

不饱和土壤 CH_4 的吸收与氧化

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摘要: 不饱和土壤是已知唯一的 CH_4 生物壑。综述了不饱和土壤 CH_4 的吸收、氧化过程及其影响因素。不饱和土壤中 CH_4 氧化的临界浓度低, 因而甲烷氧化菌可氧化大气 CH_4 并将其当作唯一的碳源和能源。土壤 CH_4 吸收率与土壤湿度通常呈负相关关系。土壤湿度过高, 大气 CH_4 和 O_2 向土壤中扩散受阻; 或土壤湿度过低引起水分胁迫均导致甲烷氧化菌活性下降。 NH_4^+ 对土壤中 CH_4 氧化的抑制作用可归结为 NH_3 和 CH_4 在甲烷单氧酶水平上的竞争、由氧化作用向硝化作用的转移以及 NH_4^+ 氧化生成的 NO_2^- 的毒性。 NH_4^+ 对 CH_4 氧化的抑制作用与土壤有效氮含量成正比。各类氮肥对 CH_4 氧化抑制作用: 化肥 > 有机肥; 铵态氮肥 > 尿素。 NO_3^- 对 CH_4 氧化没有抑制效应。阳离子代换量(CEC)高的土壤 NH_4^+ 对 CH_4 氧化的抑制作用轻。 CH_4 氧化菌对大气 CH_4 的高亲和力及 CH_4 氧化所需较低的活化能导致其温度系数 Q_{10} 较小。地温较低时, 土壤氧化 CH_4 的能力随温度升高而升高。当地温高于 CH_4 氧化的最佳温度时, CH_4 氧化菌难以与硝化细菌及其他微生物竞争利用土壤空气中的 O_2 , 导致其活性降低。甲烷氧化菌对 pH 值变化不敏感。团粒结构较好的壤土可保护 CH_4 氧化菌免受干扰。未受干扰的森林土壤 CH_4 氧化率的峰值一般出现在亚表层(5~10cm)。由于耕作破坏了表土结构, 农田土壤的 CH_4 氧化率在耕层以下才有较大增加。耕地、草地和森林土壤的平均 CH_4 吸收率分别为 0.28, 0.52 和 1.51mg/(m² · d)。植物吸收氮素养分可减轻 NH_4^+ 对土壤 CH_4 氧化菌的抑制作用。维持与提高农业土壤氧化 CH_4 潜力的重要措施包括免耕、施硝态氮肥和/或有机肥。

关键词: 甲烷氧化; 甲烷吸收; 不饱和土壤; 土壤水分; 土壤氮素; 土壤结构

Methane uptake and oxidation by unsaturated soil

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Abstract: Unsaturated soils are the only known biogenic sinks of CH_4 . In this paper we summarized the CH_4 oxidizing process in unsaturated soil and its influent factors. Methanotrophs can use atmospheric methane as the only source of carbon and energy because of the low critical concentration for methane oxidation. In General, CH_4 absorption rate is inversely proportional to soil moisture. The activity of methanotrophs becomes small if the transfer of CH_4 and O_2 from atmosphere to soils is prevented when soil moisture is over high, or water stress occurs at low soil moisture conditions. The inhibitory effect of NH_4^+ on CH_4 oxidation can be attributed to its competition with CH_4 for O_2 by the methane monooxygenases, the transfer of oxidation to nitrification and the toxicity of NO_2^- produced. The inhibitory effect of NH_4^+ on CH_4 oxidation is proportional to available nitrogen. Chemical fertilizers are stronger than manures, and ammonium are stronger than urea in inhibiting CH_4 oxidation. NO_3^- has no inhibitory effect on CH_4 oxidation. High cation exchange capacity (CEC) can alleviate the inhibitory effect of NH_4^+ on CH_4 oxidation. The high affinity of methanotrophs to atmospheric CH_4 and low activation energy for CH_4 oxidation leads to a small coefficient of temperature (Q_{10}). When soil temperature is low, the ability of CH_4 oxidation by soils is proportional to soil temperature. When soil temperature is higher than the optimal value, the activity of methanotrophs will decrease because

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it is difficult for methanotrophs to compete with nitrifiers and other microbes for the limited O₂ in soil air. Methanotrophs are very insensitive to pH value. Good granular structure of soil favors the activity of CH₄-oxidizing bacteria from being disturbed. The peak of CH₄-oxidizing rate in the undisturbed forest soil is usually in sub-topsoil (5~10cm). In farm soil, CH₄-oxidizing rate increases obviously under the depth of farming layer (25cm) because tillage destroys the structure of topsoil. The average CH₄ absorption rates of farmland, grassland and forest soil are 0.28, 0.52 and 1.51mg/(m²·d), respectively. The absorption of N by plants can alleviate the inhibitory effect of NH₄⁺ on CH₄-oxidizing bacteria. No-tillage, the use of nitrate fertilizer and (or) organic fertilizer favor CH₄ oxidization in farm soil.

Key words: methane oxidation; methane uptake; unsaturated soil; soil moisture; soil nitrogen; soil structure

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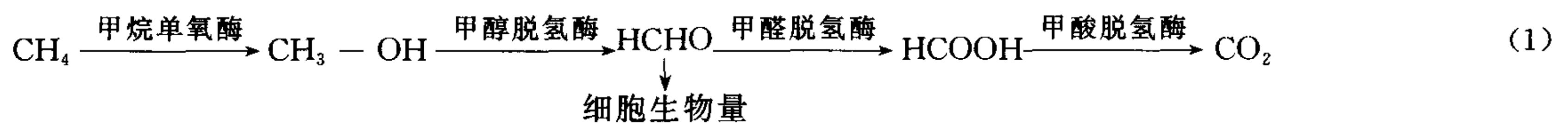
甲烷(CH₄)是大气中含量仅次于CO₂和CFCs的温室气体,其辐射增温效应是CO₂的20~30倍^[1,2]。在对流层,CH₄被氧化生成其它温室气体(CO和CO₂),其温室效应被进一步放大。少量CH₄被输送到平流层,对O₃层起到了间接的破坏作用^[3,4]。对极地冰芯的研究表明:工业革命前大气中甲烷的浓度约为0.6~0.8μl/L^[5]。受人类活动影响,大气CH₄的浓度不断升高。20世纪70~80年代大气CH₄浓度的年增长率达1%左右^[1],到20世纪80年末增幅变缓,1992年甚至出现了负增长,其原因还不清楚^[6]。目前地表大气中CH₄的平均浓度为1.7μl/L,北半球比南半球平均高出0.14μl/L,季节波动为0.03μl/L^[6]。

IPCC^[5]估计,全球大气CH₄的源总量为525Tg/a,其中自然源约占30%,人为源约占70%。自然源以湿地土壤为主,还包括海洋、淡水、白蚁和野生反刍动物等。人为源包括家养反刍动物、稻田、城市固体废弃物和污水处理、生物体燃烧、化石燃料开采过程中的泄露等。其中家养反刍动物和稻田约占全部CH₄源的15%~40%,因而农业是主要的人为源。据估计,全球大气中消耗的CH₄为470Tg/a,其中透气土壤吸收的CH₄为30Tg/a^[5]。土壤是已知唯一的CH₄生物壑。大气CH₄浓度的增长是由于人类活动增加了CH₄源的同时也减弱了其土壤壑的缘故。CH₄的土壤壑虽然相对较小,但如果失去它,大气CH₄浓度的增长率将是现在的1.5倍^[7]。

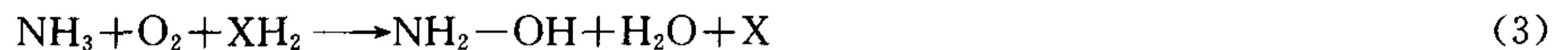
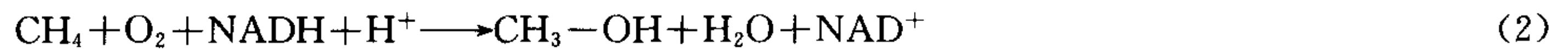
Harriss等^[8]最早发现大气CH₄被排水后的湿地土壤氧化。此后在森林^[9,10]、草原^[11,12]、苔原^[13]和沙漠^[14]都观测到土壤对CH₄的吸收作用。许多研究表明,农业活动对土壤氧化CH₄的能力有负面影响^[15~21]。本文综述了不饱和土壤(透气土壤)中CH₄的吸收、氧化过程及其影响因素,并在此基础上探讨了增加土壤CH₄吸收的途径。

1 土壤中CH₄的氧化过程

在有氧条件下,土壤中的甲烷氧化菌可氧化CH₄并将其当作唯一的碳源和能源。土壤CH₄氧化的过程如下^[23]:



甲烷单氧酶(methane monooxygenases,MMOs)作为甲烷氧化菌关键的酶,对底物的专一性极低,可与许多化合物进行代谢反应。甲烷氧化菌氧化CH₄的途径与氨氧化菌氧化NH₃非常相似^[22]。甲烷单氧酶催化如下两个过程:



虽然甲烷氧化菌氧化NH₃的速率比硝化菌要低两个数量级,但迄今为止所有被调查的甲烷氧化菌(如:Methylobacter albus, Methylosinus trichosporium)都可把NH₃氧化为NO₂⁻^[23]。NH₃对CH₄氧化的抑制作用对农田、草地和森林土壤中的甲烷氧化菌有重要的生态学意义。

2 影响土壤吸收、氧化CH₄的因素

2.1 大气与土壤空气中的CH₄浓度

Heipieper和de Bont^[24]发现,当空气中CH₄浓度小于1μl/L时,草地土壤仍能吸收CH₄。空气CH₄浓度升高,土壤CH₄吸收也随之增加,且农田土壤CH₄吸收的增加量大于森林和草原土壤^[25]。研究表明,无CH₄氧化发生时的土壤空气CH₄浓度并不为零,即土壤氧化CH₄存在一个临界浓度^[26]。Bender和Conrad^[27]推测土壤中存在两类甲烷氧化菌:一类在高浓度CH₄(>40ml/m³)下生长,对CH₄的亲和力低,其临界浓度高;另一类在与大气CH₄浓度相近的条件下生长,对CH₄的亲和力高,其临界浓度低。第一类甲烷氧化菌主要存在于湿地和稻田土壤中,以土壤内部产生的高浓度CH₄为底物。旱地土壤(不饱和土壤)则以第二类甲烷氧化菌为主,其氧化CH₄的临界浓度通常小于大气CH₄的浓度,因而这些甲烷氧化菌可以靠消耗大气CH₄为生。对于高亲和力的甲烷氧化细菌种群目前了解得还不很清楚^[28]。

土壤氧化CH₄的临界浓度可随环境条件的改变而发生变化。一般土壤在高浓度CH₄下培养一段时间其临界浓度会有所升

高。长年施用大量铵态氮肥,土壤氧化CH₄的临界值可能升得很高,需在很高的CH₄浓度下(如高于1000μl/L)培养几天才可恢复氧化CH₄的能力^[29],对于野外常年暴露于大气CH₄中的透气土壤来说这是不可能的。

2.2 土壤水分与氧的有效性

不同的土壤类型和土地利用方式,不同的土壤湿度范围,CH₄氧化率与土壤湿度的关系可能会有所不同。热带森林和大草原土壤对CH₄的吸收在旱季最大,在雨季则很低^[30,31]。土壤CH₄吸收率与土壤湿度通常呈负相关关系^[10,32~34]。而沙漠土壤甲烷吸收率则与土壤湿度呈正相关^[14]。

甲烷氧化菌的活性通常受氧的有效性限制^[35]。甲烷氧化菌消耗CH₄的能力一般超过CH₄由大气向土壤中扩散的潜力^[36],因而土壤中气体扩散的速率成为CH₄氧化的调节因子^[10,37,38]。由于气体扩散速率在液相中比在气相中慢得多,土壤水分含量成为CH₄氧化的主要影响因素。水分胁迫限制了土壤对CH₄的吸收^[39]。因为土壤湿度过低影响微生物活性,从而影响对CH₄的氧化^[36]。土壤湿度较低时,土壤CH₄吸收率随土壤湿度增加而上升。当土壤湿度超过田间持水量后,由于大气CH₄和O₂向土壤中扩散受阻,甲烷氧化菌活性开始下降^[40,41],土壤CH₄的吸收率随土壤湿度增加而降低。

在土壤有机质含量较高的土壤铵化作用进行很快^[42],即便土壤湿度低时也是如此。但较干的土壤NH₄⁺的硝化需要很长时间,结果导致NH₄⁺在土壤中积累^[43],从而抑制了CH₄的氧化。表土干湿交替大大抑制了CH₄氧化^[53]。此外,施肥常常降低土壤水势,也可能导致表层土壤CH₄的吸收率的下降^[43]。

2.3 土壤氮素

Mac Donald等^[44]观测到森林每年46kg/hm²的N沉降输入增加了土壤NH₄⁺-N含量,使土壤CH₄壑的强度降低了50%。受施肥和N的干湿沉降影响,表土的NH₄⁺含量高于亚表层土壤,使表层CH₄的氧化受到抑制^[45,46]。NH₄⁺对CH₄氧化的抑制作用与土壤有效氮含量或施肥量成正比^[47~49]。各类肥料对土壤CH₄吸收抑制作用的大小顺序是:铵态氮肥>尿素>硝态氮肥^[50,51]。施入NH₄Cl、(NH₄)₂SO₄和尿素后,土壤CH₄氧化立即被抑制了80%~96%。即使土壤NH₄⁺浓度几乎降为零,CH₄氧化仍被抑制了20%^[52]。长期施用粪肥提高了土壤有机质含量,土壤微生物的生物量增加,甲烷氧化菌的数量也相应增加,从而抵消了粪肥中N素对CH₄氧化的抑制作用^[53],使其抑制效果低于同等含N量的化肥。NO₃⁻对CH₄氧化没有抑制效应^[20]。不仅如此,硝态氮肥减轻土壤酸化还可能对CH₄氧化菌有利^[53]。Reay等^[54]发现,在温度、水分适宜的条件下,硝酸盐含量高的林地土壤没有或只有很低的氧化CH₄的能力。这可能不是由于NO₃⁻,而是盐分过高所致。CH₄氧化菌对渗透势很敏感。由于盐分的加入降低了水势,明显抑制了CH₄的氧化^[52]。根据土壤类型,K⁺能或多或少地从粘粒表面和内部改变NH₄⁺的有效性,这种内源NH₄⁺的直接效果是抑制了CH₄的氧化^[55]。土壤阳离子代换量(CEC)高时,施用大量的NH₄⁺对CH₄氧化仅有微弱的影响。反之,在低CEC的土壤,少量的NH₄⁺也会强烈抑制CH₄氧化^[56]。

NH₄⁺对土壤中CH₄氧化的抑制作用可归结为NH₃和CH₄在甲烷单氧酶水平上的竞争、由氧化作用向硝化作用的转移以及NH₄⁺氧化生成的NO₂⁻的毒性^[29,57]。NH₃和CH₄氧化相互排斥。由于甲烷单氧酶对底物的专一性极低^[22],施入土壤的NH₄⁺立即被甲烷单氧酶氧化,直到NH₄⁺被消耗殆尽,CH₄氧化才得以开始^[52]。长期施用NH₄⁺使土壤氧化CH₄的能力完全丧失^[29]。NH₄⁺的抑制效应一般不完全可逆。但腐殖土(humisol)中NH₄⁺的抑制效应则完全可逆^[58]。据推测,甲烷氧化菌从抑制效应中恢复过来的能力取决于NH₄⁺的浓度和有效作用时间,腐殖土具有极高的自然硝化率,CH₄氧化菌可能被很好地保护起来从而免受NH₄⁺的影响。

NO₂⁻是CH₄氧化菌氧化NH₄⁺的最终产物,它比NH₄⁺能更有效地抑制CH₄氧化^[52,59],其抑制时间也更长。施入NH₄⁺-N的大约65%被土壤颗粒吸收,而NO₂⁻则完全留在土壤溶液中,可更直接地对微生物造成毒害^[52]。NO₂⁻对CH₄氧化的抑制作用在加入的NH₄⁺进行硝化作用后仍然持续^[29]且变得不可逆转。但在CH₄浓度高于100ml/m³时此抑制作用可被消除^[60]。NH₄⁺和尿素对CH₄氧化的抑制效应主要不是通过NO₂⁻,因为NO₂⁻产生后立即被氧化而很少在土壤中累积^[52]。

2.4 土壤pH值

Van der Weerden等^[61]发现,在玉米田长年施N肥降低了土壤pH值从而抑制了土壤CH₄的氧化。苜蓿作绿肥也可引起土壤pH值的显著下降,土壤酸化导致CH₄氧化量的减少。与产甲烷细菌相比,甲烷氧化菌对pH值变化的耐受性更强^[58]。Dörr等^[62]分析了中欧约50个点的实验资料,发现CH₄吸收与土壤pH值没有关系。由于各地土地利用方式和农业管理措施不同,土壤吸收CH₄的适宜pH范围也会有所不同。在温带和亚北极地区的泥炭土壤甲烷氧化菌消耗CH₄的最适pH值为5.0~6.5^[58]。森林土壤中甲烷氧化菌的最适pH值为5.8,当pH值为6.8~7.0时则丧失了活性^[63]。在草地土壤,当pH值从6.3降至5.6时,CH₄吸收率降低了近一半;pH值为4时CH₄吸收率仅为pH值为6时的1/4;在更低的pH值下CH₄吸收完全被抑制^[19]。Mac Donald等^[64]采用分子生态学方法揭示了嗜酸的甲烷氧化菌可存在于pH值小于4.7的泥炭土中。实验表明,水溶液中NH₃的浓度主要取决于pH值:pH值<6时,NH₄⁺占100%;pH值为9.25时NH₄⁺和NH₃各占50%;pH值>12时就只有

NH_3 了。由于 NH_3 同 CH_4 竞争甲烷单氧酶的活性部分, pH 值从中性变为碱性使 NH_3 的抑制 CH_4 氧化的能力增强^[65,66]。

生活在土壤微小团粒中的 CH_4 氧化菌可在其周围形成了 pH 值或 O_2 的梯度^[67]。土块的 pH 值并不一定反映微生物活动所处的环境条件。无论土壤 pH 值如何, 细胞内的 pH 值应接近中性, 并在酶水平上调控各种比率^[68]。这可能是甲烷氧化菌对 pH 值变化不敏感的一个重要原因。

2.5 土壤温度

Sitaula 等^[47]发现在挪威森林平均温度低于 1℃ 的土壤中仍有大量的 CH_4 氧化菌存在。森林土壤中的 CH_4 氧化菌在 -5~10℃ 时受温度变化影响, 在 10~20℃ 时则不随温度变化。森林土壤 CH_4 氧化率与 0~10℃ 地温成正比^[48]。10~20℃ 时各种土壤平均 CH_4 吸收率为常数^[69]。森林土壤 CH_4 吸收日变化不显著^[70,71], 但季节变化明显: 夏天高, 冬天低, 春、秋介于二者之间^[70,72]。日平均土壤 CH_4 吸收率随土壤温度增加而线性增加^[32]。

温度对 CH_4 氧化的影响可用温度系数 Q_{10} 来表征。Crill 等^[50]测得泥炭土 CH_4 氧化的 Q_{10} 为 1.27~2.25; 类似地, Dunfield 等^[73]计算得到的 Q_{10} 为 1.40~2.10。 CH_4 氧化菌对温度的敏感性不如产甲烷细菌^[73], 这主要是因为 CH_4 氧化菌对大气 CH_4 的亲和力高且 CH_4 氧化所需活化能较低导致其温度系数 Q_{10} 较小的缘故^[74]。当大气 CH_4 和 O_2 扩散进入土壤的速率等于土壤中 CH_4 和 O_2 消耗的速率时, 此时的土壤温度就是 CH_4 氧化的最佳温度。当地温高于最佳温度时, 由于 CH_4 氧化菌难以与利用 O_2 能力更强的硝化细菌和其它微生物竞争利用土壤空气中的 O_2 , 使得土壤中 CH_4 氧化菌的繁殖和活性降低^[74], 土壤氧化 CH_4 的能力也随之下降。

2.6 土壤质地与结构

CH_4 氧化菌在团粒结构较好的壤土中可保护自己免受干扰; 而在沙质土壤中则易失去其高活力的生态位。沙土易受干扰影响, 与壤土和粘土相比, 撂荒后土壤 CH_4 氧化的恢复也较快^[53]。土壤有机层阻隔了大气 CH_4 或 O_2 向土壤中 CH_4 氧化菌的扩散^[70]。在未受干扰的森林土壤, CH_4 浓度随深度下降很快, 表层 0~5cm 土壤 CH_4 浓度从 1.7 降至 1.0 $\mu\text{l/L}$ ^[59,75]。由于表层土壤 NH_4^+ 含量较高, CH_4 氧化菌活性受到抑制^[76], 因而土壤 CH_4 氧化率的峰值通常出现在亚表层(5~10cm)^[24, 42, 55, 75~78], 25cm 以下土层则基本没有 CH_4 氧化活性^[76]。但也有研究表明, 由于耕作破坏了表土结构, 使得农田土壤 CH_4 氧化率在耕层深度(25cm)以下才有较大增加^[42]。在土豆地, 垄的 CH_4 吸收最大, 其次是未压实的土壤, 而压实的土壤则有显著的 CH_4 排放^[79]。

2.7 植被覆盖与土地利用方式

不同的植被覆盖与土地利用方式对土壤 CH_4 吸收有很大影响。耕地、草地和森林土壤的平均 CH_4 吸收率分别为 0.28、0.52 和 1.51 $\text{mg}/(\text{m}^2 \cdot \text{d})$ ^[53]。植物吸收大量养分可把包括 CH_4 氧化菌在内的土壤微生物从 NH_4^+ 等底物的有害影响中部分解救出来^[53]。木本植物的生物量一般大于草本植物, 其吸收土壤养分的量也通常大于草本植物, 这可能是森林土壤的平均 CH_4 吸收率大于草原土壤的原因之一。靠近城市或城市中的林地土壤 CH_4 吸收率低, 其原因是空气污染造成有机质分解和养分循环变慢。空气污染(特别是 O_3)对树叶造成伤害, 降低了树叶的分解率, 其结果是从凋落物到土壤中 CH_4 氧化菌种群的物质流中的 C/N 比下降^[80], 而 C/N 比与土壤 CH_4 吸收率呈正相关关系^[81]。森林和草地变为农田土壤 CH_4 的净吸收降低主要是由耕作和施 N 肥引起的。实验表明: 多年种植的冬黑麦田土壤 CH_4 吸收率高于多年种植的玉米田。这可能不是由于植物生长本身的影响, 而是施用不同的杀虫剂的结果^[82]。

3 维持与提高土壤 CH_4 吸收率的途径

维持与提高农业土壤氧化 CH_4 潜力的重要措施包括: 免耕^[42]、施硝态氮肥^[20]和/或有机肥^[83]。保持土壤 CH_4 氧化率最好的方法是免耕^[84]。Kessavalou 等^[85]发现免耕地的 CH_4 吸收率高于耕过的地块。免耕 15a 后, 土壤 CH_4 吸收率比连续耕作、同等施 N 量的地块高了 4.5 到 11 倍^[42]。但也有的耕地撂荒后土壤 CH_4 氧化率仍然很低。这表明停止耕作和施 N 肥后 CH_4 氧化的恢复是一个缓慢过程。

在农田只施硝态氮肥可阻止土壤 CH_4 浓度进一步减小。但这同时也带来了其他相关环境问题: 如无氧条件下, NO_3^- 在反硝化过程中生成了同样是温室气体的 N_2O 。当然, N_2O 也可由透气土壤中 NH_4^+ 的硝化产生。其次, NO_3^- 容易被淋溶到地下污染水源, 特别是在秋冬当作物吸收 N 素较少无法阻止 N 淋溶发生的时候。假如由于各种原因要施用尿素或铵态氮肥, 建议在被犁过的土壤进行表施, 这样大气 CH_4 的吸收不会受到过多的妨碍。在免耕地应避免将铵态氮肥和尿素施于土壤 5~15cm 深, 那里是 CH_4 氧化潜力最大的地方^[53]。施用有机肥虽然也抑制土壤 CH_4 的氧化, 但其抑制作用远小于铵态氮肥和尿素。我国向来有施有机肥的传统, 在增加产量的同时如何提高土壤 CH_4 的吸收率, 这方面还有很大的潜力可挖。

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