

Nitrogen fixation

Biological

Biological nitrogen fixation (BNF) occurs when atmospheric nitrogen is converted to ammonia by a nitrogenase enzyme.^[1] The overall reaction for BNF is:



The process is coupled to the hydrolysis of 16 equivalents of ATP and is accompanied by the co-formation of one equivalent of H_2 .^[14] The conversion of N_2 into ammonia occurs at a metal cluster called FeMoco, an abbreviation for the iron-molybdenum cofactor. The mechanism proceeds via a series of protonation and reduction steps wherein the FeMoco active site hydrogenates the N_2 substrate.^[15] In free-living diazotrophs, nitrogenase-generated ammonia is assimilated into glutamate through the glutamine synthetase/glutamate synthase pathway. The microbial nif genes required for nitrogen fixation are widely distributed in diverse environments.^[16]

For example, decomposing wood, which generally has a low nitrogen content, has been shown to host a diazotrophic community.^{[17][18]} The bacteria enrich the wood substrate with nitrogen through fixation, thus enabling deadwood decomposition by fungi.^[19]

Nitrogenases are rapidly degraded by oxygen. For this reason, many bacteria cease production of the enzyme in the presence of oxygen. Many nitrogen-fixing organisms exist only in anaerobic conditions, respiring to draw down oxygen levels, or binding the oxygen with a protein such as leghemoglobin.^{[20][21]}

Importance of nitrogen

Atmospheric nitrogen is inaccessible to most organisms,^[22] because its triple covalent bond is very strong. Most take up fixed nitrogen from various sources. For every 100 atoms of carbon, roughly 2 to 20 atoms of nitrogen are assimilated. The atomic ratio of carbon (C) : nitrogen (N) : phosphorus (P) observed on average in planktonic biomass was originally described by Alfred Redfield,^[23] who determined the stoichiometric relationship between C:N:P atoms, The Redfield Ratio, to be 106:16:1.^[23]

Nitrogenase

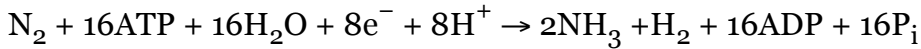
The protein complex nitrogenase is responsible for catalyzing the reduction of nitrogen gas (N_2) to ammonia (NH_3).^{[24][25]} In cyanobacteria, this enzyme system is housed in a specialized cell called the heterocyst.^[26] The production of the nitrogenase complex is genetically regulated, and the activity of the protein complex is dependent on ambient oxygen concentrations, and intra- and extracellular concentrations of ammonia and oxidized nitrogen species (nitrate and nitrite).^{[27][28][29]} Additionally, the combined concentrations of both ammonium and nitrate are thought to inhibit N_{Fix} , specifically when intracellular concentrations of 2-oxoglutarate (2-OG) exceed a critical threshold.^[30] The specialized heterocyst cell is necessary for the performance of nitrogenase as a result of its sensitivity to ambient oxygen.^[31]

Nitrogenase consist of two proteins, a catalytic iron-dependent protein, commonly referred to as MoFe protein

In 1901, Beijerinck showed that *Azotobacter chroococcum* was able to fix atmospheric nitrogen. This was the first species of the *azotobacter* genus, so-named by him. It is also the first known diazotroph, species that use diatomic nitrogen as a step in the complete nitrogen cycle.

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Nitrogenase consist of two proteins, a catalytic iron-dependent protein, commonly referred to as MoFe protein and a reducing iron-only protein (Fe protein). There are three different iron dependent proteins, molybdenum-dependent, vanadium-dependent, and iron-only, with all three nitrogenase protein variations containing an iron protein component. Molybdenum-dependent nitrogenase is the most commonly present nitrogenase.^[32] The

different types of nitrogenase can be determined by the specific iron protein component.^[33] Nitrogenase is highly conserved. Gene expression through DNA sequencing can distinguish which protein complex is present in the microorganism and potentially being expressed. Most frequently, the *nifH* gene is used to identify the presence of molybdenum-dependent nitrogenase, followed by closely related nitrogenase reductases (component II) *vnfH* and *anfH* representing vanadium-dependent and iron-only nitrogenase, respectively.^[34] In studying the ecology and evolution of nitrogen-fixing bacteria, the *nifH* gene is the biomarker most widely used.^[35] *nifH* has two similar genes *anfH* and *vnfH* that also encode for the nitrogenase reductase component of the nitrogenase complex.^[36]

Evolution of Nitrogenase

Nitrogenase is thought to have evolved sometime between 1.5-2.2 billion years ago (Ga),^{[37][38]} although some isotopic support showing nitrogenase evolution as early as around 3.2 Ga.^[39] Nitrogenase appears to have evolved from maturase-like proteins, although the function of the preceding protein is currently unknown.^[40]

Nitrogenase has three different forms (*Nif*, *Anf*, and *Vnf*) that correspond with the metal found in the active site of the protein (Molybdenum, Iron, and Vanadium respectively).^[41] Marine metal abundances over Earth's geologic timeline are thought to have driven the relative abundance of which form of nitrogenase was most common.^[42] Currently, there is no conclusive agreement on which form of nitrogenase arose first.

Microorganisms

Diazotrophs are widespread within domain Bacteria including cyanobacteria (e.g. the highly significant *Trichodesmium* and *Cyanothece*), green sulfur bacteria, purple sulfur bacteria, Azotobacteraceae, rhizobia and *Frankia*.^{[43][44]} Several obligately anaerobic bacteria fix nitrogen including many (but not all) *Clostridium* spp. Some archaea such as *Methanosarcina acetivorans* also fix nitrogen,^[45] and several other methanogenic taxa, are significant contributors to nitrogen fixation in oxygen-deficient soils.^[46]

Cyanobacteria, commonly known as blue-green algae, inhabit nearly all illuminated environments on Earth and play key roles in the carbon and nitrogen cycle of the biosphere. In general, cyanobacteria can use various inorganic and organic sources of combined nitrogen, such as nitrate, nitrite, ammonium, urea, or some amino acids. Several cyanobacteria strains are also capable of diazotrophic growth, an ability that may have been present in their last common ancestor in the Archean eon.^[47] Nitrogen fixation not only naturally occurs in soils but also aquatic systems, including both freshwater and marine.^{[48][49]} Indeed, the amount of nitrogen fixed in the ocean is at least as much as that on land.^[50] The colonial marine cyanobacterium *Trichodesmium* is thought to fix nitrogen on such a scale that it accounts for almost half of the nitrogen fixation in marine systems globally.^[51] Marine surface lichens and non-photosynthetic bacteria belonging in Proteobacteria and Planctomycetes fixate significant atmospheric nitrogen.^[52] Species of nitrogen fixing cyanobacteria in fresh waters include: *Aphanizomenon* and *Dolichospermum* (previously Anabaena).^[53] Such species have specialized cells called heterocytes, in which nitrogen fixation occurs via the nitrogenase enzyme.^{[54][55]}

Algae

One type of organelle can turn nitrogen gas into a biologically available form. This nitroplast was discovered in algae.^[56]

Root nodule symbioses

Legume family

Plants that contribute to nitrogen fixation include those of the legume family —Fabaceae— with taxa such as kudzu, clover, soybean, alfalfa, lupin, peanut and rooibos.^[44] They contain symbiotic rhizobia bacteria within nodules in their root systems, producing nitrogen compounds that help the plant to grow and compete with other plants.^[57] When the plant dies, the fixed nitrogen is released, making it available to other plants; this helps to fertilize the soil.^{[20][58]} The great majority of legumes have this association, but a few genera (e.g., *Styphnolobium*) do not. In many traditional farming practices, fields are rotated through various types of crops, which usually include one consisting mainly or entirely of clover.

Fixation efficiency in soil is dependent on many factors, including the legume and air and soil conditions. For example, nitrogen fixation by red clover can range from 50 to 200 lb/acre (56 to 224 kg/ha).^[59]



Nodules are visible on this broad bean root

Non-leguminous

The ability to fix nitrogen in nodules is present in actinorhizal plants such as alder and bayberry, with the help of *Frankia* bacteria. They are found in 25 genera in the orders Cucurbitales, Fagales and Rosales, which together with the Fabales form a *nitrogen-fixing clade* of eurosids. The ability to fix nitrogen is not universally present in these families. For example, of 122 Rosaceae genera, only four fix nitrogen. Fabales were the first lineage to branch off this nitrogen-fixing clade; thus, the ability to fix nitrogen may be plesiomorphic and subsequently lost in most descendants of the original nitrogen-fixing plant; however, it may be that the basic genetic and physiological requirements were present in an incipient state in the most recent common ancestors of all these plants, but only evolved to full function in some of them.^[60]



A sectioned alder tree root nodule

In addition, *Trema* (*Parasponia*), a tropical genus in the family Cannabaceae, is unusually able to interact with rhizobia and form nitrogen-fixing nodules.^[61]

Non-legumious nodulating plants

Family	Genera	Species
<u>Betulaceae</u>	<u>Alnus</u> (alders)	Most or all species
<u>Boraginaceae</u>	<u>Phacelia</u>	<u>Phacelia tanacetifolia</u>
<u>Cannabaceae</u>	<u>Trema</u> (Parasponia)	<u>Trema orientale</u> <u>Trema lamarckiana</u>
<u>Casuarinaceae</u>	<u>Allocasuarina</u> <u>Casuarina</u> <u>Ceuthostoma</u> <u>Gymnostoma</u>	
<u>Coriariaceae</u>	<u>Coriaria</u>	<u>Coriaria arborea</u> <u>Coriaria myrtifolia</u>
<u>Datiscaceae</u>	<u>Datisca</u>	
<u>Elaeagnaceae</u>	<u>Elaeagnus</u> (silverberries) <u>Hippophae</u> (sea-buckthorns) <u>Shepherdia</u> (buffaloberries)	
<u>Myricaceae</u>	<u>Comptonia</u> (sweetfern) <u>Myrica</u> (babyberries)	
<u>Posidoniaceae</u>	<u>Posidonia</u> (seagrass)	
<u>Rhamnaceae</u>	<u>Ceanothus</u> <u>Colletia</u> <u>Discaria</u> <u>Kentrothamnus</u> <u>Retanilla</u> <u>Talguenea</u> <u>Trevoa</u>	
<u>Rosaceae</u>	<u>Cercocarpus</u> (mountain mahoganies) <u>Chamaebatia</u> (mountain miseries) <u>Dryas</u> <u>Purshia</u> /Cowania (bitterbrushes/cliffroses)	

Other plant symbionts

Some other plants live in association with a cyanobiont (cyanobacteria such as Nostoc) which fix nitrogen for them:

- Some lichens such as Lobaria and Peltigera
- Mosquito fern (Azolla species)
- Cycads^[62]
- Gunnera
- Blasia (liverwort)
- Hornworts^[63]

Some symbiotic relationships involving agriculturally-important plants are:^[64]

- Sugarcane and unclear endophytes

- Foxtail millet and Azospirillum brasilense
- Kallar grass and Azoarcus sp. strain BH72
- Rice and Herbaspirillum seropedicae
- Wheat and Klebsiella pneumoniae
- Maize landrace 'Sierra Mixe' / 'olotón'^[65] and various Bacteroidota and Pseudomonadota

Industrial processes

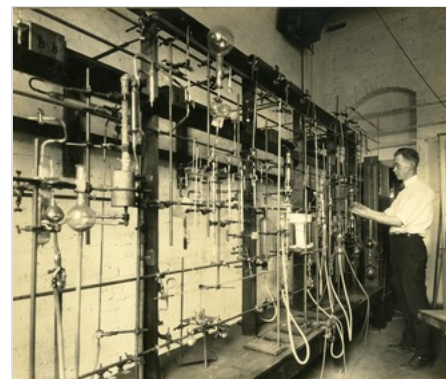
Historical

A method for nitrogen fixation was first described by Henry Cavendish in 1784 using electric arcs reacting nitrogen and oxygen in air. This method was implemented in the Birkeland–Eyde process of 1903.^[66] The fixation of nitrogen by lightning is a very similar natural occurring process.

The possibility that atmospheric nitrogen reacts with certain chemicals was first observed by Desfosses in 1828. He observed that mixtures of alkali metal oxides and carbon react with nitrogen at high temperatures. With the use of barium carbonate as starting material, the first commercial process became available in the 1860s, developed by Margueritte and Sourdeval. The resulting barium cyanide reacts with steam, yielding ammonia. In 1898 Frank and Caro developed what is known as the Frank–Caro process to fix nitrogen in the form of calcium cyanamide. The process was eclipsed by the Haber process, which was discovered in 1909.^{[67][68]}

Haber process

The dominant industrial method for producing ammonia is the Haber process also known as the Haber-Bosch process.^[69] Fertilizer production is now the largest source of human-produced fixed nitrogen in the terrestrial ecosystem. Ammonia is a required precursor to fertilizers, explosives, and other products. The Haber process requires high pressures (around 200 atm) and high temperatures (at least 400 °C), which are routine conditions for industrial catalysis. This process uses natural gas as a hydrogen source and air as a nitrogen source. The ammonia product has resulted in an intensification of nitrogen fertilizer globally^[70] and is credited with supporting the expansion of the human population from around 2 billion in the early 20th century to roughly 8 billion people now.^[71]



Equipment for a study of nitrogen fixation by alpha rays (Fixed Nitrogen Research Laboratory, 1926)

Homogeneous catalysis

Much research has been conducted on the discovery of catalysts for nitrogen fixation, often with the goal of lowering energy requirements. However, such research has thus far failed to approach the efficiency and ease of the Haber process. Many compounds react with atmospheric nitrogen to give dinitrogen complexes. The first dinitrogen complex to be reported was $\text{Ru}(\text{NH}_3)_5(\text{N}_2)^{2+}$.^[72] Some soluble complexes do catalyze nitrogen fixation.^[73]

Lightning

Nitrogen can be fixed by lightning converting nitrogen gas (N_2) and oxygen gas (O_2) in the atmosphere into NO_x (nitrogen oxides). The N_2 molecule is highly stable and nonreactive due to the triple bond between the nitrogen atoms.^[74] Lightning produces enough energy and heat to break this bond^[74] allowing nitrogen atoms to react

with oxygen, forming NO_x . These compounds cannot be used by plants, but as this molecule cools, it reacts with oxygen to form NO_2 ,^[75] which in turn reacts with water to produce HNO_2 (nitrous acid) or HNO_3 (nitric acid). When these acids seep into the soil, they make NO_3 (nitrate), which is of use to plants.^{[76][74]}



Lightning heats the air around it in a high-temperature plasma, breaking the bonds of N_2 , starting the formation of nitrous acid (HNO_2).

See also

- Birkeland–Eyde process: an industrial fertilizer production process
- Carbon fixation
- Denitrification: an organic process of nitrogen release
- George Washington Carver: an American botanist
- Heterocyst
- Nitrification: biological production of nitrogen
- Nitrogen cycle: the flow and transformation of nitrogen through the environment
- Nitrogen deficiency
- Nitrogen fixation package for quantitative measurement of nitrogen fixation by plants
- Nitrogenase: enzymes used by organisms to fix nitrogen
- Ostwald process: a chemical process for making nitric acid (HNO_3)

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