Production, modification, and consumption of atmospheric trace gases by microorganisms

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ABSTRACT

Some trace gases are contained in the atmosphere in appreciable amounts: methane, carbon monoxide, hydrogen, nitrous oxide. The bulk of these gases is of biological origin. Hydrogen is a primary product of microbial metabolism under anaerobic conditions. However, before reaching the atmosphere, it is converted by methane bacteria to methane, by nitrate reducing bacteria to nitrogen and to nitrous oxide and by sulfate reducing bacteria to hydrogen sulfide. Carbon monoxide is produced from certain organic compounds. Hydrogen, methane, and carbon monoxide are quickly oxidized by microorganisms under aerobic conditions. However, especially methane and carbon monoxide reach the atmosphere. The literature dealing with the microorganisms and biochemical reactions involved in the production and conversion of trace gases is reviewed.

Gaseous and volatile compounds are key intermediates in the cycle of matter. During mineralisation the organic carbon is converted to carbon dioxide, which escapes into the atmosphere. If organic matter is decomposed under anaerobic conditions several gases are produced in addition to carbon dioxide. However, only minor quantities of the primary gaseous products reach the atmosphere unchanged; the major amount is converted to secondary products which give rise to the atmospheric trace gases.

Hydrogen is the most important primary gas produced from organic substances during anaerobic decay, besides carbon dioxide of course. Hydrogen is then used by several groups of microorganisms, which produce methane, hydrogen sulfide, nitrogen, nitrous oxide (Fig. 1). Hydrogen, therefore, plays a predominant role in the cycle of trace gases. Only minor amounts of the organic carbon is liberated in the form of carbon monoxide. Since CO evolution apparently mainly occurs under aerobic conditions, a major proportion of the primary product escapes, and less is converted to CO_2 or CH_4 in secondary biological reactions. Methane arises under strictly anaerob conditions and is the major product of the hydrogen produced within the same habitat.

The microorganisms, their ecology and the reactions involved in these transformations are adequately presented in textbooks of general microbiology (Brock, 1970; Stanier, et al., 1971; Schlegel, 1972). Outstanding recent original papers and reviews will be cited.

Hydrogen formation

The biological formation of molecular hydrogen can be considered as a device for disposal of reducing equivalents (electrons) released in metabolic oxidations under anaerobic conditions. The anaerobic mode of life poses special problems for the cell. The cellular metabolism aims at the generation of energy (ATP). Energy production is accompanied by oxidations. Under anaerobic conditions such oxidations occur as intramolecular disproportions, resulting in carbon dioxide and highly reduced organic compounds such as alcohols and fatty acids. Many anaerobes are able to dispose of the reducing equivalents by producing gaseous hydrogen. This disposal system thus acts like a "hydrogen valve".

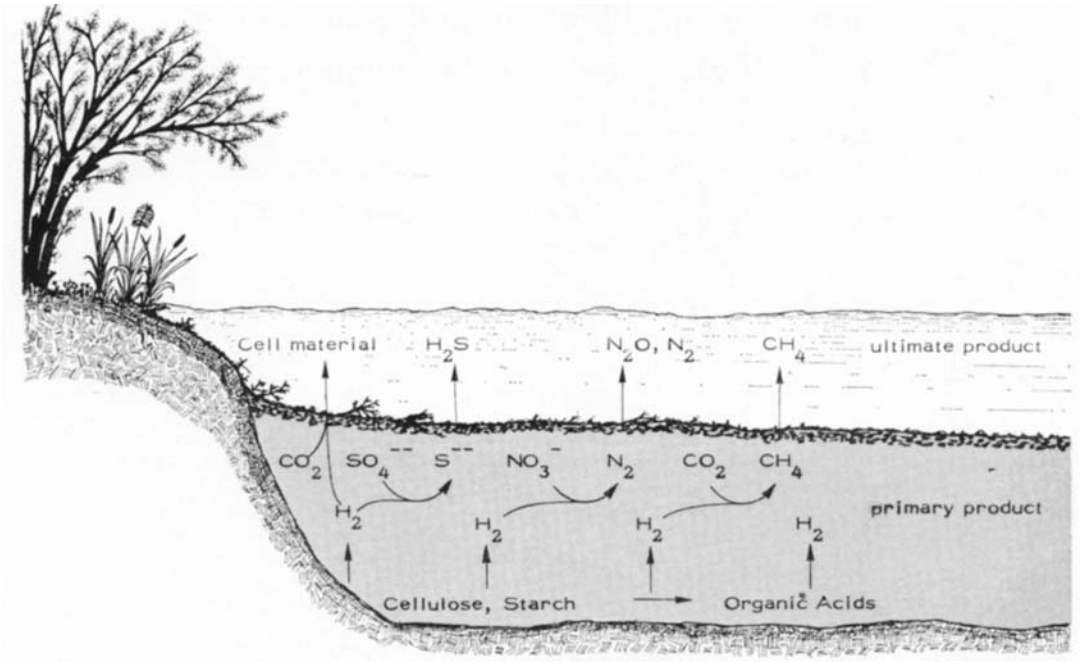

Fig. 1. The ecology of hydrogen production and consumption. Hydrogen is produced in enormous quantities during anaerobic decomposition of organic materials (cellulose and other carbohydrates, proteins, heterocyclic rings). It is then used within the same anaerobic habitat by other microorganisms. The ultimate product which reaches the atmosphere depends on the hydrogen-acceptor available in the habitat: sulfate is reduced to hydrogen sulfide; nitrate and nitrite are reduced to nitrous oxide and nitrogen; carbon dioxide is reduced to methane.

One encounters the ability to produce H_2 in many microbial species. Representative organisms can be separated into four categories (Gray & Gest, 1965). Category I comprises heterotrophic strict anaerobes, whose growth is inhibited by H_2. The primary electron donors for H_2-formation are pyruvate, reduced two-carbon compounds, amino acids, purines or pyrimidines. Representative organisms are *Clostridium butyricum*, *C. pasteurianum*, *C. kluyveri*, *Peptostreptococcus elsdenii*, *Veillonella alcalescens*. Organisms in category II are heterotrophic facultative anaerobes. They evolve hydrogen from formate; representatives: *Escherichia coli*, *Bacillus macerans*. Category III is designed for *Desulfovibrio desulfuricans* which can produce H_2 from pyruvate or formate, if sulfate is absent. Category IV consists of phototrophic microorganisms: nonsulfur purple bacteria (*Rhodospirillum*), sulfur purple bacteria (*Chromatium*), green bacteria (*Chlorobium*), and anaerobically adapted green algae.

Molecular hydrogen is produced through the effect of hydrogenases, which catalyze the reaction

$$2\ e^- + 2\ H^+ \rightleftharpoons H_2$$

In group I to III hydrogen is evolved in course of fermentations, the hydrogen being liberated by one of the following reactions.

(*a*) In clostridia and related organisms the electron transfer is mediated by a non-heme iron protein of an extreme low redox potential, ferredoxin ($E_0' \approx -420$ mV). The electrons are mainly derived from the thioclastic reaction of pyruvate, however, may even be transferred from $NAD(P)H_2$ by a $NAD(P)H_2$-ferredoxin reductase system.

$$\begin{array}{c} H_2 \\ \uparrow \\ \text{Pyruvate} \rightarrow \text{Ferredoxin} \leftarrow NAD(P)H_2 \end{array}$$

(*b*) In bacteria of category II, formate produced by the phosphoroclastic reaction is converted to CO_2 and H_2 by a sequence of reactions

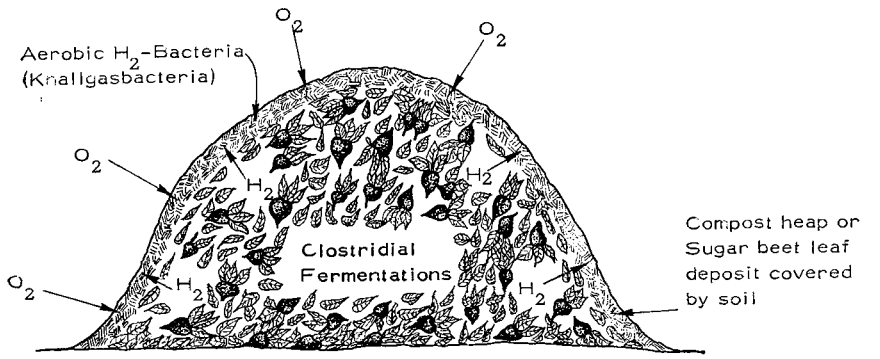

Fig. 2. The ecology of hydrogen production and consumption. Hydrogen produced by anaerobic decomposition of carbohydrates and proteins is used by autotrophic hydrogen bacteria (Knallgas-bacteria) if atmospheric oxygen becomes available in a diffusion zone. The graph symbolizes a compost heap or a sugar beet leaf deposit covered by soil. Besides lactic acid fermentations clostridial butyric acid fermentations occur which are accompanied by H_2-evolution. The gases H_2 and CO_2 penetrating to the top soil layer give rise to the growth of Knallgas-bacteria.

catalyzed by the formic hydrogenlyase enzyme complex.

(*c*) In phototrophic microorganisms, bacteria as well as anaerobically adapted algae, a photoproduction of H_2 occurs under conditions, in which reduced pyridine nucleotides ($NAD(P)H_2$) and ATP are in excess of the demands of the biosynthetic apparatus. This light-dependent H_2-formation may be regarded as a regulatory mechanism maintaining the concentrations of these important substances at adequate levels. Under appropriate conditions, with organic substrates or thiosulfate as H-donors, hydrogen formation may be brought about even in the dark. Furthermore, the nitrogenase system is apparently involved in disposing excess hydrogen by H_2-formation.

The quantitative contribution of the microorganisms and reactions mentioned to the liberation of molecular hydrogen in natural habitats is unknown. If hydrogen would escape and would not be consumed simultaneously or successively by other microorganisms associated in the same microhabitat, hydrogen would certainly be classified as a major component of the atmosphere rather than a trace gas.

Hydrogen consumption

Molecular hydrogen is a favoured hydrogen and energy donor for microorganisms. In the presence of air, hydrogen is used by the hydrogen or Knallgas-bacteria. These are autotrophs and perform a chemolithoautotrophic type of metabolism

$$6H_2 + CO_2 + 2CO_2 \rightarrow \langle CH_2O \rangle + 5H_2O$$

Hydrogen bacteria are widely distributed in the soil and apparently in the top soil layer act as a catalyst, which oxidizes H_2 diffusing from lower soil layers (Fig. 2). They belong to several genera and species like *Hydrogenomonas*, *Mycobacterium*, *Arthrobacter*, *Pseudomonas*, and *Nocardia* (Schlegel, 1966, 1973).

Since hydrogen is produced under anaerobic conditions, it is not astonishing that many anaerobic bacteria are able to use it as a H-donor (Fig. 3). Methane bacteria reducing carbon dioxide inhabit the anaerobic zones of ponds, lakes, rivers, and swamps and are cultivated in the sewage fermentation tanks. Their close association with fermentative H_2-producing bacteria is a symbiotic relationship.

If nitrate, nitrite, or nitrous oxide are present in the aquatic environment, facultative bacteria of the type of *Micrococcus denitrificans* perform a nitrate respiration. This process results in the reduction of these ions or compounds to molecular nitrogen (N_2) and is a mode of denitrification.

$$5H_2 + 2HNO_3 \rightarrow N_2 + 6H_2O$$

The presence of sulfate gives rise to sulfate respiration. The reduction of sulfate to sulfide by H_2

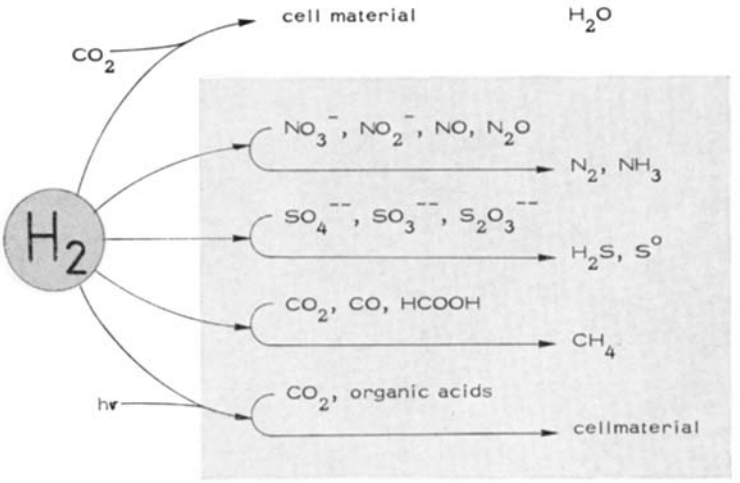

Fig. 3. The basic processes of hydrogen utilization under aerobic conditions (white) and under anaerobic conditions (grey) in the presence of different hydrogen-acceptors.

$$4H_2 + H_2SO_4 \rightarrow H_2S + 4H_2O$$

is catalyzed by strict anaerobes (*Desulfovibrio*, *Desulfotomaculum*). These bacteria oxidize and incorporate organic materials performing a mode of respiration by using sulfate as the H-acceptor. In the presence of hydrogen they are able to activate it by a constitutive hydrogenase. Since sulfate reduction by H_2 continues in resting, non-growing cells, large amounts of hydrogen sulfide are produced by relatively low numbers of bacteria. The blackening of mud is largely due to the precipitation of iron by the hydrogen sulfide produced by these bacteria.

The so-called "anaerobic corrosion of iron" is essentially due to the oxidation of hydrogen in the presence of sulfate by these bacteria, too. If e.g., an iron pipe is buried in water-logged soil, iron is polarized

$$4Fe^\circ + 8H^+ \rightarrow 4Fe^{++} + 4H_2.$$

Normally, the H_2 protects the iron surface from further decomposition. If, however, sulfates, and sulfate-reducing bacteria are present, cathodic depolarization occurs, and iron is oxidized even in the absence of oxygen.

$$4Fe^\circ + SO_4^{--} + 2H_2O \rightarrow FeS + 3Fe(OH)_2$$

Finally, hydrogen is utilized by several phototrophic bacteria as a reductant for CO_2-fixation.

Carbon monoxide production

Carbon monoxide is produced by animals, plants, and bacteria (Chappelle, 1962*a*). The observation of CO in mammalian blood goes back to the end of the last century (Grehant, 1894). It is an ever-present component of the alveolar air of man (Sjostrand, 1970). The source of CO in exhaled air was traced back to the degradation of hemoglobin to verdoglobin. This reaction has been demonstrated in vivo and in vitro. CO is probably derived from the α-carbon of the methane bridges of the tetrapyrrole ring. Evidence for the production of CO from hemoproteins by bacteria has been obtained recently (Engel et al., 1972). When the alpha-hemolytic *Streptococcus mitis* and the hemolytic *Bacillus cereus* were incubated aerobically with erythrocytes, hemoglobin, myoglobin, cytochrome *c*, Fe-hematin, or Fe-protoporphyrin under aerobic conditions at 37°C for 18 hours, CO was evolved. None of the bacteria formed CO anaerobically or from bilirubin.

Neither was CO produced by non-hemolytic bacteria. Since porphyrin derivatives are contained in all aerobic organisms, they would represent a major source of CO if all porphyrins would be degraded with CO-production.

Another source is the oxidation of L-dihydroxyphenylalanine (DOPA) by tyrosinase. The reaction may be related to the well-known CO evolution during autoxidation of pyrogallol

in alkaline solution (Miyahara & Takahashi, 1971).

Another animal known for its ability to form CO is the siphonophore *Physalia physalis*, the portuguese man-of-war. Up to 13 % CO were found in the float bladders of these organisms. The evolution of CO is apparently due to serine metabolism and the involvement of folic acid (Wittenberg, 1960).

Carbon monoxide as a product of plant metabolism is known since the gas was discovered in the float bladder of the brown alga *Nereocystis luetkeana*. The bladders contain up to 5 % CO. There are several reports on the production of CO from plant material indicating that it is formed as a degradation product of the tetrapyrrole nucleus of the chlorophyll pigments. However, no definitive studies have been made.

One of the most opulent sources of CO in nature apparently is the degradation of flavonoids. Experiments with *Aspergillus flavus* revealed a degradation pathway for rutin (Simpson et al., 1960; Westlake et al., 1961; Simpson et al., 1963). The fungus when grown on rutin excretes an enzyme that degrades the glycoside to water-soluble products; the first step is a hydrolysis (by rutinase) resulting in quercetin and rutinose. Quercetin is subsequently degraded by an enzyme tentatively referred to as quercetinase in the presence of oxygen to yield CO and a depside.

Carbon monoxide consumption

The consumption of carbon monoxide by soil or soil bacteria is well known (Lantzsch, 1922; Hasemann, 1927). Irrefutable proof for the utilization of CO by an aerobic bacterium was obtained by Kistner (1953, 1954). He isolated a Gram-negative monotrichously flagellated rod from sewage sludge by liquid enrichment culture. Since this bacterium was able to grow on $H_2 + CO_2$, too, he named it *Hydrogenomonas carboxydovorans*. When the cells were grown in a CO-containing atmosphere (80 % CO + 20 % O_2), they were able to oxidize CO according to

$$2CO + O_2 \rightarrow 2CO_2$$

Cells grown under a CO_2-containing atmosphere of hydrogen and oxygen or on lactate were unable to oxidize CO. The enzyme system for CO utilization is, therefore, an inducible one.

The successful isolation of CO oxidizing aerobic bacteria was achieved by Russian colleagues (Nozhevnikova & Zavarzin, 1973; Nozhevnikova & Savelieva, 1972; Savelieva & Nozhevnikova, 1972). From enrichment cultures under a CO-air-atmosphere they isolated several CO utilizing bacteria. One of them is *Seliberia carboxydohydrogena*, other strains are similar to Knallgasbacteria. All of them are strict aerobs, utilizing CO by an inducible enzyme system. They all are able to grow on hydrogen, carbon dioxide and oxygen. Under these conditions growth is ten times faster than on CO. These bacteria are similar to ordinary inhabitants of polluted water, and the authors are rather certain that these bacteria account for the natural aerobic CO sink.

Anaerobic conversion of carbon monoxide has been well proven. After early observations on the anaerobic oxidation of CO by soil (Wehmer, 1926) and in sludge from an anaerobic sewage fermentation tank (Fischer et al., 1931) a methane producing bacterium was isolated (Barker, 1936). *Methanosarcina barkeri* is able to convert a mixture of CO and H_2 according to the following equation

$$CO + 3H_2 \rightarrow CH_4 + H_2O$$

(Kluyver & Schnellen, 1947). According to manometric measurements (in the absence and presence of alkali) the conversion of pure CO proceeds via CO_2:

$$4CO + 4H_2O \rightarrow 4CO_2 + 4H_2$$
$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$$

Sum: $4CO + 2H_2O \rightarrow 3CO_2 + CH_4$

Some evidence for CO utilization by a photosynthetic bacterium has been obtained (Hirsch, 1968). Experiments with ^{14}CO and green algae indicate that CO is incorporated by *Chlorella* and *Scenedesmus* as well as by the cyanobacterium *Anacystis nidulans*. CO apparently is oxidized to CO_2 and enters the reductive pentosephosphate cycle (Chappelle, 1962*a* und *b*). Previous experiments by Krall & Tolbert (1957) showed that CO was incorporated by intact barley leaves. The CO-carbon initially appeared in serine, suggesting the conversion of CO to an active one-carbon unit. The utilization and conversion of CO by higher plants expects further studies.

Methane production

Methane is produced by a small group of strictly anaerobic bacteria (rev. by Wolfe, 1971; McBride & Wolfe, 1971). Methane formation occurs with alcohols, organic acids, carbon dioxide plus hydrogen or carbon monoxide as substrates.

The main habitates of methane bacteria are swamps, lakes, paddy fields, fermentation tanks of sewage disposal plants, and the rumen of cattle. In all cases, the methane producing bacteria inhabit environments of strictly anaerobic conditions. They perform the last reaction of a sequence of fermentations. In the course of these fermentations effected by other bacteria, fatty acids, alcohols, carbon dioxide, and gaseous hydrogen are formed from carbohydrates (cellulose, starch) and proteins. The primary fermentation products are further converted to methane.

There are two sources of the methane carbon. (1) Some methane bacteria use carbon dioxide as an electron acceptor for a mode of anaerobic respiration coupled with the oxidation of hydrogen

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$$

(2) Some bacteria produce methane from organic substrates, such as methanol, acetic acid, or butyric acid. In this case, methane preferentially arises from the methyl carbon and reduced carbon atoms of the organic acid.

Although methane-producing bacteria are known since the beginning of this century (Söhngen, 1906), the group is still poorly known. These bacteria are difficult to cultivate, and even under optimal conditions growth is slow. *Methanobacterium omelianskii* (Barker, 1940) was presumed to be a pure culture and to produce methane from hydrogen, ethanol, primary and secondary alcohols. However, it has been found to consist of an association of two strictly anaerobic bacteria (Bryant et al., 1967). One bacterium (M.o.H. strain) produces methane from CO_2 and H_2

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$$

The other bacterium (S-strain) oxidizes ethanol with the production of H_2 (Reddy et al., 1972)

$$CH_3 - CH_2OH + H_2O \rightarrow CH_3 - COOH + 2H_2$$

If the S-organism is kept in axenic culture without a H_2-consuming organism it grows poorly on ethanol. Hydrogen produced from ethanol inhibits growth. Recently a thermophilic methane-producing bacterium, *Methanobacterium thermoautotrophicum*, has been isolated which grows readily under an atmosphere of 80 % H_2 + 20 % CO_2 at 65–70°C (Zeikus & Wolfe, 1972).

Consumption of gaseous alkanes

The gaseous hydrocarbons methane, ethane, propane, and *n*-butane are readily utilized by soil microorganisms. Although numerous genera of bacteria and yeasts are able to grow on liquid and solid *n*-alkanes (Schlegel, 1960; Fuhs, 1961), only a few microorganisms are known to use the gaseous members of the series.

Methane consumption

Methane is utilized as a growth substrate mainly by bacteria and only under aerobic conditions. In addition to some methane oxidizing bacteria known since a long time like *Pseudomonas methanica* (Söhngen, 1906; Dworkin & Foster, 1956; Leadbetter & Foster, 1960) or *Methylococcus capsulatus* (Foster & Davis, 1966) over a 100 methane utilizing bacteria were isolated recently (Whittenbury, 1969; Whittenbury et al., 1970). Most of the methane oxidizing bacteria are obligately bound to this substrate; they use neither long chain hydrocarbons nor are able to grow on the conventional substrates. Since they use only methane, methanol or dimethylether, they are now grouped together as "obligate methylotrophs" (Quayle, 1972).

Reports on the growth of eukaryotic microorganisms on methane are rare. Whether *Chlorella* (Enebo, 1967) and *Graphium* really grow on methane (Zajic et al., 1969).

When the ethane or natural gas (containing ethane and methane in a ratio of 1:8 are employed as substrates for enrichment cultures almost invariably ethane utilizing bacteria are selected (Davis et al., 1956; Dworkin & Foster, 1958). Apparently a great number of species is able to utilize ethane; they belong to the genera *Mycobacterium*, *Flavobacterium* and *Nocardia*. Even a fungus, *Graphium*, has been used for biomass production from ethane and ethane-

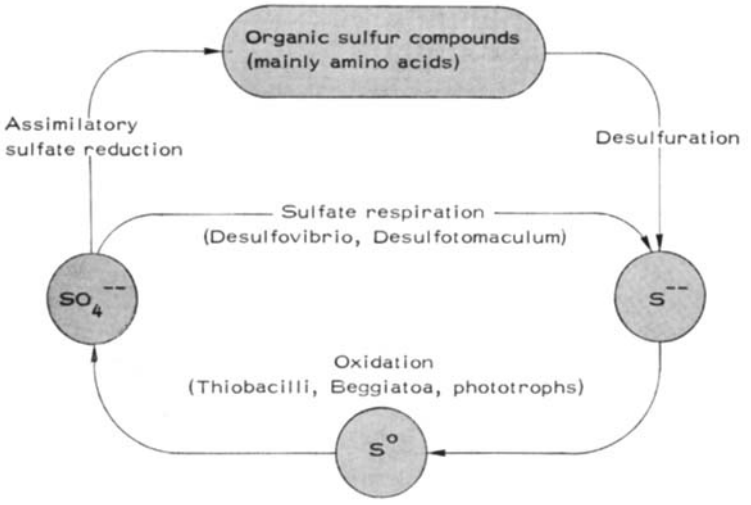

Fig. 4. The biological sulfur cycle.

methane mixtures (Volesky & Zajic, 1971). Propane is used by still a greater number of species (Bokova, 1954; Kuznetsov & Telegina, 1957; Blevins & Perry, 1972; O'Brien & Brown, 1968; Siebert, 1969). *n*-Butane is utilized by bacteria and fungi (Telegina, 1967; Coty, 1967; O'Brien & Brown, 1968; McLee et al., 1972). Species of *Arthrobacter* and *Brevibacterium* as well as *Penicillium nigricans*, *Allescheria boydii* and *Graphium cumeiferum* were identified. Even *n*-pentane is utilized by microorganisms (Takahashi et al., 1970).

Ethylene is produced by ripening fruits and initiates the ripening process by increasing respiration. Its formation is due to an enzymatic process from methionine and 4-methylmercapto-2-ketobutyrate and from linolenic acid as substrates (Mapson, 1969, 1970). Ethylene is evolved in soils, too. The evolution of the gas is greatly stimulated by the addition of methionine and glucose to the soil. *Mucor hiemalis* and a soil yeast were the most active ethylene producers when grown on glucose-methionine agar slopes (Lynch, 1972).

Although no biological process of acetylene production is known to me, the gaseous hydrocarbon may be produced from rare carbides. Acetylene is an inhibitor of biological nitrogen-fixation and is itself reduced by N_2-fixing bacteria with the formation of ethylene (Schöllhorn & Burris, 1966; Dilworth, 1966). The measurement of ethylene production from acetylene has become a common test for the nitrogenase system in vivo and in vitro and is applied even for the evaluation of the occurrence of nitrogen fixing organisms in soil and water (Burris, 1972; Hardy et al., 1972). As an energy and carbon source, acetylene is used, e.g. by *Mycobacterium lacticola* (Birch–Hirschfeld, 1932)

Nitrogen oxides

Denitrifying bacteria account for the production of nitrous oxide (N_2O) and nitric oxide (NO) in nature. A large number of facultative anaerobic bacteria (*Pseudomonas denitrificans*, *Micrococcus denitrificans*, *Thiobacillus denitrificans*, and many other soil and water bacteria) are able to perform an anaerobic respiration with nitrate or nitrite as the electron-acceptor.

Nitrate ammonification

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \begin{cases} \nearrow NH_2OH \rightarrow NH_3 \\ \searrow N_2O \longrightarrow N_2 \end{cases}$$

Denitrification

The final product of denitrification is nitrogen (N_2). However, under certain conditions, and by several bacteria, N_2O and NO, which are normal intermediates of nitrate reduction, are liberated and eventually reach the atmosphere (Renner & Becker, 1970). Nitrous oxide and

nitric oxide are further reduced with the formation of N_2.

Many denitrifiers are able to grow with N_2O as the sole electron-acceptor. However, N_2O serves as an electron-acceptor and is only used if oxygen is absent, i.e. under anaerobic conditions.

Hydrogen sulfide

Hydrogen sulfide has essentially two sources in nature (Fig. 4). It is a product of the decomposition of amino acids containing thiolgroups (Methionine, Cysteine, Cystin). However, the major amount of hydrogen sulfide, liberated into the atmosphere, is the product of sulfate respiration (Postgate, 1969). Only two strictly anaerobic genera of bacteria account for this important process in nature, *Desulfovibrio* and *Desulfotomaculum*. Both utilize organic acids as H-donors and use sulfate as the H-acceptor.

Wherever organic matter is decomposed under anaerobic conditions in the presence of sulfates, large amounts of hydrogen sulfide are produced. Since sea water is a sulfate solution, H_2S-production is most intensive and striking in estuaries and other marine habitats. Biochemically the reduction of sulfate is well-known (Peck, 1968). The final steps have been elucidated just recently (PoLee & Peck, 1971), in *Desulfovibrio gigas* trithionate and thiosulfate are intermediates of the reduction of sulfite to sulfide.

Sulfide is an autoxidizable compound. Biologically it is used as H-donor by colorless filamentous sulfur bacteria (e.g. *Beggiatoa*, *Thiotrix*) and by the phototrophic purple bacteria (*Chromatium*, *Thiospirillum*). Sulfide oxidation proceeds via sulfur, which is transiently accumulated within the cells and further oxidized with sulfate formation. The phototrophic sulfur bacteria are widely distributed in shallow ponds, in lakes and in aestuaries. (For further information on the sulfur cycle see Postgate, 1969; Pfennig, 1967; Peck, 1968; Trudinger, 1969.)

For completeness, a few volatile sulfur compounds produced by microorganisms may be mentioned (Kadota & Ishida, 1972). As a degradation product of methionine by many microorganisms, methylmercaptane (CH_3–SH) and dimethyldisulfide (CH_3–S–S–CH_3) are formed. These compounds are formed e.g., when cabbage leaves and tissues of other crucifers are decomposed. Dimethylsulfide (CH_3S–CH_3) is a component of the flavor of swiss cheese and formed during the fermentation by *Propionibacterium shermanii*.

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ПРОИЗВОДСТВО, МОДИФИКАЦИЯ И ПОТРЕБЛЕНИЕ МИКРООРГАНИЗМАМИ АТМОСФЕРНЫХ ТРАССЕРНЫХ ГАЗОВ

Некоторые трассерные газы содержатся в атмосфере в заметных количествах: метан, окись углерода, водород, окись азота. Основная часть этих газов биологического происхождения. Водород является основным продуктом микробного метаболизма при анаэробных условиях. Однако, прежде чем достигнуть атмосферы, он превращается в метан метановыми бактериями, восстанавливающими нитраты и в сероводород бактериями, восстанавливающими сульфаты. Окись углерода получается из некоторых органических веществ. Водород, метан и окись углерода быстро окисляются микроорганизмами в аэробных условиях. Однако метан и окись углерода переходят и в атмосферу. Дается обзор литературы, в которой рассматриваются микроорганизмы и биохимические реакции, связанные с производством и превращениями трассерных газов.