doi.org/10.1038/nrmicro888

Hansen, S., Lewis, K., & Vulic, M. (2008). Role of global regulators and nucleotide metabolism in antibiotic tolerance in *Escherichia coli*. *Antimicrobial Agents and Chemotherapy*, *52*(8), 2718–2726. https://doi.org/10.1128/AAC.00144-08

Harris, M. C., Speck, W. T., Campos, J. M., & Polin, R. A. (1981). Induction of gentamicin resistance by visible light. *Pediatric Research*, *15*(6), 952–955. https://doi.org/10.1203/00006450-198106000-00014

Harrison, J. J., Turner, R. J., Joo, D. A., Stan, M. A., Chan, C. S., Allan, N. D., Vrionis, H. A., Olson, M. E., & Ceri, H. (2008). Copper and quaternary ammonium cations exert synergistic bactericidal and antibiofilm activity against *Pseudomonas aeruginosa*. *Antimicrobial Agents and Chemotherapy*, *52*(8), 2870–2881. https://doi.org/10.1128/AAC.00203-08

Hassard, F., Gwyther, C. L., Farkas, K., Andrews, A., Jones, V., Cox, B., Brett, H., Jones, D. L., McDonald, J. E., & Malham, S. K. (2016). Abundance and distribution of enteric bacteria and viruses in coastal and estuarine sediments-a review. *Frontiers in Microbiology*, *7*, 1692. https://doi.org/10.3389/fmicb.2016.01692

Heinemann, J. A., Ankenbauer, R. G., & Amábile-Cuevas, C. F. (2000). Do antibiotics maintain antibiotic resistance? *Drug Discovery Today*, *5*(5), 195–204. https://doi.org/10.1016/S1359-6446(00)01483-5

Herndl, G. J., Müller-Niklas, G., & Frick, J. (1993). Major role of ultraviolet-B in controlling bacterioplankton growth in the surface layer of the ocean. *Nature*, *361*(6414), 717–719. https://doi.org/10.1038/361717a0

Hershberg, R. (2017). Antibiotic-independent adaptive effects of antibiotic resistance mutations. *Trends in Genetics: TIG*, *33*(8), 521–528. https://doi.org/10.1016/j.tig.2017.05.003

Hobby, G. L., Meyer, K., & Chaffe, E. (1942). Observations on the mechanism of action of penicillin. *Experimental Biology and Medicine*, *50*(2), 281–285. https://doi.org/10.3181/00379727-50-13773

Hockberger, P. E. (2002). A history of ultraviolet photobiology for humans, animals and microorganisms. *Photochemistry and Photobiology*, *76*(6), 561. https://doi.org/10.1562/0031-8655(2002)076 < 0561:Ahoupf > 2.0.Co;2

Hu, J. L., Zhao, F. Z., Zhang, X. X., Li, K., Li, C. R., Ye, L., & Li, M. (2018). Metagenomic profiling of ARGs in airborne particulate matters during a severe smog event. *The Science of the Total Environment*, *615*, 1332–1340. https://doi.org/10.1016/j.scitotenv.2017.09.222

Huang, G., Xia, D., An, T., Ng, T., Yip, H., Li, G., Zhao, H., & Wong, P. (2015). Dual roles of capsular extracellular polymeric substances in photocatalytic inactivation of *Escherichia coli*: Comparison of *E. coli* BW25113 and isogenic mutants. *Applied and Environmental Microbiology*, *81*(15), 5174–5183. https://doi.org/10.1128/AEM.00775-15

Huang, S., Li, L., Vleugels, J., Wang, P., & Van der Biest, O. (2003). Thermodynamic prediction of the nonstoichiometric phase Zr1–zCezO_2–x in the ZrO_2–$CeO_{1.5}$–CeO_2 system. *Journal of the European Ceramic Society*, *23*(1), 99–106. https://doi.org/10.1016/S0955-2219(02)00073-0

Idil, O., Ozkanca, R., Darcan, C., & Flint, K. P. (2010). Escherichia coli: dominance of red light over other visible light sources in establishing viable but nonculturable state. *Photochemistry and Photobiology*, *86*(1), 104–109. https://doi.org/10.1111/j.1751-1097.2009.00636.x

Jacobsen, K. A. (1910). Mitteilungen über einen variablen Typhusstamm (Bacterium typhi mutabile), sowie über eine eigentümliche hemmende Wirkung des gewöhnlichen agar, verursacht durch autoklavierung. *Zentralbl. Bakteriol. [Orig. A]*, *56*, 208–216.

Javid, B., Sorrentino, F., Toosky, M., Zheng, W., Pinkham, J. T., Jain, N., Pan, M., Deighan, P., & Rubin, E. J. (2014). Mycobacterial mistranslation is necessary and sufficient for rifampicin phenotypic resistance. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(3), 1132–1137. https://doi.org/10.1073/pnas.1317580111

Jia, S. Y., Shi, P., Hu, Q., Li, B., Zhang, T., & Zhang, X. X. (2015). Bacterial community shift drives antibiotic resistance promotion during drinking water chlorination. *Environmental Science & Technology*, *49*(20), 12271–12279. https://doi.org/10.1021/acs.est.5b03521

Jiang, M., Shao, W. L., Perego, M., & Hoch, J. A. (2000). Multiple histidine kinases regulate entry into stationary phase and sporulation in *Bacillus subtilis*. *Molecular Microbiology*, *38*(3), 535–542. https://doi.org/10.1046/j.1365-2958.2000.02148.x

Jiang, Q., Yin, H., Li, G., Liu, H., An, T., Wong, P., & Zhao, H. (2017). Elimination of antibiotic-resistance bacterium and its associated/dissociative *blaTEM-1* and *aac(3)-II* antibiotic-resistance genes in aqueous system via photoelectrocatalytic process. *Water Research*, *125*, 219–226. https://doi.org/10.1016/j.watres.2017.08.050

Kahl, B. C., Becker, K., & Löffler, B. (2016). Clinical significance and pathogenesis of *Staphylococcal* small colony variants in persistent infections. *Clinical Microbiology Reviews*, *29*(2), 401–427. https://doi.org/10.1128/CMR.00069-15

Keren, I., Shah, D., Spoering, A., Kaldalu, N., & Lewis, K. (2004). Specialized persister cells and the mechanism of multidrug tolerance in *Escherichia coli*. *Journal of Bacteriology*, *186*(24), 8172–8180. https://doi.org/10.1128/JB.186.24.8172-8180.2004

Khakimova, M., Ahlgren, H. G., Harrison, J. J., English, A. M., & Nguyen, D. (2013). The stringent response controls catalases in *Pseudomonas aeruginosa* and is required for hydrogen peroxide and antibiotic tolerance. *Journal of Bacteriology*, *195*(9), 2011–2020. https://doi.org/10.1128/JB.02061-12

Khanna, M., & Stotzky, G. (1992). Transformation of Bacillus subtilis by DNA bound on montmorillonite and effect of DNase on the transforming ability of bound DNA.

Applied and Environmental Microbiology, *58*(6), 1930–1939. https://www.ncbi.nlm.nih.gov/pubmed/1622268 https://doi.org/10.1128/AEM.58.6.1930-1939.1992

Knapp, C. W., McCluskey, S. M., Singh, B. K., Campbell, C. D., Hudson, G., & Graham, D. W. (2011). Antibiotic resistance gene abundances correlate with metal and geochemical conditions in archived Scottish soils. *PLoS One* , *6*(11), e27300. https://doi.org/10.1371/journal.pone.0027300

Kuczyńska-Wiśnik, D., Stojowska, K., Matuszewska, E., Leszczyńska, D., Algara, M. M., Augustynowicz, M., & Laskowska, E. (2015). Lack of intracellular trehalose affects formation of *Escherichia coli* persister cells. *Microbiology (Reading, England)*, *161*(Pt 4), 786–796. https://doi.org/10.1099/mic.0.000012

Kumar, J., Babele, P. K., Singh, D., & Kumar, A. (2016). UV-B radiation stress causes alterations in whole cell protein profile and expression of certain genes in the rice phyllospheric bacterium *Enterobacter cloacae*. *Frontiers in Microbiology*, *7*, 1440. https://doi.org/10.3389/fmicb.2016.01440

Lachowicz, T. M., Morzejko, E., Panek, E., & Piątkowski, J. (1996). Inhibitory action of serine on growth of bacteria of the genus *Bacillus* on mineral synthetic media. *Folia Microbiologica*, *41*(1), 21–25. https://doi.org/10.1007/BF02816334

Laxminarayan, R., Duse, A., Wattal, C., Zaidi, A. K. M., Wertheim, H. F. L., Sumpradit, N., Vlieghe, E., Hara, G. L., Gould, I. M., Goossens, H., Greko, C., So, A. D., Bigdeli, M., Tomson, G., Woodhouse, W., Ombaka, E., Peralta, A. Q., Qamar, F. N., Mir, F., … Cars, O. (2013). Antibiotic resistance—the need for global solutions. *The Lancet. Infectious Diseases*, *13*(12), 1057–1098. https://doi.org/10.1016/S1473-3099(13)70318-9

Lehtinen, S., Blanquart, F., Croucher, N. J., Turner, P., Lipsitch, M., & Fraser, C. (2017). Evolution of antibiotic resistance is linked to any genetic mechanism affecting bacterial duration of carriage. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(5), 1075–1080. https://doi.org/10.1073/pnas.1617849114

Leimer, N., Rachmuhl, C., Palheiros Marques, M., Bahlmann, A. S., Furrer, A., Eichenseher, F., Seidl, K., Matt, U., Loessner, M. J., Schuepbach, R. A., & Zinkernagel, A. S. (2016). Nonstable *Staphylococcus aureus* small-colony variants are induced by low pH and sensitized to antimicrobial therapy by phagolysosomal alkalinization. *The Journal of Infectious Diseases*, *213*(2), 305–313. https://doi.org/10.1093/infdis/jiv388

Leszczynska, D., Matuszewska, E., Kuczynska-Wisnik, D., Furmanek-Blaszk, B., & Laskowska, E. (2013). The formation of persister cells in stationary-phase cultures of *Escherichia coli* is associated with the aggregation of endogenous proteins. *PLoS One*, *8*(1), e54737. https://doi.org/10.1371/journal.pone.0054737

Leung, V., & Levesque, C. M. (2012). A stress-inducible quorum-sensing peptide mediates the formation of persister cells with noninherited multidrug tolerance. *Journal of Bacteriology*, *194*(9), 2265–2274. https://doi.org/10.1128/JB.06707-11

Levy-Booth, D. J., Campbell, R. G., Gulden, R. H., Hart, M. M., Powell, J. R., Klironomos, J. N., Pauls, K. P., Swanton, C. J., Trevors, J. T., & Dunfield, K. E. (2007). Cycling of extracellular DNA in the soil environment. *Soil Biology and Biochemistry*, *39*(12), 2977–2991. https://doi.org/10.1016/j.soilbio.2007.06.020

Li, G., Chen, X., Yin, H., Wang, W., Wong, P., & An, T. (2020). Natural sphalerite nanoparticles can accelerate horizontal transfer of plasmid-mediated antibiotic-resistance genes. *Environment International*, *136*, 105497. https://doi.org/10.1016/j.envint.2020.105497

Li, G., Liu, X., An, J., Yang, H., Zhang, S., Wong, P., An, T., & Zhao, H. (2015). Photocatalytic and photoelectrocatalytic degradation and mineralization of small biological compounds amino acids at TiO_2 photoanodes. *Catalysis Today*, *245*, 46–53. https://doi.org/10.1016/j.cattod.2014.05.040

Li, G., Liu, X., An, T., Yang, H., Zhang, S., & Zhao, H. (2015). Photocatalytic and photoelectrocatalytic degradation of small biological compounds at TiO_2 photoanode: A case study of nucleotide bases. *Catalysis Today*, *242*, 363–371. https://doi.org/10.1016/j.cattod.2014.04.029

Li, G., Liu, X., Zhang, H., An, T., Zhang, S., Carroll, A. R., & Zhao, H. (2011). In situ photoelectrocatalytic generation of bactericide for instant inactivation and rapid decomposition of Gram-negative bacteria. *Journal of Catalysis*, *277*(1), 88–94. https://doi.org/10.1016/j.jcat.2010.10.011

Li, G., Liu, X., Zhang, H., Wong, P. K., An, T., & Zhao, H. (2013). Comparative studies of photocatalytic and photoelectrocatalytic inactivation of *E. coli* in presence of halides. *Applied Catalysis B: Environmental*, *140-141*, 225–232. https://doi.org/10.1016/j.apcatb.2013.04.004

Li, J., Cao, J. J., Zhu, Y. G., Chen, Q. L., Shen, F. X., Wu, Y., Xu, S. Y., Fan, H. Q., Da, G., Huang, R. J., Wang, J., de Jesus, A. L., Morawska, L., Chan, C. K., Peccia, J., & Yao, M. S. (2018). Global survey of antibiotic resistance genes in air. *Environmental Science & Technology*, *52*(19), 10975–10984. https://doi.org/10.1021/acs.est.8b02204

Li, J., Ji, L., Shi, W., Xie, J., & Zhang, Y. (2013). Trans-translation mediates tolerance to multiple antibiotics and stresses in *Escherichia coli*. *The Journal of ntimicrobial Chemotherapy*, *68*(11), 2477–2481. https://doi.org/10.1093/jac/dkt231

Li, K., Wang, P., Chen, C., Chen, C., Li, L., & Song, T. (2017). Light irradiation helps magnetotactic bacteria eliminate intracellular reactive oxygen species. *Environmental Microbiology*, *19*(9), 3638–3648. https://doi.org/10.1111/1462-2920.13864

Liang, Z., Yu, Y., Ye, Z., Li, G., Wang, W., & An, T. (2020). Pollution profiles of antibiotic resistance genes associated with airborne opportunistic pathogens from typical area, Pearl River Estuary and their exposure risk to human. *Environment International*, *143*, 105934. https://doi.org/10.1016/j.envint.2020.105934

Lin, H., Ye, C., Chen, S., Zhang, S., & Yu, X. (2017). Viable but non-culturable *E. coli* induced by low level chlorination have higher persistence to antibiotics than their culturable counterparts. *Environmental Pollution (Barking, Essex : 1987)*, *230*, 242–249. https://doi.org/10.1016/j.envpol.2017.06.047

Ling, A. L., Pace, N. R., Hernandez, M. T., & LaPara, T. M. (2013). Tetracycline resistance and Class 1 integron genes associated with indoor and outdoor aerosols. *Environmental Science & Technology*, *47*(9), 4046–4052. https://doi.org/10.1021/es400238g

Lopatkin, A. J., Meredith, H. R., Srimani, J. K., Pfeiffer, C., Durrett, R., & You, L. (2017). Persistence and reversal of plasmid-mediated antibiotic resistance. *Nature Communications*, *8*(1), 1689. https://doi.org/10.1038/s41467-017-01532-1

Lorenz, M. G., Aardema, B. W., & Krumbein, W. E. (1981). Interaction of marine sediment with DNA and DNA availability to nucleases. *Marine Biology*, *64*(2), 225–230. https://doi.org/10.1007/BF00397113

Lu, Z. H., Na, G. S., Gao, H., Wang, L. J., Bao, C. G., & Yao, Z. W. (2015). Fate of sulfonamide resistance genes in estuary environment and effect of anthropogenic activities. *The Science of the Total Environment*, *527-528*, 429–438. https://doi.org/10.1016/j.scitotenv.2015.04.101

Mack, D., Becker, P., Chatterjee, I., Dobinsky, S., Knobloch, J. K., Peters, G., Rohde, H., & Herrmann, M. (2004). Mechanisms of biofilm formation in *Staphylococcus epidermidis* and *Staphylococcus aureus*: functional molecules, regulatory circuits, and adaptive responses. *International Journal of Medical Microbiology: IJMM*, *294*(2-3), 203–212. https://doi.org/10.1016/j.ijmm.2004.06.015

Malachová, K., Praus, P., Rybková, Z., & Kozák, O. (2011). Antibacterial and antifungal activities of silver, copper and zinc montmorillonites. *Applied Clay Science*, *53*(4), 642–645. https://doi.org/10.1016/j.clay.2011.05.016

Mao, D. Q., Luo, Y., Mathieu, J., Wang, Q., Feng, L., Mu, Q., Feng, C. Y., & Alvarez, P. J. (2014). Persistence of extracellular DNA in river sediment facilitates antibiotic resistance gene propagation. *Environmental Science & Technology*, *48*(1), 71–78. https://doi.org/10.1021/es404280v

Margaryan, A., Badalyan, H., & Trchounian, A. (2016). Comparative analysis of UV irradiation effects on *Escherichia coli* and *Pseudomonas aeruginosa* bacterial cells utilizing biological and computational approaches. *Cell Biochemistry and Biophysics*, *74*(3), 381–389. https://doi.org/10.1007/s12013-016-0748-3

Martinez, J. L. (2011). Bottlenecks in the transferability of antibiotic resistance from natural ecosystems to human bacterial pathogens. *Frontiers in Microbiology*, *2*, 265. https://doi.org/10.3389/fmicb.2011.00265

Mihara, M., Ishino, Y., Minakata, S., & Komatsu, M. (2005). Novel synthesis of gem-dichloroaziridines from imines via the KF/Al2O3-promoted generation of dichlorocarbene from chloroform . *The Journal of Organic Chemistry*, *70*(13), 5320–5322. https://doi.org/10.1021/jo050321z

Mordukhova, E. A., & Pan, J. G. (2014). Stabilization of homoserine-O-succinyltransferase (MetA) decreases the frequency of persisters in *Escherichia coli* under stressful conditions. *PLoS One*, *9*(10), e110504. https://doi.org/10.1371/journal.pone.0110504

Morrison, K. D., Underwood, J. C., Metge, D. W., Eberl, D. D., & Williams, L. B. (2014). Mineralogical variables that control the antibacterial effectiveness of a natural clay deposit. *Environmental Geochemistry and Health*, *36*(4), 613–631. https://doi.org/10.1007/s10653-013-9585-0

Muela, A., Garcia-Bringas, J. M., Arana, I. I., & Barcina, I. I. (2000). The effect of simulated solar radiation on *Escherichia coli*: The relative roles of UV-B, UV-A, and photosynthetically active radiation. *Microbial Ecology*, *39*(1), 65–71. https://doi.org/10.1007/s002489900181

Murakami, K., Ono, T., Viducic, D., Kayama, S., Mori, M., Hirota, K., Nemoto, K., & Miyake, Y. (2005). Role for *rpoS* gene of *Pseudomonas aeruginosa* in antibiotic tolerance. *FEMS icrobiology Letters*, *242*(1), 161–167. https://doi.org/10.1016/j.femsle.2004.11.005

Nandy, P., Chib, S., Seshasayee, A., & Ellermeier, C. D. (2020). A mutant RNA polymerase activates the general stress response, enabling escherichia coli adaptation to late prolonged stationary phase. *mSphere*, *5*(2), e00092-20. https://doi.org/10.1128/mSphere.00092-20

Ng, T. W., An, T., Li, G., Ho, W. K., Yip, H. Y., Zhao, H., & Wong, P. K. (2015). The role and synergistic effect of the light irradiation and H_2O_2 in photocatalytic inactivation of *Escherichia coli*. *Journal of Photochemistry and Photobiology. B, Biology*, *149*, 164–171. https://doi.org/10.1016/j.jphotobiol.2015.06.007

Nguyen, D., Joshi-Datar, A., Lepine, F., Bauerle, E., Olakanmi, O., Beer, K., McKay, G., Siehnel, R., Schafhauser, J., Wang, Y., Britigan, B. E., & Singh, P. K. (2011). Active starvation responses mediate antibiotic tolerance in biofilms and nutrient-limited bacteria. *Science (New York, N.Y.)*, *334*(6058), 982–986. https://doi.org/10.1126/science.1211037

Nie, X., Li, G., Gao, M., Sun, H., Liu, X., Zhao, H., Wong, P.-K., & An, T. (2014). Comparative study on the photoelectrocatalytic inactivation of *Escherichia coli* K-12 and its mutant *Escherichia coli* BW25113 using TiO_2 nanotubes as a photoanode. *Applied Catalysis B: Environmental*, *147*, 562–570. https://doi.org/10.1016/j.apcatb.2013.09.037

Norman, A., Hansen, L. H., & Sorensen, S. J. (2009). Conjugative plasmids: vessels of the communal gene pool. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1527), 2275–2289. https://doi.org/10.1098/rstb.2009.0037

Nowakowska, J., & Oliver, J. D. (2013). Resistance to environmental stresses by Vibrio vulnificus in the viable but nonculturable state. *FEMS Microbiology Ecology*, *84*(1), 213–222. https://doi.org/10.1111/1574-6941.12052

O'Gara, J. P. (2007). ica and beyond: biofilm mechanisms and regulation in *Staphylococcus epidermidis* and *Staphylococcus aureus*. *FEMS Microbiology Letters*, *270*(2), 179–188. https://doi.org/10.1111/j.1574-6968.2007.00688.x

Ochiai, Y., Yamada, F., Yoshikawa, Y., Mochizuki, M., Takano, T., Hondo, R., & Ueda, F. (2017). Sequential transition of the injury phenotype, temperature-dependent survival and transcriptional response in *Listeria monocytogenes* following lethal H_2O_2 exposure. *International Journal of Food Microbiology*, *259*, 52–58. https://doi.org/10.1016/j.ijfoodmicro.2017.08.001

Omoike, A., & Chorover, J. (2006). Adsorption to goethite of extracellular polymeric substances from *Bacillus subtilis*. *Geochimica et Cosmochimica Acta*, *70*(4), 827–838. https://doi.org/10.1016/j.gca.2005.10.012

Onodera, Y., Sunayama, S., Chatterjee, A., Iwasaki, T., Satoh, T., Suzuki, T., & Mimura, H. (2001). Bactericidal allophanic materials prepared from allophane soil. *Applied Clay Science*, *18*(3-4), 135–144. https://doi.org/10.1016/S0169-1317(00)00039-9

Orman, M. A., & Brynildsen, M. P. (2013). Establishment of a method to rapidly assay bacterial persister metabolism. *Antimicrobial Agents and Chemotherapy*, *57*(9), 4398–4409. https://doi.org/10.1128/AAC.00372-13

Overballe-Petersen, S., Harms, K., Orlando, L. A., Mayar, J. V., Rasmussen, S., Dahl, T. W., Rosing, M. T., Poole, A. M., Sicheritz-Ponten, T., Brunak, S., Inselmann, S., de Vries, J., Wackernagel, W., Pybus, O. G., Nielsen, R., Johnsen, P. J., Nielsen, K. M., & Willerslev, E. (2013). Bacterial natural transformation by highly fragmented and damaged DNA. *Proceedings of the National Academy of Sciences*, *110*(49), 19860–19865. https://doi.org/10.1073/pnas.1315278110

Pakulski, J. D., Baldwin, A., Dean, A. L., Durkin, S., Karentz, D., Kelley, C. A., Scott, K., Spero, H. J., Wilhelm, S. W., Amin, R., & Jeffrey, W. H. (2007). Responses of heterotrophic bacteria to solar irradiance in the eastern Pacific Ocean. *Aquatic Microbial Ecology*, *47*, 153–162. https://doi.org/10.3354/ame047153

Pakulski, J. D., Kase, J. P., Meador, J. A., & Jeffrey, W. H. (2008). Effect of stratospheric ozone depletion and enhanced ultraviolet radiation on marine bacteria at Palmer Station, Antarctica in the early austral spring. *Photochemistry and Photobiology*, *84*(1), 215–221. https://doi.org/10.1111/j.1751-1097.2007.00222.x

Pal, C., Bengtsson-Palme, J., Kristiansson, E., & Larsson, D. G. (2016). The structure and diversity of human, animal and environmental resistomes. *Microbiome*, *4*(1), 54. https://doi.org/10.1186/s40168-016-0199-5

Pang, Y. C., Huang, J. J., Xi, J. Y., Hu, H. Y., & Zhu, Y. (2016). Effect of ultraviolet irradiation and chlorination on ampicillin-resistant *Escherichia coli* and its ampicillin resistance gene. *Frontiers of Environmental Science & Engineering*, *10*(3), 522–530. https://doi.org/10.1007/s11783-015-0779-9

Pattison, D. I., & Davies, M. J. (2006). Actions of ultraviolet light on cellular structures. *Cancer: Cell Structures, Carcinogens and Genomic Instability*, (96), 131–157. https://doi.org/10.1007/3-7643-7378-4_6

Pfeifer, G. P. (1997). Formation and processing of UV photoproducts: effects of DNA sequence and chromatin environment. *Photochemistry and Photobiology*, *65*(2), 270–283. https://doi.org/10.1111/j.1751-1097.1997.tb08560.x

Pietramellara, G., Ascher, J., Borgogni, F., Ceccherini, M. T., Guerri, G., & Nannipieri, P. (2009). Extracellular DNA in soil and sediment: fate and ecological relevance. *Biology and Fertility of Soils*, *45*(3), 219–235. https://doi.org/10.1007/s00374-008-0345-8

Proctor, R. A., von Eiff, C., Kahl, B. C., Becker, K., McNamara, P., Herrmann, M., & Peters, G. (2006). Small colony variants: A pathogenic form of bacteria that facilitates persistent and recurrent infections. *Nature Reviews. Microbiology*, *4*(4), 295–305. https://doi.org/10.1038/nrmicro1384

Proia, L., von Schiller, D., Sanchez-Melsio, A., Sabater, S., Borrego, C. M., Rodriguez-Mozaz, S., & Balcazar, J. L. (2016). Occurrence and persistence of antibiotic resistance genes in river biofilms after wastewater inputs in small rivers. *Environmental Pollution (Barking, Essex : 1987)*, *210*, 121–128. https://doi.org/10.1016/j.envpol.2015.11.035

Pruden, A., & Arabi, M. (2011). *Quantifying anthropogenic impacts on environmental reservoirs of antibiotic resistance (Antimicrobial Resistance in the Environment* (pp. 173–201). John Wiley & Sons, Inc. https://doi.org/10.1002/9781118156247.ch10

Pruden, A., Pei, R., Storteboom, H., & Carlson, K. (2006). Antibiotic resistance genes as emerging contaminants: studies in Northern Colorado. *Environmental Science & Technology*, *40*(23), 7445–7450. https://doi.org/10.1021/es060413l

Pu, Y., Li, Y., Jin, X., Tian, T., Ma, Q., Zhao, Z., Lin, S. Y., Chen, Z., Li, B., Yao, G., Leake, M. C., Lo, C. J., & Bai, F. (2019). ATP-dependent dynamic protein aggregation regulates bacterial dormancy depth critical for antibiotic tolerance. *Molecular Cell*, *73*(1), 143–156 e144. https://doi.org/10.1016/j.molcel.2018.10.022

Pu, Y., Zhao, Z., Li, Y., Zou, J., Ma, Q., Zhao, Y., Ke, Y., Zhu, Y., Chen, H., Baker, M. A., Ge, H., Sun, Y., Xie, X. S., & Bai, F. (2016). Enhanced efflux activity facilitates drug tolerance in dormant bacterial cells. *Molecular Cell*, *62*(2), 284–294. https://doi.org/10.1016/j.molcel.2016.03.035

Ravanat, J. L., Douki, T., & Cadet, J. (2001). Direct and indirect effects of UV radiation on DNA and its components. *Journal of Photochemistry and Photobiology B: Biology*, *63*(1-3), 88–102. https://doi.org/10.1016/S1011-1344(01)00206-8

Robertson, J. M. C., J. Robertson, P. K., & Lawton, L. A. (2005). A comparison of the effectiveness of TiO_2 photocatalysis and UVA photolysis for the destruction of three pathogenic micro-organisms. *Journal of Photochemistry and Photobiology A: Chemistry*, *175*(1), 51–56. https://doi.org/10.1016/j.jphotochem.2005.04.033

Rong, X. M., Huang, Q. Y., & Chen, W. L. (2007). Microcalorimetric investigation on the metabolic activity of *Bacillus thuringiensis* as influenced by kaolinite, montmorillonite and goethite. *Applied Clay Science*, *38*(1-2), 97–103. https://doi.org/10.1016/j.clay.2007.01.015

Ruiz-Gonzalez, C., Simo, R., Sommaruga, R., & Gasol, J. M. (2013). Away from darkness: A review on the effects of solar radiation on heterotrophic bacterioplankton activity. *Frontiers in Microbiology*, *4*, 131. https://doi.org/10.3389/fmicb.2013.00131

Runger, T. M., & Kappes, U. P. (2008). Mechanisms of mutation formation with long-wave ultraviolet light (UVA). *Photodermatology, hotoimmunology & Photomedicine*, *24*(1), 2–10. https://doi.org/10.1111/j.1600-0781.2008.00319.x

Sakatos, A., Babunovic, G. H., Chase, M. R., Dills, A., Leszyk, J., Rosebrock, T., Bryson, B., & Fortune, S. M. (2018). Posttranslational modification of a histone-like protein regulates phenotypic resistance to isoniazid in mycobacteria. *Science Advances*, *4*(5), eaao1478. https://doi.org/10.1126/sciadv.aao1478

Sancar, A., & Sancar, G. B. (1988). DNA repair enzymes. *Annual Review of Biochemistry*, *57*, 29–67. https://doi.org/10.1146/annurev.bi.57.070188.000333

Sand, K. K., & Jelavic, S. (2018). Mineral facilitated horizontal gene transfer: A new principle for evolution of life? *Frontiers in Microbiology*, *9*, 2217. https://doi.org/10.3389/fmicb.2018.02217

Santos, A. L., Moreirinha, C., Lopes, D., Esteves, A. C., Henriques, I., Almeida, A., Domingues, M. R., Delgadillo, I., Correia, A., & Cunha, A. (2013). Effects of UV radiation on the lipids and proteins of bacteria studied by mid-infrared spectroscopy. *Environmental Science & Technology*, *47*(12), 6306–6315. https://doi.org/10.1021/es400660g

Santos, A. L., Oliveira, V., Baptista, I., Henriques, I., Gomes, N. C., Almeida, A., Correia, A., & Cunha, A. (2012). Effects of UV-B radiation on the structural and physiological diversity of bacterioneuston and bacterioplankton. *Applied and Environmental Microbiology*, *78*(6), 2066–2069. https://doi.org/10.1128/AEM.06344-11

Schluter, A., Szczepanowski, R., Puhler, A., & Top, E. M. (2007). Genomics of IncP-1 antibiotic resistance plasmids isolated from wastewater treatment plants provides evidence for a widely accessible drug resistance gene pool. *FEMS Microbiology Reviews*, *31*(4), 449–477. https://doi.org/10.1111/j.1574-6976.2007.00074.x

Schrammel, B., Cervero-Arago, S., Dietersdorfer, E., Walochnik, J., Luck, C., Sommer, R., & Kirschner, A. (2018). Differential development of *Legionella* sub-populations during short- and long-term starvation. *Water Research*, *141*, 417–427. https://doi.org/10.1016/j.watres.2018.04.027

Schultz, R. A., Barbis, D. P., & Friedberg, E. C. (1985). Studies on gene transfer and reversion to UV resistance in xeroderma pigmentosum cells. *Somatic Cell and Molecular Genetics*, *11*(6), 617–624. https://doi.org/10.1007/BF01534726

Shah, D., Zhang, Z. G., Khodursky, A., Kaldalu, N., Kurg, K., & Lewis, K. (2006). Persisters: A distinct physiological state of *E. coli*. *BMC Microbiology*, *6*(1), 53. 53. https://doi.org/10.1186/1471-2180-6-53

Shah, S., Colquhoun, D., Nikuli, H., & Sorum, H. (2012). Prevalence of antibiotic resistance genes in the bacterial flora of integrated fish farming environments of Pakistan and Tanzania. *Environmental cience & Technology*, *46*(16), 8672–8679. https://doi.org/10.1021/es3018607

Shi, H., Li, G., Sun, H., An, T., Zhao, H., & Wong, P.-K. (2014). Visible-light-driven photocatalytic inactivation of *E. coli* by Ag/AgX-CNTs (X = Cl, Br, I) plasmonic photocatalysts: Bacterial performance and deactivation mechanism. *Applied Catalysis B: Environmental*, *158-159*, 301–307. https://doi.org/10.1016/j.apcatb.2014.04.033

Singh, D. V., Choudhury, R., & Panda, S. (2012). Emergence and dissemination of antibiotic resistance: A global problem. *Indian Journal of Medical Microbiology*, *30*(4), 384. https://doi.org/10.4103/0255-0857.103756

Slater, F. R., Bailey, M. J., Tett, A. J., & Turner, S. L. (2008). Progress towards understanding the fate of plasmids in bacterial communities. *FEMS Microbiology Ecology*, *66*(1), 3–13. https://doi.org/10.1111/j.1574-6941.2008.00505.x

Slon, V., Hopfe, C., Weiß, C. L., Mafessoni, F., de la Rasilla, M., Lalueza-Fox, C., Rosas, A., Soressi, M., Knul, M. V., Miller, R., Stewart, J. R., Derevianko, A. P., Jacobs, Z., Li, B., Roberts, R. G., Shunkov, M. V., de Lumley, H., Perrenoud, C., Gušić, I., … Meyer, M. (2017). Neandertal and denisovan DNA from pleistocene sediments. *Science (New York, N.Y.)*, *356*(6338), 605–608. https://doi.org/10.1126/science.aam9695

Storteboom, H., Arabi, M., Davis, J. G., Crimi, B., & Pruden, A. (2010). Identification of antibiotic-resistance-gene molecular signatures suitable as tracers of pristine river, urban, and agricultural sources. *Environmental Science & Technology*, *44*(6), 1947–1953. https://doi.org/10.1021/es902893f

Stotzky, G. (1986). Influence of soil mineral colloids on metabolic processes, growth, adhesion, and ecology of microbes and viruses. In P. M. Huang & M. Schnitzer (Eds.), *Interactions of Soil Minerals with natural Organics and Microbes* (pp. 305–428). https://doi.org/10.2136/sssaspecpub17.c10

Stotzky, G., & Rem, L. T. (1966). Influence of clay minerals on microorganisms. I. Montmorillonite and kaolinite on bacteria. *Canadian Journal of Microbiology*, *12*(3), 547–563. https://doi.org/10.1139/m67-202

Stotzky, G., & Rem, L. T. (1967). Influence of clay minerals on microorganisms. IV. Montmorillonite and kaolinites on fungi. *Canadian Journal of Microbiology*, *13*(11), 1535–1550. https://doi.org/10.1139/m67-202

Sun, H., Li, G., & An, T. (2017). Bacterial oxidative stress responses and cellular damage caused by photocatalytic and photoelectrocatalytic inactivation. In *Advances in Photocatalytic Disinfection* (pp. 259–272). https://doi.org/10.1007/978-3-662-53496-0_12

Sun, H., Li, G., An, T., Zhao, H., & Wong, P. (2016). Unveiling the photoelectrocatalytic inactivation mechanism of *Escherichia coli:* Convincing evidence from responses of parent and anti-oxidation single gene knockout mutants. *Water Research*, *88*, 135–143. https://doi.org/10.1016/j.watres.2015.10.003

Sun, H., Li, G., Nie, X., Shi, H., Wong, P., Zhao, H., & An, T. (2014). Systematic approach to in-depth understanding of photoelectrocatalytic bacterial inactivation mechanisms by tracking the decomposed building blocks. *Environmental Science & Technology*, *48*(16), 9412–9419. https://doi.org/10.1021/es502471h

Sundqvist, M. (2014). Reversibility of antibiotic resistance. *Upsala Journal of Medical Sciences*, *119*(2), 142–148. https://doi.org/10.3109/03009734.2014.903323

Takahashi, Y., Suzuki, K., Niimura, T., Kano, T., & Takashima, S. (1991). A production of monoclonal antibodies by a simple electrofusion technique induced by ac pulses. *Biotechnology and Bioengineering*, *37*(8), 790–794. https://doi.org/10.1002/bit.260370814

Takeuchi, N., Kaneko, K., & Koonin, E. V. (2014). Horizontal gene transfer can rescue prokaryotes from Muller's ratchet: benefit of DNA from dead cells and population subdivision. *G3 (Bethesda, Md.)*, *4*(2), 325–339. https://doi.org/10.1534/g3.113.009845

Templeton, M. R., Oddy, F., Leung, W. K., & Rogers, M. (2009). Chlorine and UV disinfection of ampicillin-resistant and trimethoprim-resistant *Escherichia coli*. *Canadian Journal of Civil Engineering*, *36*(5), 889–894. https://doi.org/10.1139/L09-040

Tikhomirova, A., Trappetti, C., Standish, A. J., Zhou, Y., Breen, J., Pederson, S., Zilm, P. S., Paton, J. C., & Kidd, S. P. (2018). Specific growth conditions induce a Streptococcus pneumoniae non-mucoidal, small colony variant and determine the outcome of its coculture with Haemophilus influenzae. *Pathogens and Disease*, *76*(7). https://doi.org/10.1093/femspd/fty074

Toprak, E., Veres, A., Michel, J. B., Chait, R., Hartl, D. L., & Kishony, R. (2011). Evolutionary paths to antibiotic resistance under dynamically sustained drug selection. *Nature Genetics*, *44*(1), 101–105. https://doi.org/10.1038/ng.1034

Tseng, C. C., Tsai, Y. H., Hu, A. R., Liou, J. W., Chang, K. C., & Chang, H. H. (2016). Altered susceptibility to the bactericidal effect of photocatalytic oxidation by TiO_2 is related to colistin resistance development in Acinetobacter baumannii. *Applied Microbiology and Biotechnology*, *100*(19), 8549–8561. https://doi.org/10.1007/s00253-016-7654-x

van Grieken, R., Marugan, J., Pablos, C., Furones, L., & Lopez, A. (2010). Comparison between the photocatalytic inactivation of Gram-positive *E. faecalis* and Gram-negative *E. coli* faecal contamination indicator microorganisms. *Applied Catalysis B: Environmental*, *100*(1-2), 212–220. https://doi.org/10.1016/j.apcatb.2010.07.034

Vega, N. M., Allison, K. R., Khalil, A. S., & Collins, J. J. (2012). Signaling-mediated bacterial persister formation. *Nature Chemical Biology*, *8*(5), 431–433. https://doi.org/10.1038/nchembio.915

Vestergaard, M., Paulander, W., & Ingmer, H. (2015). Activation of the SOS response increases the frequency of small colony variants. *BMC Research Notes*, *8*, 749. https://doi.org/10.1186/s13104-015-1735-2

Volzing, K. G., & Brynildsen, M. P. (2015). Stationary-phase persisters to ofloxacin sustain DNA damage and require repair systems only during recovery. *mBio*, *6*(5), e00731–00715. https://doi.org/10.1128/mBio.00731-15

Vulin, C., Leimer, N., Huemer, M., Ackermann, M., & Zinkernagel, A. S. (2018). Prolonged bacterial lag time results in small colony variants that represent a sub-population of persisters. *Nature Communications*, *9*(1), 4074. https://doi.org/10.1038/s41467-018-06527-0

Wang, J., Li, G., Yin, H., & An, T. (2020). Bacterial response mechanism during biofilm growth on different metal material substrates: EPS characteristics, oxidative stress and molecular regulatory network analysis. *Environmental Research*, *185*, 109451. https://doi.org/10.1016/j.envres.2020.109451

Wang, W., Li, G., Xia, D., An, T., Zhao, H., & Wong, P. (2017). Photocatalytic nanomaterials for solar-driven bacterial inactivation: recent progress and challenges. *Environmental Science: Nano*, *4*(4), 782–799. https://doi.org/10.1039/C7EN00063D

Williams-Nguyen, J., Bueno, I., Sargeant, J. M., Nault, A. J., & Singer, R. S. (2016). What is the evidence that point sources of anthropogenic effluent increase antibiotic resistance in the environment? Protocol for a systematic review. *Animal Health Research Reviews*, *17*(1), 9–15. https://doi.org/10.1017/S1466252316000037

Williams, L. B., Metge, D. W., Eberl, D. D., Harvey, R. W., Turner, A. G., Prapaipong, P., & Poret-Peterson, A. T. (2011). What makes a natural clay antibacterial? *Environmental Science & Technology*, *45*(8), 3768–3773. https://doi.org/10.1021/es1040688

Wilson, D. N., & Nierhaus, K. H. (2007). The weird and wonderful world of bacterial ribosome regulation. *Critical Reviews in Biochemistry and Molecular Biology*, *42*(3), 187–219. https://doi.org/10.1080/10409230701360843

Windels, E. M., Michiels, J. E., Fauvart, M., Wenseleers, T., Van den Bergh, B., & Michiels, J. (2019). Bacterial persistence promotes the evolution of antibiotic resistance by increasing survival and mutation rates. *The ISME Journal*, *13*(5), 1239–1251. https://doi.org/10.1038/s41396-019-0344-9

Withey, J. H., & Friedman, D. I. (2003). A salvage pathway for protein structures: tmRNA and trans-translation. *Annual Review of Microbiology*, *57*, 101–123. https://doi.org/10.1146/annurev.micro.57.030502.090945

Wong Fok Lung, T., Monk, I. R., Acker, K. P., Mu, A., Wang, N., Riquelme, S. A., Pires, S., Noguera, L. P., Dach, F., Gabryszewski, S. J., Howden, B. P., & Prince, A. (2020). *Staphylococcus aureus* small colony variants impair host immunity by activating host cell glycolysis and inducing necroptosis. *Nature Microbiology*, *5*(1), 141–153. https://doi.org/10.1038/s41564-019-0597-0

Wu, C., Martel, J., Young, D., & Young, J. (2009). Fetuin-A/albumin-mineral complexes resembling serum calcium granules and putative nanobacteria: Demonstration of a dual inhibition-seeding concept. *PLoS One*, *4*(11), e8058. https://doi.org/10.1371/journal.pone.0008058

Wu, Y., Vulic, M., Keren, I., & Lewis, K. (2012). Role of oxidative stress in persister tolerance. *Antimicrobial Agents and Chemotherapy*, *56*(9), 4922–4926. https://doi.org/10.1128/AAC.00921-12

Xia, D., Liu, H., Jiang, Z., Ng, T., Lai, W., An, T., Wang, W., & Wong, P. (2018). Visible-light-driven photocatalytic inactivation of *Escherichia coli* K-12 over thermal treated natural magnetic sphalerite: Band structure analysis and toxicity evaluation. *Applied Catalysis B: Environmental*, *224*, 541–552. https://doi.org/10.1016/j.apcatb.2017.10.030

Xia, D., Ng, T., An, T., Li, G., Li, Y., Yip, H., Zhao, H., Lu, A., & Wong, P. (2013). A recyclable mineral catalyst for visible-light-driven photocatalytic inactivation of bacteria: natural magnetic sphalerite. *Environmental Science & Technology*, *47*(19), 11166–11173. https://doi.org/10.1021/es402170b

Xia, D., Wang, W., & Wong, P. (2017). Visible-light-driven photocatalytic treatment by environmental minerals. In *Advances in Photocatalytic Disinfection* (pp. 41–61). https://doi.org/10.1007/978-3-662-53496-0_3

Xie, J. W., Jin, L., Luo, X. S., Zhao, Z., & Li, X. D. (2018). Seasonal disparities in airborne bacteria and associated antibiotic resistance genes in $PM_{2.5}$ between urban and rural sites. *Environmental Science & Technology Letters*, *5*(2), 74–79. https://doi.org/10.1021/acs.estlett.7b00561

Yang, X. G., Li, Y., Lu, A. H., Yan, Y. H., Wang, C. Q., & Wong, P. K. (2011). Photocatalytic reduction of carbon tetrachloride by natural sphalerite under visible light irradiation. *Solar Energy Materials and Solar Cells*, *95*(7), 1915–1921. https://doi.org/10.1016/j.solmat.2011.02.020

Yin, H., Chen, X., Li, G., Chen, Y., Wang, W., An, T., Wong, P. K., & Zhao, H. (2019). Sub-lethal photocatalysis bactericidal technology cause longer persistence of antibiotic-resistance mutant and plasmid through the mechanism of reduced fitness cost. *Applied Catalysis B: Environmental*, *245*, 698–705. https://doi.org/10.1016/j.apcatb.2019.01.041

Yin, H., Li, G., Chen, X., Wang, W., Wong, P., Zhao, H., & An, T. (2020). Accelerated evolution of bacterial antibiotic resistance through early emerged stress responses driven by photocatalytic oxidation. *Applied Catalysis B: Environmental*, 118829. *269* https://doi.org/10.1016/j.apcatb.2020.118829

Yoshida, M., Reyes, S. G., Tsuda, S., Horinouchi, T., Furusawa, C., & Cronin, L. (2017). Time-programmable drug dosing allows the manipulation, suppression and reversal of antibiotic drug resistance in vitro. *Nature Communications*, *8*, 15589 https://doi.org/10.1038/ncomms15589

Yu, W. H., Li, N., Tong, D. S., Zhou, C. H., Lin, C. X., & Xu, C. Y. (2013). Adsorption of proteins and nucleic acids on clay minerals and their interactions: A review. *Applied Clay Science*, *80-81*, 443–452. https://doi.org/10.1016/j.clay.2013.06.003

Zbinden, A., Quiblier, C., Hernandez, D., Herzog, K., Bodler, P., Senn, M. M., Gizard, Y., Schrenzel, J., & Francois, P. (2014). Characterization of *Streptococcus tigurinus* small-colony variants causing prosthetic joint infection by comparative whole-genome analyses. *Journal of Clinical Microbiology*, *52*(2), 467–474. https://doi.org/10.1128/JCM.02801-13

Zhang, H., Chang, F., Shi, P., Ye, L., Zhou, Q., Pan, Y., & Li, A. (2019). Antibiotic resistome alteration by different disinfection strategies in a full-scale drinking water treatment plant deciphered by metagenomic assembly. *Environmental Science & Technology*, *53*(4), 2141–2150. https://doi.org/10.1021/acs.est.8b05907

Zhang, S., Ye, C., Lin, H., Lv, L., & Yu, X. (2015). UV disinfection induces a VBNC state in *Escherichia coli* and *Pseudomonas aeruginosa*. *Environmental Science & Technology*, *49*(3), 1721–1728. https://doi.org/10.1021/es505211e

Zhao, Y., Yang, Q. E., Zhou, X., Wang, F.-H., Muurinen, J., Virta, M. P., Brandt, K. K., & Zhu, Y. G. (2020). Antibiotic resistome in the livestock and aquaculture industries: Status and solutions. *Critical Reviews in Environmental Science and Technology*, 1–38. https://doi.org/10.1080/10643389.2020.1777815