

REVIEW

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Dioxin impacts on lipid metabolism of soil microbes: towards effective detection and bioassessment strategies

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Abstract

Dioxins are the most toxic known environmental pollutants and are mainly formed by human activities. Due to their structural stability, dioxins persist for extended periods and can be transported over long distances from their emission sources. Thus, dioxins can be accumulated to considerable levels in both human and animal food chains. Along with sediments, soils are considered the most important reservoirs of dioxins. Soil microorganisms are therefore highly exposed to dioxins, leading to a range of biological responses that can impact the diversity, genetics and functional of such microbial communities. Dioxins are very hydrophobic with a high affinity to lipidic macromolecules in exposed organisms, including microbes. This review summarizes the genetic, molecular and biochemical impacts of dioxins on the lipid metabolism of soil microbial communities and especially examines modifications in the composition and architecture of cell membranes. This will provide a useful scientific benchmark for future attempts at soil ecological risk assessment, as well as in identifying potential dioxin-specific-responsive lipid biomarkers. Finally, potential uses of lipid-sequestering microorganisms as a part of biotechnological approaches to the bio-management of environmental contamination with dioxins are discussed.

Keywords: Dioxins, Soil microbes, Lipid metabolism, Biotetection, Bioremediation

Introduction

Dioxins, polychlorinated dibenzodioxins (PCDDs) and polychlorinated dibenzofurans (PCDFs), are the most toxic group of persistent organic pollutants (POPs) that have been described to date (WHO 2016). Chemically, dioxins consist of two aromatic rings linked via either one or two atoms of oxygen, and give rise, respectively, to PCDFs or PCDDs. This extremely stable structure contains one to eight positions that can be chlorinated, which confers both high structural stability and extreme hydrophobicity. Depending on the number and position of chlorination ($P=1-8$), the dioxin group includes 75 PCDD and 135 PCDF congeners that vary significantly in

terms of their overall toxicity (Pollitt 1999; Caruso et al. 2003). Congeners with chlorine atoms substituted in the lateral 2, 3, 7 and 8 positions of the aromatic rings are considered as the most toxic. Of these, 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD), with a toxic equivalency factor (TEF) of 1.0, is the most toxic congener of all the dioxins (WHO 2002; Van den Berg et al. 2006).

In modern settings, dioxins are mainly produced by industrial, municipal and domestic incineration (Tuppurainen et al. 2003; Tue et al. 2016; Chen et al. 2005) as well as during industrial processes involving chlorinated aromatic and aliphatic compounds, such as pesticides and herbicides synthesis (Lee et al. 1984). Also, the accidental or deliberate incineration of forest-derived and other solid materials releases considerable amounts of dioxins into the environment (Nzihou et al. 2012; Coutinho et al. 1998; Travis and Hattemer-Frey 1989).

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Due to their high structural stability and their extreme hydrophobicity, dioxins tend to persist in the environment and bioaccumulate in both human and animal food chains (Stockholm 2001). This means that humans can be exposed to dioxins through the consumption of contaminated food, which constitutes a potential health risk (WHO 2002; IPCS 2003). According to the US National Institute of Environmental Health Sciences (NIEHS), more than 90% of human exposure to dioxins occurs via ingested food rather than alternative routes such as via skin contact or inhalation (NIEHS 2017). Overall, dioxins are known to cause irreversible biological damage in human, animals, plant and microorganisms, leading to wider ecological, environmental and economic impacts (Hanano et al. 2014b, c, 2015b, 2016b, 2018b, d, 2019a, b; Latchoumycandane et al. 2003; Angrish et al. 2013; Woeller et al. 2019; Ssebugere et al. 2019; Prokopec et al. 2020).

At the beginning of many food chains, PCDD/Fs have a strong tendency to associate with soil organic materials due to their high organic carbon–water partition (KOC) coefficient. This low mobility together with low water solubility results in a high accumulation of PCDD/Fs in several types of soil (Xu et al. 2020; Meijer et al. 2001). Along with sediments, soil contains the largest reservoirs of these contaminants (Krauss and Wilcke 2003; Yao et al. 2018; Mertes et al. 2018). As a consequence, soil microorganisms are liable to be exposed to dioxins, leading to a range of biological responses that impacts the diversity, genetics and functional of affected microbial communities (Hanano et al. 2014c; Kimura and Kamagata 2009).

The cytotoxicity of dioxins in biological systems, including microorganisms, occurs mainly via their high affinity for biological macromolecules containing lipid moieties, including unbound lipids, lipoproteins and liposaccharides, thereby affecting their biological functions in living cells (Lawrence and Kerkvliet 1998; Hanano et al. 2015c, 2019b; Cranmer-Byng et al. 2015). In terms of their high octanol/water partition coefficients (K_{ow}), estimated at about 7.0 for TCDD, dioxins are the most lipophilic contaminants described to date (Hanson et al. 2019; Sarna et al. 1984; Marple et al. 1986; Shlu et al. 1988). This extremely high K_{ow} value acts as a driving force enabling dioxins to rapidly attack lipidic macromolecules in exposed organisms, including microbes. In this context, it is important to learn more about the impacts of PCDD/Fs on the lipid metabolism of soil microbial communities. This will help in identifying potential dioxin-specific-responsive lipid biomarkers as new parameters for the soil ecological risk assessment.

This review surveys the alterations in lipid metabolism of soil microbial communities in response to dioxin exposure. It begins with a brief background on

the nature of dioxins as lipophilic environmental contaminants and examines their impacts on microbial lipid metabolism with respect to the composition of cellular fatty acids (FAs). It then looks at the modifications of cell membrane architecture, especially the increased levels of unsaturated FAs that occur in response to dioxin exposure. Finally, the possible uses of lipid-sequestering microorganisms for biotechnological approaches to bio-management of dioxin in contaminated environments are outlined.

Sources of dioxins in the environment

Dioxins are released into the environment through natural sources such as volcanic activities or forest fires (Hay 1981). Such episodes are becoming more common with particular increases in the incidence of large-scale forest fires over the last decade (Salamanca et al. 2016; Zhang et al. 2016; Oliveira et al. 2020). Dioxins are also discharged into the environment by various manufacturing processes involving synthesis of chlorinated aromatic and aliphatic compounds, such as pesticide and herbicides (Chen et al. 2005) as well as paper production (Haq and Raj 2020). Other unintentional sources of dioxins include wastes containing chlorinated aromatic compounds from chemical facilities, sewage sludge, incineration of municipal and medical wastes, incineration of fossil fuels and fly ash storage (Hippelein et al. 1996). Moreover, the destruction of electronic waste (e-waste) is a considerable source of PCDD/Fs for surrounding environments, and the amount of e-waste is expected to grow to 52.2 million tons by 2021 (Jin et al. 2020). Plastic materials, such as PVC, account for about 26% of the volume of e-waste (Zheng et al. 2008; Tsydenova and Bengtsson 2011), while brominated flame retardants are used for the package of e-wastes (Kiddee et al. 2013). The methods for the processing of e-waste, such as manual disassembly, roasting, acid leaching and open burning (Nishimura et al. 2017; Ma et al. 2009; Zheng et al. 2008), lead to the formation of PCDD/Fs. Automobile emissions are another important source of PCDD/Fs. Even though leaded fuel has been banned across most of the world, diesel fuel contains Cl in minor amounts (Dyke et al. 2007; Zhao et al. 2014) as do the dispersants, added to retain dirt in suspension in diesel fuel mixtures (Dyke et al. 2007). This suggests that PCDD/Fs can be formed together with other POPs in diesel engines. Finally, road transport emissions have also been identified as an important source of several halogenated POPs, such as PCDD/Fs, PCBs and polybrominated diphenyl ethers (PBDEs) (Chen et al. 2017a; Kim et al. 2003; Fuster et al. 2001; Laroo et al. 2011).

Fate and transport of dioxins in the environment

Research conducted on the processes through which dioxins move into the environment shows that, although their formation occurs at local levels, their environmental distribution is much wider, from regional to global in reach. Once released into the environment, dioxins are distributed between specific environmental compartments. This section outlines the fate and transport processes for dioxins in the atmospheric, terrestrial and aquatic environments although, clearly, these systems are not mutually exclusive and so interact with each other. After their release, dioxins are transported through the atmosphere and deposited to terrestrial and/or aquatic surfaces. The travel distance before deposition depends upon several factors including the height of release, temperature, prevailing meteorological conditions and particle size.

Dioxins are relatively volatility and can exist in both the gaseous phase and/or bound to particles in the atmosphere, depending upon the prevailing environmental conditions, most notably temperature (Hippelein et al. 1996). Dioxins can continuously exchange between particle and vapor phases. In summer, when temperatures are high, the less chlorinated dioxin congeners tend to be found predominantly in the vapor phase, but are more likely to be bound to particles when temperatures are lower in winter (Wu et al. 2009; Shih et al. 2006; Hermanson et al. 2020; Fang et al. 2017; Birgul and Tasdemir 2011; Cindoruk and Tasdemir 2010). This is important because dioxins in the vapor phase can more readily undergo photochemical transformation to less toxic derivatives than those bound to solid substrates (Birla and Kamens 1994).

Atmospheric dioxins can move into and between terrestrial environments by direct deposition onto soil, vegetation and water surfaces via either wet or dry processes. Aquatic surfaces can be contaminated with dioxins via a direct wet or dry deposition, although direct inputs from industrial effluents and run-off from soil may also be important (Kjeller and Rappe 1995). In water, dioxins partition rapidly to solid organic matter and therefore accumulate in sediments (Beurskens et al. 1993). Interestingly, dioxins can readily partition into sedimentary clays, such as ball clays, which are fine grained and highly plastic materials with a large surface area-to-volume ratio that readily bind to such hydrophobic molecules. Subsequently, dioxins can accumulate in aquatic fauna as a direct consequence of the ingestion of contaminated organic matter, for example by filter feeding animals. As a result, the concentration of dioxins in marine animal tissues is found to increase as one moves up the food chain, a phenomenon known as biomagnification (Ahn et al. 2008; Tratnyek et al. 2020).

Due to their poor solubility in water, dioxins accumulate in most soil types, making soils the most important reservoirs of such contaminants. Above-ground terrestrial vegetation can also be exposed to dioxins by a direct deposition of atmospheric dioxins on leaves or via absorption from soil via root systems and transport via the vascular system to aerial tissues such as leaves and flowers (Reischl et al. 1988; Chrostowski and Foster 1996; Engwall and Hjelm 2000; Hanano et al. 2015b, 2018b, d). Here, it is important to note that leafy crops, such as salads, are less affected by direct deposition of dioxins because of their relatively brief lifetime in the field, which is often limited to a few weeks. However, even leafy crops can be exposed to dioxins indirectly from contaminated soil due to their active root systems (Hanano et al. 2014b, 2018b). Longer lived perennial and woody plants can accumulate considerable amount of dioxins from the surrounding atmosphere as well as via their well-developed root systems (Hanano et al. 2016b, 2018d). More research is needed to define and evaluate the modalities by which plants can be exposed to dioxins, compared to animals that are directly exposed via contaminated feed (Torres et al. 2013; Diletti et al. 2007).

Bioavailability of dioxins

The bioavailability of a soil contaminant is routinely defined by the degree to which it may be absorbed and metabolized by biological systems (ISO/FDIS 2008). Some of limitations of this definition, notably in terms of the temporal and species dependence are discussed in detail by Harmsen et al. (2005). Semple et al. (2003) addressed these limitations by proposing two different components of bioavailability: (i) the bioavailability component where a compound is freely available to cross an organism's cellular membrane at a given time. After transfer has occurred, storage, transformation, assimilation or degradation within the organism can occur. These processes are distinct from the original transfer from the medium. (ii) The bioaccessibility component, where a compound can cross an organism's cellular membrane from the environment only if the organism has a direct access to the chemical. Although the details of these definitions have been debated, it is obvious that organic compound bioavailability is intimately related to three factors: (i) the physicochemical properties of the compound; (ii) the physicochemical properties of the soil type, and finally; (iii) the current environmental conditions at the time of potential exposure (Meric et al. 2014; Smidova et al. 2017).

The bioavailability of dioxins is conditioned by their extremely low water solubility and strong affinity to organic particles in soils, which in turn, are also continuously targeted by soil microorganisms. This can

facilitate the initial interactions between dioxins and soil microorganisms. The uptake mechanism of hydrophobic compounds in general, and dioxins in particular, is a key aspect of their biodegradation process within cells, because they need to cross the cell membrane in order to be accessible to the relevant membrane-bound enzymes. Some soil microorganisms are able to increase the bioavailability of dioxins by quantitative and qualitative modification of cell membrane lipids, hence modulating the fluidity and permeability of the cell membrane and facilitating the uptake of the dioxins (Aguilar-Uscanga and Francois 2003; Hanano et al. 2019b). It was also reported that the most active microorganisms in term of dioxin uptake from the aquatic environment are those that produce biosurfactants as secreted substances that tend to reduce liquid surface tensions, thereby acting as emulsifying agent for the dioxins (Hanano et al. 2014a, 2015c).

Several microbiological methods have been developed to measure the bioavailability of dioxins. They include measurement of dioxin biodegradability because the biodegradable fraction is also considered to be the bioavailable fraction (Richterich et al. 1998). Mineralization assays are also used where the conversion of ^{14}C -labeled dioxins into $^{14}\text{CO}_2$ gives a measure of the microbially available fraction of the contaminant (Hatzinger and Alexander 1995; Semple et al. 2003). Microbial toxicity tests have also been applied, but these do not necessarily measure the bioavailable compound fraction (Jacobs et al. 1993). Another technique in microbial measurement is the use of microbial biosensors, which has widespread applications in environmental monitoring and toxicity assessment and considerable advantages in terms of sensitivity, cost and time compared to using higher organisms (Steinberg et al. 1995).

In this context, genetic manipulation can enhance the sensitivity of biosensor towards a target compound and reporter genes for bacterial bioluminescence (lux) have been used (Palmer et al. 1998). In this strategy, which has been used for a range of hydrophobic organic pollutants including dioxins, a given metabolic stress induced by an environmental toxicant results in a decline in luminescence that is directly proportional to the toxicant concentration (Boyd et al. 1997; Sousa et al. 2009).

Lipophilicity of dioxins

The lipophilicity of dioxins, i.e., their extreme affinity for cellular lipids, is a major determinant factor of their toxicity (Geyer et al. 1993). The lipophilicity of an organic compound is experimentally described by a partition coefficient, $\text{Log}P$, defined as the ratio of the concentration for an unionized compound at equilibrium between organic and aqueous phases (Marple et al. 1986). Different dioxin congeners (there are 210 in total) possess a

range of physicochemical properties. Seventeen of them are of interest for their potential toxicity to humans and other organisms. Therefore, knowledge of properties of individual dioxins is necessary in order to determine the behavior of dioxins pool, which are typically found as mixtures in the environment, and this is important for predicting and possibly mitigating the fate, transport and the toxicological effects of dioxins in humans.

In environmental modeling, *n*-octanol partitioning is routinely used as a more convenient alternative to biological systems. Hence, the ability of dioxins to partition between air or water and *n*-octanol is used as a proxy measure of their ability to bio-concentrate in plants, animals and fish. Here, two main parameters are described, namely the *n*-octanol:water or *n*-octanol:air partition coefficients, K_{ow} and K_{oa} , respectively, although for many of dioxin congeners there is substantial uncertainty about their value (Mackay et al. 1982; Marple et al. 1986). Table 1 summarizes the octanol:water partition coefficient (K_{ow}) values of the most potent congeners of dioxins. This table shows that values of K_{ow} are positively correlated with the chlorination degree of dioxins. Thus, a high value K_{ow} value reflects a high affinity to cellular fats and possibly a high subsequent toxicity in an organism. However, the tetrachlorinated dibenzo-*p*-dioxin congeners, known for their extreme toxicity in biological systems, do not have the highest K_{ow} values. Obviously,

Table 1 Octanol–water partition coefficient (log K_{ow}) of some PCDDs

Dioxin substituent	Log K_{ow}	References
Dibenzo- <i>p</i> -dioxin	4.30	Shlu et al. (1988)
1-Chloro-	4.75	Sarna et al. (1984)
2-Chloro-	5.00	Hanson et al. (2019)
2,3-Dichloro-	5.60	Sarna et al. (1984)
2,7-Dichloro-	5.75	Hanson et al. (2019)
2,8-Dichloro-	5.60	Shlu et al. (1988)
1,2,4-Trichloro-	6.35	Hanson et al. (2019), Shlu et al. (1988)
1,2,3,4-Tetrachloro-	6.60	Sarna et al. (1984)
1,2,3,7-Tetrachloro-	6.90	Burkhard et al. (1994), Shlu et al. (1988)
1,3,6,8-Tetrachloro-	7.10	Sarna et al. (1984)
1,3,7,9-Tetrachloro-	7.10	Marple et al. (1986)
2,3,7,8-Tetrachloro-	7.20	Marple et al. (1986)
1,2,3,4,7-Pentachloro-	7.40	Shlu et al. (1988), Sarna et al. (1984)
1,2,3,4,7,8-Hexachloro-	7.80	Marple et al. (1986)
1,2,3,4,6,7,8-Heptachloro-	8.00	Sarna et al. (1984), Shlu et al. (1988)
1,2,3,4,6,7,8,9-Octachloro-	8.20	Marple et al. (1986), Shlu et al. (1988)

the high toxicity of such substituents of dioxins is conditioned by their efficiency in penetrating biological systems and their subsequent interactions with cellular components. For this reason, the ‘Toxic Equivalent’ (TEQ) concept is used to assess the potential toxicity of a mixture of dioxins in exposed organisms (Safe 1990). This factor indicates the degree of toxicity compared to 2,3,7,8-TCDD, the most toxic congener of dioxins which has been universally assigned a TEF value of 1.

Lipids are promising cellular components to be targeted for bio-environmental studies. This is because lipids are highly abundant and ubiquitous across all organisms, and their profiles can often be substantially modified in response to a wide range of environmental stimuli (Depatie et al. 2020; Tang et al. 2018). Such lipidic alterations can allow organisms to maintain essential biological functions while adapting to environmental changes including toxic contaminants. Much research has been conducted to determine the major metabolic responses in lipid metabolism of microorganisms exposed to environmental stressors, including persistent toxicants (Tartu et al. 2017). The overall lipidic profile of an organism, or part thereof, at a given time is referred to as the lipidome. The relatively new discipline of lipidomics helps us to understand the biofeedback processes affecting lipid metabolism in responding to historical environmental changes, and can help predict similar responses in the future (Depatie et al. 2020). Lipid metabolism can be affected at anabolic and catabolic levels due to the regulation of enzymes controlling lipid metabolism at transcriptional and biochemical levels (Pakiet et al. 2019; Russo et al. 2020; Sollai et al. 2019). Cell membrane lipids, which are the first lipidic barrier enabling the cell to manage communication with the surrounding milieu, are typically subjected to considerable qualitative and quantitative alterations according to the nature and level of exposure to environmental contaminants (Albergamo et al. 2016). These interactive responses in lipid metabolism of microorganisms exposed to dioxins are reviewed in detail as follows.

Effects of dioxins on lipid metabolism in soil microorganisms

There are multiple lines of genetic, molecular and biochemical evidence demonstrating that dioxins, notably TCDD, alter lipid metabolism by affecting the activity of certain key enzymes in fatty acids (FAs) biosynthesis, levels of triacylglycerols, cholesterol and free FAs in plasma of animals, plants and humans exposed to dioxins. In contrast, relatively little is known about similar exposure patterns involving soil microorganisms (Hanano et al. 2014b, 2015b, 2016b, 2018c, 2019a, b).

Soil microorganisms are readily subjected to dioxin exposure and respond by a range of biological alterations that can influence microbial diversity and functionality (Cerniglia 1984; Hanano et al. 2014c). Enzymatic activity is now considered as one of the most useful indicators for assessing exposure levels of microbial communities to stressors (Yao et al. 2018; Field and Sierra-Alvarez 2008; Anasonye et al. 2014; Le et al. 2017). Consequently, many bacterial and somewhat fewer fungal species have been identified and characterized as potential bioindicators and/or biodegraders of dioxins (Hiraishi et al. 2001, 2003b; Hanano et al. 2019a; Stella et al. 2017; Magan et al. 2010; Rubilar et al. 2011). Omics-based studies, including genomics, transcriptomics, proteomics, and metabolomics have given much useful information about microbial responses to environmental challenges. This has enabled the extrapolation of results from a relatively small-scale omics studies to a wide diversity of organisms, and the compilation of risk assessments and remediation strategies applicable to entire ecosystems (Brinke and Buchinger 2017).

Lipidomics is an emerging field where hundreds to thousands of lipid molecular species are simultaneously measured qualitatively and quantitatively (Koelmel et al. 2020). Lipids participate in metabolic reactions controlling cellular energy balance and also serve as major structural components in membranes, as well as acting as substrates for the generation of signaling compounds and other cellular mediators (Konings et al. 2002). Therefore, lipidomics can be used to determine lipid biomarkers against a specific contaminant exposure that affects certain biochemical pathways, including FA biosynthesis, lipid peroxidation and oxidative stress (Albergamo et al. 2016). Several biological systems have been evaluated for biodegradation of dioxins, such as bacterial angular dioxygenases (Sato et al. 1997; Armengaud et al. 1998; Habe et al. 2001), peroxidases of white-rot fungi and anaerobic dehalogenases from microbial consortia (Bumpus et al. 1985; Bunge et al. 2003). The effects of dioxins on lipid metabolism of soil microorganisms have been studied *in vitro* using a selected microorganism isolated from dioxin-exposed environment and this approach has been used with a large variety of soil microorganisms, including bacteria, yeast and fungi (Hanano et al. 2014c, 2019a, b).

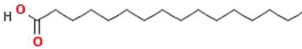
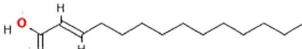
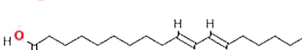
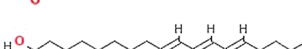

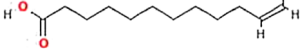
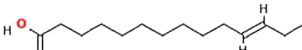

In the 1970s, Fulco et al. were the first to shed light on the biological connection between exposure to dioxins and cytochrome P450 in *Bacillus megaterium* ATCC 14581, which was initially characterized as an oxygenase of monounsaturated FAs (Matson et al. 1977). In the 1980s, the same group reported a detailed characterization of three different isoforms of cytochrome P450 in *B. megaterium*, referred as to P450_{BM-1}, P450_{BM-2} and

P450_{BM-3} (Kim and Fulco 1983; Narhi et al. 1983; Schwab et al. 1985). Of these, P450_{BM-3}, the best characterized isoform, is a catalytically self-sufficient monooxygenase that requires NADPH and O₂ to catalyze the hydroxylation and epoxidation of monounsaturated FAs (Matson et al. 1977; Ruettinger and Fulco 1981; Narhi and Fulco 1987). Interestingly, orthologs of these bacterial P450s were identified in hepatic microsomal fractions of rat and human that can metabolize dioxins via multiple catalytic mechanisms (Inouye et al. 2002; Sakaki et al. 2002; Shinkyo et al. 2003a, b; Sulistyaningdyah et al. 2004). More recently, a homolog of P450_{BM-1} has been identified and characterized in strain BmA14K of *B. megaterium*, isolated from soil contaminated with dioxins which showed a remarkable ability to grow in the presence of TCDD as the sole carbon source (Hanano et al. 2019b). As a direct consequence of its exposure to TCDD, BmA14K exhibited a morphological and biophysical profile typified by high levels of biosurfactant production, surface hydrophobicity and cell membrane permeability. This is consistent with earlier reports demonstrating such behavior in *B. megaterium* (Thavasi et al. 2008, 2011) and other microorganisms (Bouassida et al. 2018; Paraszkiwicz et al. 2018; Plaza et al. 2016; Hanano et al. 2015d).

At the cellular level, it was shown that TCDD-grown BmA14K cells have a specific FA profile typified by low ratios of branched-chain/straight chain FAs (BCFAs/

SCFAs) and saturated/unsaturated FAs (SFAs/USFAs), plus an unusual “signature” due to the presence of branched-chain unsaturated FAs (BCUFAs), which are absent in non-exposed bacteria (Hanano et al. 2019b). In addition to their use as biomarkers in bacterial taxonomy (Guinebretiere et al. 2013), bacterial FAs compositions are considerably modulated by various environmental factors. This is known as a part of bacterial responses to environmental changes including temperature, nutrients, salts, irradiation, pressure and hydrophobic pollutants (Braganza and Worcester 1986; Diomande et al. 2015; Sikkema et al. 1995; Ayari et al. 2009; Hanano et al. 2019b). The various functions of different types of FAs in terms of environmental responses are due to their diverse structures as summarized in Table 2. FAs compositions in the genus *Bacillus* in general and in *B. megaterium* species in particular are characterized by numerous branched-chain FAs (BCFAs), with a predominance of *iso* and *anteiso* BCFAs composed of 14–17 carbons, and smaller amounts of straight chain FAs (Kaneda 1966, 1977; Choi et al. 2000; Nickels et al. 2017a, b). However, an opposite scenario, with low ratios of BCFAs/SCFAs and SFAs/USFAs, was found in TCDD-exposed bacteria (Hanano et al. 2019b). This observation is consistent with earlier reports suggesting that adaptation of certain Bacilli to environmental changes, such as decreasing temperature and pH, involves a reduced level of BCFAs

Table 2 Environmental implications of different types of microbial membrane FAs

Type of fatty acids	Structure of fatty acids ^a	Response to environment factors	References
Saturated fatty acids (SFAs)		Decrease, low SFAs/USFAs	Nichols et al. (1997), Hanano et al. (2019b)
Mono-unsaturated fatty acids (MUFAs)		Decrease, low SFAs/USFAs	Hanano et al. (2019b)
Di-unsaturated fatty acids (DUFAs)		Increase	Kim et al. (2011), Fulco (1970)
Poly-unsaturated fatty acids (PUFAs)		Increase	Silbert et al. (1973), Chen et al. (2017b), Nichols et al. (1997)
<i>cis</i> -Straight chain fatty acids (<i>cis</i> -SCFAs)		Increase	Pedrotta and Witholt (1999), Hanano et al. (2019b)
<i>trans</i> -Straight chain fatty acids (<i>trans</i> -SCFAs)		Increase	Keweloh and Heipieper (1996), Hanano et al. (2019b)
<i>iso</i> -Branched chain fatty acids (<i>iso</i> -BCFAs)		Decrease, low BCFAs/SCFAs	Kaneda (1966), Nickels et al. (2017a), Chen et al. (2017b)
<i>anteiso</i> -Branched-chain fatty acids (<i>anteiso</i> -BCFAs)		Decrease, low BCFAs/SCFAs	Choi et al. (2000), Nickels et al. (2017a, b), Chen et al. (2017b)

^a Source: <https://pubchem.ncbi.nlm.nih.gov/>

and an increased level of USFAs (Silbert et al. 1973; Kaneda 1977; Chen et al. 2017b; Hong et al. 2017). In other words, TCDD-exposed bacteria exhibit a specific lipidic “signature” due to the presence of BCUFAs. The creation of such signatures can be explained by the activation of membrane-bound desaturases that act on existing branched-chain saturated FAs (BCSFAs) to produce their corresponding BCUFAs. Importantly, this lipidic “signature” was absent in bacteria grown in catechol, an intermediate of the TCDD-biodegradation pathway, suggesting that the BCUFA “signature” is specific to dioxins. In line with this, molecular and biochemical evidence have demonstrated that *B. subtilis* can respond rapidly to thermal changes by desaturation of existing FAs leading to a rapid modulation of membrane fluidity (Aguilar et al. 2001).

The accumulation of certain types of FAs in *B. megaterium* A14K as a function of dioxin exposure raises the question of their subsequent metabolizing systems and particularly about the roles of cytochrome P450 monooxygenases. In this regard, TCDD-grown *B. megaterium* A14K showed enhanced levels of P450_{BM-1}, the smallest but the most abundant FA monooxygenase in *B. megaterium* (Schwalb et al. 1985). This highlights the roles of such monooxygenases in bacterial responses to TCDD and also their possible TCDD-induced subcellular targeting because these supposedly soluble enzymes also contain a putative transmembrane domain (Williams et al. 2000; Xiao et al. 2018). Interestingly, a similar scenario is found in plants and animals where the involvement of FA-metabolizing enzymes and their targeting into cytosolic lipid droplets as dioxin-responsive elements have been demonstrated (Lakshman et al. 1988, 1989; Al-Bayati and Stohs 1987, 1991; al-Bayati et al. 1988; Hanano et al. 2015b, 2016a). Together, these studies indicate that TCDD-exposed bacteria exhibit a specific profile of oxygenated FAs typified by high levels of hydroxylated and epoxidized FAs synthesized via TCDD-induced P450_{BM-1} and possibly other monooxygenases (Harmsen et al. 2005; Narhi and Fulco 1987; Ruettinger and Fulco 1981; Schwalb et al. 1985).

Oxygenated FAs, also termed oxylipins, are well known as essential molecules enabling animals, plants and microorganisms to respond to various forms of biotic and abiotic stress (Mohammadpour et al. 1988; Bestervelt et al. 1994; Hanano et al. 2018d). In microorganisms, oxylipins play crucial roles in regulating the biosynthesis of secondary metabolite (Hanano et al. 2018a, 2019a), as well as the production of biosurfactants and their emulsifying activity towards hydrophobic compounds (Hanano et al. 2014a, 2015c, 2017, 2019b). Oxylipins have also roles in altering bacterial membrane fluidity as a function of environmental stress (Denich et al. 2003). For

these reasons, the signatures of the various FAs and their metabolites have been proposed to be used as biomarkers for biomonitoring the exposure of animals, plants and soil microorganisms to dioxins (Hiraishi et al. 2003a; Basompierre et al. 2007; Hanano et al. 2018d, 2019b).

Soil fungi can also be exposed to soil contaminants, such as dioxins, and hence could be used to assess their toxicity and possibly their biodegradation (Miao et al. 2020; Bilal et al. 2019). The in vitro exposure of a soil-dwelling strain of the fungus *Aspergillus flavus* to dioxin results in a phenotype typified by a reduction in vegetative growth and a tendency to conidiation, which has similarities with the ‘wasting syndrome’ observed in animals experimentally exposed to TCDD (Tuomisto et al. 1995; Tsujimoto et al. 2013; Hutin et al. 2018; Hanano et al. 2019a). Furthermore, dioxin-exposed fungi exhibit an unusual cellular FA profile (Hanano et al. 2019a). This dioxin-specific FA pattern in fungal cells is related to an enhanced level of a lipid-binding caleosin/peroxygenase, called AfPXG, which catalyzes the reduction of FA hydroperoxides (FA-OOH) to their corresponding alcohols (AF-OH), similarly to the action of orthologous caleosin/peroxygenases in plants (Hanano et al. 2006, 2018c). The biological impacts of such peroxygenase activity in oxylipin biosynthesis pathway have been well characterized in plants (Blee et al. 2014; Charuchinda et al. 2015), but much less in fungi (Fan et al. 2015). However, an *AfPXG* gene knockout in *A. flavus* resulted in a considerable accumulation of FA-OOH in fungal tissues combined with developmental anomalies and a reduced level of aflatoxin production (Hanano et al. 2015a).

Beside of its enzymatic activity, AfPXG has a structural role in cellular lipid droplet (LD) assembly. Caleosin-encoding genes are present in many, but not all, publicly available fungal genomic sequences including all *Aspergillus* sp. The encoded caleosin protein sequences harbor at least one copy of a highly conserved lipid-binding domain enabling the proteins to be integrated into the monolayer membrane of LDs as well as into conventional bilayer membranes (Murphy 2012; Rahman et al. 2018; Hanano et al. 2015a). The structural role of fungal caleosins in impacting the assembly and the stability of LDs is well demonstrated (Froissard et al. 2009; Jamme et al. 2013; Ortiz-Urquiza et al. 2016; Zhu et al. 2015; Zeng et al. 2017). In connection with exposure to dioxin, TCDD-exposed fungi expressed more AfPXG and accumulated more LDs than controls, which probably aids the fungal cells to sequester dioxin into LDs. Similar induction of caleosin isoforms was also reported in plants experimentally exposed to TCDD (Hanano et al. 2016b, 2018d). These data highlight the possible effects of dioxins on aflatoxicogenicity of *A. flavus*. The presence

of fungal-derived toxins could be a major problem in certain foods, with implications for human health and also for wider food security. In conclusion, soil microbes directly exposed to dioxins experience significant but predictable changes to their cellular lipid metabolism and their subsequent lipid profiles. Such alterations can assist in the identification of dioxin-specific lipid biomarkers in soil microorganisms as a part of strategies to monitor, control and remediate such contaminants.

Effects of dioxins on cell membrane lipids

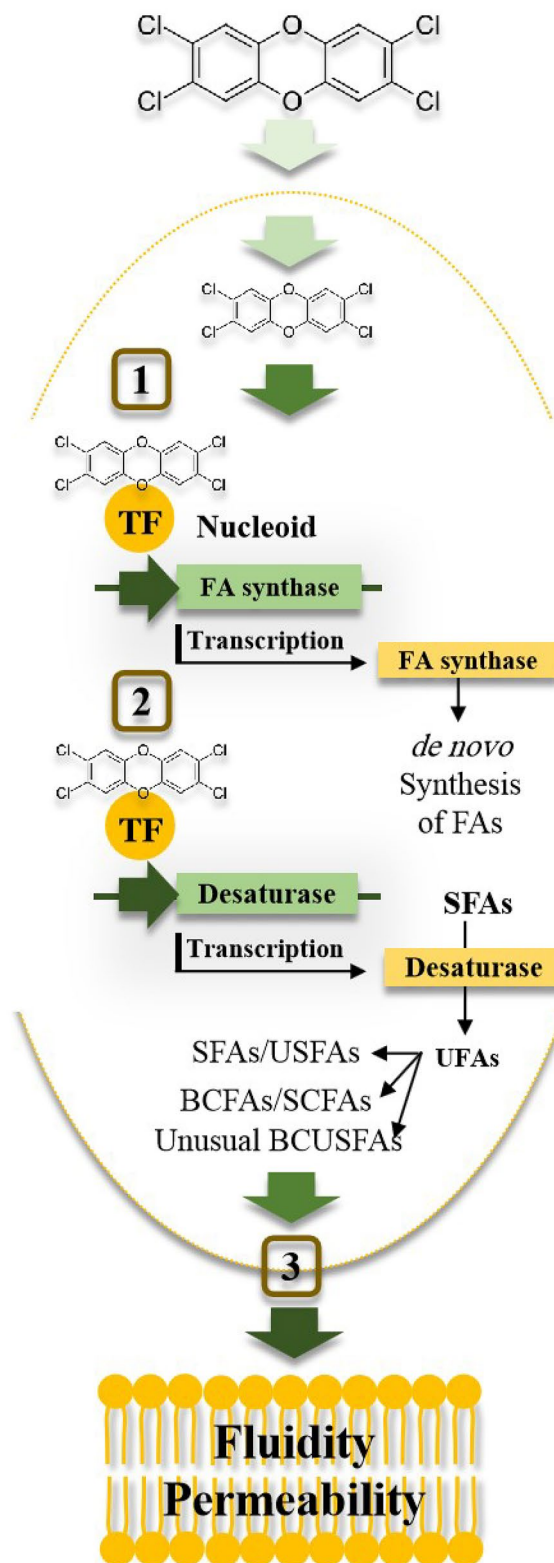
Bacterial cell membranes have important homeostatic functions in maintaining optimal intercellular conditions for metabolism and energy transduction. To achieve this, bacteria can dynamically modify the structure of their cell membrane as a function of environmental changes. The modulation of membrane lipid composition is the most common adaptive strategy used by soil microorganisms for responding to environment changes such as temperature and pH, a phenomenon known as homeoviscous adaptation (Di Pasqua et al. 2006; Heipieper et al. 2003; Holtwick et al. 1999; Russell and Fukunaga 1990). Unlike eukaryotes, bacteria can modulate membrane fluidity by changing the proportion of *iso*- and *anteiso*-branched FAs, by isomerization of *cis* unsaturated FAs (UFAs) to corresponding *trans* isomers, and also by altering the average FAs chain length, protein binding, and overall FA composition (Fujita et al. 2007; Fulco 1983).

Lipids have many important functions in microbial cells, both as membrane components and more broadly as metabolic intermediates (Cronan and Gelmann 1975; Fulco 1983; Russell and Fukunaga 1990). In particular, lipids are involved in environmental sensing and adaptation; hence variations in temperature, pH, ethanol concentration, salts, irradiation, antibiotics and toxic compounds, that affect microbial growth and transition to the stationary phase, can also lead to alteration in FAs content and membrane viscosity (Russell 1984). For example, there is a universally conserved microbial adaptive response in modulating FAs unsaturation to adjust membrane fluidity (Suutari et al. 1990; Suutari and Laakso 1994; Hanano et al. 2015d, 2019b; Loffeld and Keweloh 1996; Keweloh and Heipieper 1996). The lipophilic character of dioxins enables them to partition into the lipid bilayer of bacterial cell membranes, disturbing the overall lipid and protein packing, hence rendering the membrane more permeable (Evans et al. 1998; Bayer et al. 2000; Mrozik et al. 2004). It was found that the total FA content and the percentage of membrane PUFAs, notably C16:2 and C18:2, were significantly increased in a strain of baker's yeast, *Saccharomyces cerevisiae*, grown on aromatic hydrocarbons (Hanano et al. 2015d). This adaptive modification proceeded at two levels. Quantitatively,

the increase of total FAs is explained by activation of FA biosynthesis from correspondingly terminally hydroxylated alkanes that are accumulated proximately to the endoplasmic reticulum via adjacent peroxisomal fatty alcohol oxidases and fatty aldehyde dehydrogenases (Fukui and Tanaka 1981). On the other hand, increases in PUFAs can be explained by their architectural necessity in the cell membrane to enhance its fluidity. Several reports have suggested that *S. cerevisiae* increases unsaturated FAs in the membrane and this increases membrane fluidity in the presence of alcohols (Kim et al. 2011). As *S. cerevisiae* does not naturally produce polyunsaturated FAs (Ratledge and Wynn 2002), the appearance of PUFAs, notably C16:2 and C18:2, in aromatic hydrocarbon-grown yeast is surprising. Although *S. cerevisiae* produces monounsaturated FAs of 16- and 18-carbons via a $\Delta 9$ -desaturase, which is capable of producing C16:1 and C18:1 (Stukey et al. 1989), other species of *Saccharomyces* such as *S. kluyveri* can produce di-unsaturated FAs C16:2 and C18:2 via a $\Delta 12$ -desaturase (Kainou et al. 2006). However, the presence of new isoforms of desaturase in yeast grown with aromatic hydrocarbons remains to be demonstrated. A similar adaptive scenario was recently reported for TCDD-exposed *B. megaterium* A14K that exhibited a specific lipidic "signature" due to the presence of branched-chain unsaturated fatty acids (BCUFAs) (Hanano et al. 2019b). This suggests a possible activation of membrane-bound desaturases that act on existing branched-chain saturated FAs (BCSFAs) in cell membrane to produce the corresponding BCUFAs, which are tentatively considered as lipid biomarkers to dioxin exposure (Hanano et al. 2019b).

As reported by Russell (1984), the mechanisms by which bacterial cells can alter the unsaturation ratio of membrane FAs depend on the mechanism of FA biosynthesis. The author described two distinct and mutually exclusive UFAs biosynthetic pathways in bacteria, an anaerobic and an aerobic pathway. The former is used by anaerobes and some facultative aerobes and produces UFAs by de novo synthesis through the action of a FA synthase (de Mendoza et al. 1983; Russell 1984). The latter produces only saturated FAs, via multisubunit membrane desaturase enzymes (Russell 1997). Figure 1 summarizes the possible cellular and molecular pathways by which dioxins can impact the synthesis of FAs, and subsequently, the composition of cell membrane, modifying its fluidity and permeability. On the other hand, adaptation to pH in *Escherichia coli* and *Salmonella enterica* resulted in a decrease of UFA content, suggesting that the mechanism depends on the type of stressor (Yuk and Marshall 2004; Chiou et al. 2004). Increased FA length is another important membrane alteration to increase survival in acidic environments and a similar mechanism

Fig. 1 Schematic model of molecular and biochemical impacts of dioxins on lipid biosynthesis and cell membrane composition in soil microorganisms. Due to their extreme lipophilicity, dioxins show a high affinity towards cellular lipids. After their uptake, dioxins can affect the metabolism of microbial FAs by two distinct and mutually exclusive UFA biosynthetic pathways in bacteria, an anaerobic and an aerobic pathway. (1) The first is used by anaerobes and some facultative aerobic microorganisms leading to produce UFAs by de novo synthesis under the action of an FA synthase. (2) The other produces only saturated FAs, via multisubunit associated-membrane desaturases. This generally modifies the composition of cellular FAs leading to decreasing ratios of saturated FAs/unsaturated FAs (SFAs/USFAs), branched-chain FAs/straight chain FAs (BCFAs/SCFAs). It also leads to the generation of an unusual FAs such as branched-chain unsaturated FAs (BCUSFAs), which enhances the fluidity and permeability of the cell membrane. The spectrum of unusual FAs produced as part of dioxin responses in these bacteria gives rise to specific “lipidic signatures” that can be used as part of diagnostic and remediation strategies to address such environmental pollutants



probably occurs when the cells grow in the presence of antimicrobial compounds. In *E. coli* O157:H7, short-medium chain FAs (C4–C14) and long chain FAs (C20–C22) were either absent or present in low concentrations under control conditions (Fozo and Quivey 2004a, b).

Biotechnological strategies and future prospects

The ultimate goal of research into microbe–contaminant interactions is to identify microbes that can effectively take up, metabolize, and thus minimize the environmental concentration of contaminant, a process known as biodegradation (Gavrilescu and Chisti 2005; Wagner et al. 2002). Most research into biodegradation involves a “single-microorganism” strategy. However, selection of the “best” microorganism that removes a given contaminant from the environment in a “perfect” manner remains a big challenge. Indeed, identifying the “best” microorganism is often frustrating because of the traditional culturing methods of microorganisms that did not guarantee a full success. This process is applied particularly to culturable microorganisms, although it is estimated that only 0.1–10% of soil microorganisms can be cultured *in vitro*. Therefore, traditional laboratory-based approaches provide very limited information on the true diversity of soil microbial community and hence the potential utility of hitherto uncultivated species (Kalivas et al. 2017; Kakirde et al. 2010; Shen et al. 2007).

It is therefore necessary to ‘think outside the box’, for example where modern environmental metagenomics is revealing a huge diversity of hitherto undiscovered and uncultivated soil-dwelling species that might have interesting biotechnological properties for removing of contaminants. In this regard, it was interestingly shown that archaea have novel ether-based FAs, rather than the ester-based FAs found in bacteria and eukaryotes. Archaeal membranes containing such ether-based lipids are known to have uniquely resilient properties allowing their adaptation to many forms of environmental stresses, including highly extreme stresses (Gurr et al. 2016).

Another challenge is selecting a microbe in a natural environment, where it is quite hard to predict its biological/functional behavior in different habitats and as part of a wider microbial community at a given environmental site (Koelmel et al. 2020). In this respect, it is worth noting that dioxin biodegradation is a complex biochemical process. This is due to the diversity of dioxin-metabolizing microbial systems, to the biochemical diversity of the enzymes initiating the first step in dioxin biodegradation, and finally to the diversity of environmental factors required by a given microbial species. To minimize this complexity, alternative approaches basing on the culture-independent genomic analysis of microbial communities,

i.e., metagenomics, have been developed (Schloss and Handelsman 2003; Rondon et al. 2000; Shen et al. 2007).

Metagenomics approaches are derived from the statistical concept of meta-analysis (the process of statistically combining separate analyses) and genomics (the comprehensive analysis of an organism’s genetic material) (Rondon et al. 2000). In metagenomics, two complementary approaches, function-driven analysis and sequence-driven analysis, are combined to extract biological information from metagenomics datasets. The former is initiated by identification of clones expressing desired traits, followed by their characterization via sequence and biochemical analysis. This allows a rapid identification of functional clones that have potential involvement in dioxin biodegradation pathways. The sequence-driven analysis approach uses highly conserved DNA sequences to design hybridization probes or PCR primers to screen metagenomics libraries for clones that contain sequences of interest.

Significant discoveries have also emerged from random sequencing of metagenomic clones carrying phylogenetic anchors, such as the *16S rRNA* gene and the archaeal DNA repair gene (*radA*) (Beja et al. 2000a, b, 2001; Quaiser et al. 2002; Schleper et al. 1998; Suzuki et al. 2001), and have provided functional information about the organisms from which these clones were derived. Without doubt, the use of metagenomics for studying interactions between soil microbes and contaminants in general, and dioxins in particular, will considerably assist the screening of soil microbes including bacteria, archaea, viruses and fungi, irrespective of their culturability and taxonomic identities. As a result, it is possible that such approaches could lead to modification of the current conventional microbiological strategy for dioxin degradation based on single microbe-based analysis to a more sophisticated and biologically relevant community-based analysis, thus leading to new strategies for dioxin bio-management.

With respect to dioxin specificity, the use of lipidomics, in combination with metagenomics, can help to better characterize lipidic signatures symptomatic of soil microorganisms subjected to dioxins exposure. To date, the limited number of environmental lipidomics studies does not reflect the potential applicability of this approach in environmental science, rather, it may reflect: (i) an unawareness of lipidomics as a tool for environmental scientists; (ii) the cost of sample analysis using high-resolution mass spectrometers, and (iii) the high-level of bioinformatics expertise needed for data processing and interpretation. Somewhat more controversially, genetically engineered microorganisms have attracted some attention and might be a complementary biotechnological strategy for remediation of dioxin-contaminated

environments. For example, it might be possible to engineer microorganisms with combinations of enzyme systems, such as angular dioxygenase, cytochrome P450, lignin peroxidase, and dehalogenase that could act as efficient dioxin-metabolizing biosystems (Sakaki and Munetsuna 2010).

Conclusions

Soils, and therefore soil microbial communities, can be highly exposed to dioxin contamination. Due to their extreme lipophilicity, dioxins tend to mostly affect lipid metabolism in exposed microbes, leading to the production of dioxin-specific “signatures” of specific cellular FAs, and the modulation of the FA composition of cell membranes. This review emphasizes the importance of lipidic signatures in term of their specificity and consequent ability for use as tools to assess and monitor the exposure of soil microbes to dioxins. It also underlines the use of metagenomics coupled with lipidomics as potentially powerful approaches to providing an overall image of the lipidic responses of soil microbial communities after exposure to dioxins. It finally suggests that effective remediation strategies for dioxins in contaminated soil require approaches based on community dynamics rather than targeting single microbes. Future biotechnological approaches for biosensing and bioremediation of dioxin-contaminated environments will be greatly facilitated by use of data provided by such metagenomic/lipidomic approaches.

Abbreviations

PCDDs: Polychlorinated dibenzodioxins; PCDFs: Polychlorinated dibenzofurans; POPs: Persistent organic pollutants; TCDD: Tetrachlorodibenzo-*p*-dioxin; PCDD/Fs: Polychlorinated dibenzo-*p*-dioxin/furans; TEF: Toxic equivalency factor; KOC: Organic carbon–water partition; Kow: Octanol/water partition coefficients; Koa: Octanol/air partition coefficients; FAs: Fatty acids; TEQ: Toxic equivalent; PCBs: Polychlorinated biphenyls; LogP: Partition coefficient; BCFAs/SCFAs: Branched-chain/straight chain FAs; SFAs/USFAs: Saturated/unsaturated FAs; BCUFAS: Branched-chain unsaturated FAs; AfPXG: Caleosin/peroxygenase; LDs: Lipid droplets; radA: Archaeal DNA repair gene.

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