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Soil Microorganisms as Controllers of Atmospheric Trace Gases (H_2, CO, CH_4, OCS, N_2O, and NO)

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IMPORTANCE OF ATMOSPHERIC TRACE GASES

The composition of Earth's atmosphere is the result of dynamic processes; it has changed in the past and is changing at the present. The most dramatic change in the past was that from an anoxic to an oxic atmosphere. This change occurred slowly over about 2.5 Gyr and was caused by the emergence of oxygenic photosynthesis (239, 458). The dramatic changes occurring in the atmosphere at present are due to the steady increase in the amount of CO_2 and several other trace gases (124, 405). Atmospheric theory predicts that changes in the concentrations of these gases will have dramatic consequences for the habitability of our planet (78, 83, 131–133, 135, 152, 367, 413, 414, 537). These consequences include (i) global warming due to the increased abundance of greenhouse gases,

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TABLE 1. Contribution of soil to the global cycles of atmospheric trace gases

Trace gas	Mixing ratio (ppbv)	Lifetime (days)	Total budget (Tg yr^{-1})	Annual increase (%)	Contribution (%) of soils as:		Importance	References
					Source	Sink		
H_2	550	1,000	90	0.6	5	95	Insignificant	88, 271
CO	100	100	2,600	1.0	1	15	Tropospheric chemistry	88, 272
CH_4	1,700	4,000	540	<0.8	60	5	Greenhouse effect; tropospheric and stratospheric chemistry	84, 270, 405, 512
OCS	0.5	1,500	2.3	0	25	?[a]	Formation of stratospheric aerosol	12, 80, 81, 366, 432
N_2O	310	60,000	15	0.2–0.3	70	?	Stratospheric chemistry; greenhouse effect	52, 140, 273, 405
NO	<0.1	1	60	?	20	?	Tropospheric chemistry	91, 140
DMS	<0.1	<0.9	38	?	<0.1	0	Cloud formation	78, 397
CH_3CCl_3	0.14	2,200	0.20	−3.4	0	0	Calibration of OH	406
CF_2Cl_2	0.48	44,000	0.45	<5	0	0	Stratospheric chemistry; greenhouse effect	83, 135, 405

[a] Unknown.

mainly CO_2, CH_4, and N_2O; (ii) destruction of the stratospheric ozone layer due to the increased abundance of halogenated compounds and N_2O; (iii) an increase in the amount of tropospheric ozone due to the increased emission of NO_x, CO, and hydrocarbons; and (iv) changes in the density of clouds in the troposphere and aerosol in the stratosphere due to changed emissions of dimethyl sulfate (DMS) and OCS, respectively. Many of the theoretical predictions have been confirmed by recent observations, e.g., the destruction of stratospheric ozone at higher latitudes (517, 569). However, many of the mechanisms responsible for changes in atmospheric composition are uncertain, as is the extent of future change (405). The biosphere in particular is one of the least understood components in the cycles of CO_2 and of atmospheric trace gases.

With the exception of the main constituents, i.e., N_2, O_2, Ar, and CO_2, trace gases in the atmosphere occur at mixing ratios of less than 20 ppmv (261). Atmospheric scientists preferentially describe the abundance of a compound in terms of volume mixing ratios (e.g., ppmv = 10^{-6} and ppbv = 10^{-9}), which can be converted to concentrations (e.g., moles per cubic meter) if the pressure and temperature are known (564). With exception of the noble gases Ar, Ne, Kr, and Xe, which slowly accumulate in the atmosphere, all other constituents undergo cycles that are more or less dominated by the biosphere, including humans (261). Only a few trace gases (e.g., He and Rn) exhibit cycles that are governed purely by physicochemical processes. Others (e.g., the freons $CFCl_3$ and CF_2Cl_2) are biologically inert and are being introduced into the atmosphere by human activity (210, 367). However, most of the atmospheric trace gases undergo cycles that have significant biospheric components or are even dominated by biospheric processes. For purposes of understanding trace gas dynamics, the biosphere can be separated into habitats (ocean, soil) and organisms (vegetation, animals). Soils are of particular interest, since they are one of the most important habitats for microorganisms. For example, in an agricultural soil, microorganisms are present at billions per g of soil and constitute a biomass of approximately 500 kg of C per ha (250), which corresponds to about 1 sheep per 100 m^2 (13).

CONTRIBUTION OF SOILS TO THE BUDGETS OF ATMOSPHERIC TRACE GASES

Soils contribute to the budgets of many atmospheric trace gases by acting as sources or sinks. The most important of these trace gases include CH_4, CO, OCS, H_2, N_2O, and NO (Table 1). CCl_2F_2, CH_3CCl_3, and DMS are also important for various reasons but are largely unaffected by soils. CCl_2F_2 and CH_3CCl_3 are produced exclusively by industry, and DMS is produced almost exclusively by plants and oceanic phytoplankton. The absolute values of total budgets and percent contributions by soils should not be taken for granted, because the individual source and sink strengths are highly uncertain. The uncertainty is illustrated by looking, e.g., at the budget of CH_4 as it was repeatedly updated over the years (43, 84, 134, 164, 274, 405). Two points are striking: (i) the large range for most of the source strengths and (ii) the variations of the mean values estimated by the various authors.

There are a number of reasons for the variations, which cannot be discussed here in detail. The ranges of the soil sources and sinks, in particular, are highly uncertain. Although fluxes of trace gases between soil and atmosphere can be measured with some reliability by using various approaches (343), it is not trivial to estimate atmospheric budgets from field fluxes (516). The problem is that the fluxes generally show a high variability with respect to site and time. Integration of fluxes over larger areas and extended periods does not necessarily solve the problem, since each individual flux event is caused by deterministic processes that change in a nonlinear way when conditions change even slightly. In addition, soils are presently looked upon as a macroscopic system, although the function is controlled predominantly on a microscopic level, i.e., the level of the microorganisms. Perhaps only 1 to 10% of the existing soil bacterial species are known (61, 542). It is possible that a group of microorganisms with a particular function consists of populations of many different species, but virtually nothing is known about the dynamics of these populations and their regulation in soil. Clearly, we need to learn more about this microscopic level before we can safely make adaptations to the right scaling of flux measurements or of other experiments that aim to understand the role of soils in the dynamics of the composition of the atmosphere.

TABLE 2. Microorganisms and reactions important in the production and consumption of atmospheric trace gases in aerated upland soils and anoxic wetland soils

Trace gas	Production in:		Consumption in:	
	Upland soil	Wetland soil	Upland soil	Wetland soil
H_2	N_2-fixing bacteria	Fermenting bacteria	Abiontic soil hydrogenases	Methanogens, sulfate reducers, ferric iron reducers, (Knallgas bacteria)[a]
CO	Chemical conversion of organic carbon	Uncharacterized anaerobic bacteria	Ammonium oxidizers	Uncharacterized anaerobic bacteria, (carboxydotrophs)
CH_4	Unknown	Methanogens	Unknown methanotrophs	(Common methanotrophs)
OCS	Microbes with thiocyanate hydrolase, unknown reactions	Microbes with thiocyanate hydrolase, unknown reactions	Microbes with carbonic anhydrase, unknown reactions	Microbes with carbonic anhydrase, unknown reactions
N_2O	Nitrifiers, denitrifiers, DNRA	Denitrifiers, DNRA, (nitrifiers)	Denitrifiers	Denitrifiers
NO	Nitrifiers, denitrifiers, DNRA, chemical decomposition of nitrite	Denitrifiers, DNRA, (nitrifiers)	Denitrifiers, heterotrophic bacteria, methanotrophs	Denitrifiers, (methanotrophs, heterotrophic bacteria)

[a] Parentheses indicate that the enclosed is important only in oxic niches such as the soil surface or rhizosphere.

MECHANISMS OF PRODUCTION AND CONSUMPTION OF TRACE GASES

Some aspects of soil processes involved in the exchange of the trace gases CH_4, H_2, CO, OCS, N_2O, and NO between the soil and the atmosphere have been reviewed recently (94–96, 223). In principle, one has to distinguish between the processes that are known to produce or consume these gases but are probably irrelevant at the low concentrations typical of atmospheric trace gases and the processes that really play some role in the gas exchange between soil and atmosphere. The latter processes are summarized separately for upland and lowland soils (for definitions, see below) in Table 2. Three different categories of soil processes play a role in trace gase exchange: chemical processes, enzymatic processes, and microbial processes.

Chemical Processes

Chemical reactions in soil can be distinguished from biological reactions by autoclaving or similar procedures (60). These procedures often create ambiguous results, because chemical reactions are also affected. A better approach involves testing for the existence of a temperature optimum. The latter is an unambiguous indication of a biological reaction (411).

Chemical production of H_2 often occurs as an artifact when wet environmental samples are brought into contact with material consisting of iron or steel. The H_2 production that is caused by corrosion of elemental iron can serve as energy source for chemolithotrophic bacteria, e.g., sulfate reducers and methanogens (190, 577). Chemical H_2 production has also been observed in the saturated zone of deep aquifers, partially as an artifact during drilling, but apparently also as a product of various chemical reactions taking place in the rock material in situ (39). This chemical source of H_2 can apparently support the growth of chemolithotrophic bacteria (e.g., methanogens) in deep aquifers (515). The role of chemical H_2 production in soil has not been investigated explicitly, but it seems to be negligible compared with that of H_2 consumption processes (113).

CO production in soil is dominated by chemical reactions. Autoclaved or otherwise killed soil samples show higher CO release rates than do live soil samples (114, 118). Autoclaving probably alters soil organic matter so that it can more easily decompose to CO. In fresh soil, CO production rates increase with temperature according to the Arrhenius law without reaching an optimum temperature (118), demonstrating that CO production is dominated by chemical processes. CO is apparently produced from the thermal decomposition of humic acids and other organic material (118). In the field, the CO flux between soil and atmosphere is strongly dependent on the magnitude of chemical production which results in net CO emission when the level of organic carbon in soil is high or the soil temperature is high, i.e., during early afternoon (119, 453).

Chemical processes also seem to be involved in the production and consumption of OCS in soil, since autoclaving or γ-ray treatment does not completely abolish activity (315). However, one of four soils tested exhibited a clear temperature optimum for both production and consumption. The chemical reactions involved in OCS production and consumption in soil are unknown.

Nitrous oxide (N_2O) can be produced chemically by decomposition of hydroxylamine, but this reaction seems to be of no or little importance under field conditions (55, 363). On the other hand, NO production in soil can be caused by chemical processes, most importantly the decomposition of nitrite (74, 352). Since nitrite is destroyed during autoclaving, lack of NO production in autoclaved soil is not necessarily proof of biological NO production (141, 353). On the other hand, readdition of nitrite to autoclaved soil or addition of small amounts of nitrite to natural soil often increases the NO production dramatically (44, 141, 486). This effect is probably caused by contact of the added nitrite with reactants that otherwise would not have led to its chemical decomposition. Sterilization of soil with γ-rays instead of autoclaving results in a similar effect since it stimulates nitrite production from nitrate (73). Therefore, it is presently not possible to exactly quantify the contribution of nitrite decomposition to NO production. However, in most soils, nitrite concentrations are very low. Chemical decomposition would rapidly deplete this pool, if it were not replenished by the microbial activity (nitrifiers and nitrate reducers). Under steady-state conditions, microorganisms thus control NO production, even if the mechanism of production is chemical. However, a peak of chemical NO production can be initiated by desiccation of soil. Desiccation probably increases nitrite concentrations and decreases pH, thus creating reactive levels within microsites (141).

In contrast, it is relatively easy to assess the contribution of chemical processes to the decomposition of NO. Autoclaving

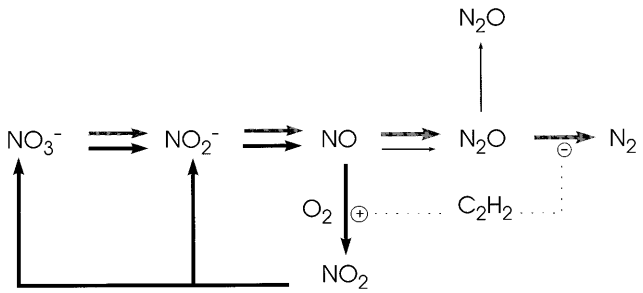

FIG. 1. Scheme of the effect of >0.1% acetylene (C_2H_2) on the transformation of nitrogen by denitrification and the production of N_2O.

soil usually abolishes any NO uptake at low concentrations (254, 424). This observation is reasonable since the chemical oxidation of NO to NO_2 by O_2 is a termolecular reaction that depends on the square of the NO concentration. Hence, chemical NO oxidation is significant only at relatively high NO mixing ratios. Whereas at 10 ppbv the half-life of NO is about 10^4 h, it is on the order of <1 h at mixing ratios of >100 ppmv (201).

Recently, we observed that the reaction of trace amounts of NO with O_2 is strongly enhanced if acetylene is present in mixing ratios of >0.1% (45, 46). Under natural conditions, this reaction is not relevant. However, it does play a role when denitrification rates in aerated soils are assayed by the acetylene blocking technique (143, 287, 391). In this case, the acetylene-catalyzed oxidation of NO results in the scavenging of nitrogen that would otherwise have accumulated as N_2O and thus results in a significant underestimation of the denitrification rate (Fig. 1).

Soil Enzymatic Processes

Soil enzymatic processes refer to the so-called abiontic enzymes (which by definition are free extracellular enzymes, enzymes bound to inert soil particles, enzymes within dead or nonproliferating cells, and enzymes associated with dead cell fragments) (498). Although the definition is straightforward, in practice it is difficult to differentiate between abiontic soil enzymes and the normal enzymes that are active in living microorganisms. The usual approach is to test enzyme activity after application of sterilizing agents, assuming that after inactivation of the living microbes, the residual enzymatic activity is due to abiontic soil enzymes. This approach is ambiguous, since the killing of microorganisms does not necessarily inactivate all of their enzymes. An example is the use of toluene as the sterilizing agent, which, however, can also be used to permeabilize (and kill) microorganisms for the assay of intracellular enzymes (249, 390).

Nevertheless, the criteria for abiontic soil enzymes are firmly established in soil science (68, 151, 497), and by applying these criteria, it can be shown that H_2 oxidation in soil is due to abiontic soil hydrogenases (115). In addition, no microorganism has so far been found that would fit the kinetic properties of active soil, i.e., exhibiting a K_m in the range of tens of ppmv of H_2 (equivalent to tens of nanomoles per liter in soil solution), although many different microorganisms and soil isolates have been tested (112, 122, 225, 291, 469). Obviously, the enzyme(s) responsible for the oxidation of atmospheric H_2 has to be isolated directly from soil to find out its molecular nature and origin. So far, abiontic soil hydrogenases are the only enzymes that appear to be important for trace gas exchange between soil and atmosphere. In fact, this activity represents about 95% of the global sink strength in the atmospheric H_2 budget (88).

Soil catalase reaction has been proposed to be involved in the decomposition of N_2O (548, 549), but this possibility has not been pursued.

Microbial Processes

Most of the trace gas production and consumption processes in soil are probably due to microorganisms. Trace gases can play different roles in the metabolism of microorganisms, i.e., as growth substrates, as cometabolites, as stoichiometric products, and as miscellaneous products, sometimes of unclear origin.

Growth on a substrate requires that the utilization of the substrate allow the generation of sufficient energy to cover maintenance plus biosynthesis costs. For the consumption of atmospheric trace gases, this means that two conditions must be met. (i) The Gibbs free energy of the consumption reactions at the actual ambient concentration must be sufficiently exergonic. This is not a problem for oxidation reactions with O_2, nitrate, or ferric iron as the electron acceptor but is a problem for other electron acceptors, especially bicarbonate reduction to acetate or CH_4 (see below). (ii) The consumption reaction must be sufficiently fast to match the maintenance requirements. This means that the V_{max}/K_m ratio must be at least as high as the maintenance coefficient (87). Since there are limits for increasing V_{max}, i.e., the number of active enzyme molecules per cell, the ability to consume trace gases at low ambient concentrations is actually limited by the relative magnitude of the K_m, which must be sufficiently low. This kinetic limitation applies generally and is critical for aerobic reactions, such as the oxidation of trace gases with O_2 (87).

Because of these constraints, it is not unexpected that trace gases are seldom utilized at ambient concentrations for growth. However, they can instead be used as additional substrates with supporting microbial growth or as cometabolites without supporting growth. The constraints outlined above do not apply for additional substrates or cometabolites. A rigorous test for support of growth is to show that the trace compound is assimilated into biomass (easily done by applying radiocarbon tracers in the case of CO and CH_4), that it supports the generation of ATP, or that the growth yield is increased by the utilization of the trace gas. If these tests are negative, it is likely that the trace gas is cometabolized. There are several enzymes that are known to catalyze the conversion of trace gases in addition to the conversion of the physiologically meaningful substrate (see below).

To test whether the trace gas metabolism in soil can be caused by a particular microorganism, it is useful to study the kinetics of the consumption of a trace gas in both systems (87). In particular, the K_m and threshold values that are observed in the microbial cultures should be consistent with those observed in the soil. This is a necessary criterion whenever microorganisms with a particular K_m dominate the consumption process in soil, independent of whether they use the trace gas for growth or cometabolism. However, this criterion is often not fulfilled (Table 3), and then the responsible microorganisms must be considered as unknown. An example is as follows. Consumption of atmospheric CH_4 in soil is achieved by a microbial activity with a low K_m value for CH_4, typically in the nanomolar range (33, 34, 136, 160). Known cultures of methanotrophs have K_m values in the micromolar range (281). So far, the microorganisms that oxidize atmospheric CH_4 have escaped isolation. All the methanotrophs that have been isolated from soils thus far do not possess the required kinetic properties

TABLE 3. Kinetic characteristics of trace gas consumption by soil, microorganisms, and microbial enzymes

Trace gas	Soil or microorganism	Threshold (nM)	K_m (nM)	Reference(s)
H_2	Upland soil	<0.01	10–70	88, 226, 469
	Aerobic H_2-oxidizing bacteria	>0.35	>800	88, 225, 291
	Wetland soil	10–180[a]	2,000–16,000	89, 207, 302, 440, 562
	Methanogenic bacteria	10–70	2,000–13,000	89, 123
CO	Upland soil	<0.01	5–50	88, 198
	Carboxydotrophic bacteria	<0.01	400–950	105, 198
	NH_4^+-oxidizing nitrifiers	?[b]	>97	257
	Methanotrophic bacteria	?	2,700	176
	Wetland soil	3–20[a]	?	110, 302
	Acetogenic bacteria	?	>10,000	355
CH_4	Upland soil	0.03–0.7	20–200	34, 136, 160
	Methanotrophic bacteria	<1.0	800–66,000	29, 70, 280, 464, 465
	NH_4^+-oxidizing nitrifiers	?	6,600–2,000,000	29
	Wetland soil, oxic rhizosphere and surface layers	1–300	2,500–10,700	193, 280, 282
OCS	Upland soil	<5[a]	>9	315
	Bacteria with carbonic anhydrase	?	8,900	408
	Phototrophic bacteria	?	2,200	170
	N_2-fixing bacteria	?	>3,100,000	480
N_2O	Soil, anoxic incubation	<0.8	700,000–1,000,000	40, 184
	Denitrifiers, DNRA bacteria	?	500–100,000	184, 531
NO	Soil, anoxic incubation	<0.01	1.6–8.5	26, 424, 475
	Denitrifying bacteria	<0.01	0.6–7.3	351, 424, 457
	Soil, oxic incubation	<0.01	1.8–>26.0	424, 443, 475
	Heterotrophic *Pseudomonas* spp.	<0.01	>7.5	298
	Flexibacter canadensis	?	>67	582

[a] Values are probably compensation concentrations between simultaneously operating production and consumption reactions. The actual thresholds should be lower.
[b] Unknown.

(281). We have to assume that these latter methanotrophs have an ecological niche that is characterized not by oxidation of atmospheric CH_4 but by oxidation of relatively high CH_4 concentrations that emerge in the vicinity of CH_4 production zones, e.g., in wetlands (420).

In summary, microbial processes involved in trace gas production and consumption in soil are still not well known and often seem to involve microorganisms that are unknown and have not been isolated or physiologically characterized.

Thresholds. Thresholds are the concentrations below which trace gases are no longer consumed. Thresholds have been observed in soil and in microbial culture for most of the atmospheric trace gases (Table 3). Threshold concentrations should not be confused with compensation concentrations. Compensation occurs when consumption is balanced by simultaneous production (see below) (93). Many of the H_2-consuming bacteria are able to produce small, nonstoichiometric amounts of H_2 when they grow heterotrophically (see below). However, the thresholds observed in aerobic H_2-oxidizing bacteria after the consumption of H_2 as sole substrate were not due to H_2 production, since removal of H_2 to levels lower then the threshold did not result in an increase of H_2 (98).

Threshold concentrations exist for growth but also for substrate degradation. The first are defined by the substrate concentration that still allows the generation of energy beyond the rate required for maintenance purpose. This subject has recently been reviewed (445). The thresholds required for growth are higher than the thresholds below which substrate degradation stops. The mechanisms that determine the latter thresholds are unclear.

In anaerobic bacteria, the magnitude of the H_2 thresholds seems to depend on the thermodynamics of the H_2 consumption reaction. Thus, the threshold concentrations decrease with increasing redox potential of the energy-yielding reaction, so that the H_2 threshold for H_2 utilization decreases in the following order: homoacetogenesis > methanogenesis > sulfate reduction > nitrate reduction (Fig. 2). Consequently, it was proposed that the H_2 concentration measured in the environment is an indication for the electron acceptor used in the H_2-utilizing process (331). By using chemostat cultures of anaerobic bacteria, it was found that the H_2 thresholds are equivalent to a certain amount of Gibbs free energy, the so-called critical Gibbs free energy, ΔG_c (484). Thresholds that are similarly characterized by a ΔG_c were also observed for the anaerobic degradation of benzoate by syntrophic bacterial consortia (563). The magnitude of the ΔG_c is in the range of energy required to translocate 1 mol of protons through a fully energized membrane (462, 463), suggesting that the stoichiometric conversion of one substrate molecule is obligatorily coupled to the translocation of at least one proton.

However, the ΔG_c obviously increases with the increasing redox potential of the energy-yielding reaction (484). In Fig. 2, the Gibbs free energies of H_2-consuming reactions with different electron acceptors are plotted as a function of the H_2 partial pressure. The diagram includes the H_2 threshold values and the ΔG_c values that were observed for the different H_2-consuming reactions. It is obvious that homoacetogens are the most efficient H_2 utilizers, which leave the smallest amount of free energy (in the form of the substrate H_2) unused. The other physiological groups of H_2 utilizers leave the more energy

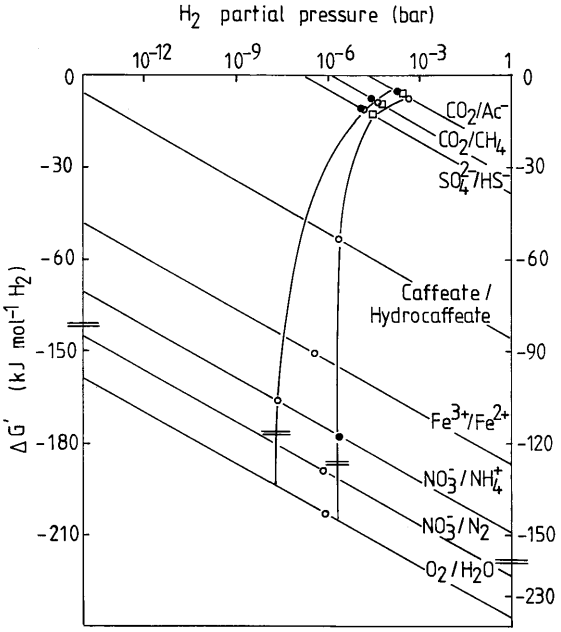

FIG. 2. Relation between the H_2 thresholds and the critical Gibbs free energies (ΔG_c) of different microbial H_2 oxidation reactions as function of the electron acceptor. The H_2 thresholds (○) and the ΔG_c values for H_2 consumption (●) and for growth on H_2 (□) were taken from the literature (127, 225, 291, 332, 484) and are plotted on the line that is given by the Nernst equation of the individual reactions. For simplicity, the Nernst equation was calculated by assuming standard conditions at pH 7 except for the partial pressure of H_2. The curves show the upper and lower range of the data.

unused the more their characteristic electron acceptors make available. However, the H_2 thresholds of the H_2 oxidation reactions with highly negative Gibbs free energies, i.e., those using ferric iron, nitrate, or O_2 as the oxidant, are all similar and are much higher than necessary for thermodynamic reasons. Obviously, the H_2 threshold is then no longer a function of the energetics of the reaction but is due to other unknown mechanisms.

Trace Gases as Substrates for Growth and Maintenance

Trace gases can support the growth of bacteria. Most of them (H_2, CO, CH_4, and OCS) serve as electron donors in oxidation reactions and yield energy for biosynthetic purposes. For most of the oxidation reactions, O_2, nitrate, ferric iron, sulfate, or bicarbonate can serve as an alternative electron acceptor. Only oxidation of CH_4 requires O_2 for the initial monooxygenase reaction (but see the discussion on anaerobic CH_4 oxidation, below). The nitrogen gases (N_2O and NO), by contrast, serve as electron acceptors for growth of denitrifying bacteria on reduced compounds such as organic substrates and H_2.

H_2. Hydrogen is a good growth substrate for a large diversity of bacteria. For example, the aerobic H_2-oxidizing bacteria grow with H_2, O_2, and CO_2 as sole energy and carbon substrates (14). The key enzyme is a membrane-bound Ni/Fe-containing uptake hydrogenase (195). A few species also contain a cytoplasmic hydrogenase (195). However, they all oxidize H_2 only at concentrations that are much higher than those in the ambient atmosphere (Table 3). Therefore, they cannot be responsible for the degradation of atmospheric H_2 by soil and probably play no role as controllers of the flux of atmospheric H_2 into soil. Instead, this role is covered by abiontic soil hydrogenases (88). However, the aerobic H_2-oxidizing bacteria are able to scavenge H_2 whenever it arises at high concentrations, e.g., at sites with geothermal H_2 production (101), in composting material (30), and at N_2-fixing root nodules with bacteroids lacking uptake hydrogenase activity (309, 401, 470). Especially in the latter case, H_2-oxidizing bacteria may contribute to reduce the release of H_2 from soils which are covered by N_2-fixing legumes and are at least temporarily a net source of atmospheric H_2 (113). Aerobic H_2-oxidizing bacteria may also scavenge some of the H_2 which is produced in anoxic soil, e.g., rice fields, as it diffuses over the anoxic-oxic interface on the surface of rice roots and is released into the atmosphere via the vascular gas transport system of the rice plants (476). Indeed, aerobic H_2-oxidizing bacteria are found in the rhizosphere of rice (209, 312).

Hydrogen also serves as a growth substrate for different anaerobes, notably the methanogenic bacteria. It is one of the important precursors of CH_4 in anoxic soils, contributing approximately 10 to 50% to total CH_4 production (396, 440, 478, 518, 525). As for the aerobic H_2-oxidizing bacteria, anaerobic H_2 utilization is characterized by threshold concentrations that are usually higher than those found in the ambient atmosphere (Table 3).

CO. Carbon monoxide serves as a growth substrate for a similar diversity of bacteria to those served by H_2. However, it has not received much attention. The best-studied bacterial groups are the aerobic CO-oxidizing (carboxydotrophic) bacteria (357, 367, 593) and the CO-utilizing homoacetogenic bacteria (154, 597). There is a marked difference in the key enzymes for CO oxidation by these two groups. The aerobic carboxydotrophs possess a molybdopterin cofactor and dehydrogenate CO plus water to CO_2 plus reducing equivalents (367). The homoacetogens catalyze the same reaction with a nickel-containing enzyme whose main function, however, is the synthesis or degradation of acetyl coenzyme A (CoA) (412, 580). CO consumption has also been reported for methanogens which possess the Ni-containing CO dehydrogenase (179). This CO dehydrogenase activity is part of an acetyl-CoA decarbonylase synthase complex (212). A nickel-containing CO dehydrogenase is also present in sulfate-reducing bacteria (355, 586). An interesting mechanism of CO consumption has been reported for phototrophic bacteria which hydrolyze CO with water to H_2 and CO_2 (171, 545). This CO dehydrogenase also contains nickel and iron sulfur clusters but has a simpler structure than the CO dehydrogenase of homoacetogens and lacks the ability to catalyze the synthesis or degradation of acetyl-CoA (47, 268). A recently isolated thermophilic anaerobic CO utilizer also hydrolyzes CO to H_2 and CO_2 (522). Interestingly, recent studies indicate that the production of H_2 from CO also occurs in aerobic carboxydotrophic bacteria, i.e., those with the molybdopterin-containing CO dehydrogenase (454). In addition to these bacteria that are all able to grow on CO, CO can be oxidized by monooxygenases without being used for bacterial growth (see below). For the most recent review of the different CO dehydrogenases, see reference 180.

So far, no conclusive ecological niche has been found for the CO-utilizing mode of bacterial growth (88, 95). In contrast to aerobic H_2 utilization, a threshold for aerobic CO utilization has not been reported (114). However, the affinity of the commonly known aerobic CO-utilizing bacteria (K_m in the low micromolar range) is much lower than that observed in soils (K_m in tens of nanomoles per liter) (Table 3). Therefore, these bacteria cannot account for the CO consumption in soil. Instead, the CO-cooxidizing nitrifying bacteria may be responsible for CO consumption in soil (see below). Also, unknown oligotrophic bacteria have been suggested as possible agents

for atmospheric CO consumption (116). However, these bacteria have not been isolated in pure culture. A thermophilic actinomycete was reported to grow aerobically on CO with a relatively low K_m (70 nM), which is on the same order as that observed in soil (7 to 33 nM) (198). The CO-oxidizing microorganisms in soil seem not to grow with CO and assimilate only minor amounts of ^{14}CO into biomass (22).

The role that the anaerobic CO utilizers (acetogens, methanogens, etc.) may play in anoxic soils is unexplored. Concentrations of CO in paddy soils and sediments are in the nanomolar range (Table 3). Turnover of CO is probably low but has so far not been investigated systematically. Submerged paddy soil seems to be only a small source of atmospheric CO, but the plants of these wetlands produce and emit significant amounts of CO (110, 598). Peat soils emit small amounts of CO when the water table is high but act as a sink for atmospheric CO when the water table is low (197). It is possible that the CO production at high water table is due to photodynamic effects acting on the *Sphagnum* plants (88, 526).

CH_4. The only known group of bacteria able to grow on CH_4 are the aerobic methylotrophic bacteria which oxidize CH_4 with O_2 to CO_2 (85, 223, 233). The methanotrophs are subdivided into two major groups, type I and type II (280, 374). Type I methanotrophs (the genera *Methylobacter* and *Methylomonas*) belong to the γ-subdivision of the *Proteobacteria* and use the ribulose monophosphate pathway for formaldehyde assimilation. Type II methanotrophs (the genera *Methylosinus* and *Methylocystis*) belong to the α-subdivision and use the serine pathway. A third group, type X, is often proposed for *Methylococcus capsulatus* (γ-subdivision), because this bacterium has characteristics of both of the other groups. The oxidation pathway is initiated by the methane monooxygenase (MMO) which requires both O_2 and reducing equivalents for activity. The MMO exists in two different forms. The membrane-bound enzyme is evolutionarily related to the ammonium monooxygenase (AMO) of the nitrifying bacteria (240) and is synthesized only in the presence of sufficient concentrations of copper but is apparently present in all methanotrophs (374). The soluble MMO, on the other hand, is found only in type II and type X methanotrophs and is expressed when the copper concentration is low (<1 μM) (280, 373). The K_m values for CH_4 that are observed in bacterial culture or in enzyme preparations are in the range of 1 to 92 μM, with those of the particulate MMO possibly at the lower end (280). Chemostat and gradient culture studies suggest that type I methanotrophs dominate at lower CH_4 concentrations (10, 211). Studies by Lidstrom's group (318) indicate that copper-sufficient and copper-insufficient forms of the particulate MMO exist, with the copper-sufficient form having a lower K_m for CH_4 than the copper-insufficient form. However, all of the culture studies so far have shown K_m values that are much higher than those observed for oxidation of low CH_4 concentrations in soil ($K_m <$ 200 nM [Table 3]). The existing methanotrophs are unable to grow on atmospheric CH_4, an activity that is obviously accomplished by unknown and as yet unisolated bacteria in soils (33).

In principle, methanotrophs must have either a high affinity for CH_4 or a low maintenance requirement to grow on atmospheric CH_4 (87). Methanotrophs with low affinities seem to account for the activity that is induced in soils preincubated with high CH_4 concentrations (33, 37, 466). The activity can be maintained over long periods but is lost when soils are incubated under atmospheric CH_4 concentrations (466). Bock and Sand (42) recently claimed to demonstrate the existence on the surface of building stones of methanotrophs that are able to grow on atmospheric CH_4. However, experimental details were not presented. Measurements of $^{14}CH_4$ oxidation in soil generally demonstrated CH_4 assimilation into microbial biomass even at low atmospheric CH_4 concentrations (438, 466, 575). Probably, this activity is due to the same unknown high-affinity bacteria that were shown to be responsible for atmospheric CH_4 oxidation (33). As tested in soil samples, they are apparently inhibited by ammonia and nitrite as described for methanotrophic bacteria in culture (160, 284, 465).

Methanotrophs that have a K_m for CH_4 in the micromolar range (Table 3) cannot account for atmospheric CH_4 oxidation but are able to oxidize CH_4 at anoxic-oxic interfaces, such as the surface layer of methanogenic sediments and paddy soil (279, 283) and the rhizosphere of rice and other aquatic plants (203, 204, 282). For example, CH_4 concentrations in the micromolar range exist in the oxic surface layers of submerged soils where CH_4 diffuses from below (107, 441). The micromolar K_m values for CH_4 oxidation in this layer and in excised rice roots are typical for methanotrophs in culture (Table 3). Micromolar K_m values are sufficient to allow the methanotrophs in these zones to reduce the emission flux of CH_4 from wetlands, rice fields, and other methanogenic environments and to exert an important control on the budget of atmospheric CH_4 (75, 477). A similar role is played by methanotrophs in the cover soil of landfills (255). When exposed to high CH_4 concentrations, the methanotrophic populations in this environment respond to high CH_4 by shifts in K_m from 1.6 to 32 μM (276).

Methane oxidation is obviously also important under anoxic conditions, especially in marine and hypersaline sediments. The evidence for anaerobic CH_4 oxidation is based on the use of $^{14}CH_4$, on diffusive models, and on $\delta^{13}CH_4$ profiles (6, 247, 248). The data usually show a coincidence of anaerobic CH_4 oxidation with sulfate reduction. Anoxic CH_4 oxidation has also been suggested to operate in the subsoil of rice fields (364). There, it coincided with reduction of ferric iron. However, microorganisms able to consume CH_4 in the absence of O_2 have not been isolated thus far. It has been suggested recently that the anaerobic CH_4 oxidation is due to a reverse methanogenesis, producing CO_2 plus H_2 from CH_4, which is thermodynamically possible if the H_2 partial pressure is kept low by H_2-utilizing sulfate reducers (237). This hypothesis is analogous to that for "*Reversibacter*," a homoacetogen, which is able to convert acetate to H_2 and CO_2 if the H_2 partial pressure is low (313). The hypothesis is not unreasonable, since methanogens are known to keep a certain H_2 partial pressure even when growing on acetate, methanol, or isopropanol (97, 125, 330). However, the hypothesis has so far not been supported by defined coculture studies. Inhibitor experiments are also inconclusive (7). It is also unclear how the methanogens could reverse the strongly exergonic final reactions of the methyl transferase, methyl-CoM reductase, and heterodisulfide reductase (371, 468).

OCS. Growth on carbonyl sulfide, as well as on carbon disulfide, has been obtained with *Thiobacillus thioparus* (506). The K_m for OCS is unknown, but that for CS_2 is 16.5 μM. Recently, other eubacteria that are able to grow on OCS as the sole energy source have been isolated (259). These bacteria grow on a wide variety of sulfur compounds (including DMS, COS, and CS_2) aerobically and as denitrifiers. There is no indication that the hydrolysis of OCS would yield energy and/or support growth (267, 506). Therefore, we may assume that the bacteria just grow by oxidizing the H_2S that is produced by hydrolysis of OCS. The nature of the OCS-hydrolyzing enzyme in thiobacilli is not known. However, by analogy to autotrophic plants (407–409), OCS hydrolysis may be catalyzed by a carbonic anhydrase that functions in autotrophic CO_2

fixation. In fact, OCS may be a cometabolite in many more bacteria if they possess enzymes able to hydrolyze OCS.

N_2O. Nitrous oxide is an obligate intermediate in the denitrification pathway and can serve as the sole electron acceptor to support the growth of denitrifying bacteria (28, 294, 384, 602). Interestingly, N_2O can also be reduced to N_2 by some but not all bacteria that normally reduce nitrate to ammonia, i.e., the so-called DNRA (dissimilatory reduction of nitrate to ammonia) bacteria (452, 474, 531). N_2O reduction is the only known process important for N_2O turnover in soil. The bacterial K_m values for N_2O range from 0.5 to 100 μM, and values in soil are even higher (Table 3). The reason for this large variability is probably an analytical bias due to diffusion limitation during the experiments (538). However, it is obvious that the K_m values are large compared with the concentration of atmospheric N_2O, which is equivalent to an aqueous concentration of about 8 nM. Although soils usually act as net sources for atmospheric N_2O, uptake of N_2O from the atmosphere has been observed occasionally (72, 158, 446, 499). A threshold for N_2O uptake has not been observed; i.e., it is below the detection limit of N_2O analysis (40).

NO. Nitric oxide is an obligate intermediate in the denitrification pathway. Nitric oxide is produced by nitrite reductase and is reduced to N_2O by nitric oxide reductase (589, 601). Some fungi can denitrify (492), but they possess a NO reductase with a different molecular structure from that of bacteria (491). Theoretically, denitrifiers should be able to grow on NO as the sole electron acceptor, since the redox potential is high ($E_0' = +1{,}173$ mV for NO/N_2O) and since N_2O, the product of NO reduction, could equally serve as an electron acceptor ($E_0' = +1{,}355$ mV for N_2O/N_2). However, since NO is usually toxic to bacteria at the high concentrations that are required for testing growth (337), there are almost no reports on successful growth of denitrifiers by NO reduction (399). Nonetheless, it has been demonstrated that NO as an electron acceptor can support vectorial proton translocation and thus allow the generation of energy (489, 554). It has been shown that the reduction of NO by denitrifiers is important for NO turnover in soil (424) and that the K_m value for NO is very low in both soil and denitrifying bacteria (<8 nM; Table 3). However, there seem to be additional processes for NO consumption in soil, e.g., NO consumption by methanotrophs (35, 301). It is unknown whether NO consumption is beneficial for methanotrophs and also whether it is due to a reduction or an oxidation mechanism. Oxidation of NO to nitrate rather than reduction to N_2O has recently been found to be the dominant NO consumption mechanism in some soils (27, 161, 443). This oxidation reaction is possibly due to cooxidation of NO by heterotrophic bacteria (27, 298). A threshold for NO uptake has not been reported.

Trace Gases as Cometabolites

Monooxygenase. MMO of methanotrophic bacteria is able to oxidize not only CH_4 but also NH_3 and CO (29). Likewise, AMO also oxidizes CH_4 and CO. The physiology and environmental relevance of these reactions have been reviewed in detail (29). Both monooxygenases have overlapping ranges of K_m values for CH_4 (Table 3). AMO has a much lower V_{max} with CH_4 than does MMO, so that nitrifiers must be proportionally more numerous than methanotrophs in soil to exert the same activity (29). On the other hand, both nitrifiers and methanotrophs oxidize CO at similar rates per cell, so that the ratio of CH_4 to CO oxidized is higher in methanotrophs than in nitrifiers (258). Castro et al. (71) showed that in nitrogen-fertilized soils, rates of CO oxidation were similar but those of CH_4 oxidation were lower than in the control soil, and they thus concluded that upon fertilization, nitrifiers became relatively more important for CH_4 oxidation than did methanotrophs.

Tests for assimilation of $^{14}CH_4$ in nitrifiers gave contradictory results (29). At present, it cannot be excluded that CH_4 oxidation could be beneficial, at least for some species of nitrifiers, such as those (e.g., *Nitrosococcus* species) belonging to the γ-subgroup of *Proteobacteria* which exhibited $^{14}CH_4$ incorporation into biomass (256, 558). However, none of the nitrifiers is able to grow with CH_4.

The soluble MMO has relatively high K_m values for CO (2.7 μM), which cannot explain the CO oxidation activity in soil which has K_m values of <50 nM (Table 3). AMO, on the other hand, has a much lower K_m for CO (>97 nM), which comes close to the K_m observed in soil (Table 3). Incubation experiments with soils showed that the uptake of atmospheric CO was enhanced when the population of nitrifiers was enriched (35). Nitrifiers do not assimilate ^{14}CO in large amounts (257), similarly to the results found for soils (22). The low assimilation is probably due to fixation of $^{14}CO_2$, the oxidation product of ^{14}CO, in the presence of ammonium as the energy substrate (257). In summary, it appears that cometabolism of CO by the AMO of nitrifiers may contribute to the uptake of atmospheric CO by soil.

Carbonic anhydrase. The carbonic anhydrase of cyanobacteria, algae, lichens, and plants is apparently able to react with OCS as a structural analog of CO_2 and thus to catalyze the hydrolysis of OCS to CO_2 and H_2S (21, 215, 359, 407–409) by the following reactions:

$$OCS + OH^- \rightarrow CO_2 + HS^-$$
$$CO_2 + OH^- \rightarrow HCO_3^-$$

The K_m value (Table 3) of the carbonic anhydrase for OCS is in the same range as or lower than that for CO_2 (269, 408, 409). Carbonic anhydrase is an enzyme that may be widespread among autotrophic soil microorganisms. For example, any microorganism which assimilates CO_2 by using an enzyme with CO_2 as the active species (e.g., ribulose-1,5-bisphosphate carboxylase) potentially contains carbonic anhydrase to facilitate the equilibration between bicarbonate and CO_2. In soils with many autotrophic bacteria (e.g., autotrophic nitrifiers), carbonic anhydrase could be responsible for much of the OCS consumption. However, systematic studies are lacking. The uptake of OCS in soil was found to be a first-order reaction for OCS mixing ratios of >400 ppbv, equivalent to about 8.8 nM in soil solution (315). Soil OCS uptake at lower mixing ratios has not yet been tested. However, atmospheric OCS mixing ratios are typically around 0.5 ppbv, equivalent to 11 pM. Because of the lack of data, it cannot be excluded that a second OCS degrading activity exists in soil that is predominantly active at concentrations below 4 nM and thus may have a K_m value in the picomolar range (315).

CO dehydrogenase and nitrogenase. Carbonyl sulfide can also be reduced to CO and H_2S by the CO dehydrogenase of *Rhodospirillum rubrum* (170) and the nitrogenase of *Azotobacter vinelandii* (480). The CO dehydrogenase has a K_m for OCS ($K_m = 2.2$ μM) lower than that for its natural substrate, CO_2 ($K_m = 190$ μM). The K_m for OCS of the nitrogenase is much higher ($K_m = 3.1$ mM). Degradation of OCS has also been observed in cultures of homoacetogenic bacteria but only at relatively high mixing ratios (percent level) and without growth (504). Since homoacetogens also possess a CO dehydrogenase, OCS degradation may be due to this enzyme. However, the environmental significance of OCS hydrolysis by CO dehydrogenase and nitrogenase remains unclear.

Peroxidase. Peroxidases are believed to be involved in the decomposition of NO within tissues of higher organisms and to catalyze the oxidation of NO to nitrate (244, 389, 510). Recently, we isolated a new *Pseudomonas* species that also oxidizes NO with O_2 to nitrate by a membrane-bound enzyme (27, 298). This bacterium cannot nitrify or denitrify, and growth is not supported by NO oxidation. Therefore, it is likely that NO is consumed by cooxidation. Other heterotrophic microorganisms also seem to be able to consume low NO concentrations under oxic conditions (27). Oxidation of NO to nitrate has been demonstrated to occur in certain soils, although it is still unknown how widespread this NO consumption mechanism is in comparison with the reduction by denitrifying bacteria (27, 161, 443). Both activities can occur in the same soil; the oxidative pathway was active under oxic conditions, the reductive pathway was active under anoxic conditions, and the K_m value of NO oxidation seemed to be at least four times higher than that of NO reduction to N_2O (443). This feature may provide an experimental tool to distinguish oxidative and reductive NO consumption in soil (95).

Trace Gases as Stoichiometric Products

Several trace gases are stoichiometric products of dissimilatory pathways, i.e., H_2, CH_4, N_2O, and NO. However, only the production of CH_4, N_2O, and NO has a large impact on atmospheric budgets. Microbial production of H_2 in soil plays only a minor role.

H_2. Hydrogen is an important product of bacterial fermentation and allows for the regeneration of redox carriers in their oxidized state. Even bacteria that are unable to grow fermentatively under anaerobic conditions, e.g., methylotrophs or Knallgas bacteria, can produce some H_2 by fermentation when they are kept under anoxic conditions or with limiting O_2 supply (264, 307, 552). However, the extent of H_2 formation depends on the redox potential of the particular H_2-generating reaction and the H_2 partial pressure according to thermodynamic theory. For example, H_2 generation by fermentation of pyruvate is thermodynamically not restricted, because of the negative redox potential of the reaction, whereas H_2 generation by fermentation of propionate is thermodynamically restricted. This subject is covered in several reviews (97, 156, 462, 511). In soil, H_2 production by fermentation can be observed in two different situations.

(i) In anoxic methanogenic soil, H_2 production is usually in steady state with H_2 consumption by methanogenic bacteria. The turnover time of H_2 is within minutes and creates steady-state H_2 concentrations that are typically in the nanomolar range. The H_2 concentration is often only slightly higher than the threshold of methanogens for H_2 (Table 3). Thus, methanogenic soils are only a negligible source in the budget of atmospheric H_2 (88, 476).

(ii) When oxic soils are flooded, a phase of H_2 production usually precedes the phase of methanogenesis (104, 566). Production of H_2 then occurs transiently and is probably caused by fermentation of substrates (e.g., sugars) that have no thermodynamic restriction for the production of H_2 at high concentrations. Concentrations of H_2 in this phase can reach percentage levels. The source strength of this transient soil state for atmospheric H_2 has not been estimated so far. Such a transient state may also occur in microniches within generally oxic soil (95). However, it is probably not of widespread importance, because field studies indicate that soils usually act as a sink for atmospheric H_2.

The only incidences of a significant net emission of H_2 into the atmosphere (2.4 to 4.9 Tg $year^{-1}$) were reported for soils covered with N_2-fixing legumes (88, 113). Here, however, H_2 is not produced by fermentation but, rather, is a side product of nitrogenase (166).

CH_4. The production of CH_4 in anoxic natural environments is understood in principle and has been reviewed repeatedly (89, 275, 594, 596, 600). Methane is an important degradation product of organic matter under anoxic conditions. Cellulose carbon, for example, is converted methanogenically to 50% CO_2 and 50% CH_4. The degradation is achieved by a complex microbial community consisting of hydrolytic, fermenting, syntrophic, acetogenic, and methanogenic bacteria. Methane production in anoxic environments such as sediments and flooded rice fields creates the most important source in the budget of atmospheric CH_4 (84, 405). The actual production of CH_4 is accomplished by methanogenic bacteria. The biochemical pathways of CH_4 production and the enzymes involved have been intensively studied during the past decades and are now understood in principle (178). However, further research is needed to learn something about the community structure of methanogenic environments and also about the populations of methanogens involved (see below).

NO and N_2O. The microbial basis of the production of NO and N_2O in soil is more complicated than that of CH_4. Both NO and N_2O are intermediates in the sequential reduction pathway of nitrate by denitrifiers (177, 589, 601), and thus, both are produced and consumed by this microbial group. Production of NO and N_2O has also been demonstrated among bacteria that respire nitrate to nitrite and those that dissimilate nitrate to ammonium (DNRA) (96, 538). NO and N_2O are also produced by nitrifiers apparently producing the nitrogenous gases by reduction of nitrite (403, 422). NO and N_2O can be produced in soil during both oxidation of ammonium and reduction of nitrate (143, 288, 289, 423), presumably involving nitrifiers and denitrifiers, respectively. However, since denitrifiers, nitrate respirers, and DNRA cannot be differentiated in situ, and since autotrophic and heterotrophic nitrifiers cannot always be differentiated either, the exact microbial basis of NO and N_2O production and consumption is still not clear (96). The problem is compounded by the fact that these physiologically defined groups are obviously widespread among the various taxa including the *Proteobacteria*, gram-positive bacteria, and fungi. In addition, the enzymatic basis of the NO-producing and NO-consuming reactions is not well understood. The level of understanding is best for denitrification (177, 589, 601); however, the biochemical pathways and enzymes involved in NO and N_2O production by other physiological groups are poorly understood (96).

Trace Gases as Miscellaneous Products

Oxic soils sometimes produce sufficient CH_4 to act as a net source of atmospheric CH_4 (145, 208, 265, 588). In contrast to the vigorous CH_4 production in anoxic soil, the microbial basis for the production of small amounts of CH_4 in oxic soils is still unclear. Whereas large amounts of acetate (in the millimolar range) are produced by anaerobic acetogenic bacteria in forest soil, production of CH_4 is minor as long as the soil is not completely anoxic (308). However, methanogens are present (though in small numbers) in every soil, even in dry desert soil (395), and methanogenesis can be initiated in these oxic soils if they are water saturated (308, 396, 557). Temporarily flooded soils apparently produce more CH_4 with longer flooding periods (11). Since methanogens are sensitive to O_2 and are unable to form resting stages, it is unclear how they could survive or even proliferate in soils that are generally oxic. If we assume that methanogenesis in oxic soil starts only if anoxic mi-

croniches have become sufficiently numerous (e.g., after heavy rain), we still have the problem of explaining how methanogens can survive when no anoxic microniches are present. A similar enigma occurs with respect to CH_4 production in epilimnetic surface water of lakes and oceans (493, 494). There are several conceivable answers (or combinations of them) to this problem. (i) There are methanogens in soil that are less sensitive to O_2 but have not yet been cultured. Interestingly, *Methanosarcina* species were shown to become active at redox potentials as high as +50 mV (182). Also, up to 5% of the methanogenic population of rice field soil was able to survive desiccation of the soil under oxic conditions (181). (ii) Even completely oxic soils contain microniches suitable for the survival of methanogens, e.g., in the guts of small animals. As a result, methanogens can be reinoculated continuously by the soil microfauna and mesofauna, which distribute methanogens with their feces. This possibility is largely unexplored, although a study of various arthropod taxa suggests that only a few taxa, i.e., termites (*Isoptera*), cockroaches (*Blattidae*), millipedes (*Diplopoda*), and scarab beetles (*Scarabaeidae*), have methanogenic symbionts (220). Anoxic microsites could also be created in consortia with O_2-respiring microorganisms. This possibility was explored as a way to explain the CH_4 production in oxic seawater (494). (iii) Methane is produced in a minor side reaction, e.g., degradation of methionine by clostridia (431) that are able to survive in dry oxic soil as spores. Such low rates of CH_4 production have also been reported for sulfate reducers and other bacteria (402). Methane can also be produced by aerobic reactions such as bacterial degradation of methylphosphonates (139).

The microbial basis for the production of OCS is unclear. It has been observed that OCS production in soil is stimulated after the addition of thiocyanate (56, 315, 361). A OCS-producing enzyme, thiocyanate hydrolase, has been purified from *Thiobacillus thioparus* (262). The same bacterium also produced OCS by hydrolysis of CS_2 (506). However, the mechanism of OCS production in soils that are not treated with thiocyanate is still unknown.

Although the majority of CO production in soil seems to be caused by chemical processes (see above), microbial production is also possible. Carbon monoxide can be produced from oxidation of the methin bridges in porphyrins (530, 590). Thus, CO production was found in heme- and hydroxocobalamin-degrading bacteria (167, 168, 232). Carbon monoxide production has also been reported for the microbial degradation of flavonoids (572), rutin (573), and aromatic acids (236) and has also been observed in cultures of various microorganisms as a result of unspecified processes (65, 410). All these processes can in principle take place in soil, but their actual biogeochemical role is unknown.

Worth mentioning also is the production of H_2 and CO in nonstoichiometric amounts by methanogens, acetogens, and sulfate-reducing bacteria. Both compounds are found in trace quantities in cultures of these bacteria (97, 121, 125, 153, 330, 334). Hydrogen and CO are formed as intermediates in metabolism and probably equilibrate to some extent with the medium. The production of small amounts of H_2 during acetate catabolism by *Methanosarcina* species is sufficient to serve as an electron donor for sulfate reducers (398). Likewise, the small amounts of H_2 produced by methanol-utilizing acetogens are sufficient as electron donors for methanogens or sulfate reducers (126). These cases of interspecies H_2 transfer have been observed primarily in defined bacterial cocultures, but some evidence points to their occurrence in anoxic paddy soil (3).

DEFINITION OF SOIL AND SOIL MICROORGANISMS

When characterizing trace gas metabolism in soil, one problem is a suitable definition of soil and soil microorganisms. The definition of soil in the various atmospheric budgets of trace gases usually assumes that it is a terrestrial site which is covered by some vegetation. These sites comprise farmland soils, which are dominated by mineral soils, as well as wetland soils, which are often dominated by living and dead plant biomass, e.g., *Sphagnum* bogs. The various soils usually also contain animals, which may produce trace gases on their own. From the viewpoint of a microbiologist, it is appropriate to assess the effects of plants and animals (mainly worms and arthropods) separately from those of microorganisms. However, the term "microorganisms" may also be ambiguous. Often the term is used as a proxy for members of the *Bacteria*, *Archaea*, fungi, and protozoa. However, from a practical point of view, the soil microbiota is best defined as including all organisms that are too small to be separated from the soil matrix by mechanic tools (e.g., forceps and sieves). Thus, soil microorganisms in a practical sense would comprise bacteria (*Bacteria* and *Archaea*), fungi, algae, and protozoa but also the micro- and mesofauna smaller than about 1 mm, e.g., rotifers, nematods, acari, and collembols (524).

Role of Vegetation

In practice, the distinction between soil and vegetation is often not trivial and usually not solved simply by removing the plants, since plant processes and soil processes interact in various ways, e.g., metabolism of trace gases by the plants, transport of trace gases through the plants, or metabolism of trace gases in the rhizosphere of plants.

Trace gases that are metabolized by the plants include CO (24, 483, 526), OCS (64, 205, 407, 528), and NO/NO_2 (253, 481, 500, 536). The plant metabolism may create a trace gas flux that adds to the flux generated in the soil. In these cases, it is impossible to assess the effect of the soil if the vegetation is not removed.

Plants can serve as conduits for the transport of trace gases between the soil and the atmosphere. This phenomenon is especially important for wetland soils which are covered with aquatic plants that have a vascular gas transport system to provide the roots with O_2 (15). Vascular transport is most important for the flux of CH_4 (477), but other gases are transported as well, e.g., CO, H_2, and N_2O (110, 368, 476). It is almost impossible to measure realistic gas fluxes from wetland soils when aquatic plants are removed. However, it is relatively easy to assess the contribution of plant-mediated flux to total flux, if the plants are cut below the water level (e.g., in flooded rice fields) (149, 242, 478). This allows the measurement of the momentary contribution of vascular transport to the total flux. In the long term, however, the ongoing production of trace gas in the soil will result in another transport pathway, e.g., ebullition (75, 76).

Some trace gases are specifically metabolized in the rhizosphere. For example, H_2 is released into the atmosphere if soils are covered with N_2-fixing legumes (113). Hydrogen is produced by nitrogenase of the bacteroids in the root nodules and is only partially recycled by uptake hydrogenases of the bacteroids. Similar phenomena probably exist for *Frankia* root nodules (437, 485), although H_2 fluxes caused by *Frankia* symbiosis have not yet been measured in a soil system.

Role of Animals

Since the biomass and the overall contribution of the soil fauna to litter decomposition are relatively minor compared with those of soil microorganisms, they have usually been neglected (165). However, soil animals may affect the trace gas flux by directly producing trace gases, by affecting trace gas-metabolizing soil microorganisms through grazing, or by accelerating the gas transport between soil and atmosphere.

Some soil arthropod taxa, e.g., termites, produce H_2 and CH_4, since they contain fermenting and methanogenic bacteria in their guts (57–59, 220, 599). Protozoa may also contain fermenting and methanogenic bacteria and thus release H_2 or CH_4 into the soil (174, 175, 183). Since small animals usually cannot be removed selectively from soil, it is very hard to assess the contribution of individual arthropods to trace gas metabolism in soil.

Little is known about the grazing pressure and other effects of soil animals on soil microorganisms in general (165). Nothing is known on this subject with respect to microorganisms that metabolize trace gases.

Soil animals may also affect the diffusive transport of trace gases in wetland soils, but this issue has not been studied explicitly. Benthic animals may affect the trace gas exchange between sediment and water by changing the topography of the surface, e.g., by creating mounds that in turn affect the water flow at the surface, the diffusive boundary layer, and the penetration of water flow into the sediment according to Bernouille's law (especially if it is a sandy sediment) (49, 219). Burrowing animals possibly accelerate the exchange of O_2 beyond diffusional transport by actively ventilating their burrowing holes with a stream of water (192, 305). Analogously, the exchange of trace gases may also be enhanced.

TRACE GAS FLUXES BETWEEN SOIL AND ATMOSPHERE

From the viewpoint of microbial trace gas metabolism, it is appropriate to distinguish at least two different groups of soils. Upland soils are not water-saturated, well-aerated soils which are generally oxic. Wetland soils are water-saturated soils that are generally anoxic. These two groups of soils have different characteristics with respect to microbial production and consumption of trace gases. This issue has been reviewed recently (94, 95). Perhaps even more importantly, however, the gas exchange mechanism itself is organized in different ways (see Fig. 3 to 5).

As a result, wetland soils are usually sources of atmospheric trace gases. Wetland soils are especially important sources of atmospheric CH_4. They act as sinks for atmospheric CH_4 only when the water is drained (231). Fluxes of CH_4 in various types of wetlands have been investigated intensively. The rates of CH_4 emission have frequently been compiled and reviewed (20, 23, 347, 360, 380). There are several studies of emission rates of NO (199, 310) and N_2O (191, 311, 323, 324, 340, 345, 459, 501, 502) in wetland soils (e.g., paddy fields, fens, and wet tundra). All these studies show that the fluxes of NO and N_2O from wetland soils are small compared with aerated soils, probably because a larger percentage of the produced NO and N_2O is further reduced by denitrifiers to N_2. Submerged rice fields seem to act occasionally even as a sink for atmospheric N_2O (362).

Upland soils, on the other hand, are both sources of and sinks for atmospheric trace gases. They are net sinks for atmospheric H_2 (88), CO (88), and CH_4 (420) but net sources of N_2O and NO (140, 354, 578).

The flux of a trace gas between the soil and the atmosphere is the result of three basic processes: production, consumption, and transport. The interaction of these basic processes is different in upland and wetland soils (see Fig. 3 to 5).

Wetland Soils

Wetland soils are submerged and generally anoxic. However, O_2 penetrates from the surface and creates a thin (1- to 5-mm-deep) oxic soil layer. It also penetrates from roots of aquatic plants with gas vesicular systems into deeper soil layers.

Vertical redox gradients. The depth of the oxic surface layer is the result of a balance between the influx of O_2 from above and the O_2 consumption by the soil microflora. The O_2 influx is mainly due to molecular diffusion but may be enhanced by bioirrigation of the soil fauna (see above) and by photosynthetic O_2 production by benthic algae (19, 430). The O_2 consumption and thus the O_2 penetration depth are a function of the availability of degradable organic matter present in the surface layers (421, 429). However, O_2 consumption in the surface layer is also a function of the production of reduced compounds such as CH_4, ammonium, ferrous iron, and sulfide in the anoxic layers below. These compounds diffuse upward until they reach the oxic zone, and there they contribute to the microbial (and chemical) O_2 demand (523).

In general, O_2 is depleted rapidly with distance from the soil surface or the root surface, resulting in a redox stratification (595). This stratification theoretically creates relatively well-defined habitats for the different groups of trace gas-metabolizing microorganisms, which may be studied separately to some extent. The different redox zones are characterized by the dominance of the electron acceptors O_2, NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, and CO_2 (Fig. 3) (595). Experimentally, the different zones may be distinguished by spatial sampling, but few studies in which profiles of manganese and iron were measured simultaneously with other electron acceptors have been performed. These profiles (all in marine sediments) showed the existence of redox zones, which, however, were not sharply separated (507, 532). The different redox processes can also be studied on a temporal basis, for example, by observing the sequential reduction of the different electron acceptors when oxic soils are submerged and become anoxic (393, 400).

Most wetland soil is devoid of O_2 (below 2 to 3 mm deep) and also contains no other electron acceptors (below a few centimeter deep) other than CO_2 and H^+. Therefore, this zone is dominated by fermentation and methanogenesis (Fig. 3). Production of H_2 by fermentation is intensive, but most of the produced H_2 (together with CO_2) is immediately converted by methanogens to CH_4, so that the steady-state concentration of H_2 is typically in the nanomolar range (10 to 180 nM, corresponding to about 8 to 140 ppmv in the gas phase [Table 3]). It must be emphasized that this concentration range, although low with respect to substrate requirements by methanogens, still represents a substantial supersaturation with respect to the atmospheric H_2 concentration (0.55 ppmv).

Methane is an end product of the microbial metabolism in this zone and occurs in concentrations equivalent to mixing ratios of up to 90% (191). The pathways of CH_4 production (89, 275, 594, 596, 600) have frequently been reviewed. Further trace gases that seem to be produced in the anoxic soil zone are CO (110, 197, 302) and OCS (234, 235, 361). However, the mechanism for production of these gases is not clear (see above).

The sulfate reduction zone can also be quite extensive in wetland soils, especially in marshes that are influenced by seawater. Sulfate reducers consume H_2 and, in steady state, re-

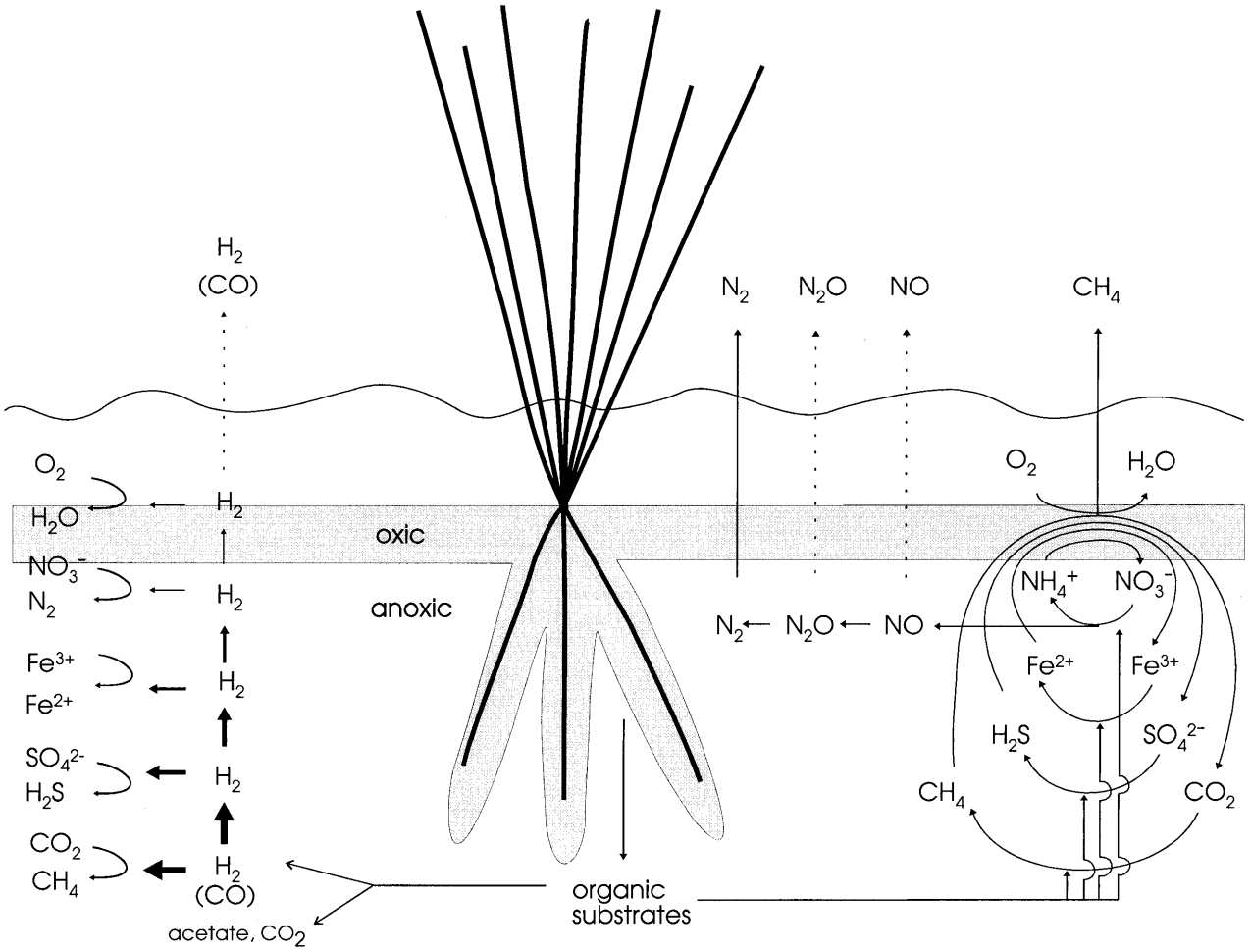

FIG. 3. Conceptual scheme of the vertical distribution of different redox reactions that influence the flux of H_2 and other trace gases (CO, CH_4, NO, and N_2O) from submerged vegetated soil and of the reoxidation of reduced inorganic electron acceptors by O_2 in the oxic layers at the soil-water interface and the rhizosphere of aquatic plants.

duce the H_2 concentration to lower values than found in the methanogenic zone, typically less than 2 to 10 nM (2, 331, 358). Therefore, there will be a flux of H_2 from the methanogenic into the SO_4^{2-}-reducing zone (Fig. 3). However, this soil zone is still substantially supersaturated with respect to atmospheric H_2. Nothing is known about the metabolism of CO in this zone, although one could theoretically expect CO turnover by sulfate reducers (334). The Fe^{3+}-reducing zones should further reduce the H_2 concentration, since iron reducers are able to metabolize H_2 more efficiently than are sulfate reducers (331).

The NO_3^- reduction zone is the site where H_2 concentrations are kept at a low partial pressure by the action of, e.g., denitrifiers or DNRA bacteria (127, 225). However, partial pressures are not necessarily lower than those in the Fe^{3+}-reducing zone (see above) (Fig. 2). Consumption of CO and OCS should theoretically be also possible, since carboxydotrophs and thiobacilli, respectively, that reduce nitrate are known (267, 367).

The NO_3^- reduction zone is also the zone where production and consumption of NO and N_2O occur by the action of denitrifiers and DNRA. A conceptual model of the effect of soil water status on the production of N_2O was presented by Keller (265). The vertical zonation in soil and sediment of nitrifying and nitrate-reducing activities and the regulation of these activities have been studied in great detail by means of chemical microsensors and ^{15}N isotope pairing (251, 252, 382, 447, 448). The results show that nitrification of ammonium in the oxic surface layer is an important source of nitrate and that denitrification is often tightly coupled to this process (Fig. 3). The fluxes of NO and N_2O into the atmosphere are relatively small, mainly because most of the produced NO and N_2O is further reduced to N_2. The ratio of N_2 to N_2O produced increases with the saturation of the soil pore space with water (568).

The oxic zone is dominated by consumption of trace gases, i.e., oxidation of CH_4, H_2, CO, and H_2S with O_2 as the electron acceptor (Fig. 3). The concentration of trace gases at the base of the oxic zone is generally much higher than the concentrations detected in the atmosphere or the gaseous pore space of upland soils. This allows the development of trace gas-oxidizing microbial communities that are different from those dominant in upland soils (95). The best-studied example so far is the oxidation of CH_4, which is obviously achieved by common methanotrophs in the CH_4-rich oxic zone of wetland soils but is achieved by unknown bacteria with high affinity for CH_4 in the upland soils, where CH_4 is supplied mainly from the atmosphere (33).

Although the zonation in wetland soil is usually relatively well defined, activity overlaps may occur. For example, al-

though CH_4 production is usually inhibited by the presence of SO_4, Fe^{3+} or NO_3^-, mainly since sulfate reducers, iron reducers, and nitrate reducers outcompete methanogens for common electron donors (331, 562), the simultaneous operation is possible if electron donors are not limiting, e.g., in organic-rich soils and sediments (2, 328, 370, 571). However, more complex interactions on the community level have also been discussed (3) (see below).

Radial redox gradients. The same redox zonation as in the vertical dimension theoretically also occurs radially around the roots of O_2-transporting aquatic plants. The release of O_2 by aquatic plants and increased redox potentials around the roots have been documented (15, 16, 82, 187, 189, 194, 243, 293). The availability of O_2 allows the operation of chemical and microbial oxidation reactions in the rhizosphere. Thus, the rhizosphere of aquatic plants is an important site for the oxidation of CH_4 (144, 203, 204, 241, 282). Oxidation of H_2 and the presence of aerobic H_2-oxidizing bacteria in the rhizosphere has also been documented (209, 312, 476). Other reduced compounds, such as ferrous iron (31), ammonium (18, 169, 419), and sulfide (579), are also oxidized in the rhizosphere. Although little is known about the actual zonation of the individual redox-active substances because of methodological difficulties, theoretical models have been constructed for the distribution of O_2 (17, 150, 547) and ferric iron (31, 285, 286).

Experiments with ^{15}N-labelled ammonium or urea and flux measurements in microcosms have indicated that denitrification in bulk soil is tightly coupled to nitrification in the oxic rhizosphere, which in turn can influence the production of N_2O and NO (18, 419). The importance of rhizospheric processes for the emission of NO and N_2O has not yet been properly quantified, but field measurements of total fluxes, including diffusion, ebullition, and plant transport, indicate that wetlands constitute only a weak source of atmospheric NO and N_2O (see above).

The roots of aquatic plants are also sources of organic material, which is either actively excreted or derived from sloughed-off cells or decomposing dead roots (Fig. 3) (322, 565). One of the seasonal maxima of CH_4 emission from rice fields which is usually observed when the rice plants are in their maximum growth phase is ascribed to stimulation of the methanogenic bacterial community by root exudation (242, 383, 455). Recently, it has been demonstrated that the roots of rice plants are colonized with methanogenic bacteria (320, 321) and that root preparations of aquatic plants produce CH_4 (52, 138, 277, 282, 320). However, the percent contribution of these particular methanogenic populations to total CH_4 emission from wetlands is unknown. Also, the amount of microbially available organic substrates should influence the extent of the redox layers around the root, since these substrates fuel the reduction of O_2, NO_3^-, Fe^{3+}, SO_4^{2-}, and CO_2. However, no experimental data exist.

Flux into the atmosphere. The flux of trace gases between wetland soil and the atmosphere is driven by the concentration gradient from the soil to the atmosphere. The transport processes have been studied in some detail for the emission of CH_4 from wetlands (75, 76, 89, 92, 223, 477) but should, by analogy, also apply to other trace gases and wetlands. There are basically three different pathways of CH_4 transport: plant vascular transport, ebullition, and diffusion through soil and flooding water.

The transport is driven by the CH_4 concentration gradient between the anoxic soil and the atmosphere (Fig. 3 and 4). The gradient is built up by microbial production of CH_4 in the anoxic methanogenic zone of the soil but is modulated to a large extent by CH_4 oxidation taking place both in the oxic surface layer and around the roots. More than 80% of the diffusive CH_4 flux appears to be oxidized in the oxic surface layer of freshwater wetlands (53, 107, 223, 279, 283, 523). The CH_4 oxidation efficiency in the rhizosphere usually does not quite reach the efficiency that is typical of the oxic soil surface (>80%) but seems to be mostly in a range of only 20 to 50% (148, 172, 203, 204, 478). The flux of CH_4 by plant vascular transport is usually the dominating emission pathway when the wetland soil is covered by the appropriate vegetation. This has been well documented in rice fields and other wetlands (76, 77, 241, 242, 478).

The process of ebullition has been reviewed (75, 76). Ebullition is especially important in unvegetated wetlands. The ebullition flux of CH_4 (and other trace gases contained in the bubbles) does not seem to be under the control of CH_4-oxidizing bacteria. However, the ebullition events can create channels in the soil and thus enlarge the surface area that is in direct contact with the oxic flooding water and consequently can enlarge the oxic boundary layer at the soil-water interface, which constitutes a suitable habitat for methanotrophic bacteria (339).

In marine environments, aerobic CH_4 oxidation is sometimes small (247, 387). Hypersaline microbial mats exhibited no aerobic CH_4 oxidation at all (102). Addition of salt to rice fields resulted in a stronger inhibition of CH_4 oxidation than of CH_4 production (147). The reason is probably the insufficient adaptation of methanotrophic bacteria to high salt concentrations (280, 467). Although a potential activity of halotolerant methanotrophs has recently been found in hypersaline lagoons (508), it is unclear how much this potential activity attenuates the diffusive CH_4 flux in situ.

The CH_4 that has passed the CH_4-oxidizing zone in the soil surface layer enters the flooding water and is more or less homogeneously mixed. The CH_4 emission from the water phase into the atmosphere is then a function of the CH_4 concentration gradient between water and air. The CH_4 flux can be modelled from this concentration gradient and the gas transfer velocity between the water and the atmosphere. The transfer velocity is mainly a function of the wind speed (326, 336). Comparison of the calculated CH_4 fluxes with those actually measured indicate that some CH_4 is consumed at the water-air interface, presumably by microorganisms living in the aquatic surface layer (neuston layer) (120, 224, 476). Hence, the diffusive flux of CH_4 from the anoxic methanogenic soil layers into the atmosphere seems to be not only under the control of CH_4 production and CH_4 oxidation at the soil-water interface but also under the control of CH_4 oxidation at the water-atmosphere interfaces.

Upland Soils

Although upland soils are generally well aerated, they may contain anoxic microniches (238, 488, 539, 592). One may assume that gases are transported by diffusion or convection within the soil gas phase rather than within the water phase. Individual soil crumbs may then be considered units of trace gas metabolism. In nonaggregated soils, similar units may be represented by sand grains that are covered by a microbial biofilm (Fig. 5).

Soil crumbs. Microorganisms in the soil crumbs or on sand grains are the actual units of trace gas metabolism. However, we know very little about the distribution of trace gas-metabolizing microorganisms and of their activities on this microscopic scale. The CH_4-oxidizing activity per gram (dry weight) or per surface area was highest in a soil fraction consisting of

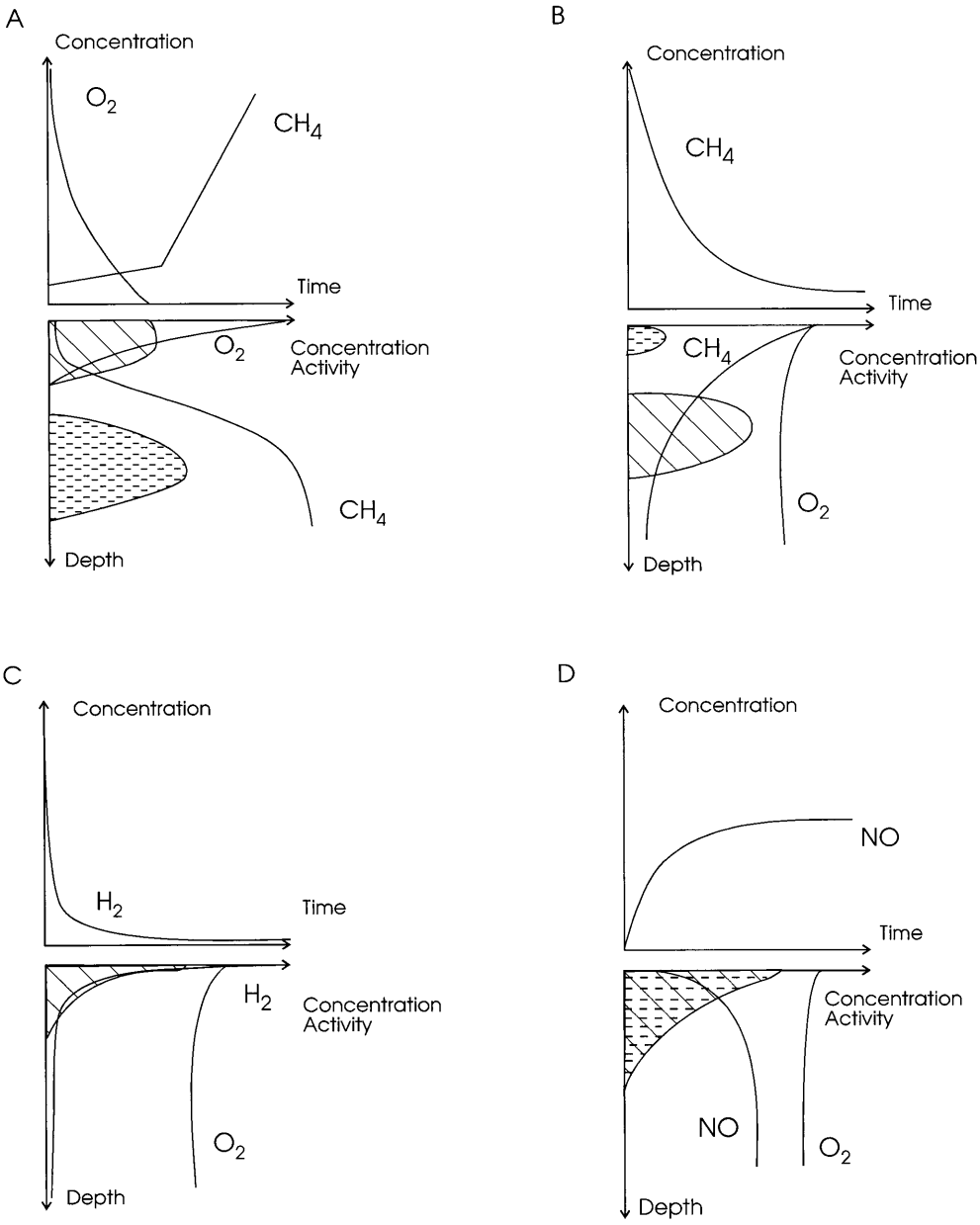

FIG. 4. Change of trace gas concentrations with time in the headspace and of the initial vertical profiles of trace gases and trace gas-consuming and/or trace gas-producing activities in incubated soil cores, such as are typical for CH_4 in wetland soil (A), CH_4 in upland soil (B), H_2 in upland soil (C), and NO in upland soil (D). Hatched areas indicate zones of consumption activity, and stippled areas indicate zones of production activity.

relatively large soil particles (0.5 to 2 mm in diameter) (36). The activity of the abiontic soil hydrogenase was found mainly in soil particles of 0.1 to 0.5 mm in diameter, i.e., also in somewhat large soil particles (227). These observations differed from the finding that bulk microbial biomass and microbial ATP levels generally slightly increased with decreasing particle sizes and were greatest in the clay fractions 3 to 10 μm in diameter (227). Hence, individual activities in soil crumbs and on sand grains may be quite heterogeneous.

Because of this heterogeneity, individual soil crumbs or sand grains are likely to exhibit different redox gradients. However, the redox stratification in soil crumbs is not well known because of methodological difficulties. Gradients can be measured only with microelectrodes on relatively large soil crumbs that are usually prepared for this purpose. Studies of gradients of O_2 and N_2O are noteworthy (238, 488, 592). However, we are far from understanding the dynamics of processes in soil crumbs. A central problem is the fact that soil crumbs are very heterogeneous. Most are probably dominated by aerobic metabolism, but some may be dominated by anaerobic metabolism. The extent of the two processes depends mainly on the availability of O_2, which again is a function of diffusion and microbial consumption (214, 428).

A further complication is that soil crumbs are not static. Metabolic processes in an individual soil crumb continue only as long as suitable substrates are available. Eventually, metabolic degradation will cease if no substrates are supplied from the outside. The lifetime of a soil crumb is thus limited.

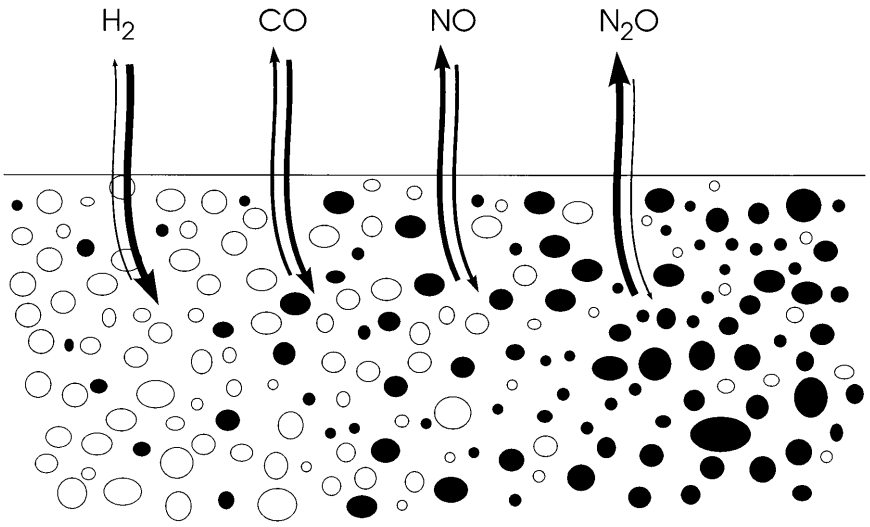

FIG. 5. Conceptual scheme of the bidirectional fluxes of H_2, CO, NO, and N_2O between the upland soil and atmosphere as a result of the relative amounts of soil entities (e.g., soil crumbs) that either release trace gas into the soil atmosphere (open symbols) or take it up (solid symbols).

Crumbs may aggregate after rainfall or bioturbation by the soil fauna. New soil crumbs will be formed from fecal pellets. Crumbs will form anew upon desiccation, especially in clay soil. All these processes will have dramatic effects at the microscopic level, where the trace gas-metabolizing microorganisms are active.

Compensation concept. Soil crumbs may show net production or net consumption, with both occurring simultaneously in the same bulk soil sample (Fig. 4 and 5). The simultaneous operation of both production and consumption has in fact been shown for many trace gases, and this observation is the basis for the compensation concept (93).

Trace gas consumption generally increases with trace gas concentration (first-order kinetics, Michaelis-Menten kinetics, etc.), in contrast to trace gas production, which is usually independent of end product concentration. Therefore, there is a concentration at which production equals consumption, i.e., the compensation point,

$$m_c = P/k$$

where m_c is the compensation mixing ratio, P is the production rate, and k is the first-order uptake rate constant of the trace gas. Compensation points have been demonstrated in upland soils for most trace gases, e.g., H_2, CO, NO, N_2O, and OCS, and this has recently been reviewed (93, 94).

To determine the production rate and consumption rate separately in a soil system, one must measure the kinetics of release or uptake in a way that allows the determination of both k and m_c. This can be done in a dynamic or a static system, as described in detail elsewhere (93). P can then be calculated from the equilibrium equation above, which assumes compensation between production and consumption at zero flux.

The determination of a production rate (P) should not be confused with the determination of a release rate (R). Whereas the former (P) is a gross rate, the latter (R) is a net rate, which is given by

$$R = P - km$$

Both P and R are similar only if the simultaneously operating consumption process (k) is negligible. Release rates of NO, for example, can be much lower than the NO production rates, since NO consumption is of a similar magnitude to NO production. For understanding the actual flux of NO at the soil surface on a theoretical basis, it is thus better to know both the production and consumption rates than only the resulting release rates.

In fact, the actual NO flux at the soil-atmosphere interface was successfully calculated from NO production and consumption rates by using a simple diffusion model that is based on the compensation concept (200, 426, 442, 444). Nitric oxide is a good example, since it shows both high and variable production and consumption rates in soil and, consequently, highly dynamic compensation points (25, 303, 450). However, the basic equations should also be applicable to other trace gases. A good example for future research would be CO, which also shows highly variable compensation points under both laboratory and field conditions (114, 119, 319).

The compensation concept provides a useful theoretical framework for measuring trace gas metabolism in upland soils. However, there are some caveats. The situation may be more complicated when production and consumption are not distributed homogeneously. Legume fields, for example, both release and take up H_2. The detection of a particular compensation point for a given field situation or for planted soil microcosms was used to quantify the gross rates of H_2 release and H_2 uptake (111, 113, 470). On a smaller scale, however, e.g., for soil samples taken from the legume field, the compensation concept would give completely different results, since the soil samples either are devoid of H_2-producing root nodules or contain them in a different state of activity. Root nodules themselves are small entities that show both production of H_2 by nitrogenase and consumption of H_2 by uptake hydrogenase (166). Nodules are again surrounded by soil in which H_2 consumption is achieved by processes, i.e., the action of aerobic H_2-oxidizing bacteria, different from those in bulk soil, i.e., the action of abiontic soil hydrogenases (88, 309, 401, 470).

Methane uptake. The compensation concept can probably not be applied for the flux of CH_4 between upland soils and the atmosphere. Actually, compensation points for CH_4 have so far not been demonstrated, either in the field or in the laboratory. In most upland soils, CH_4 production is usually absent

or marginal and the CH_4 flux is dominated by CH_4 oxidation. However, examples of upland soils with a low CH_4 production activity also exist, although the production processes are still unclear (see above). It seems that CH_4 production and oxidation processes are not homogeneously distributed but are vertically separated from each other (Fig. 4). Therefore, any "compensation point" that may be measured in the field would have an ambiguous meaning, and the compensation concept is not useful for modelling the CH_4 flux.

If CH_4 production were localized preferentially in surface soil, e.g., in anoxic microniches of the litter layer (487), then CH_4 would be released into the atmosphere despite a relatively strong CH_4 consumption in deeper soil layers. Exactly this kind of CH_4 profile has been observed in forest soils of the Appalachian mountains (587). On the other hand, other forest soils (Adirondack) exhibited highest activities of CH_4 production and consumption in the organic litter layers (588). Only in the latter case might the compensation concept be applied.

However, in most soils, atmospheric CH_4 consumption seems to be located in the subsoil, usually between the A and B horizons (4, 136, 160, 297, 465, 574). This zonation contrasts with that of other trace gases (H_2, CO, NO, and N_2O) for which maximum production and consumption activities are found in surface soil (Fig. 4) (117, 173, 319, 442–444, 482), where most of the microbial biomass is located. The deeper location of CH_4 oxidation is possibly caused by edaphic factors in the surface soil that are suboptimal or inhibitory for the growth of CH_4-oxidizing bacteria. Thus, the higher abundance of ammonium in surface soil than in subsoil may cause inhibition of CH_4 oxidation (465). The relatively large fluctuations of soil moisture in the upper horizon may also restrict methanotrophic activity to deeper layers, since methanotrophs seem to be sensitive to water stress (467). The ecology of methanotrophic bacteria has recently been reviewed (223, 280, 281). The subsurface location of methanotrophs means that energy requirements for maintenance and growth are obtained from CH_4 concentrations that are lower than atmospheric. Goulding et al. (208) have hypothesized that methanotrophic populations may persist only at soil sites that are adjacent to methanogenic microniches. However, this hypothesis is not supported by the vertical CH_4 profiles that have so far been reported in soil.

ROLE OF MICROORGANISMS AS CONTROLLERS OF TRACE GAS FLUXES

Most of our knowledge about trace gas metabolism in soil is derived from functional studies, i.e., the determination of activities in soil and in microbial culture. However, we know very little about the microbial populations and communities in soil that are actually performing the observed reactions. To correlate soil function with soil microbial populations, it is important to know the physiological groups and the taxa of the microorganisms involved, their numbers, and their localization in the soil.

Diversity of Trace Gas-Metabolizing Microorganisms

One possibility for differentiating the various activities involved in trace gase metabolism involves the use of inhibitors specific (385) for particular groups of microorganisms or particular enzymes. For example, the selective contribution of fungi and bacteria to atmospheric CO consumption was analyzed by using cycloheximide or streptomycin to inhibit the two respective groups (114). Production of NO and N_2O by either nitrifiers or denitrifiers is usually differentiated by the addition of AMO inhibitors such as nitrapyrin or acetylene (143, 288, 289, 423). An unambiguous routine assay for differentiating between CH_4-oxidizing methanotrophs and nitrifiers has not been reported yet (29, 386, 387).

Functional groups of bacteria are usually detected and enumerated by their ability to grow under specific conditions. For example, CH_4-oxidizing bacteria are enumerated by using growth in media with CH_4 as the sole energy source. However, this procedure does not cover any bacteria that cooxidize CH_4 without using it for growth. Therefore, the classical enumeration procedures have only a very restricted usefulness for the study of trace gas-metabolizing microorganisms. It is very likely that the functional groups of microorganisms involved in trace gas metabolism consist of several species. Many species belonging to the same functional groups are probably present in soil but have not yet been cultured. It is likely that the most active bacteria in soil are unknown. Therefore, it is necessary to assess the microbial diversity involved in trace gas metabolism by methods others than cultivation techniques. Study of the reassociation kinetics of single-stranded soil DNA has demonstrated that 1 g of soil contains about 4,000 different bacterial genomes (542).

A possible approach to the study of soil microbial populations without culturing them is to investigate macromolecules that are characteristic of the bacteria of interest. These macromolecules can either be directly isolated from soil or be detected in soil by the use of labelled antibodies or nucleic acid probes. The most promising target molecules are nucleic acids (8, 388, 456, 561) and lipids (544, 550), as reviewed elsewhere. Most of the techniques address the microbial diversity at the phylogenetic level, e.g., 16S rRNA genes or lipids that are diagnostic for specific bacterial taxa. The assessment of microbial diversity at the physiological level is more difficult, since it requires the detection and quantification of macromolecules that are typical of a physiological function, e.g., structural genes or the mRNA of an enzyme or the enzyme itself. Such techniques have not been applied to a great extent to the study of microbial trace gas metabolism in soil or sediment. However, some examples do exist.

Progress has recently been made with respect to the detection of CH_4-oxidizing bacteria in soil and peat by using PCR techniques that target the genes of either soluble methane monooxygenase or group-specific sequences of the 16S rRNA (349, 375). The results indicate the existence of so far unknown "species" of methanotrophs in soil and water. The presence and abundance of methanotrophs in soil were also assessed by analyzing signature phospholipid fatty acids (218, 381, 519).

Phylogenetic hybridization probes have been developed for methanogens and successfully applied to the analysis of the composition of the methanogenic community in anaerobic reactors (416, 417). Methanogenic microbial communities in digestors have also been studied by using immunological probes, which give some information on their topography in digestor flocs (217, 335). Signature lipids of methanogens have been used for a coarse analysis of the methanogenic community of an Antarctic lake sediment (338). Similar studies should also be possible in other CH_4-producing habitats, e.g., soil. By using rice soil microcosms, cloning and sequencing techniques have recently been applied to determine the dominant methanogenic populations (320). The results indicate that methanogens related to the genera *Methanobacterium* and *Methanosaeta* are most frequent in the anoxic bulk soil while methanogens related to the genus *Methanosarcina* and to a new branch within the *Methanomicrobacteria* were dominant in the rhizosphere of the rice plants (320, 321).

The composition of the natural communities of microorgan-

isms which belong to a well-defined physiological group but are polyphyletic and spread over several taxa cannot be readily analyzed by using probes and primers that are based on rRNA genes. Instead, functional probes and primers based on the genes of dissimilatory enzymes may be used. For analyzing communities of denitrifiers, probes and primers against nitrate reductase, nitrite reductase, and N_2O reductase (503, 559) and antibodies against nitrite reductases (128, 295) have been developed. Both approaches have been applied to natural environments (325, 560). The study of soil environments demonstrated the presence of bacteria that possess genes for denitrifying enzymes (325, 503). However, because of cross-reactions and false-positive results on the one hand and of too narrow a specificity of the probes on the other hand, the techniques targeting functional genes or enzymes are of very limited use for analyzing the community of denitrifiers (including uncultured ones) in soil.

Similarly, hybridization probes against the hydrogenase gene of aerobic H_2-oxidizing bacteria were used to characterize H_2-consuming bacterial isolates from soil, but with limited success (292). The problem is that the probes and primers were designed for a rather limited range of bacterial species but are intended to target a large number of unknown and usually uncultured bacteria that by definition share only the characteristic of possessing a hydrogenase gene. The design of primers and probes with such a broad specificity is very difficult. However, probes and primers with a narrow specificity, e.g., against the hydrogenase gene of bacteria related to *Alcaligenes eutrophus*, were successfully applied to retrieve sequence information for so far uncultured Knallgas bacteria in soil (312). Primers and probes against a limited group of hydrogenase genes, e.g., those of the sulfate-reducing genus *Desulfovibrio*, have also been applied successfully to detect these bacteria in anaerobic reactors and microbial mats (567). Communities of hydrogenase gene-containing sulfate reducers in oil fields and soil have also been analyzed by reverse sample genome probing, in which the environmental DNA is used as the probe and is assayed against a selection of cultured bacteria to test whether they might be present in the particular environment (529, 553). However, sulfate reducers are related to each other closely enough that their communities in microbial mats can also be analyzed by phylogenetic (16S rRNA) probing (9, 415).

Recently, PCR amplification of the gene (*mcr*) of the methyl-CoM reductase, the key enzyme of CH_4 production, has been used to detect and characterize populations of methanogens in peat soil (221).

Composition of the Microbial Community and Control of Trace Gas Flux

Microbial metabolism is one of the controls of the trace gas flux between soil and atmosphere. Metabolic processes are affected by environmental variables (e.g., temperature and nutrients) acting either on the enzyme activities that have been expressed by the resident microbial populations, on the synthesis of new enzyme activities, or on the proliferation of particular soil microorganisms. All these levels of control are important. However, the role of microbial community composition is the least understood. I will give a few examples.

Effect of nitrogen fertilization on methane uptake. A number of studies have shown that nitrogen addition reduces the uptake of atmospheric CH_4 by soil (71, 130, 206, 222, 369, 379, 495, 513). However, some investigators have observed no effect of nitrogen fertilization (62, 188, 527), found only a long-term but no short-term effect (245, 246), or even observed a stimulation associated with a change in vegetation (306). These

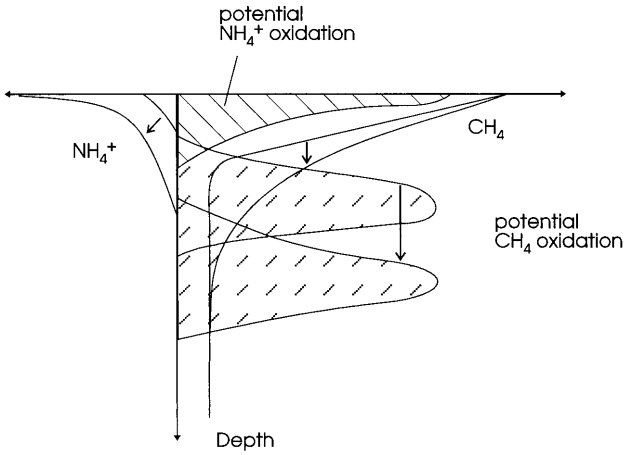

FIG. 6. Conceptual scheme of the inhibitory effect of ammonium fertilizer on CH_4 uptake by soil as a result of the displacement of potential CH_4-oxidizing activities to deeper soil layers.

different observations have been interpreted as either direct inhibition of CH_4 oxidation by ammonium, gradual competitive displacement of the CH_4-oxidizing methanotrophs by CH_4-oxidizing nitrifiers, or more complex changes in the soil. Direct inhibition of CH_4 oxidation by ammonium has been demonstrated in pure cultures of methanotrophs as well as in soil samples (29, 35, 63, 160, 284, 465). Castro et al. (71) and Steudler et al. (514) observed that the ratio of CH_4 to CO oxidation became lower upon nitrogen fertilization and attributed this to a shift from methanotrophs to nitrifiers as the prevailing CH_4-oxidizing population. On the other hand, Bender and Conrad (35) observed no decrease in CH_4 oxidation rates when soil samples were enriched in the population of ammonium-oxidizing nitrifiers. Quite in contrast, the addition of ammonium to these soils was less inhibitory to CH_4 oxidation than to the control soils. Hence, it remains unclear whether and how much a population shift from methanotrophs to nitrifiers can contribute to the fertilizer effects observed in field studies.

The interpretations of most of the field studies suffer from a lack of information about the vertical distribution of the activities of CH_4 oxidation in the context of nitrogen transformation. Dunfield et al. (163) recently showed that fertilization had no effect on the CH_4 uptake by peat soil, since the CH_4-oxidizing activity was localized in subsoil but the ammonium added was immobilized, volatilized as NH_3, or oxidized to nitrate in the soil surface layers.

A conceptual model of the effects of nitrogen fertilizers on CH_4 uptake by soil is presented in Fig. 6. This model is based on the observation that the zone of ammonium oxidation is located in the soil surface layers and thus is separated from the zone of CH_4 oxidation, which is located in deeper soil layers (465). This separation is thought to be due to the inhibition of CH_4 oxidation by ammonium. Populations of methanotrophs can therefore persist only in subsoil, where ammonium concentrations are usually below the inhibitory level. As a consequence, CH_4 has to diffuse from the surface down to the subsoil to become oxidized. The CH_4 oxidation activity in subsoil extends over depths where sufficient CH_4 is available and ceases when CH_4 concentrations decrease below a threshold. Fertilization temporarily increases the ammonium concentration in the surface layer. If the ammonium oxidation activity in the surface layers is too low to prevent vertical transport, the

ammonium concentrations may reach inhibitory levels in the zone of CH_4 oxidation, so that CH_4 has to diffuse to still deeper layers to become oxidized. Consequently, the vertical CH_4 gradient would become less steep and the CH_4 flux would decrease. The inhibitory effect of the ammonium fertilizer would thus basically be a displacement of the CH_4 oxidation activity to deeper soil layers. On the other hand, if the ammonium oxidation activity in surface soil (or other ammonium removal mechanisms) is high enough to prevent leakage of ammonium to deeper layers, fertilization would have no immediate effect on CH_4 oxidation. This would particularly be the case when soil plots have received fertilizers for a long time, so that nitrogen turnover in surface soil is more active and the zone of CH_4 oxidation is displaced to greater depth. Cores of such soil plots would exhibit lower CH_4 uptake rates than those of unfertilized control plots and would be less prone to react to short-term fertilization (188, 245, 527). Natural soil with a relatively deep location of the CH_4 oxidation zone or high activity of the ammonium oxidation zone would behave similarly (163).

Initiation of methanogenesis. Production of CH_4 in periodically submerged wetland soils is initiated some time after flooding. Methanogenesis is initiated after the sequential reduction of O_2, nitrate, manganese(IV), iron(III), and sulfate. The sequential reduction process occurs largely according to the thermodynamic theory, which predicts that electron acceptors with a more positive redox potential are preferred (595). The general operation of the sequential reduction process has been repeatedly shown in soils that become anoxic after being flooded (393, 400). However, the exact mechanism that controls the initiation of CH_4 production and the dynamics of the microbial populations involved is still unclear.

One possibility is that methanogens are present only as a marginal population and increase in number as soon as the nonmethanogenic electron acceptors are reduced and thermodynamic conditions become favorable for CH_4 production. Indeed, the numbers of methanogens increased in soils that had never been flooded before, e.g., desert soil (396). On the other hand, however, the numbers of methanogens were relatively stable at a high titer throughout the annual drainage and flooding periods of rice fields (19, 348, 478). Obviously, the nonsporulating, obligately anaerobic methanogens are able to survive in soil under adverse conditions to a greater extent than was previously believed possible (181). However, because of the presence of yet uncultured methanogens in soil (221, 320, 321), we cannot be sure that the composition of the community of methanogens remains unaltered during the initiation of methanogenesis upon flooding of soil.

Irrespective of whether the methanogens grow first or are already present in sufficient numbers, a central question is which environmental factor triggers the initiation of CH_4 production. One possible factor is the concentration of methanogenic substrates. For example, the H_2 concentration has to be higher than the threshold value required for a favorable thermodynamic reaction (Fig. 2) (see above). Similarly, the acetate concentration has to be sufficiently high to allow exergonic CH_4 production from acetate. Theoretically, the concentrations of both substrates should be kept below the threshold of methanogens by the thermodynamically more favorable consumption activities of sulfate reducers and ferric iron reducers, which are active as long as sulfate and ferric iron are available. After depletion of sulfate and ferric iron, the steady-state concentrations of H_2 and acetate would increase and thus trigger the initiation of CH_4 production. This theory is supported by observations in a river sediment which exhibited increasingly higher H_2 concentrations during the successive reduction of sulfate and ferric iron and stabilized at the methanogenesis-specific threshold when production of CH_4 was the only redox process (331). Similarly, in anoxic lake sediment and paddy soil, inhibition of CH_4 production by sulfate or ferric iron was paralleled by a decrease of H_2 to concentrations that were thermodynamically nonpermissive for CH_4 production (2, 329). In this case, a too low substrate concentration was probably the factor that turned CH_4 production off. However, the theory was not supported by observations in four different submerged soils, which showed H_2 and acetate concentrations that were sufficient for exergonic methanogenesis but in which CH_4 production was nevertheless not initiated before sulfate and ferric iron were depleted (396). In this case, the methanogenic substrates cannot have acted as the signal for initiation of CH_4 production.

Another potential signal for initiation of methangenesis is the soil redox potential (E_h). Rates of CH_4 emission from rice fields correlate negatively with the soil redox potential (342). Production of CH_4 in *Methanosarcina barkeri* starts as soon as the redox potential of the medium drops below +50 mV (182). As the redox potential of the medium was buffered by a mixture of ferrous and ferric iron, one could hypothesize that CH_4 production in methanogens is switched on by a regulator protein that reacts with iron similarly to the global regulation of aerobic and anaerobic metabolism in *Escherichia coli* (546). Indications of soil redox potential as a signal for initiation of methanogenesis were recently obtained when several upland soils were flooded, resulting in anoxic and methanogenic soils (396). The possible importance of redox potential in addition to that of thermodynamically permissive substrate concentrations was also demonstrated for methanogenic paddy soil that was temporarily aerated or drained and subsequently showed suppression of CH_4 production until all the sulfate and ferric iron that were produced during the aeration phase was reduced again (418). It is possible that both the concentration of methanogenic substrates and the redox potential (mediated by a redox active compound, e.g., iron) act as signals depending on the type of methanogenic community involved, but the dynamics of the latter have not yet been investigated.

Effect of temperature on methanogenesis. Methane production increases exponentially with increasing temperature of submerged peat or paddy soil (162, 479, 487, 521, 570, 571). In addition, temperature seems to affect the contribution of acetate relative to H_2 plus CO_2 as precursors for CH_4 production. At low temperatures, the contribution of H_2 plus CO_2 to methanogenesis is small, with CH_4 being derived mainly from acetate (79, 109, 471, 472, 520). Existing cultures of methanogens all cease to produce CH_4 from H_2 plus CO_2 if temperatures are lower than 15 to 20°C (51, 600). On the other hand, there are psychrotrophic homoacetogenic cultures that are able to convert H_2 plus CO_2 to acetate at low temperatures (100, 299, 300). Setting up cultures on H_2 plus CO_2 with soil or sediment as the inoculum usually results in the enrichment of bacteria producing acetate instead of CH_4 at low temperature (100, 299, 300, 471). On the other hand, at high temperature, some acetogens can convert acetate to H_2 plus CO_2 (313). This acetate cleavage is then followed by H_2-dependent methanogenesis in thermophilic digestor sludge (5, 314).

From these observations, one is tempted to conclude that H_2-dependent methanogens do not operate at low temperature and are replaced by H_2-dependent homoacetogens. However, this is probably not the case. Although psychrotrophic methanogens have not been isolated thus far, there are reports of H_2-dependent methanogenesis in sediments and submerged soil at low temperatures (69, 377, 378, 570). Therefore, it is likely that psychrotrophic H_2-consuming methanogens do exist

but have not been cultured. In addition, thermodynamic calculations have often indicated that H_2-dependent homoacetogenesis is endergonic at in situ H_2 concentrations (79, 439, 471, 533). A more likely explanation for the decreased contribution of H_2 to methanogenesis at low temperature is a shift in the fermentation pathway of organic matter. It has been shown that the production of H_2 by syntrophic proton-reducing bacteria is especially sensitive to low temperatures (79, 109, 471). For example, a decrease in the temperature of methanogenic paddy soil from 30 to 15°C resulted in both a decrease in the H_2 concentration and an increase in the concentration of fatty acids, indicating that syntrophic fatty acid degraders were inhibited at the lower temperature (79). An increase in the temperature of cold profundal lake sediment from 4 to 20°C, on the other hand, resulted in increased H_2 concentrations, increased production of fatty acids, and increased contribution of H_2 to CH_4 production (471). These observations suggest that temperature has a decisive influence on the pathway of organic matter degradation to CH_4. Presently available experiments and observations indicate that at low temperature, organic matter degradation is dominated by homoacetogenesis followed by acetotrophic methanogenesis, whereas at high temperature organic matter degradation is dominated by fermentation followed by syntrophic H_2 production plus H_2-dependent methanogenesis. The assumption that the syntrophic bacteria rather than the H_2-dependent methanogens constitute the step that is actually limited by low temperature is supported by the following observation: an increase in the concentration of H_2 but not in cellulose stimulated H_2-dependent methanogenesis in lake sediment at low temperature (472). The enhancement of syntrophic bacteria and H_2-dependent methanogenesis by increasing temperature may be one of the reasons why the aggregation of syntrophic and methanogenic bacteria seemed to intensify in a lake sediment during summer stratification (103).

Interspecies hydrogen transfer in microbial aggregates. Interspecies H_2 transfer is a key process in the anaerobic degradation of organic matter to CH_4 (156, 462, 511, 594, 596). Interspecies H_2 transfer is accomplished between fatty acid- or alcohol-oxidizing H^+-reducing acetogenic syntrophic bacteria and H_2-consuming methanogenic bacteria. The process is obligatory for the syntrophs which depend on the maintenance of a low H_2 concentration by the methanogens for thermodynamic reasons. Characterization of the kinetics and thermodynamics of the H_2 transfer reaction in anoxic digestors, sediments, and soil has shown that syntrophs and methanogens are juxtaposed; i.e., they operate within a microbial aggregate (90, 99, 106, 108). Hydrogen may be replaced by formate as the transferred electron equivalent in some situations (50, 157, 535). The formation of microbial aggregates to achieve syntrophic degradation of fatty acids and alcohols probably facilitates the diffusional transfer of H_2 or formate between the two bacterial groups and thus alleviates the energetic problems involved (50, 463).

Nothing is known about the actual composition of the microbial aggregate communities in anoxic soil and sediment. In fact, evidence for the existence of microbial aggregates in soil and sediment is only circumstantial and is not based on direct microscopic observations (90). However, information exists for anaerobic digestor flocs which may be considered to be a model system for microbial aggregates with interspecies H_2 transfer (217, 228, 551, 583–585). Harmsen (228) investigated the architecture of different digestor flocs by using phylogenetic DNA probes and showed that the syntrophic and methanogenic bacteria existed in distinct clusters in the interior of the flocs, whereas the bacteria fermenting the primary substrates formed the outer layer of the flocs. However, a lattice-type rather than a cluster-type arrangement of the syntrophic partner cells has also been observed (159, 534). Schink (462) suggested that because of continuous cell division, small lattice-type aggregates inadvertently turn into cluster-type aggregates until the whole floc is mixed up again. Soils and sediments probably can contain only small microbial aggregates because of spatial limitations. The observation that the contribution of juxtaposed interspecies H_2 transfer to total CH_4 production increased during the season in the relatively fluffy sediment of Lake Mendoata was interpreted as being due to increased formation of microbial aggregates (103). In anoxic paddy soil, on the other hand, CH_4 production by juxtaposed H_2 transfer was maximal from the onset of CH_4 production (104). Possibly, syntrophic bacterial aggregates that produce CH_4 consist of only a few bacteria which are confined together in or on a soil crumb or grain.

The digestor flocs exhibited a very high bacterial diversity including not only fermenting bacteria, homoacetogens, syntrophs, and methanogens, as theoretically expected, but also sulfate reducers (583) and even aerobic heterotrophs (263). The aerobes allow the operation of CH_4 production even in an oxic environment. The sulfate reducers, on the other hand, may function as syntrophs themselves and convert ethanol or lactate to acetate plus H_2 in the presence of H_2-consuming methanogens (66, 350). There is strong evidence that sulfate reducers can function as syntrophs in digestor flocs (534, 583). Phylogenetic analysis indicated a close relationship of syntrophic propionate-oxidizing bacteria to sulfate reducers (229, 230, 556).

Circumstantial evidence from kinetics studies indicates that sulfate reducers may function as syntrophic partners in methanogenic aggregates in Lake Mendota sediment (103). In this case, the immediate inhibition of methanogenesis by addition of sulfate may actually be the result of a diversion of the electron flow (Fig. 7): the fatty acid- or alcohol-degrading sulfate reducers stop producing H_2 syntrophically and instead reduce sulfate, maybe even competing with the methanogens for H_2 produced by other bacteria (89).

We recently interpreted the inhibition of acetate-dependent methanogenesis by sulfate in anoxic paddy soil in a similar way (3). In this particular soil, the population of acetate-utilizing sulfate reducers was very small and was confined to spores of *Desulfotomaculum*. However, H_2-utilizing *Desulfovibrio* species were present and were able to decrease the H_2 concentration in the presence of sulfate so much that H_2-dependent methanogenesis was thermodynamically no longer feasible. Inhibition and radiotracer experiments indicated that the decrease in H_2 concentration could have resulted in the conversion of the methyl group of acetate to CO_2 instead to CH_4 and in the transfer of the reducing equivalents as H_2 to the sulfate reducers (Fig. 7). Such an interspecies H_2 transfer has been shown for cocultures of acetate-utilizing *Methanosarcina* and H_2-utilizing *Desulfovibrio* species (398). It is questionable whether similar explanations hold for the inhibition of acetate-dependent methanogenesis by iron(III) and nitrate (2, 3, 260, 290). However, not only is there a close phylogenetic relationship among the genus *Pelobacter* (functioning as a fermenting or syntrophic bacterium), sulfate- or sulfur-reducing bacteria, and Fe^{3+}-reducing bacteria, but also members of all of these functionally defined groups are able to reduce Fe^{3+} (86, 333). Therefore, one could imagine that a bacterium functions in a microbial aggregate once as the syntrophic partner but also as a sulfate reducer or ferric iron reducer when sulfate or Fe^{3+} becomes available. A similar situation may also be imagined with respect to nitrate, as, for example, *Desulfovibrio desulfu-*

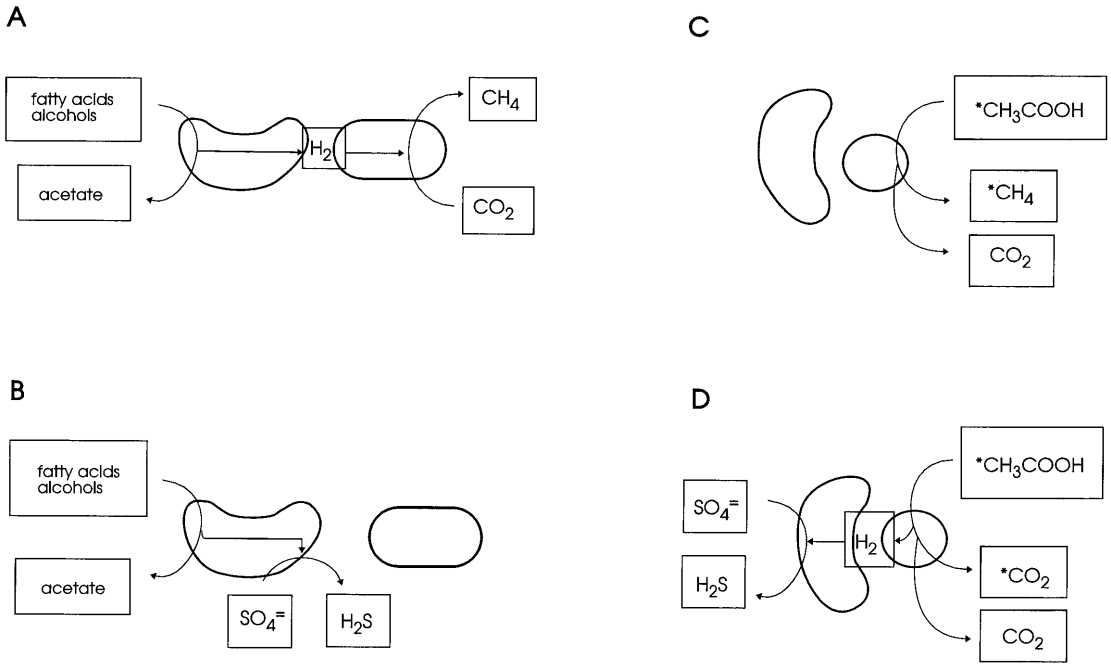

FIG. 7. Conceptual scheme of the interspecies H_2 transfer between sulfate-reducing and methanogenic bacteria. (A and B) Sulfate reducer degrading fatty acids or alcohols either in syntrophy with a methanogen or in unitrophy by using sulfate as electron acceptor. (C and D) Methanogen converting the methyl group of acetate to CH_4 in unitrophy or to CO_2 in syntrophy with a sulfate reducer.

ricans can function not only as a sulfate reducer but also as nitrate reducer, as a ferric iron reducer, and as a syntroph with methanogens (86, 127, 484). In fact, this bacterium can also function as an O_2 respirer, reducing O_2 preferentially before NO_3^- and SO_4^{2-} (304). Investigation of both function and community structure will be necessary to elucidate these kinds of microbial interactions in soil and other environments.

Production of NO and N_2O. NO and N_2O flux between the soil and the atmosphere results from complex and little-understood interactions of different processes in soil that occur simultaneously. Since processes involved in production (e.g., nitrification) often differ from those involved in consumption (e.g., denitrification), production and consumption are regulated differently (96). Furthermore, NO production and N_2O production are a composite of different processes, such as nitrification and denitrification, that vary in relative significance depending on soil conditions (141–143, 289, 394, 423, 433, 475, 496, 543). Even one particular process, e.g., denitrification, can be a composite of different bacterial species that may be phylogenetically distant from each other and express different types of enzymes. For example, the NO-producing nitrite reductase can be either a copper-type or a cytochrome *cd*-type enzyme (128). Both NO production and N_2O production in denitrifiers are a function of the relative activity of the producing and the consuming enzymes, i.e., nitrite reductase and NO reductase for NO production and NO reductase and N_2O reductase for N_2O production (38, 351, 591). The actual turnover of nitrogen by these enzymes depends on substrate concentrations and the kinetic properties of the enzymes. The specific activities of the enzymes depend on biosynthesis (transcription and translation) and inactivation. The available information on the regulation of enzyme synthesis suggests that O_2 partial pressure and concentrations of nitrogen substrates are major regulators (538). More importantly, however, the patterns of regulation seem to be different in different species of denitrifiers (32, 48, 129, 296, 351, 425, 581). The expression of denitrifying enzymes shows different O_2 sensitivities for the different bacterial strains. There are also bacteria that dentrify under aerobic conditions (327, 435, 436). The different effects of O_2 on the expression of the various bacterial nitrite reductases, NO reductases, and N_2O reductases will affect whether NO or N_2O is the dominant product when the O_2 availability in soil changes. Therefore, knowledge of the composition of the community of denitrifiers in soil is important for understanding of the production of NO and N_2O. Unfortunately, there are only a few studies of expression of denitrifying enzymes in soil after the onset of anaerobiosis (146, 186, 505). The results indicate that synthesis of nitrate reductase and nitrite reductase starts within hours whereas synthesis of nitrous oxide reductase is delayed for more than 1 day, so that N_2O is produced. None of these studies involved the investigation of the composition the microbial community or looked for the metabolism of NO. Therefore, it remains unclear whether the pattern of NO and N_2O production are affected by the composition of the denitrifier community in natural soil. Community effects are not unlikely, since soil which is amended with different denitrifiers exhibits completely different patterns of production of NO and N_2O (1, 372).

There are reports that the soil microbial communities which reduce nitrate differ as a function of temperature (202, 278, 449) and pH (41, 392, 490). There are also numerous reports that the production and release of NO and N_2O from soil into the atmosphere are affected by soil temperature and pH (213, 434, 451, 578). However, the available information does not allow a synthesis of the observed patterns of release or production of NO and N_2O with patterns of microbial community composition.

These examples provide a narrow focus on denitrification and on three of the most conspicuous soil variables, i.e., aeration (soil water), temperature, and pH. The real situation,

however, is much more complex and involves a hierarchy of environmental controls that affect denitrification rates on the one hand (538) and the fraction of NO and N_2O produced on the other hand (185). Furthermore, the real situation in soil probably involves many more types of microbial metabolism, such as autotrophic and heterotrophic nitrification, nitrate respiration, and DNRA, which produce and consume NO and N_2O (96). This complexity will be understood only when more is known about the microorganisms involved and their metabolism.

CONTROL ON THE ECOSYSTEM LEVEL

Trace gases are produced and consumed by defined reactions in individual microorganisms. Any control of the production or consumption process is exerted at this level initially. However, it is also relevant to ask whether the microbial diversity and community structure in soil have any consequences at the ecosystem level (461). Although a microbiologist may tend to answer this question in the affermative, the true answer is by no means clear.

In fact, much of the spatial and temporal variability of trace gas fluxes between the soil and the atmosphere can often be explained by only a limited number of factors, including soil and parent material, climate, vegetation, and topography (346). Thus, empirical models that are based on correlation analysis involving easily measureable soil variables (e.g., temperature, moisture, texture, and organic carbon) often predict trace gas fluxes quite well. Statistical techniques, such as multiple regression or multivariate data analysis, help to assess the optimum set of variables to be measured. For example, water table position, temperature, and degree of peat humification explained 91% of the variance in the logs of CH_4 flux from a peatland in Northern Minnesota (155). Weaker but still significant correlations of CH_4 flux to a few predictors have also been reported for other sites (67, 196). Emission rates of N_2O from some soil environments (e.g., prairie ecosystems) have also been predicted amazingly well from a few soil variables such as temperature, moisture, and inorganic nitrogen (460). The strong correlations of CH_4 emission with water table height and of N_2O emission to inorganic nitrogen compounds are easily understood, since microbial methanogenesis requires anoxia and microbial N_2O production requires either ammonium or nitrate as a substrate. Empirical models based on various physical and chemical parameters are successful without considering the structure of the microbial community. Even largely mechanistic models of NO and N_2O production that differentiate between nitrification and denitrification neglect microbial community structure (316, 317, 404).

In some studies, it was found that trace gas fluxes were controlled largely by a single ecosystem function that created a bottleneck in substrate flow. For example, rates of N_2O emission from tropical soils were strongly correlated with rates of net nitrogen mineralization which limited nitrification and denitrification and thus also N_2O production (344). On the other hand, although NO release should be limited by nitrogen mineralization in the same way as N_2O release is limited, the release rates of these gases have often been found to be anticorrelated because of the different reactions of the gases to changing soil moisture (266). Annual fluxes of N_2O were correlated with the annual aboveground net primary production in a tallgrass prairie landscape (216). Similarly, rates of CH_4 emissions from wetlands correlated well with the net ecosystem productivity, i.e., the amount of the net primary production that is left in the ecosystem and is not immediately liberated by microbial decomposition (576). A control of CH_4 production by primary productivity was supported by the observation that CH_4 emission rates increased when wetland vegetation was exposed to elevated CO_2 concentrations (137). On the other hand, net ecosystem productivity was not a decisive controller of CH_4 emission in Swedish peatlands (555).

Relevant trace gas flux measurements on the ecosystem or landscape level are still scarce. In addition, the classification of ecosystems is not satisfactory, and the possible mosaic structure of an ecosystem is also subject of debate (427). The microbial community structure in the soil of the various ecosystems and ecosystem mosaics is largely unknown. Therefore, it cannot be assessed safely at present whether the soil community structure is important for the trace gas flux. In addition, we do not know the scale in space and time on which it is possibly important. Therefore, it remains unclear whether trace gas flux at the ecosystem level is finally controlled by a few processes only or whether changes in the diversity and composition of microbial species are also important. However, by analogy to ecological studies of plant and animal communities (376, 473, 540, 541), I would dare to predict that microbial species diversity is an important factor in ecosystem function.

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