CHAPTER 10

METABOLISM OF SUBSTRATES OTHER THAN GLUCOSE

UTILIZATION OF SUGARS OTHER THAN GLUCOSE

Glucose is the preferred carbon source for most of the common heterotrophic bacteria. Nevertheless, microorganisms possess remarkable versatility in their ability to use a wide range of other compounds as sources of carbon and energy. Most (if not all) of these pathways invariably lead to the production of intermediates that can enter one of the central pathways described in Chapter 8 (i.e., EMP, Entner-Doudoroff, pentose shunt, TCA cycle, or glyoxylate cycle). Many of these alternate carbon sources are utilized only after a period of induction of the enzymes required for their transport and metabolism. The presence of glucose in the growth medium generally inhibits the expression of catabolic enzymes for these substrates.

Monod first described this glucose effect in 1947 for the inhibition of β-galactosidase synthesis in *Escherichia coli*, and in 1961 Magasanik coined the term catabolite repression for this phenomenon. In media containing glucose and another carbohydrate, bacteria exhibit two complete growth cycles (diauxic growth) separated by a lag period. Glucose prevents entry of the second substrate by a process known as inducer exclusion and represses induction of the genes coding for the enzymes required for utilization of the second substrate. The details of the genetic regulation of carbohydrate metabolism are in Chapter 5.

**Lactose**

In *E. coli*, lactose utilization requires the induction, under the control of the lac operon, of a specific permease for its transport, and β-galactosidase, the enzyme that cleaves it to form D-galactose and D-glucose (Fig. 10-1). The D-galactose is phosphorylated to galactose-1-phosphate and metabolized via the Leloir pathway to yield fructose-6-phosphate (Fig. 10-2). Fructose-6-phosphate is ultimately utilized via the EMP pathway.
UTILIZATION OF SUGARS OTHER THAN GLUCOSE

**Fig. 10-1.** Lactose utilization in *E. coli.*

**Fig. 10-2.** The tagatose and Leloir pathways of galactose utilization.
Some organisms, such as *Lactobacillus casei*, do not contain the *lac* operon system but possess a PEP phosphotransferase system (PTS) that phosphorylates lactose via a specific enzyme II (see Chapter 5). The intracellular lactose is split by phospho-β-galactosidase to yield glucose and galactose-6-phosphate. Galactose-6-phosphate is metabolized via the tagatose-6-phosphate pathway to yield glyceraldehyde-3-phosphate and dihydroxyacetone phosphate (Fig. 10-2). In both cases, the D-glucose is metabolized via the EMP pathway. In *Staphylococcus aureus*, the tagatose-6-phosphate pathway is required for the utilization of galactose as well as lactose. Strains of *Klebsiella* lacking both *lac* and *gal* operons (*Lac−Gal−*) give rise to lactose-utilizing mutants that transport lactose via the PEP-PTS and metabolize lactose via phospho-β-galactosidase. The resultant galactose-6-phosphate is metabolized via the tagatose phosphate pathway.

**Galactose**

The inducible enzyme system required for galactose utilization in *S. cerevisiae* is under the control of a complex system of structural and regulatory genes that includes a galactose permease (encoded by *GAL2*) and three enzymes of the Leloir pathway: galactokinase, galactose-1-phosphate uridylyltransferase, and uridine diphosphoglucose-4-epimerase encoded by the structural genes *GAL1*, *GAL7*, and *GAL10*. The enzyme phosphoglucomutase converts glucose-1-phosphate to glucose-6-phosphate, which then enters the glycolytic pathway. The galactose pathway enzymes are coordinately controlled by a positive factor required for the expression of structural genes and a negative factor that interacts with the inducer (galactose) to modulate the function of the positive factor. Expression of the structural genes is controlled by carbon catabolite repression.

**Maltose**

Utilization of maltose, a disaccharide of glucose, by *E. coli* requires the expression of genes concerned with maltose uptake (*malEGF*, *malK*, and *lamB*) and induction of amyloglactase and maltodextrin phosphorylase (encoded by the *malPG* operon). Expression of these genes is induced by maltose and is mediated indirectly by the *malT* activator. The cAMP receptor protein (CRP) binds to cAMP and positively regulates the *malT* gene and the *malEGF* operon. The MalT protein mediates the action of cAMP-CRP on *malPQ* genes. Amyloglactase hydrolyzes maltose with the production of D-glucose and the polysaccharide maltodextrin (Fig. 10-3). Maltodextrin is converted to G-1-P by maltodextrin phosphorylase. With the isomerization of G-1-P to G-6-P by phosphoglucomutase, both products are utilized via the EMP pathway. Similar systems for the utilization of maltose are active in a number of other organisms.

**Mannitol**

Catabolism of mannitol and other hexitols (D-glucitol or sorbitol, and D-galactitol) by *E. coli* involves transport by specific enzyme II's of the PEP-PTS. The phosphorylated derivative is then oxidized to the corresponding sugar phosphate by a specific hexitol phosphate dehydrogenase (Fig. 10-4). The catabolic enzymes for mannitol, glucitol, and galactitol are encoded within three operons (*mtl, gut*, and *gat*) in *E. coli*. All
three operons have the same gene order: a regulatory gene (C), the hexitol-specific enzyme II of the PEP-PTS (A), and the hexitol phosphate dehydrogenase (D). In the case of mannitol, mannitol-1-phosphate is oxidized by a specific NAD-dependent dehydrogenase to yield F-6-P, which enters the EMP pathway. *Bacillus subtilis* transports D-glucitol (sorbitol) through an inducible permease. The free hexitol is oxidized to D-fructose by an inducible glucitol dehydrogenase. D-Fructose then enters the EMP pathway via F-6-P.

Mannitol is also produced as an end product of glucose metabolism in *E. coli*, *Staphylococcus aureus*, *Lactobacillus brevis*, *Leuconostoc mesenteroides*, *Absidia glauca*, and *Rhodococcus erythropolis*. Many organisms utilize a mannitol cycle as a means of regenerating NADP through the NADP-dependent mannitol dehydrogenase that oxidizes mannitol to fructose (Fig. 10-4). The fruiting body of *Agaricus bisporous* accumulates large amounts of mannitol, whereas only low amounts are found in the mycelium. *E. coli* can also convert D-mannitol to D-ribose utilizing a pathway involving the synthesis of ribulose-5-phosphate (Fig. 10-4).

**Fucose and Rhamnose**

*E. coli* uses interesting parallel pathways for L-fucose and L-rhamnose metabolism. These pathways involve the induction of specific permeases, kinases, isomerases, and aldolases (Fig. 10-5). A cluster of genes at 60.2 minutes on the *E. coli* genetic map encodes the enzymes involved in fucose utilization. The *fuc* genes are organized into four operons under the influence of *fucR*, a positive regulatory protein. Fuculose-1-phosphate is a true inducer. The genes for the rhamnose system constitute a well-defined operon, whereas the fucose system maintains the gene for aldolase (*ald*) under separate
control. The pathways converge with the formation of dihydroxyacetone phosphate and lctaldehyde. Dihydroxyacetone phosphate enters the central metabolic pathway at the triose level. Under aerobic conditions an NAD-linked dehydrogenase oxidizes \( L \)-lactaldehyde to \( L \)-lactate and an FAD-linked dehydrogenase oxidizes \( L \)-lactate to pyruvate, which then enters the central pathway. Anaerobically, a single NAD-linked oxidoreductase...

Fig. 10-4. Pathways of metabolism of sorbose and mannitol. In many organisms the mannitol cycle functions as a means of regulating reduced NADP levels.
is induced by either L-fucose or L-rhamnose and serves both pathways. In either case, L-1,2-propanediol is formed and excreted. However, each methyl pentose exerts its influence at a different level. L-fucose is a transcriptional activator of \textit{fucO}, whereas L-rhamnose functions posttranscriptionally. The L-fucose pathway can be recruited for the utilization of 6-deoxy-L-talitol and D-arabinose. Identical systems for the dissimilation of L-fucose and L-rhamnose are present in \textit{S. enterica} and \textit{K. pneumoniae}.

**Mellibiose, Raffinose, Stachyose, and Guar Gum**

These compounds all contain α-1,6-linked galactose residues, as shown in Figure 10-6. Many species of enteric bacteria can ferment mellibiose and raffinose, but relatively few can utilize galactomannans such as guar gum. \textit{Bacteroides ovatus}, an obligately anaerobic resident of the intestinal tract of humans, develops α-galactosidase activity when grown on mellibiose, raffinose, or galactomannan. However, β-D-mannanases,
enzymes that degrade the mannose backbone of guar gum (galactomannan), are produced only during growth on this substrate. The α-galactosidase I differs from the α-galactosidase II produced during growth on melibiose, raffinose, or stachyose.

PECTIN AND ALDOHEXURONATE PATHWAYS

Pectin, a highly methylated form of poly-β-1,4-D-galacturonic acid, is a major constituent of plant cell walls. The ability to degrade pectin contributes to the virulence of bacterial and fungal phytopathogens such as *Erwinia chrysanthemi* and *E. carotovora*, *Moloinia fructigena*, *Cladosporium cucumerinum*, and *Botrytis cinerea*. The rumen bacteria, *Butyrivibrio fibrisolvens* and *Lachnospira multiparus*, provide nutrients to the ruminant animal because of their ability to degrade pectin and cellulose.
Fig. 10-7. Pathways of pectin catabolism in bacteria. The three-letter designation for the structural enzymes are: Pem, pectin methylesterase (PME); polygalacturonate (PGA) lyases (PelA to PelE) are extracellular enzymes. Further degradation of the breakdown products are conducted by: Ogh, oligogalacturonate hydrolase; Ogl, oligogalacturonate lyase; KduI, 4-deoxy-l-threo-5-hexoseulose uronate isomerase; KduD, keto-deoxyuronate dehydrogenase; KdgK, 2-keto-3-deoxygluconate kinase; KdgA, 2-keto-3-deoxy-6-phosphogluconate aldolase; UxaA, altronate hydrolase; UxaB, altronate oxidoreductase; UxaC, uronate isomerase.
Bacteroides thetaiotaomicron, a gram-negative anaerobe found in the human intestinal flora, can also degrade pectin and other plant polysaccharides.

E. chrysanthemi and E. carotovora initiate the degradation of pectin by means of a group of enzymes acting sequentially as shown in Figure 10-7. Pectin methylesterase (Pem) removes methoxyl groups linked to C-6 to yield polygalacturonate, which is degraded by pectate lyases (encoded by pelABCDE) to form unsaturated digalacturonate. Alternatively, an exopolygalacturonase produces digalacturonate. The polygalacturonate residues are then degraded via either of the two alternative pathways that lead to the formation of 2-keto-3-deoxy-6-phosphogluconate (KDPG) as shown in Figure 10-7. This metabolite then follows the Entner-Doudoroff pathway to pyruvate and triose phosphate.

CELLULOSE DEGRADATION

Cellulose is a $\beta$-1,4-linked glucose polymer that occurs in crystalline or amorphous forms and is usually found along with other oligosaccharides in the walls of plants and fungi. Cellulose-digesting microorganisms in the rumen of herbivorous animals are responsible for the ability of ruminants to use cellulose as a source of energy and building blocks for biosynthesis. A major obstacle to economical animal protein production has been the inefficient utilization of cellulose-containing materials by the rumen microflora. The ubiquitous distribution of cellulose in municipal, agricultural, and forestry waste emphasizes the potential use of cellulose for conversion to useful products such as single-cell protein or fermentation products such as methane or alcohol. As a consequence, the degradation of cellulose has been a continuing subject of intense study.

Cellulose degradation requires the combined activities of three basic types of enzymes (Fig. 10-8). Initially, an endo-$\beta$-1,4-glucanase cleaves cellulose to smaller oligosaccharides with free-chain ends. Then exo-$\beta$-1,4-glucanases remove disaccharide cellobiose units from either the reducing or nonreducing ends of the oligosaccharide chains. Cellobiose is then hydrolyzed to glucose by $\beta$-glucosidases.

These cellulolytic enzymes may be produced as extracellular proteins by organisms such as Trichoderma or Phanaerochete (filamentous fungi), or by Cellulomonas, Microbispora, or Thermomonospora (Actinomycetes). Rumen bacteria such as Ruminococcus flavofaciens and Fibrobacter succinogenes, or gram-positive anaerobes such as Clostridium thermocellum, C. cellulosorans, or C. cellulosylicum, produce a cell-bound multienzyme complex called the cellulosome. With the aid of the electron microscope, cellulosomes can be seen as protuberances on the cell surface (Fig. 10-9). The cellulosome of C. cellulosorans contains three major subunits: a scaffolding protein, CipA; an exoglucanase, ExgS; and an endoglucanase, EngE. Also present are endoglucanases EngB, EngL, and EngY, and a mannanase, ManA. The scaffolding protein serves as a cellulose-binding factor. Another component, present in duplicate and referred to as dockerin, mediates the association of cellulose fibers with the scaffolding protein. Various models have been proposed to conceptualize the complex interaction of the cellulosome with cellulose fibers during the digestion process.

A wide diversity of actively cellulolytic organisms is important in industrial applications, in the rumen of animals, and in the digestive systems of arthropods that degrade wood. Termites and other arthropods that degrade wood owe their ability to digest cellulose to the presence of specific microbial symbionts in their digestive tract.
STARCH, GLYCOGEN, AND RELATED COMPOUNDS

Starch, one of the most common storage compounds in plants, is a mixture of 25% amylose and 75% amylopectin. Amylose consists of long, unbranched chains of glucose in \( \alpha \)-(1,4) linkage. Although not truly soluble in water, amylose forms hydrated micelles in which the polysaccharide chain forms a helical coil. By comparison, amylopectin is a highly branched form of starch in which the backbone consists of glucose chains in \( \alpha \)-(1,4) linkage with \( \alpha \)-(1,6) linkages at the branch points (Fig. 10-10). Glycogen, the main storage compound in animal cells, is comparable to amylopectin in that the main backbone also consists of glucose units in \( \alpha \)-(1,4) linkage but with more frequent \( \alpha \)-(1,6) branches. Pullulan, a starch-like polysaccharide, is a 1,4:1,6-\( \alpha \)-D-glycan composed of maltotriose units in 1,6-\( \alpha \)-linkage.

Amylose can be hydrolyzed by \( \alpha \)-amylase, which cleaves the \( \alpha \)-(1,4) linkages to yield a mixture of \( \alpha \)-glucose and \( \alpha \)-maltose. Amylose is also hydrolyzed by \( \beta \)-amylase,
Fig. 10-9. Cellulosomes of *Clostridium thermocellum*. Scanning electron micrographs of ferritin-labeled cellobiose-grown cells. Prior to processing for electron microscopy, the cells were treated with cationized ferritin. Wild-type cellulose-digesting cells (a) are easily distinguishable from mutant cells (b) by the protuberances that cover the entire cell surface of the wild type. Bars = 200 nm. (source From Bayer, E. A. and R. Lamed, 1986. *J. Bacteriol.* 167:828–836.)

Fig. 10-10. Structure of amylopectin and pullulan. Amylopectin contains chains of glucose molecules in α-(1,4) linkage with occasional α-(1,6)-linked branches. The structure of glycogen is similar except that there are more frequent α-(1,6)-linked branches. Pullulan is composed of maltotriose units of three glucose molecules in α-(1,4) linkage connected by α-(1,6) linkages.
liberating β-maltose in stepwise fashion from the nonreducing end of the molecule. Thus β-amylases invert the configuration at the C-1 position during cleavage of the α-(1,4)-glucosidic bond, whereas α-amylases retain the α-configuration at the C-1 position. These enzymes also hydrolyze amylopectin or glycogen to yield glucose, maltose, and a highly branched core, limit dextrin. A debranching enzyme, α-(1,6)-glucosidase, is capable of hydrolyzing the α-(1,6) linkages in limit dextrin. The combined action of α-(1,6)-glucosidase and α-amylase is required to completely degrade amylopectin or glycogen to glucose and maltose. Thus, α-amylases are endoenzymes that can bypass the α-(1,6) branch points of amylopectin, whereas β-amylases are exoenzymes that cannot hydrolyze amylopectin internally to the α-(1,6) branch points. Both α- and β-amylases and debranching enzymes (also called pullulanases) are produced by a number of bacteria and fungi. 

The amylases secreted by a variety of Bacillus species have been studied intensively because of their industrial application. The α-amylases from B. subtilis are saccharifying enzymes that produce mostly glucose and maltose from starch. On the other hand, the α-amylases produced by B. licheniformis and B. amyloliquefaciens are liquefying enzymes that yield mostly maltosaccharides. Under the conditions of nutrient deprivation, B. subtilis activates the structural gene for α-amylase, amyE. The synthesis of α-amylase is not inducible in the classic sense in that no compound can be shown to trigger the action of amyE. However, synthesis of the enzyme is repressed by glucose and other readily metabolizable carbon sources. Several genes appear to increase the formation of α-amylase and its secretion.

For ecological as well as industrial reasons, the thermostability of α-amylases has been of considerable interest. Thermophilic species, such as B. acidocaldarius and B. stearothermophilus, produce amylases that are stable at temperatures ranging from 58 °C to 80 °C. However, mesophilic species, such as B. licheniformis and B. amyloliquefaciens, also produce amylases that are active at temperatures in excess of 75 °C. Comparative studies of the enzymes and the structural genes of mesophilic and thermophilic species reveal considerable amino acid homology between the enzymes from the two groups, indicating that these proteins are related on an evolutionary basis.

Thermophilic anaerobes produce highly active thermostable starch-degrading enzymes. Clostridium thermosulfurogenes produces an extracellular, thermoactive, and thermostable β-amylase and a cell-bound glucoamylase. It does not produce a debranching enzyme. Clostridium thermosulfuricum produces a cell-bound glucoamylase and a debranching enzyme, pullulanase, which are thermoactive and thermostable. Mixed cultures of these organisms exhibit enhanced production of β-amylase, glucoamylase, and pullulanase, with concomitant increase in ethanol production from starch. The β-amylase of C. thermosulfurogenes is expressed at high levels only when the organism is grown on maltose or other carbohydrates containing maltose units. Glucose represses β-amylase synthesis, but cAMP does not eliminate the repressive effect.

Bacteroides thetaiotaomicron, a gram-negative anaerobe found in high numbers in the human colon, can ferment a variety of polysaccharides, including amylose, amylopectin, and pullulan. In this organism the degradative enzymes are not extracellular but are cell associated, indicating that the first step in starch utilization involves binding of starch to the bacterial surface. This action is followed by translocation
through the outer membrane into the periplasm where the starch-degrading enzymes are located. *B. thetaiotaomicron* produces four maltose-inducible outer membrane proteins and one enzyme located in the cytoplasmic membrane.

A 115 kDa outer membrane protein is essential for maltoheptaose utilization, whereas the other outer membrane proteins are involved in starch utilization. Two constitutively produced outer membrane proteins are also involved in starch utilization. Various bacteria produce four types of pullulan-hydrolyzing enzymes. A glucoamylase hydrolyzes pullulan from the nonreducing ends to produce glucose. A pullulanase (type I) found in *K. pneumoniae* and *B. thetaiotaomicron* breaks α-(1,6) glucosidic linkages to produce maltotriose. An isopullulanase found in *Aspergillus niger* hydrolyzes α-(1,4) glucosidic linkages in pullulan to produce panose [a branched trisaccharide with two α-(1,4) linkages and one α-(1,6) branch]. An α-glucosidase is found in *B. thetaiotaomicron* in addition to pullulanases I and II.

Cyclodextrins are cyclic oligosaccharides containing from 6 to 12 glucopyranose units bonded through α-(1,4) linkages, as shown in Figure 10-11. These compounds are widely used in the food and pharmaceutical industry as solubilizing and stabilizing agents. They have also found application as the bonded phase for high-performance liquid chromatography (HPLC) used in the separation and identification of organic compounds. Certain organisms produce cyclodextrins in the process.

![Cyclodextrin structure](image)

**Fig. 10-11. Cyclodextrin structure.** Cyclodextrins are cyclic oligosaccharides containing from 6 to 12 glucopyranose units bonded through α-(1,4) linkage.
of degrading starch. *Bacillus stearothermophilus* degrades starch by means of the enzyme cyclodextrin glucanotransferase. Cyclodextrins are resistant to hydrolysis by many starch-splitting enzymes. *Bacillus macerans, B. coagulans, B. sphaericus,* and *C. thermohydrosulfuricum* produce a cyclodextrinase that can hydrolyze linear maltodextrins as well as cyclodextrin.

**METABOLISM OF AROMATIC COMPOUNDS**

Many microorganisms can utilize aromatic compounds as their sole source of carbon. The aromatic ring structure is degraded and the products are converted to compounds that can enter central metabolic pathways to provide carbon sources and energy. Degradation of aromatic compounds is of major importance because of the widespread occurrence of these substances in natural as well as synthetic materials. Hydrocarbon-degrading microorganisms facilitate reentry of the carbon from these compounds into the natural biological cycles, preventing their accumulation in the environment. Accumulation of toxic aromatic hydrocarbons, particularly herbicides, pesticides, and other industrial waste products, can lead to serious contamination of ground water and cause serious ecological damage.

A fundamental aspect of the metabolism of aromatic ring compounds involves the conversion of the ring structure to a form that can be cleaved to yield an open chain, which can then be metabolized to intermediates in the central metabolic pathways. Under aerobic conditions, monooxygenases or dioxygenases introduce hydroxyl groups that facilitate ring cleavage. As shown in Figure 10-12, several pathways lead to the formation of catechol or similar compounds that can undergo either ortho- or meta-cleavage to yield intermediates leading into the general metabolic schemes. The meta-cleavage pathway results in the formation of pyruvate and acetaldehyde, whereas the ortho-pathway yields β-ketoadipate, a compound that is cleaved to form succinate and acetate.

Several ring oxidation mechanisms are known. *Pseudomonas putida* mt-2 oxidizes the methyl group of toluene to form benzyl alcohol. Subsequent reactions yield catechol, the substrate for the meta-cleavage pathway that leads to keto acid formation. *P. putida* PpF1 initiates the oxidation of toluene by incorporating oxygen into the aromatic nucleus to form cis-toluene dihydrodiol, which is converted to 3-methylcatechol. This compound is then degraded via the meta-cleavage pathway to yield an α-keto acid. *P. mendocina* oxidizes toluene to p-cresol, which undergoes ortho-cleavage to form β-ketoadipate. This compound is split by succinyl-CoA transferase to yield succinate and acetate as intermediates that can be used in the TCA cycle. The keto acid intermediates formed via the meta-cleavage route ultimately lead to acetaldehyde and pyruvate, compounds that can enter the central metabolic pathways.

The demonstration by Stanier and his colleagues in 1947 of the mechanism of the oxidation of mandelate to intermediates of the TCA cycle by *P. putida* represents the first example of sequential induction of enzymes of a catabolic pathway. Sequential induction refers to the fact that each of the enzymes in the pathway is inducible by its specific substrate.

Compounds with more complex ring structures, such as naphthalene, anthracine, or phenanthrine, undergo sequential ring fission to form ring structures that can
Fig. 10-12. Metabolism of aromatic hydrocarbons. The enzymes are: (1) naphthalene oxygenase, (2) 1,2-dihydroxynaphthalene oxygenase, (3) salicylaldehyde dehydrogenase, (4) salicylate hydroxylase, (5) catechol 2,3-oxygenase, (6) 2-hydroxymuconic semialdehyde dehydrogenase, (7) 4-oxalocrotonate tautomerase, (8) 4-oxalocrotonate decarboxylase, (9) 2-hydroxymuconic semialdehyde hydrolase, (10) 4-hydroxy-2-oxovalerate aldolase, (11) catechol 1,2-oxygenase, (12) cis, cis-muconate lactonizing enzyme, (13) (+)-muconolactone isomerase, (14) β-ketoadipate enol-lactone hydrolase, (15) succinyl CoA-β-ketoadipate thiolase, (16) mandelate racemase, (17) L- (+)-mandelate dehydrogenase, (18) benzoate decarboxylase, (19) NAD- and NADP-linked benzaldehyde dehydrogenases, (20, 21) benzoic acid oxidase, (22) benzene hydroxylase, (23) phenol hydroxylase, (24) toluene hydroxylase, (25) protocatechuate ortho-cleavage enzyme.
then be degraded via the ortho- or meta-cleavage pathways (Fig. 10-12). Chlorinated compounds, such as chlorobenzoate or polychlorinated biphenyls, often require dehalogenation before the aromatic ring can be hydroxylated to facilitate ring fission. In general, the more complex the ring structures, the more resistant polyaromatic hydrocarbons are to degradation. So far in this discussion, we have mentioned primarily pseudomonads that are well known for their ability to degrade aromatic hydrocarbons. Under natural conditions, a consortium of microorganisms may be

![Diagram of aromatic compound metabolism](image)

**Fig. 10-13. Comparison of anaerobic benzoate degradation by *R. palustris* and *T. aromatica*.**

required to rapidly degrade a compound with four or more fused rings. For example, benzo[a]pyrene, a potent carcinogen that commonly occurs in complex mixtures such as diesel fuel, contains five fused rings. Rapid mineralization of this compound was best accomplished by a combination of organisms phylogenetically related to the bacterial genera Sphingobacterium, Pseudomonas, Aquabacterium, Burkholderia, Ralstonia, Sphingomonas, Mycobacterium, and Alcaligenes.

Even more complex organic materials such as lignin are resistant to microbial attack. However, many fungi and a few bacteria are capable of degrading lignin or its breakdown products. These organisms are essential for the return of the constituents of these heteropolymers to the natural carbon and nitrogen cycles. The wood-rotting fungus Phanerochaete chrysosporium is capable of degrading the pesticide DDT and other complex organic compounds because of their structural similarity to components of the lignin complex.

Studies on the degradation of aromatic compounds cited thus far have all involved the incorporation of molecular oxygen into the aromatic nucleus to form dihydroxylated intermediates. Under anaerobic conditions, the aromatic ring structures are attacked reductively. A comparison of anaerobic benzoate degradation by Rhodopseudomonas palustris and Thauera aromatica is shown in Figure 10-13. Subsequent metabolism involves the formation of intermediates leading to the formation of acetyl-CoA. Acetyl-CoA can then enter the central metabolic pathway. A wide assortment of aromatic compounds are degraded to benzyol-CoA via several novel reactions including carboxylation of phenolic compounds, reductive elimination of ring substituents such as hydroxyl or amino groups, oxidation of methyl substituents, O-demethylation reactions, and shortening of aliphatic side chains.

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**Pectin Utilization**


**Cellulose Utilization**


**Utilization of Starch, Glycogen, and Related Compounds**


**Utilization of Aromatic Hydrocarbons**


