A

► Carbon Source
► Chemolithoautotroph
► Photoautotroph

Autotrophy

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Synonyms

Primary production

Keywords

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Definition

Autotrophy is a life style in which inorganic compounds provide for all nutritional needs of an organism. Implicit in this definition is the capacity of an organism to derive all cell carbon from carbon dioxide. Energy can be derived from two sources: (1) Photoautotrophs are photosynthetic and obtain energy from sunlight. (2) Chemolithoautotrophs obtain energy by the oxidation of inorganic substances. Table 1 shows a general classification of organisms on the basis of the carbon and energy sources.

Overview

Autotrophs are capable of growth exclusively at the expense of inorganic nutrients and they are vital in the cycling of inorganic compounds (Alberts et al. 1994; Campbell and Reece 2002). Such autotrophs not only completely satisfied their own needs for reduced carbon monomers from inorganic matter but could also feed the already existing heterotrophs. Thus, autotrophic organisms are also called primary producers. Carbon dioxide that is fixed into organic compounds as a result of autotrophic activity is available for consumption or respiration by animals or heterotrophic microorganism. The end products of respiration in heterotrophic organism are carbon dioxide and this way the carbon cycle is completed (Alberts et al. 1994; Campbell and Reece 2002). Now it is accepted that autotrophy is an extremely important process on Earth and autotrophic microorganims, as primary producers, support the growth of non-autotrophic organisms (Maier et al. 2000).

Photoautotrophs

A large number of microorganisms, as well as the green plants, algae and protists, are phototrophic. They use light as energy source in the process called photosynthesis. The result of this mechanism is the generation of a proton motive force that can be used in the synthesis of ATP and the synthesis of reducing power (e.g., NADPH). Most phototrophs use energy conserved in ATP and electrons in NADPH for the assimilation of carbon dioxide as the carbon source for biosynthesis. These phototrophs are called photoautotrophs. There are also phototrophs able to use organic compounds as carbon sources with light as energy source; they are called photoheterotrophs (Table 1) (Campbell and Reece 2002; Maier et al. 2000; Madigan et al. 2003).

Chemolithoautotrophs

In the 1880s, Sergei Winogradsky (1856–1953) proposed the concept of chemolithotrophy, the oxidation of inorganic compounds as a source of energy and electrons for the autotrophic growth. Studying sulfur bacteria (*Beggiatoa* and *Thiothrix*) he concluded that these organisms obtained their carbon from CO_2 in air, and they were called autotrophs. The discovery of autotrophy in chemolithotrophic bacteria was of major significance in the advance of our understanding of cells physiology because it showed that CO_2 could be converted to organic

Autotrophy. Table 1 Classification of metabolisms according to energy, reducing power, and carbon sources

Metabolism	Energy source	Reducing power	Carbon source
Chemo-litho-autotrophic	Oxidation of inorganic compounds	Inorganic compounds	CO_2
Photo-itho-autotrophic	Visible light	Inorganic compounds	CO_2
Photo-organo-heterotrophic	Visible light	Organic compounds	Organic compounds
Chemo-organo-heterotrophic	Oxidation of organic compounds	Organic compounds	Organic compounds

carbon without photosynthesis. Chemolithotrophy is shown by members of both the Bacteria and Archaea Domains. Chemolithoautotrophs are important in the cycling of inorganic compounds in Earth, including methanogens, which produce methane, and nitrifiers, which convert ammonia to nitrate (Madigan et al. 2003; Ehrlich 2002).

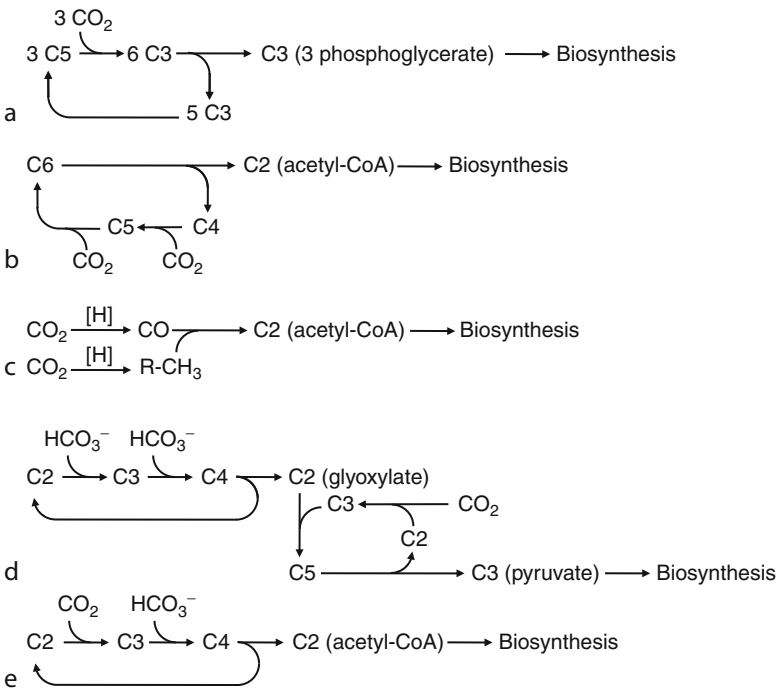
Basic Methodology and Key Research Findings

Autotrophic Pathways

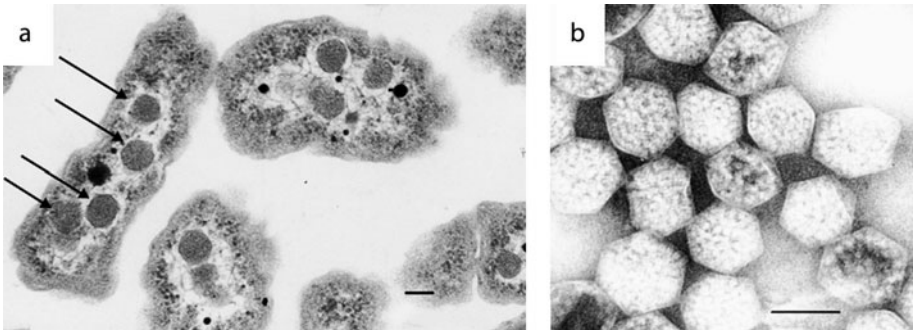
Six biochemical mechanisms are known for the autotrophic fixation of CO_2 into cell material. The pathways differ in the participating enzymes, ATP, and reducing power requirements and carbon isotope fractionation (Maier et al. 2000; Madigan et al. 2003; Berg et al. 2010).

1. The Calvin–Benson cycle, discovered in the 1950s in Melvin Calvin's lab, starts with the condensation of a 5-C sugar (ribulose 1,5-bisphosphate) with CO_2 to yield two molecules of 3-C (3-phosphoglycerate) (Fig. 1a). From these molecules both the initial 5-C sugar is regenerated and organic materials are biosynthesized. The cycle is operative in plastids of plants, algae, and protists, as well as in cyanobacteria, some aerobic or facultative anaerobic proteobacteria, CO-oxidizing mycobacteria, some iron- and sulfur-oxidizing firmicutes and green sulfur bacteria. The ability to fix carbon by this pathway is conferred by the activity of two enzymes (together with fragments of central metabolism like gluconeogenesis and the pentose phosphate pathway): ribulose 1,5-bisphosphate carboxylase-oxygenase (► Rubisco) and phosphoribulokinase (Campbell and Reece 2002; Maier et al. 2000; Madigan et al. 2003). Although Rubisco activity has been detected in some Archaea, it has not been possible to demonstrate Calvin–Benson-dependent autotrophic growth (Berg et al. 2010).

Several autotrophic prokaryotes that use the Calvin–Benson cycle for CO_2 fixation produce polyhedral cell inclusions called carboxysomes. Carboxysomes are made of polyhedral protein shells about 80–120 nm in diameter (Fig. 2). These compartments are surrounded by a thin membrane, and



Autotrophy. Figure 1 The diversity of autotrophic pathways. A scheme of stoichiometric relationships in (**a**) the Calvin–Benson cycle, (**b**) the Arnon cycle, (**c**) the Wood–Ljundahl pathway, (**d**) the hydroxypropionate bicycle, and (**e**) the hydroxypropionate/dicarboxylate-hydroxybutirate cycles. In each case, the identity of the net product of C fixation, the starting point of biosynthesis, is indicated



Autotrophy. Figure 2 (**a**) A thin-section electron micrograph of *Halothiobacillus neapolitanus* cells with carboxysomes inside. In one of the cells shown, *arrows* highlight the visible carboxysomes. (**b**) A negatively stained image of intact carboxysomes isolated from *H. neapolitanus*. The features visualized arise from the distribution of stain around proteins forming the shell as well as around the Rubisco molecules that fill the carboxysome interior. Scale bars indicate 100 nm. Figure from Tsai et al. (2007)

consist of a tightly packed crystalline array of molecules of Rubisco (Tsai et al. 2007). Thus the carboxysomes would be a mechanism to increase the amount of Rubisco in the cell to allow for higher rates of CO_2 fixation. Carboxysomes have been found in obligately chemolithotrophic sulfur-oxidizing bacteria, nitrifiying bacteria, cyanobacteria, and prochlorophytes. They are not present in facultative autotrophs like purple anoxygenic phototrophs, despite the fact that when these organisms grow as photoautotrophs, they use the Calvin–Benson cycle to fix CO_2. Thus, the carboxysome may be an evolutionary adaptation to life under strictly autotrophic conditions (Madigan et al. 2003).

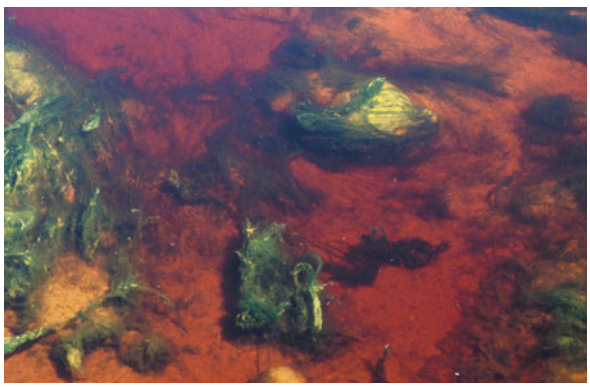
2. In the green sulfur bacterium *Chlorobium*, CO_2 fixation occurs by a reversal (or reductive) citric acid cycle also known as Arnon cycle (Madigan et al. 2003; Evans et al. 1966). This is the analog of a Krebs cycle operating in reverse mode (Fig. 1b). Since the Arnon cycle involves some enzymes (e.g., the carboxylating and reducing steps) that are inhibited by oxygen, this pathway is only found in microorganisms growing under anaerobic conditions. These include some proteobacteria, green sulfur bacteria, and microaerophilic bacteria like *Aquifex* (Maier et al. 2000; Madigan et al. 2003).
3. In some Gram-positive bacteria and methanogenic archaea was identified the ability to synthesize acetyl CoA from CO and/or CO_2, the Wood–Ljundahl pathway (Madigan et al. 2003; Ljundahl et al. 1965). One CO_2 molecule is reduced to CO and another one to a methyl group (attached to a cofactor). Then, acetyl CoA is synthesized from CO and the methyl group (Fig. 1c). The key enzymes of this pathway are inhibited by oxygen, thus it is restricted to obligate anaerobic microorganisms. These include some proteobacteria, planctomycetes, spirochates, and archaea (Maier et al. 2000; Madigan et al. 2003; Berg et al. 2010).
4. The 3-hydroxypropionate bicycle is present in some green non-sulfur phototrophic bacteria like *Chloroflexus* (Herter et al. 2002). A succinyl CoA molecule is synthesized from acetyl CoA and two bicarbonate molecules (Fig. 1d). Although uses the same intermediates as the hydroxypropionate-hydroxybutirate cycle (see below), most of the participating enzymes are different. The final product of the cycle is glyoxylate. Its assimilation requires a second metabolic cycle. This pathway is restricted to the family Chloroflexaceae and might represent an early attempt of autotrophy in anoxygenic phototrophs (Maier et al. 2000; Madigan et al. 2003).
5. The hydroxypropionate-hydroxybutirate cycle occurs in some aerobic archaea, like *Sulfolobus*. Albeit this pathway is formally the same as the 3-hydroxypropionate bicycle, the nonhomologous participating enzymes indicate that both pathways evolved independently in a remarkable case of evolutionary convergence in metabolism (Berg et al. 2010) (Fig. 1e).
6. The dicarboxylate-hydroxybutirate cycle occurs in some anaerobic archaea like the Thermoproteales and Desulfurococcales. The pathway can be divided into two parts (Fig. 1e): (1) one acetyl CoA, one CO_2, and one bicarbonate are converted into succinyl CoA; (2) this C4 molecule is transformed into two molecules of acetyl CoA (one serves as biosynthetic precursor, the other as acceptor of the cycle) (Berg et al. 2010).

Applications

Ecology

Autotrophs are present in all ecosystems. They take energy from the environment in the form of sunlight or inorganic chemicals and use it to create energy-rich molecules such as carbohydrates. Thus, they meet their requirements easily and can be constitutive around the world. Moreover, autotrophic organisms are primary producers and, as a consequence, they are at the pyramidal base of the ecosystems. Thus, heterotrophs depend on autotrophs for the energy and raw materials they need (Maier et al. 2000). On the other hand, autotrophs, as a consequence of their poor requirements, have greater adaptability; thus, they are especially important in oligothrophic environments, like oligothrophic lakes, glaciers and ice, acid waters, geothermal systems, etc.

Rio Tinto (Huelva, Southwestern Spain) is an example of an environment dominated by autothrophic bacteria. This ecosystem is of great interest for astrobiology (Fig. 3). It is an extreme environment with a rather constant acidic pH along the entire river and a high concentration of heavy metals. The extreme conditions of the Tinto ecosystem are generated by the metabolic activity of chemolithotrophic microorganisms thriving in the rich complex sulfides of the Iberian Pyrite Belt. In this system, more than 70% of the cells are affiliated to autotrophic bacteria (iron-oxidizing bacteria), with only a minor fraction corresponding to heterotrophic. The special interest shows also autotrophic microalgae, present in the river, primary producer, together iron-oxidizing bacteria, of the system (González-Toril et al. 2003).



Autotrophy. Figure 3 Río Tinto as example of an ecosystem dominated by autotrophic microorganisms

Autotrophy and Early Evolution of Life

The autotrophic metabolism has emerged independently several times during evolution, that is, it is a polyphyletic trait (Berg et al. 2010; Pereto et al. 1999). The Calvin–Benson cycle seems idiosyncratic to bacteria, whereas the Arnon cycle and the Wood–Ljundahl pathway show a wider phylogenetic distribution. The different versions of the hydroxypropionate pathway likely emerged independently (Berg et al. 2010). At this moment, phylogenetic analysis of the participating enzymes does not allow us to infer which one is the older pathway.

Mainstream hypothesis on the ► origin of life postulate that the first prokaryotes were anaerobic heterotrophs, for example, fermenters. In the beginning, they may have fed on externally available abiotic organic molecules, either synthesized on Earth or delivered by extraterrestrial bodies. It is generally supposed that autotrophic metabolism emerged latter.

Whether the first autotrophs were chemosynthetic or photosynthetic is currently a matter of debate. One school of thought favors chemosynthetic autotrophs in the form of methanogens, which formed methane. Microorganims (methanogenic archaea) with such metabolism exist today, and they are strict anaerobes. The other school of thought favors photosynthetic prokaryotes in the bacterial domain as the first autotrophs. This notion is supported by the existence of the Warrawoona stromatolites, which is around 3.5 billion years old. Those microfossils have been interpreted, on the basis of comparison with modern counterparts, to have been formed by cyanobacteria. However, modern cyanobacteria are aerobes. Because the primordial atmosphere at this time is thought to have been almost free of oxygen, the emergence of anaerobic photosynthetic bacteria, of which modern purple and green bacteria must be a counterpart, must have preceded that of cyanobacteria (Campbell and Reece 2002).

On the other hand, in 1988, Wächtershäuser proposed the surface metabolism theory for the origin of life (Wächtershäuser 1988). According to it, life arose as a form of autocatalytic two-dimensional chemolithotrophic metabolism on a pyrite surface, using the energy and electrons of the anaerobic synthesis of FeS_2 (pyrite) from FeS and H_2S. According to this proposal, the ancestral carbon fixation pathway would be a primitive version of the Arnon cycle (Wächtershäuser 1990). The Wood–Ljundahl pathway has also been proposed as a candidate of the older autotrophic mechanism (Pereto et al. 1999; Russell and Martin 2004). The lack of experimental evidences is the weaker aspect of the autotrophic hypothesis on the origin of life.

See also

- ► Calvin–Benson Cycle
- ► Chemolithoautotroph
- ► Isotopic Fractionation (Interstellar Medium)
- ► Origin of Life
- ► Photoautotroph
- ► Rubisco

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Available Water

► Water Activity

Axial Tilt

► Obliquity and Obliquity Variations

Azane

► Ammonia

Azulmin

► HCN Polymer