4.4 Anaerobic Pathways: Life without Oxygen

Although humans have an almost constant requirement for oxygen, other organisms can survive in the absence of oxygen. There are a variety of oxygen-poor environments that do not support aerobic processes. For example, anaerobic environments occur within the human gut, in wet environments (such as swamps and waterlogged soils), deep underground, deep in the oceans, and in landfills. Even though oxygen is not available for aerobic respiration in these environments, energy-rich foods are available for any organisms that are able to use them. Biological productivity in these environments, however, is inherently low because the energy yields of anaerobic pathways are much lower than the energy yield of aerobic respiration.

There are two anaerobic processes by which certain cells and organisms can oxidize fuel molecules and generate ATP: fermentation and anaerobic respiration. Anaerobic cellular respiration uses an electron transport chain that employs an inorganic substance other than oxygen as the terminal electron acceptor. In contrast, fermentation uses an organic molecule as a final electron acceptor but does not use an electron transport chain. Thus, fermentation is not considered to be a form of respiration.

Fermentation

Imagine a cell is in an environment where the oxygen supply is either very low or absent but glucose is abundant. As you have learned, glycolysis is a universal and ancient pathway that can generate ATP. Therefore, even in the absence of oxygen, cells can take in glucose and use glycolysis for ATP production. However, in addition to glucose, glycolysis requires other reactants—most notably NAD^+, which must be present to remove hydrogen in the glycolysis pathway. Cells have a very limited supply of NAD^+. Therefore, after NAD^+ is reduced to NADH, cells must have a way of removing the hydrogen to regenerate NAD^+. A variety of organisms, including yeast and some bacteria, use fermentation reactions to oxidize NADH to NAD^+ instead of an electron transport chain (**Figure 1**). By performing fermentation, cells can regenerate NAD^+ and allow glycolysis to continue.

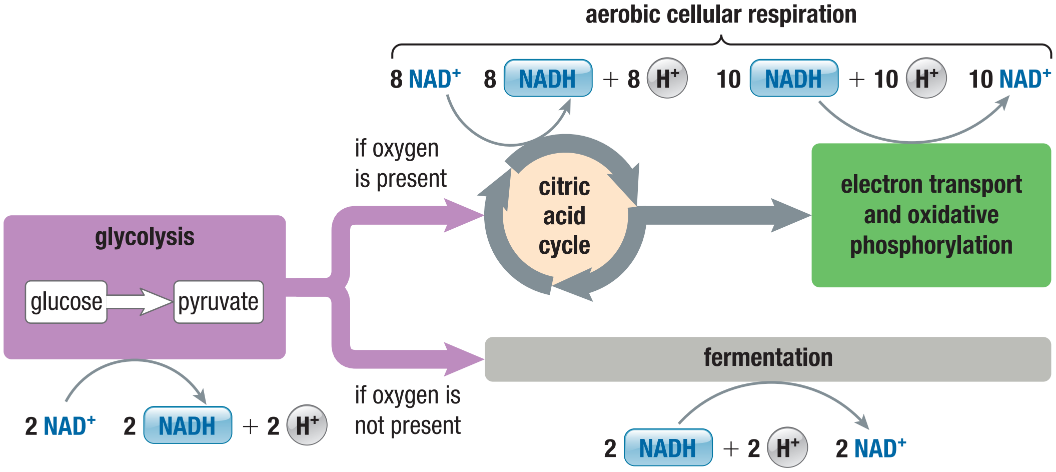

Figure 1 Energy-yielding processes differ in how NAD^+ is regenerated. In cellular respiration, an electron transport chain oxidizes NADH while fermentation reactions provide an alternative pathway for NADH oxidation.

There are several forms of fermentation that bacteria use to obtain energy, but there are two forms that eukaryotes also use: alcohol (ethanol) fermentation and lactate (lactic acid) fermentation. In some organisms, these pathways are the primary source of energy. In other organisms, these pathways are only used as optional or supplemental sources of energy when oxygen is not available in adequate supply.

Alcohol Fermentation

Alcohol fermentation (or ethanol fermentation) occurs in a variety of organisms, including certain bacteria and yeasts. In alcohol fermentation, the pyruvate that is produced by glycolysis is decarboxylated to form acetaldehyde, which is then used to oxidize NADH (**Figure 2**). The products of these final steps include a molecule of CO_2, a molecule of ethanol, and an NAD^+.

alcohol fermentation a process in which pyruvate is decarboxylated, producing a molecule each of CO_2 and of ethanol, and an NAD^+

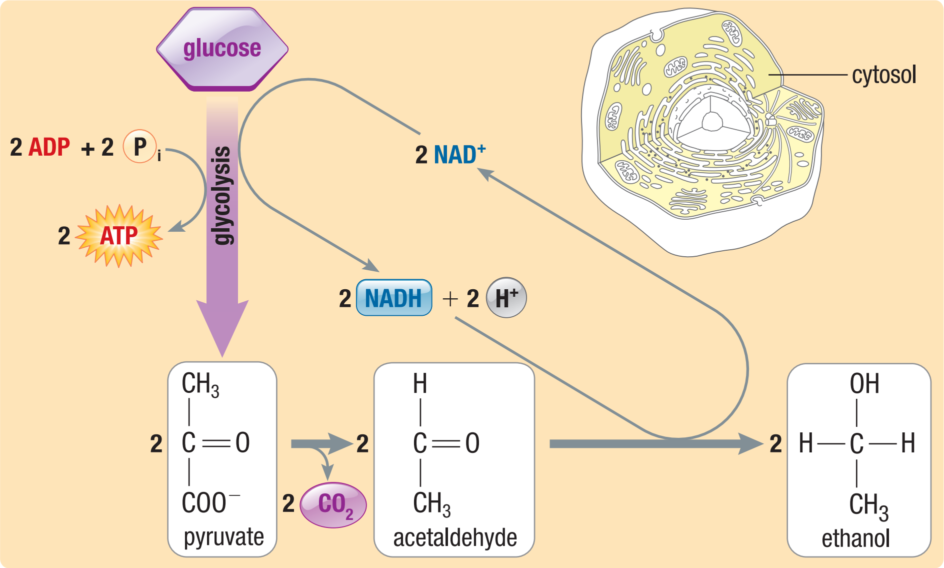

Figure 2 Fermentation reactions produce ethanol.

The following equation summarizes the final steps in alcohol fermentation:

$$\text{pyruvate} + \text{NADH} + H^+ \rightarrow NAD^+ + CO_2 + \text{ethanol}$$

When including glycolysis, which yields the two pyruvate molecules that are used in the reaction above, the overall fermentation pathway results in the formation of two ATPs and the release of carbon dioxide and ethanol waste products, as shown in the following overall equation:

$$\text{glucose} + 2\ \text{ADP} + 2\ P_i \rightarrow 2\ \text{ATP} + 2\ CO_2 + 2\ \text{ethanol}$$

Alcohol fermentation by yeasts has widespread commercial applications. Bakers use the yeast *Saccharomyces cerevisiae* to make bread dough rise. They mix the yeast with a small amount of sugar and blend the mixture into the dough, which has a low oxygen level. As the yeast cells convert the sugar into ethanol and CO_2, the gaseous CO_2 expands and creates gas bubbles that cause the dough to rise. In the oven, thermal energy evaporates the alcohol and causes further expansion of the bubbles, producing a light-textured product.

Alcohol fermentation is also used for brewing beer and wine. Winemakers rely on a mixture of wild yeasts and cultivated yeasts to produce wine (**Figure 3**). Alcohol fermentation is an important process in many industries, with over $6 billion in beer and wine produced annually in Canada. The commercial value of yeast has led to yeast being one of the best understood and most studied of all eukaryotic organisms. It was the very first eukaryote to have its entire genome sequenced. CAREER LINK

Figure 3 Alcohol fermentation occurs in nature. In this photograph, wild yeast cells are visible as a dustlike coating on grapes.

Alcohol fermentation also occurs naturally in the environment. For example, over-ripe or rotting fruit often starts to ferment, and birds that eat the fruit may actually become too intoxicated to fly.

FERMENTATION EFFICIENCIES

Fermentation produces only 2 ATP, compared with up to 38 ATP produced in aerobic respiration. The reason for so much less ATP is that ethanol is produced as a waste product during fermentation, and it is a very energy-rich compound. This is clearly demonstrated by the use of ethanol as a fuel for cooking and some race cars.

Even though fermentation produces much less ATP than aerobic respiration, it is still important in many environments. For example, a dead fish at the bottom of a deep lake is potential food for an anaerobic organism. In an oxygen-rich environment, however, even though an organism could survive using fermentation, it will be rapidly outcompeted by any aerobic organism that is able to extract 19 times as much energy from the same amount of food.

Lactate Fermentation

lactate fermentation a process in which pyruvate reacts with NADH and is converted directly into lactate and regenerates NAD^+

Lactate fermentation is used as a primary energy pathway in some bacteria, but it can also be used as a supplemental system in many eukaryotes. Just because a cell uses aerobic cellular respiration does not mean that it cannot also perform fermentation reactions. In humans, lactate fermentation occurs in our muscle cells when strenuous activity causes a demand for ATP that exceeds the rate at which O_2 can be supplied to the electron transport chain for oxidative phosphorylation. When we are breathing deeply and our heart is pumping rapidly, our circulatory system can still only provide a limited amount of oxygen gas each second. As a result, there is an upper limit on the rate at which oxygen can be supplied to cells and the rate at which aerobic pathways can generate ATP. Even as mitochondria are working rapidly to generate ATP, they are ultimately limited by the amount of available O_2. To maximize ATP production, glycolysis proceeds rapidly, yielding 2 ATPs for every glucose, and any excess pyruvate that is formed in the cytosol is converted into lactate. This pathway regenerates NAD^+, which can be used to maintain a high rate of glycolysis and increases ATP production. If high energy demands continue, significant quantities of lactate can accumulate in cells (**Figure 4**). Following strenuous exercise, when the oxygen content of the muscle cells returns to normal levels and ATP demands have fallen, the reaction is reversed. The reverse reaction regenerates pyruvate and NADH, which can be oxidized by the citric acid cycle and electron transport chain. At one time, the accumulation of lactate (in the form of lactic acids) in muscle tissue during strenuous exercise was thought to be the primary cause of muscle stiffness and soreness. This is now known not to be the case. Lactate levels in muscles generally return to normal within an hour after intense exercise.

Figure 4 Clara Hughes is a Canadian speed skater. In this photograph, she is competing in a 5000 m race. Lactate accumulates in muscle cells during such long and energy-demanding events.

During lactate fermentation, pyruvate oxidizes NADH and is converted directly into lactate and regenerates NAD^+ (**Figure 5**). This reaction commonly occurs in the cytosol.

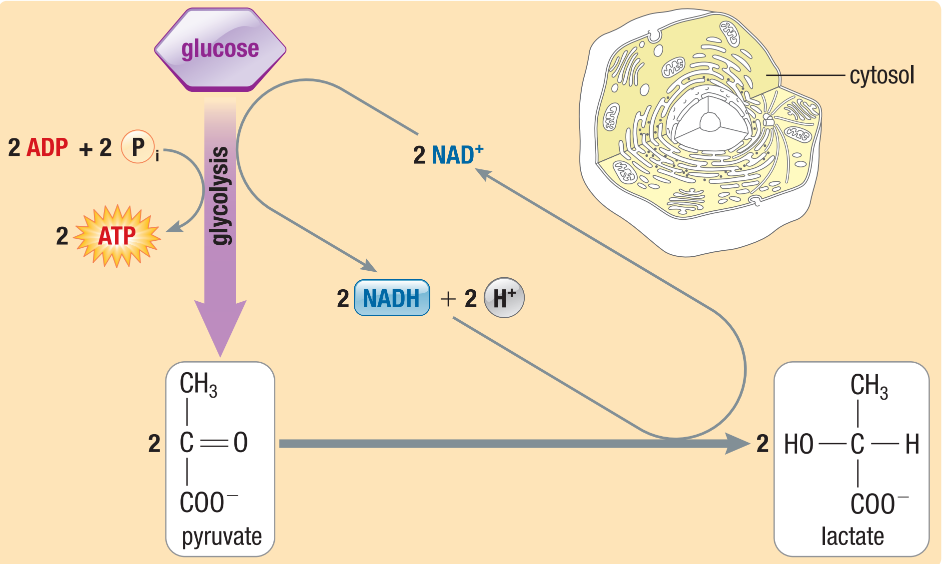

Figure 5 Fermentation reactions that produce lactate

The following equation summarizes the final steps in lactate fermentation, beginning with a single pyruvate:

$$\text{pyruvate} + \text{NADH} + H^+ \rightarrow NAD^+ + \text{lactate}$$

The efficiency of lactate fermentation is the same as the efficiency of alcohol fermentation, resulting in 2 ATPs formed per glucose and a similar overall equation:

$$\text{glucose} + 2\ \text{ADP} + 2\ P_i \rightarrow 2\ \text{lactate} + 2\ \text{ATP}$$

Notice that, in both alcohol and lactate fermentation, the only reactants other than ADP and P_i are food molecules—in this case, glucose.

Certain bacteria also produce lactate as their fermentation product. The sour taste of buttermilk, yogurt, and dill pickles is a sign of their activity. As well, lactic acid fermentation is used for making some cheeses.

LACTATE THRESHOLD AND OXYGEN DEBT

The rate at which oxygen can be supplied to mitochondria is not always sufficient to meet all of the energy demands of the cell. Therefore, lactate production is ongoing throughout the duration of highly strenuous physical activity. The lactate that is produced is transported from the muscles to the liver, where it is oxidized back to pyruvate so that it does not build up in muscle tissue. The point at which lactate production is too high for transport out of muscles to keep up is called the lactate threshold. This value can be increased by individuals through training, and it is useful for setting exercise intensity limits in endurance sports. The process of lactate fermentation results in an oxygen debt. By taking deeper and more frequent breaths, the body brings in large quantities of oxygen to diminish the oxygen debt.

Investigation 4.4.1

Observing the Products of Fermentation **(p. 200)**

In this investigation, you will test for the products of fermentation and examine the ability of yeast to use different substances as food sources.

UNIT TASK BOOKMARK

You may find the information you learn in the Research This: Putting Microbes to Work useful as you research the Unit Task on page 252.

Research This

Putting Microbes to Work

Skills: Questioning, Researching, Evaluating, Communicating — SKILLS HANDBOOK A4.1

Fermentation plays a vital role in the production of many foods and beverages. In this activity, you will investigate a commercial application that uses fermentation to make a product. Examples of products are bread, beer, wine, liquor, sauerkraut, yogurt, cheese, pickles, and Japanese fermented soybeans.

1. Choose a drink or food that is produced by fermentation.
2. Research the drink or food you chose using the Internet and other resources.

A. What is (are) the key organism(s) that drive the fermentation process? What are their scientific names? T/I

B. What physical and chemical conditions are used to create an environment for the fermentation of the product? How does the industry set up the process of fermentation? T/I

C. Name some environmental conditions that can influence the quality or success of the fermentation process. For example, how do water quality parameters, such as pH, temperature, and oxygen, affect fermentation? T/I

D. How does the action or products of fermentation create or enhance the product you chose? T/I

E. Share your results with your classmates through a poster or presentation. Be sure to mention anything especially interesting you found out while doing your research. C

WEB LINK

Anaerobic Respiration

Although they lack mitochondria, many prokaryotes have cellular respiration electron transport chains. These electron transport chains are located on internal membrane systems derived from the plasma membrane. Some are very similar to those found in the mitochondria of eukaryotes and use O_2 as the terminal electron acceptor. Other prokaryotes, however, have electron transport chains that use substances other than O_2 as the terminal electron acceptor and are said to undergo anaerobic respiration. For example, sulfate, SO_4^{2-}; nitrate, NO_3^-; and the iron ion, Fe^{3+}, are common electron acceptors used by many groups of prokaryotes that do not use O_2 as the terminal electron acceptor.

Organisms that can use these electron acceptors instead of oxygen are common in soils deep underground and in the sediments of marshes, wetlands, and lakes (**Figure 6**). Some wetlands have a strong unpleasant smell, similar to rotten eggs. This smell is produced when anaerobic sulfur-reducing bacteria in the bottom sediments release hydrogen sulfide, H_2S. During anaerobic respiration, these cells use SO_4^{2-} as the terminal electron acceptor (instead of O_2), which results in H_2S as the end product of the electron transport chain (instead of H_2O).

Figure 6 Bogs commonly have anaerobic zones that produce hydrogen sulfide, H_2S.

4.4 Review

Summary

- Fermentation pathways enable organisms to use glycolysis as a source of ATP, without an electron transport chain.
- Alcohol fermentation is performed by yeast and has significant commercial value.
- Lactate fermentation in muscles provides a supplementary source of ATP when energy demands are very high.
- Anaerobic respiration uses inorganic substances other than O_2 as terminal electron acceptors in an electron transport chain.

Questions

1. Compare aerobic respiration and fermentation in terms of the amount of ATP that can be generated from a single glucose molecule. K/U
2. (a) What is the difference between fermentation and glycolysis?
   (b) Why do cells rely on fermentation rather than glycolysis alone? K/U
3. Describe one advantage and one disadvantage of a species that is able to perform fermentation. How do the advantage and disadvantage influence the energy efficiency of the species and where the species can live? T/I
4. (a) Explain the anaerobic pathway that is used to create a loaf of bread. How does this pathway work?
   (b) Name two other products that use the same pathway.
   (c) Explain this pathway to someone who routinely bakes but is not a scientist. K/U C
5. Do our muscle cells produce alcohol? Given that alcohol and lactate fermentation both yield two ATP molecules for every glucose molecule, do you think it would make any difference which pathway was used? Explain. K/U A
6. Identify some environments in which anaerobic respiration takes place. K/U
7. Using what you know about lactic acid fermentation, explain why a person could not perform strenuous exercise indefinitely. K/U T/I
8. How could you increase the amount of time that you can exercise comfortably? K/U
9. Imagine that a muscle cell had a limited number of mitochondria but a very high oxygen supply. If this muscle cell were required to generate a great deal of power, do you think it would benefit from lactate fermentation? Why or why not? T/I
10. Some mammals have an exceptional ability to go for extended periods of time without breathing. Research the diving behaviour of sperm whales (**Figure 7**) and elephant seals. How long can these organisms go without surfacing for air? What special adaptations do these animals have to meet the oxygen and ATP demands of their cells? T/I

Figure 7

WEB LINK