Enzymes and genes involved in aerobic alkane degradation

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INTRODUCTION

Various microorganisms, including bacteria, filamentous fungi and yeasts, can degrade alkanes (van Belen et al., 2003; Wentzel et al., 2007; Wang et al., 2006). Alkanes are major constituents of crude oil. They are also present at low concentrations in diverse non-contaminated because many living organisms produce them as chemo-attractants or as protecting agents against water loss. Alkane degradation is a widespread phenomenon in nature. The numerous microorganisms, both prokaryotic and eukaryotic, capable of utilizing alkanes as a carbon and energy source, have been isolated and characterized. This review summarizes the current knowledge of how bacteria metabolize alkanes aerobically, with a particular emphasis on the oxidation of long-chain alkanes, including factors that are responsible for chemotaxis to alkanes, transport across cell membrane of alkanes, the regulation of alkane degradation gene and initial oxidation.

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Keywords: alkane degradation, hydroxylation, monoxygenase, regulations of gene expression, chemotaxis, transporter, AlmA, LadA

CHEMOTAXIS TO LINEAR ALKANES

Chemotaxis facilitates the movement of microorganisms toward or away from chemical gradients in the environment, and this process plays a role in biodegradation by bringing cells into contact with degradation substrates (Parales and Harwood, 2002; Parales et al., 2008). Alkanes are sources of carbon and energy for many bacterial species and have been shown to function as chemo-attractants for certain microorganisms. A bacterial Flavimonas oxydans isoleucinate isolate that was obtained from soil contaminated with gas oil was shown to be chemotactic to gas oil and hexadecane (Lanfranconi et al., 2003). Similarly, Pseudomonas aeruginosa PAO1 is chemotactic to hexadecane (Smith et al., 2003). The tlpS gene, which is located downstream of the alkane hydroxylase gene alkB1 in the PAO1 genome, is predicted to encode membrane-bound methyl-accepting chemotaxis proteins (MCP) that may play a role in alkane chemotaxis (Smith et al., 2003), although no experimental evidence exists. Similarly, the gene alkN is predicted to encode an MCP that could be involved in alkane chemotaxis in Pseudomonas putida G51 (van Belen et al., 2001). Our recent investigation of the genome sequence of Alcanivorax borkumensis B-5 (Lai et al., 2012) identified the alkane chemotaxis machinery of Alcanivorax, which consists of eight cytoplasmic chemotaxis proteins that transmit signals from the MCP proteins to the flagellar motors (Figure 1). This chemotaxis machinery is similar to that of Escherichia coli (Parales and Ditty, 2010). However, further investigation is necessary to confirm the mechanism of alkane chemotaxis in Alcanivorax borkumensis B-5.

m ALKANE UPTAKE IN BACTERIA

Although the genes and proteins that enable the passage of aromatic hydrocarbons across the bacterial outer membrane have been identified (van den Berg, 2005; Mooney et al., 2006; Hearn et al., 2008), the active transport mechanisms involved in alkane uptake remain unclear. Previous reviews (Rojo, 2010) discussed the observation that direct uptake of alkane molecules from the water phase is only possible for low molecular weight alkanes,
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FIGURE 1 | Schematic diagram of the chemosensory signaling system of A. dieselolei B-5. (A) MCP dimers with associated CheW and CheA proteins are shown in the presence (left) and absence of alkane (right). Cells responding to a gradient of attractant will sense the attractant bound to the periplasmic side of the cognate MCP and will continue swimming in the favorable direction due to the inability of CheA to autophosphorylate. In the absence of CheA-P, CheY remains in the inactive unphosphorylated state, and swimming behavior remains unchanged. Cells swimming down a gradient of attractant will sense the decrease in attractant concentration due to decreased occupancy of the MCPs. Under these conditions, the MCPs undergo a conformational change that is transmitted across the cytoplasmic membrane and stimulates CheA kinase activity. CheA-P phosphorylates CheY, which in its phosphorylated state binds to the FliM protein in the flagellar motor and causes a change in the direction of flagellar rotation allowing the cell to randomly reorient and swim off in a new direction.

Dephosphorylation of CheYP is accelerated by the CheZ phosphatase. Under all conditions, the constitutive methyltransferase CheR methylates specific glutamyl residues on the cytoplasmic side of the MCP. Methylated MCPs stimulate CheA autophosphorylation, thus resetting the system such that further increases in attractant concentration can be detected. The methyltransferase, CheB, becomes active when it is phosphorylated by CheA-P CheB-P competes with CheF and removes methyl groups from the MCPs. CM, cytoplasmic membrane. (B) Organization of chemotaxis genes involved in alkane metabolism in A. dieselolei B-5. The detailed information of the ORFs of MCP gene cluster is presented. MCP, methyl-accepting chemotaxis protein; CheY-1, CheY-like receiver protein; CheY-2, CheY-like receiver protein; CheW-1, CheW-like protein, signal transduction protein; CheW-2, Chemotaxis protein, signal transduction protein; CheA, CheA signal transduction histidine kinase; CheB, CheB methylesterase; CheR, CheR methyltransferase.

which are sufficiently soluble to facilitate efficient transport into cells. For medium- and long-chain n-alkanes, microorganisms may gain access to these compounds by adhering to hydrocarbon droplets (which is facilitated by the hydrophobic cell surface) or by surfactant-facilitated access, as reviewed by Rojo (2009). Surfactants have been reported to increase the uptake and assimilation of alkanes, such as hexadecane, in liquid culture (Beal and Betts, 2000; Noordman and Janssen, 2002), but their exact role in alkane uptake is not fully understood. Bacteria that are capable of oil degradation usually produce and secrete surfactants of diverse chemical nature that allow alkane emulsification (Yakimov et al., 1998; Peng et al., 2007, 2008; Qiao and Shao, 2010; Shao, 2010). Based on our understanding of biosurfactant structure and the mechanism of outer membrane transport, we speculate that biosurfactants may be excluded from entering the cell and remain in the extracellular milieu.

In P. putida, alkL in the alk operon is postulated to play an important role in alkane transport into the cell (van Beilen et al., 2008).
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2004; Hearn et al., 2009). Transcriptome analysis of A. borkumensis Sk2 revealed that the alkane-induced gene blc, encoding the outer membrane lipoprotein Blc, might be involved in alkane uptake because it contains a so-called lipocalin domain (Sabirova et al., 2011). When this domain contacts organic solvents, a small hydrophobic pocket forms and catalyzes the transport of small hydrophobic molecules. More recently, our genome analysis (Lui et al., 2012) and closer examination of A. dieselolei B-3Suggested that three outer membrane proteins that belong to the long-chain fatty acid transporter protein (FadL) family are involved in alkane transport (unpublished). The FadL homologs are present in many bacteria that are involved in the biodegradation of xenobiotics (van den Berg, 2005), which are usually hydrophobic and probably enter cells by a mechanism similar to that employed for long-chain (LC) fatty acids by FadL in E. coli.

DEGRADATION PATHWAYS OF n-ALKANES

The initial terminal hydroxylation of n-alkanes can be carried out by enzymes that belong to different families. Microorganisms degrading short-chain length alkanes (C2–C4, where the subindex indicates the number of carbon atoms of the alkane molecule) have enzymes related to methane monoxygenases (van Beilen and Funhoff, 2007). Strains degrading medium-chain length alkanes (C5–C12) frequently contain soluble cytochrome P450s and integral membrane non-heme iron monoxygenases, such as AlkB (Rojo, 2009; Austin and Groves, 2011).

Interestingly, alkane hydroxylases of long-chain length (LC-) alkanes (> C18) are unrelated to the above alkane hydroxylases as characterized recently. One such hydroxylase, AlmA, is an LC-alkane monoxygenase from Acinetobacter. A second hydroxylase is LadA, which is a thermophilic soluble LC-alkane monoxygenase from Geobacillus (Feng et al., 2007; Throne-Holst et al., 2007; Wentzel et al., 2007).

The almA gene, which encodes a putative monoxygenase homologous to the flavin-binding family, was identified from Acinetobacter sp. DSM 17674 (Throne-Holst et al., 2007; Wentzel et al., 2007). This gene encodes the first experimentally confirmed enzyme that is involved in the metabolism of LC n-alkanes of C20 and longer. We provided the first evidence that the AlmA of the genus Alcanivorax functions as an LC-alkane hydroxylase, and found that the gene alma in both A. borkumensis A-11-3 and A. dieselolei B-3 strains expressed at high levels to facilitate the efficient degradation of LC n-alkanes (Liu et al., 2011; Wang and Shao, 2012a).

The almA gene sequences were present in several bacterial genera capable of LC n-alkane degradation, including Alcanivorax, Marinobacter, Acinetobacter, and Parvibaculum (Wang and Shao, 2012b). In addition, similar genes are found in other genera such as Oceanovibrio sp. RED65, Rubitomia spp., Mycobacterium spp., Photobacterium sp., Psychrobacter spp., and Nocardioides fuscus DSM10152. However, few of these genes have been functionally characterized.

A unique LC-alkane hydroxylase from the thermophilic bacterium Geobacillus thermodenitrificans NG80-2 has been characterized. This enzyme is called LadA and oxidizes C15–C36 alkanes, generating the corresponding primary alcohols (Feng et al., 2007). The LadA crystal structure has been identified, revealing that LadA belongs to the bacterial luciferase family, which is two-component, flavin-dependent oxygenase (Li et al., 2008). LadA is believed to oxidize alkanes by a mechanism similar to that of other flavoprotein monooxygenases, and its ability to recognize and hydroxylate LC-alkanes most likely results from the way in which it captures the alkane (Li et al., 2008). Therefore, the hydroxylases involved in LC-alkane degradation appear to have evolved specifically, which is in contrast with other alkane monooxygenases such as AlkB and P450.

Interestingly, branched-chain alkanes are thought to be more difficult to degrade than linear alkanes (Purnik et al., 1974). However, Alcanivorax bacteria efficiently degrade branched alkanes (Hara et al., 2003). In A. borkumensis Sk2, isoprenoid hydrocarbon (phytane) strongly induces P450 (a) and alkB2 (Schneiker et al., 2006). In a previous report, we found that both pristane and phytane activate the expression of alkB1 and almA in A. dieselolei B-3 (Liu et al., 2011). In A. hongdengensis A-11-3, we recently found that pristane selectively activates the expression of alkB1, P450-3 and almA (Wang and Shao, 2012a). However, the metabolic pathways that mediate this activity are poorly understood, although they may involve the α- or β-oxidation of the hydrocarbon molecule (Weikinmon and Morgan, 1990).

REGULATION OF ALKANE-DEGRADATION PATHWAYS

The expression of the bacterial genes involved in alkane assimilation is tightly regulated. Alkane-responsive regulators ensure that alkane degradation genes are induced only in the presence of the appropriate hydrocarbons. Many microorganisms (Rojo, 2009; Austin and Groves, 2011) contain several sets of alkane degradation paths, each one being active on a particular kind of alkane or being expressed under specific physiological conditions. In these cases, the regulatory mechanisms should assure an appropriate differential expression of each set of enzymes. The regulators that have been characterized belong to different families, including LuxR/MalT, AraC/XylS, and other non-related families (Table 1).

REGULATION OF THE ALKANE DEGRADATION PATHWAY IN Pseudomonas spp.

Pseudomonas butanovora species oxidize C2–C8 n-alkanes into the corresponding alcohols with an alkane monooxygenase termed butane monooxygenase (BMO). BMO is a multimeric protein that is formed by the products of the bmoXTRZDC operon (Shao et al., 2002). The expression of the genes encoding BMO is activated by BmOR, a β3-dependent transcriptional regulator that recognizes alcohols and aldehydes derived from the C2–C8 n-alkanes that are substrates of BMO, although BmOR does not recognize the alkanes themselves (Kurth et al., 2008). In P. putida GP1, the OCT plasmid encodes all of the genes required for the assimilation of C2–C13 alkanes (van Beilen et al., 1994, 2004; Johnson and Hyman, 2006). The genes in this pathway are grouped into two clusters, alkRFGHKL and alkST (van Beilen et al., 1994, 2001). The alkRFGHKL operon is transcribed from a promoter named PalkR, whose expression requires the transcriptional activator AlkS and the presence of alkanes (Kok et al., 1989; Panke et al., 1999). An AlkS-dependent reporter system based on a PalkR-luxAB fusion showed that C12–C14 alkanes are efficient activators of the AlkS regulator (Sticher et al., 1997). When alkanes become available, AlkS binds and represses PalkR more efficiently.
than it does in the absence of alkanes. From this binding site, AlkS activates the PuikS2 promoter, resulting in high expression of the alkST genes (Canosa et al., 2000). Therefore, this pathway is controlled by a positive feedback mechanism that is driven by AlkS.

**REGULATION OF THE ALKANE DEGRADATION PATHWAY IN Alcanivorax spp.**

A gene similar to alkS in P. putida GPO1 is located upstream of alkB1 in A. borkumensis SK2, and AlkS is predicted to be an alkane-responsive transcriptional activator. The expression level of AlkS in strain SK2 cells grown in hexadecane is higher than that of pyruvate-grown cells (Sabirova et al., 2006). Evidence suggests that in A. borkumensis, AlkS activates the expression of alkB1, a gene that encodes an alkane hydroxylase, in response to alkanes. However, it is unlikely that AlkS regulates the expression of alkB2, despite the induction of this gene in response to alkanes (van Beljen et al., 2006). Interestingly, a gene encoding a transcriptional regulator belonging to the GntR family is located immediately upstream of alkB2; however, its role in alkB2 expression has not been reported. A. borkumensis has three genes encoding cytochrome P450 of the CYP153 family (Schnieker et al., 2006). A gene encoding a transcriptional regulator belonging to the AraC family is located immediately upstream of alkB2, however, its role in alkB2 expression has not been reported. A. borkumensis has three genes encoding cytochrome P450 of the CYP153 family (Schnieker et al., 2006). A gene encoding a transcriptional regulator belonging to the GntR family is located immediately upstream of alkB2, however, its role in alkB2 expression has not been reported. A. borkumensis has three genes encoding cytochrome P450 of the CYP153 family (Schnieker et al., 2006).

In A. hongdengensis, a gene downstream of alkB1 encodes a protein that is similar to TetR family transcriptional regulators (Wang and Shao, 2012a). In addition, a gene encoding a transcriptional regulator belonging to the GntR family is located just upstream of alkB2, although its role in the regulation of alkB2 is not known (Wang and Shao, 2012a). Genes encoding transcriptional regulators belonging to the AraC family are located near P450-1 and P450-2 (Wang and Shao, 2012a). Similar to many of the genes described above, their role in the regulation of the corresponding P450 genes requires further investigation.

Three regulators that are involved in alkane degradation were identified in the A. dieselolei strain B-5 genome sequence, and they belong to different MerR and AraC families (Table 1). Regulatory genes are located upstream of alkB1 and P450, and the proteins encoded by these genes are 46 and 64% similar to MerR and AraC from P. aeruginosa and A. borkumensis SK2, respectively (Liu et al., 2011). Downstream of alkB2, there is a gene encoding a transcriptional regulator that shares 61% similarity with AraC from Marinobacter sp. ELB17 (Liu et al., 2011). Therefore, Alcanivorax strains usually encode multiple alkane hydroxylases that are expressed under the control of different regulators encoded in the same gene cluster as the monoxygenase gene. Our lab is using strain B-5 as a model system to study how cells modulate the expression of these genes in response to different alkanes with varied chain lengths.

**GLOBAL REGULATION OF THE ALKANE DEGRADATION PATHWAY**

The expression of alkane degradation pathway genes is often downregulated by complex global regulatory controls that ensure that the genes are expressed only under the appropriate physiological conditions or in the absence of any preferred compounds.

### Table 1

| Bacterium | Gene | Family | Effector | Evidence | Reference |
|-----------|------|--------|----------|----------|-----------|
| P. putida | alkS | Lrp/MatT | C2–C6 n-alkanes | Direct | Sticher et al. (1997) and Panke et al. (1999) |
| A. borkumensis | alkS | Lrp/MatT | Not tested | Similarity | van Beilen et al. (2001) |
| A. borkumensis | alkR | GntR | Not tested | No | Schnieker et al. (2006) |
| A. borkumensis | araC | AraC/XylS | Not tested | No | Schnieker et al. (2006) |
| A. borkumensis | apr1 | Lrp/MatT | Not tested | Similarity | van Beilen et al. (2004) |
| A. hongdengensis | merR | TetR | Not tested | Similarity | Wang and Shao (2012a) |
| A. hongdengensis | arac1 | AraC/XylS | Not tested | Similarity | Wang and Shao (2012a) |
| A. hongdengensis | arac2 | AraC/XylS | Not tested | Similarity | Wang and Shao (2012a) |
| A. dieselolei | merR | MerR | C14–C26 n-alkanes | Similarity | Liu et al. (2011) |
| A. dieselolei | arac1 | AraC/XylS | C12–C26 n-alkanes | Similarity | Liu et al. (2011) |
| A. dieselolei | arac2 | AraC/XylS | C10–C26 n-alkanes | Similarity | Liu et al. (2011) |
| P. butanovora | bmrR | Xre-Dependent | C2n–C6 n-alkanes | Direct | Kurth et al. (2008) |
| P. aeruginosa | gntR | GntR | C3–C5 n-alkanes | Indirect | Marín et al. (2003) |
| Acinetobacter sp. ADP1 | alkR | AraC/XylS | C5–C10 n-alkanes | Direct | Retajczak et al. (1998) |
| Acinetobacter sp. M1 | alkR | AraC/XylS | ≥C10 n-alkanes | Indirect | Tani et al. (2001) |
| Acinetobacter sp. M1 | alkR | OnR | C2n–C7 n-alkanes | Indirect | Tani et al. (2001) |
(Rojo, 2009). Two global regulatory networks exist. One network relies on the global regulatory protein Crc (Yu and Rojo, 2001), while the other network receives information from cytochrome o ubiquinol oxidase (Cyo), which is a component of the electron transport chain (Dinamarca et al., 2002, 2003).

The Crc is an RNA-binding protein that interacts with the 5′ end of the alkS mRNA, inhibiting translation (Moreno et al., 2007). A recent study further showed that Crc inhibits the induction of thealkane degradation pathway by limiting not only the translation of their transcriptional activators but also that of genes involved in the entire alkane degradation pathway in P. putida (Hernández-Arranz et al., 2013). In addition, results of this study suggest that Crc follows a multi-step strategy in many cases, targeting the upstream regulations and the long-chain length alkane oxidation.

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CONCLUDING REMARKS

Research in the last few years has resulted in many new insights into the mechanism of alkane degradation by microorganisms, including the upstream regulations and the long-chain length alkane oxidation. Investigations using “omics” strategies will help us to better understand the global metabolic networks within a microbial cell and the overall process of bacterial alkane-dependent chemotaxis, alkane transport, gene expression regulation and complete mineralization.

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