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# 农田土壤 $N_2O$ 排放的关键过程及影响因素

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**摘要:** 一氧化二氮 ($N_2O$) 作为重要的温室气体之一，在全球气候变化研究中引人关注。随着氮肥使用量的增加，农田土壤 $N_2O$ 排放已经成为全球关注和研究的热点。人们普遍认为土壤硝化、反硝化过程是 $N_2O$ 产生的两个主导途径，而诸如施肥、灌水等农田管理措施以及土壤 pH、温度等环境因子均会影响农田土壤 $N_2O$ 产生和排放。本文系统论述了土壤 $N_2O$ 产生的各主要途径，并综述了氮源、碳源、水分含量、氧气含量、土壤 pH 和温度以及其他调控因子对 $N_2O$ 排放的影响，旨在阐明各过程对 $N_2O$ 排放的产生机制及主要环境因子的影响，以期为后续研究提供参考和理论依据。农田土壤硝化过程本身对 $N_2O$ 排放的直接贡献较小，$N_2O$ 产生的主要来源是包含硝化细菌的反硝化、硝化–反硝化耦合作用在内的生物反硝化过程。真菌反硝化和化学反硝化在酸性土壤以及硝酸异化还原成铵过程在高有机质和厌氧土壤环境中对 $N_2O$ 排放具有重要作用。未来研究可从农田土壤 $N_2O$ 的产生和消耗机制、降低 $N_2O/N_2$ 产物比、$N_2O$ 的还原过程及相关影响因素进行深入研究。此外，利用新技术方法，探究土壤物理、化学和生物学因素对氮素转化过程的影响，重点关注 $N_2O$ 峰值排放及相关联微生物的响应，并构建土壤氮素平衡和 $N_2O$ 排放模型，可进一步加深对农田土壤 $N_2O$ 排放机制和影响因素的理解。

**关键词:** 农田土壤；氧化亚氮；硝化作用；反硝化作用；环境因子

# Key production processes and influencing factors of nitrous oxide emissions from agricultural soils

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**Abstract:** Nitrous oxide ($N_2O$), as an important greenhouse gas, has been greatly concerned due to its high potential to climate warming. $N_2O$ emissions from agricultural soils become research focus with the increasing of nitrogen fertilizer application. Nitrification and denitrification are thought as the two dominant pathways for $N_2O$ emissions, and are significantly influenced by agricultural managements (e.g. fertilization, irrigation) and environmental factors (e.g. soil pH, temperature). This study summarized the main pathways and regulatory factors of $N_2O$ emissions from agricultural soils. The purpose of this study is to explore the mechanisms of $N_2O$ production and the responses of $N_2O$ emissions to the main regulatory factors (e.g. available N, available carbon, soil moisture, oxygen concentration, soil pH and temperature, etc.), which would provide scientific basis to the future research. The N losses as $N_2O$ from nitrification are little in agricultural soils. The processes of biological denitrification (including nitrifier denitrification and nitrification-coupled denitrification) are often regarded as the principal source of $N_2O$ emissions. The fungal denitrification and chemodenitrification play an important role in emission of $N_2O$ in acidic soils. Meanwhile, the $N_2O$ emissions caused by the dissimilatory nitrate reduction to

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ammonium (DNRA) cannot be ingored with high content of soil organic matter and anaeribic conditions. Future researches should focus on the mechnisms of $N_2O$ production and consumption, combining with decreasing the ratio of $N_2O$ to $N_2$ and the processes of $N_2O$ reduction and related influencing factors. Moreover, the new techniques (e.g. planar optodes, robot incubation system etc.) should be used to investigate the effects of soil physicochemical and biological factors on nitrogen transformation, to evaluate the response of related microbial diversity from the hotspots of $N_2O$ emissions, and to establish the nitrogen balance and related $N_2O$ emission models. These works may further deepen our understanding of the mechansim of $N_2O$ emission and its related influencing factors.

**Key words:** agricultural soil; nitrous oxide; nitrification; denitrification; influencing factors

一氧化二氮 ($N_2O$，俗称氧化亚氮) 作为重要的温室气体之一，其全球增温潜势为 $CO_2$ 的 190～270 倍，且浓度以每年 0.25% 的速率持续增加，加剧了全球气候变暖[1]。同时，$N_2O$ 也是破坏臭氧层的主要因子[2]。因而，$N_2O$ 的排放在全球气候和生态环境变化的研究中受到广泛关注。

农业活动是 $N_2O$ 最大的人为排放源，其中农田土壤对 $N_2O$ 排放贡献最大[3-5]。农田土壤每年 $N_2O$ 排放约占全球人为活动 $N_2O$ 排放总量 ($6.7 \times 10^6$ t) 的 42%[6]。以我国农田土壤为例，2014 年 $N_2O$ 排放量约为 1.21 Tg，占全球 $N_2O$ 排放量的 31%[7]。一般认为农田土壤 $N_2O$ 产生的主要途径为硝化和反硝化作用过程[8]，同时，环境因子 (土壤 pH、温度等) 和管理措施 (施肥、灌水等) 主要通过影响这两个过程进而影响 $N_2O$ 排放。然而，综合土壤 $N_2O$ 排放的其他过程并结合相关环境因子的分析仍缺乏系统性研究。因此，探究农田土壤各调控机制和环境因子对 $N_2O$ 排放的影响，有利于理解农田土壤氮素转化过程与 $N_2O$ 排放之间的关系，从而为进一步提出合理的 $N_2O$ 减排措施提供理论依据。

## 1 农田土壤产生 $N_2O$ 的过程

农田土壤产生 $N_2O$ 的生物学过程包括硝化作用、反硝化作用、硝化细菌的反硝化作用、硝酸异化还原成铵以及真菌反硝化作用等。通常认为反硝化和硝化作用是产生 $N_2O$ 的主导途径。近年来在土壤低氧环境条件下硝化细菌的反硝化作用对 $N_2O$ 排放的贡献受到重视。此外，硝化–反硝化耦合作用和真菌反硝化作用对 $N_2O$ 排放也有贡献。而且，化学反硝化、亚硝基化反应 (nitrosation) 等非生物学过程也是土壤 $N_2O$ 的产生途径 (图 1)。因此，全面了解与 $N_2O$ 排放有关的土壤过程，有助于实现农田土壤 $N_2O$ 减排。

### 1.1 硝化作用

硝化作用 (nitrification) 通常有两个过程：氨氧化过程和亚硝酸氧化过程 (图 1A)。氨氧化过程是自养的氨氧化细菌 (ammonia-oxidizing bacteria，AOB) 或氨氧化古菌 (ammonia-oxidizing archaea，AOA) 在氨单加氧酶 (AMO) 催化下将 $NH_3$ 催化氧化为羟胺 ($NH_2OH$)，并进一步在羟胺氧化还原酶 (HAO) 催化下产生 $NO_2^-$，该过程是硝化作用发生的限速步骤[9]。亚硝酸氧化是指 $NO_2^-$ 在亚硝酸氧化菌 (nitrite oxidation bacteria，NOB) 作用下氧化为 $NO_3^-$ 的过程。最近研究发现了完全氨氧化菌 (如 *Nitrospira*) 的存在，这类细菌能够将铵态氮直接氧化为硝态氮，称为完全硝化过程 (complete ammonia oxidizers，comammox)[10-11]，这一发现颠覆了硝化过程必须经过两步反应过程的经典认知。除自养硝化作用外，异养硝化作用是指异养微生物将有机态氮氧化为亚硝态氮或硝态氮的过程，其中参与该活动的微生物有细菌、真菌等[12-13]。

$N_2O$ 不是硝化过程的中间产物，其产生与中间产物 $NH_2OH$ 和 $NO_2^-$ 紧密相关。硝化作用对 $N_2O$ 排放的直接贡献较低，大多低于 $NH_4^+$-N 氧化总量的 1%[14]。纯培养发现，不同亚硝化螺菌氨氧化过程产生的 $N_2O$ 与其累积的 $NO_2^-$ 比例为 0.07%～0.1%[15]。Mørkved 等通过泥浆培养试验发现，土壤硝化作用产生的 $N_2O$ 与硝化终产物 $NO_3^-$ 的比值也仅为 0.02%～0.09%[16]。硝化过程对土壤 $N_2O$ 排放的贡献，或许主要体现在其为包括经典生物反硝化过程、硝化细菌的反硝化过程，甚至非生物的 $N_2O$ 产生过程等提供 $NO_3^-$ 和 $NO_2^-$ 等底物上，其中氨氧化过程产生的终产物 $NO_2^-$ 尤为重要。

进一步对比自养硝化和异养硝化作用对 $N_2O$ 排放的相对贡献来看，一般认为异养硝化作用对 $N_2O$ 的贡献较少，但在某些土壤环境条件下不容忽

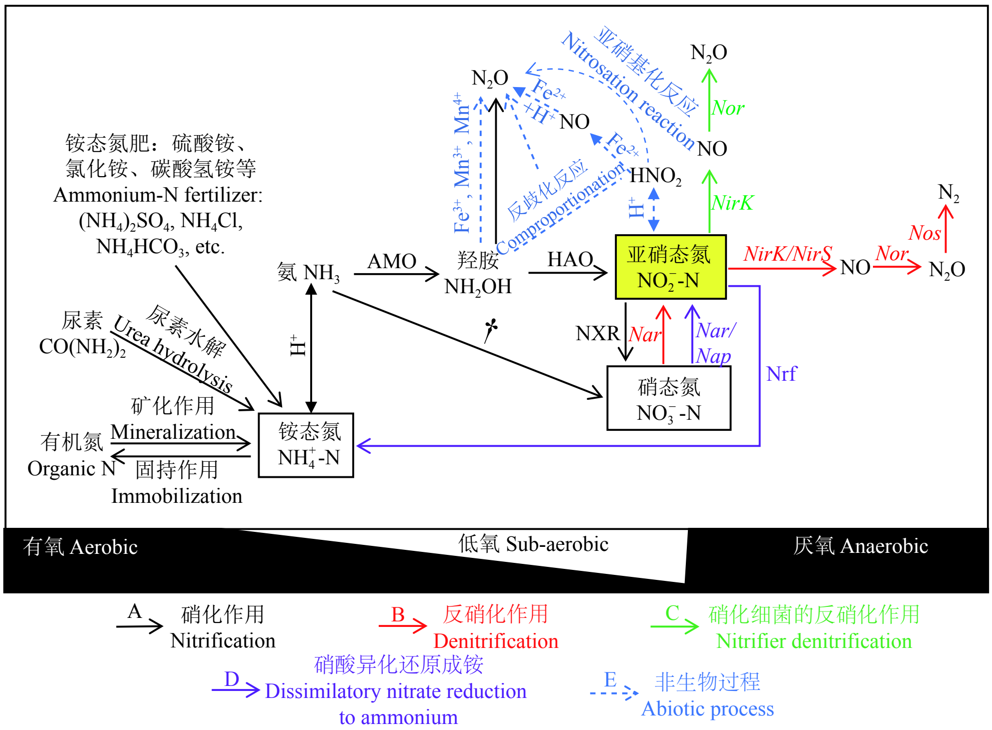

**图 1　$N_2O$ 排放的主要生物学和非生物学过程**

**Fig. 1　Biotic and abiotic processes of nitrous oxide ($N_2O$) emission from soils**

[注（Note）：AMO—氨单加氧酶 Ammonia monooxygenase；HAO—羟胺氧化还原酶 Hydroxylamine oxidoreductase；NXR—亚硝酸氧化还原酶 Nitrite oxidoreductase；Nar/Nap—硝酸异化还原酶 Membrane-bound nitrate reductase/periplasmic nitrate reductase；Nrf—亚硝酸还原酶 Cytochrome *c* nitrite reductase；NirK—含铜的亚硝酸异化还原酶 Copper-containing nitrite reductase；NirS—含有细胞色素 $cd_1$ 的亚硝酸异化还原酶 Cytochrome $cd_1$ nitrite reductase；Nor—NO 还原酶 Nitric oxide reductase；Nos—$N_2O$ 还原酶 Nitrous oxide reductase；† 该过程 (一步硝化反应) 由 *Nitrospira* 细菌作用† This process (one-step nitrification) attributed only to the *Nitrospira* bacteria[10-11]；A、B、C、D、E 分别代表硝化、反硝化、硝化细菌反硝化、硝酸异化还原成铵及非生物学过程 A，B，C，D，E represent nitrification，denitrification，nitrifier deitrification，dissimilatory nitrate reduction to ammonium and abiotic processes，respectively.]

视[17]。如，在酸性森林土壤中异养硝化作用是产生 $N_2O$ 的主要途径[18-23]，其贡献主要受土壤 pH 和 C/N 影响[20]。此外，目前还暂未有证据显示，完全硝化过程 (comammox) 具有产生 $N_2O$ 的能力，但由于其生物化学过程是经典氨氧化细菌和亚硝酸氧化细菌相关过程的结合，其存在具有产生 $N_2O$ 的可能性[21]。

## 1.2　反硝化作用

反硝化作用 (denitrification) 通常是指生物反硝化，即反硝化微生物在厌氧条件下将 $NO_3^-$ 或 $NO_2^-$ 逐渐还原为 NO、$N_2O$ 和 $N_2$ 的过程 (图 1B)[22]。该过程所需的酶包括异化硝酸盐还原酶 (*Nar* & *Nap*)、异化亚硝酸盐还原酶 (*Nir*)、一氧化氮还原酶 (*Nor*) 以及一氧化二氮还原酶 (*Nos*)，相应的编码基因分别为 *narG* 和 *napA*、*nirK/S*、*norB* 以及 *nosZ*。其中，$NO_2^-$ 还原为 NO 的过程被认为是反硝化作用中最关键的步骤[23]。亚硝酸盐还原酶 (*Nir*) 是产生 NO 的关键酶，包含由 *nirS* 基因编码的细胞色素还原酶 ($cd_1$-Nir) 和由 *nirK* 基因编码的可溶性含铜酶 (*Cu*-Nir)[24]。反硝化微生物通常只含有其中的一种，已分离的反硝化细菌中含 *nirS* 的数量占 3/4[25]，而且在许多环境中以含有 *nirS* 基因的反硝化微生物占主导[25]。

通常反硝化作用是土壤产生 $N_2O$ 的主要来源。有研究表明，反硝化作用对 $N_2O$ 排放的贡献在农田、茶园和竹园土壤中分别为 54.5%、72.8% 和 77.1%[20]。完全的反硝化作用终产物为分子态氮 ($N_2$)，然而约有 1/3 数量的反硝化细菌缺少编码 $N_2O$ 还原酶 ($N_2OR$) 的 *nosZ* 基因，导致其终产物为 $N_2O$[26]。同时，低土壤 pH 或高 $NO_3^-$ 含量会抑制 $N_2O$ 还原酶的形成[27]。此外，在土壤碳有效性较低条件下，与其他异化还原酶相比，$N_2O$ 还原酶竞争电子的能力较弱，因而也会造成 $N_2O$ 排放量增加[28]。

## 1.3　硝化细菌反硝化

硝化细菌的反硝化作用 (nitrifier denitrification，

ND) 是氨氧化微生物直接利用其在氨氧化过程产生的亚硝酸盐 ($NO_2^-$) 作为电子受体，进行反硝化的过程。通常多发生在好氧或低氧条件下，进行该反应的微生物通常为氨氧化细菌 (AOB)[29]，还未发现氨氧化古菌 (AOA) 具有这种还原能力[30]。此外，由于 AOB 缺乏 $N_2OR$ 编码基因，因而其终产物绝大部分是 $N_2O$，而非 $N_2$[31]。硝化细菌反硝化作用对土壤 $N_2O$ 排放可能占有较高比重[32-33]。Zhu 等利用双同位素标记法证实在低氧浓度条件下，施用铵态氮肥后硝化细菌反硝化作用是土壤 $N_2O$ 排放的主要来源[34]。Huang 等研究发现，集约化石灰性低碳旱作土壤中硝化细菌的反硝化作用占 $N_2O$ 排放总量的 44%～58%[35]。但也有研究对此持怀疑态度[36]，主要是由于定量硝化细菌反硝化的双同位素方法是基于氨氧化过程产生的 $NO_2^-$ 只能被自养 AOB 还原的假设。然而，事实上许多异养反硝化菌也能够直接异化还原 $NO_2^-$，从而导致高估了硝化细菌反硝化作用对 $N_2O$ 排放的贡献量。

### 1.4 硝化–反硝化耦合作用

一般认为，硝化和反硝化作用分别发生在有氧和厌氧条件下，即两个过程在不同的生态位中进行。硝化–反硝化耦合作用 (nitrification–coupled denitrification，NCD) 的实质是同时存在于两个相邻微域空间的硝化和反硝化过程的偶联；发生在有氧空间、由硝化过程产生的 $NO_2^-$ 或 $NO_3^-$ 作为底物直接被存在于厌氧或低氧空间的反硝化微生物所利用[12, 37]，从而导致在好氧–厌氧界面上 $N_2O$ 的排放。

硝化–反硝化耦合作用对污水中的氮素去除、沉积物及农田土壤的氮素转化发挥着重要作用[37-38]。有氧条件的反硝化作用和沉积物内孔隙水的对流运输可使这两个过程在空间和时间上耦合更加紧密[39]。同时，研究已经证实，沉积物中添加 $^{15}NH_4^+$ 后，由反硝化作用产生的 $^{15}N\text{-}N_2$ 几乎与氨氧化过程和亚硝酸氧化过程同步，即硝化和反硝化过程在发生时间上重叠[41]。在某些情况下硝化–反硝化耦合作用能够去除河口沉积物中 10%～80% 的人为氮素污染[40]。在土壤好氧微域环境中，如土壤表面氧化层或根际，硝化产生的 $NO_3^-$ 或 $NO_2^-$ 进入土壤厌氧微域会进一步发生反硝化作用。已有研究表明，在稻田土壤存在硝化–反硝化耦合作用，且硝化–反硝化耦合作用产生的氮损失很可能受硝化速率调控[41]。同时 Ma 等[42]研究发现，在稻田土壤 250% 和 100%WHC条件下硝化–反硝化耦合作用对 $N_2O$ 排放总量的贡献比例分别为 6.74% 和 11.5%。

### 1.5 真菌反硝化

真菌反硝化作用 (fungal denitrification) 主要是以 $NO_2^-$ 作为底物在各种酶参与下还原为 $N_2O$ 的过程[43]，其中某些真菌 (如 *Fusarium oxysporum*) 也能够将 $NO_3^-$ 还原为 $N_2O$。与细菌反硝化过程不同，由于真菌在线粒体膜上缺少 $N_2OR$，故不能将 $N_2O$ 进一步还原为 $N_2$[45]。进行反硝化作用的细菌和真菌均能利用 *NirK* 编码的亚硝酸盐还原酶将 $NO_2^-$ 还原为 NO[22, 44]。与细菌不同的是，真菌主要是在 NO 还原酶细胞色素 P450nor 的作用下，以烟酰胺腺嘌呤二核苷 (NADH，一种辅酶) 作为电子供体将 NO 还原为 $N_2O$[45]，这种 NO 还原酶在结构和功能上与细菌 NO 还原酶有较大差别[46]。

一般认为，土壤 $N_2O$ 的产生以细菌主导的反硝化作用过程为主[47]。近年来，越来越多的证据显示，真菌在不同生态系统中对土壤 $N_2O$ 的排放均有贡献[48-52]，尤其在酸性土壤条件下更明显[53-54, 61]，如真菌反硝化作用在低 pH 茶园土壤中对 $N_2O$ 排放的贡献高达 70%[55]。这主要与真菌群落在低 pH 条件下占主导，而细菌对酸性土壤环境条件较为敏感有关[56]。相反，真菌反硝化作用在碱性土壤中对 $N_2O$ 的贡献并不重要[57]。在沙漠和半干旱的草地土壤中真菌也是 $N_2O$ 产生的主要来源[52]，同时，在极端高温条件 (40℃) 出现时，酸性土壤施用有机肥后可能也会增加真菌反硝化作用对 $N_2O$ 排放的贡献[58]。Wei 等发现农田土壤田间表层施用颗粒性有机肥后 $N_2O$ 排放主要来源于真菌的反硝化作用[52]。

### 1.6 硝酸异化还原成铵

硝酸异化还原成铵 (dissimilatory nitrate reduction to ammonium，DNRA) 是硝酸异化还原的过程之一。与反硝化作用类似，DNRA 过程是以 $NO_3^-$ 或 $NO_2^-$ 作为电子受体并在厌氧条件下将其还原为 $NH_4^+$ 的过程 (图 1D)。土壤 pH、碳源含量、底物浓度 ($NO_3^-$ 和 $NO_2^-$)、C/N 等是影响 DNRA 和反硝化作用这两个氮异化还原过程竞争的重要环境因素[59]。一般认为，DNRA 更易在 pH 较高的条件下发生。如 Yoon 等已证实在酸性条件下 *Shewanella loihica PV-4* 菌株主要产物为 $N_2O$，而在碱性土壤中为 $NH_4^+$[60]。同时，在 $NO_3^-$ 或 $NO_2^-$ 底物浓度较高或电子受体充足、碳源含量相对较低的环境中，由于 DNRA 过程发生所需的自由能比反硝化作用过程自由能高，因此该条件下反硝化作用更易发生[61]。相反，在电子受体 ($NO_3^-/NO_2^-$) 不足而碳源含量充裕时，DNRA 过程则占主导[61]。

通常，DNRA 过程在海洋生态系统的氮素循环中发挥重要作用，而陆地生态系统其多发生在湿地、草地等自然土壤中[62]，其对 $N_2O$ 排放的贡献较低，甚至可以忽略。如 Kool 等通过$^{15}N$-$NH_4^+$和$^{15}N$-$NO_3^-$标记试验表明，在沙壤土中 DNRA 过程对 $N_2O$ 的贡献可以忽略[63]。然而，也有研究发现具有 DNRA 功能的细菌中含有非典型 $N_2OR$，可将 $N_2O$ 进一步还原，这对 $N_2O$ 消耗具有潜在贡献[64]。

### 1.7　非生物学过程

除生物学过程外，近年来非生物学过程对 $N_2O$ 排放的贡献再次受到关注[65-68]。非生物学产生 $N_2O$ 的过程又称为化学反硝化作用 (chemodenitrification)[69]，包括 $NO_2^-$的分解、$NO_2^-$和 $NH_2OH$ 与金属离子等作用发生的电子转移过程[70]以及光化学反应等[71-72]。非生物学过程的发生主要与硝化、反硝化过程释放的不稳定中间产物 $NH_2OH$ 和 $NO_2^-$有关 (图 1E)。它们可与金属离子 (如 $Fe^{2+}$或 $Mn^{3+}$) 或有机质发生非生物的化学反应产生 $N_2O$、NO，甚至 $N_2$[70]。其中，$NO_2^-$与有机物质的反应，被称为亚硝基化作用 (nitrosation)。一般而言，$NH_2OH$ 很少在土壤中出现累积，这与 $NH_2OH$ 具有很高的活性且其氧化的发生与土壤 pH、Mn 和土壤有机质 (SOM) 的含量有关[73]。如 Heil 等研究发现，尽管土壤中 Mn 的含量较低，但 $NH_2OH$ 会优先与 $Mn^{3+}$或 $Mn^{4+}$进行化学反应，而非 $Fe^{3+}$，这主要是因为 $Fe^{3+}$常以不溶性的形态存在，导致其不易与 $NH_2OH$ 接触进行反应[73]。$NO_2^-$既可来源于硝化过程也可能来源于反硝化过程。在高土壤 pH 条件下施用铵态氮肥后易导致 $NO_2^-$累积[74]，而 $NO_2^-$可与 $Fe^{2+}$发生反应生成 NO 和 $N_2O$。此外，土壤 $NO_2^-$也可与 SOM 发生亚硝基化反应 (图 1E)，且 $N_2O$ 产生量与 SOM 含量呈正相关[75]。

通常认为非生物学过程对 $N_2O$ 排放的贡献较少，如在 21% 和 0% 氧浓度下，粘壤土化学反硝化对 $N_2O$ 的贡献分别为 6.33% 和 0.08%；同时，Ma 等[42]发现添加 $NO_2^-$后，灭菌土壤 $N_2O$ 排放占非灭菌土壤 $N_2O$ 排放比例少于 1.1%。也有研究发现，添加 $NO_2^-$后非生物因素对总 $N_2O$ 排放量的贡献较高，达 31%～75%[80]，这可能与土壤 pH 有关。

## 2　主要环境因子对 $N_2O$ 排放的影响

### 2.1　氮源

农田土壤施入的化肥氮约有 70% 以上是以铵态氮或酰胺态氮肥的形式进入土壤[76]。土壤氨氧化过程有中间产物 $NH_2OH$ 和 $NO_2^-$的产生。这两种中间产物易于分解，因而在田间条件下的土壤中很难被监测到。特别是 $NH_2OH$，由于其极具活性，可经氧化作用产生 $NO_2^-$，发生化学作用产生 $N_2O$，也可与土壤有机质 (SOM) 发生反应。$NO_2^-$在土壤中也不稳定，同时由于土壤样品储运和处理过程较长等原因，也不易观察到其累积。但在实验室培养条件下，常常会发现 $NO_2^-$的过渡性积累，且与 $N_2O$ 排放呈极显著正相关关系[77-80]，这表明亚硝态氮作为产生 $N_2O$ 过程底物的重要性。

早期研究表明，施用化学氮肥能够增加农田土壤 $N_2O$ 的排放[81]。Shcherbak 等[82]通过元分析发现，$N_2O$ 排放随施氮量的增加呈指数而非线性增长。近年来研究发现，在覆膜水稻[83]和常规淹水水稻种植体系[84]土壤中，通过尿素氮深施可显著降低 $N_2O$ 排放。这可能由于深施后的尿素氮在土壤还原环境条件下多以铵态氮形式保存，且不易移动，降低了硝化和反硝化反应所需底物。对比不同肥料类型来看，通过田间试验大样本分析和模型显示，施用尿素产生的 $N_2O$ 排放量较硫酸铵高[85-86]，这在室内培养试验中也得到类似结论[35]。同时，施用高效氮肥如包膜氮肥可显著降低土壤 $N_2O$ 排放[87]。Liu 等[88]证实施用控释尿素土壤 $N_2O$ 排放系数显著低于尿素、硫酸铵和硝酸铵钙。Xia 等[89]通过大样本分析发现施用控释氮肥可整体减少 $N_2O$ 排放达 38.3%。与尿素[90]和硫酸铵[91]处理相比，土壤施用家禽粪肥可明显增加 $N_2O$ 排放量。大样本分析显示，与仅施用化学氮肥相比，有机肥增加 $N_2O$ 排放量平均高达 32.7%[92]。有机肥与化肥混施 (表 1) 或有机肥部分替代化肥[88]能够缓解土壤 $N_2O$ 排放。

许多研究显示，在我国北方石灰性土壤中硝化作用过程是产生 $N_2O$ 的主导途径[98-101]，并推测这可能与该土壤低的有效性碳含量有关[101]。然而，在 pH 较高的情况下，化学氮肥施入土壤后由硝化作用导致的亚硝态氮过渡性积累，从而为硝化细菌的反硝化和反硝化过程进行提供底物，或许更为重要。在高铵态氮投入的中性土壤中，氨氧化细菌 (AOB) 主导控制着硝化作用的活性[102]，而氨氧化古菌 (AOA) 通常在低 $NH_3$ 浓度的酸性土壤中发挥显著作用[103]，这主要是由于 AOA 和 AOB 对底物 ($NH_3$ 和 $O_2$) 的亲和性 ($K_m$) 存在较大差异有关[104]。Hink 等利用 1-辛炔 ($C_8H_{14}$) 区分 AOA 和 AOB 对 $N_2O$ 产生量的相对贡献证实[105]，添加铵态氮后 AOB 对土壤 $N_2O$ 总产生量起主导作用 (贡献比例为 81%～86%)，而未添加铵态氮的土壤中，AOA 对 $N_2O$ 的贡献率为

表 1 不同肥料类型和施肥方法下土壤 $N_2O$ 排放量和排放系数

Table 1 Cumulative $N_2O$ emissions and emission factors under different fertilizer types and fertilization methods

| 肥料类型 Fertilizer type | 作物 Crop | 施肥方法 Application method | 土壤质地 Soil texture | 采样时期 Sampling period (d) | 施氮量 N rate (kg/hm²) | $N_2O$ 累积排放量 Cumulative $N_2O$ emission (kg/hm²) | 排放系数 Emission factor (%) | 参考文献 Reference |
|---|---|---|---|---|---|---|---|---|
| 牛粪 Dairy manure | 草地 Grassland | 撒施 Broadcast | 沙壤土 Sandy loam | 21 | 315 | 0.65 | 0.21 | [93] |
| 尿素 Urea | 小麦–玉米 Wheat-maize | 表层滴灌 Surface fertigation | 壤土 Loam | 350 | 600 | 3.14 | 0.52 | [94] |
| 家禽粪 Poultry manure | 大葱–冬小麦 Welsh onion+ winter wheat | 基施 Basal fertilization | 粉质粘壤土 Silty clay loam | 355 | 46 | 1.51 | 1.35 | [95] |
| 家禽粪 + 磷酸氢二铵 + 尿素 Poultry manure + $(NH_4)_2HPO_4$ + urea | 大葱–冬小麦 Welsh onion+ winter wheat | 基施 Basal application | 粉质粘壤土 Silty clay loam | 355 | 646 | 4.02 | 0.42 | [95] |
| 有机肥+尿素 Manure + urea | 番茄 Tomato | 基施+追施 Basal and topdressing | 粉质粘壤土 Silty clay loam | 105 | 1550 | 19.7 | 1.06 | [96] |
| 尿素 Urea | 甘蔗 Sugarcane | 表施 Surface fertilization | 黏土 Clayey soil | 60 | 60 | 1.13 | 0.52 | [86] |
| 硝酸铵 Ammonium nitrate | 甘蔗 Sugarcane | 表施 Surface fertilization | 黏土 Clayey soil | 60 | 60 | 1.08 | 0.44 | [86] |
| 尿素 Urea | 甘蔗 Sugarcane | 表施 Surface fertilization | 黏土 Clayey soil | 30 | 120 | 1.22 | 0.83 | [86] |
| 硝酸铵 Ammonium nitrate | 甘蔗 Sugarcane | 表施 Surface fertilization | 黏土 Clayey soil | 30 | 120 | 0.47 | 0.23 | [86] |
| 固体家禽粪 Solid poultry manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 粉质黏土 Silty clay | 180 | 90 | 5.2 | 2.9 | [97] |
| 液体牛粪 Liquid dairy cattle manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 粉质黏土 Silty clay | 180 | 94.3 | 6.3 | 4.1 | [97] |
| 液体猪粪 Liquid swine manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 粉质黏土 Silty clay | 180 | 90 | 4.4 | 2.0 | [97] |
| 硝酸铵钙 Calcium ammonium nitrate | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 粉质黏土 Silty clay | 180 | 90 | 5.1 | 2.7 | [97] |
| 固体家禽粪 Solid poultry manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 沙壤土 Sandy loam | 180 | 90 | 2.2 | 2.1 | [97] |
| 液体牛粪 Liquid dairy cattle manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 沙壤土 Sandy loam | 180 | 94.3 | 1.2 | 1.1 | [97] |
| 液体猪粪 Liquid swine manure | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 沙壤土 Sandy loam | 180 | 90 | 1.3 | 1.1 | [97] |
| 硝酸铵钙 Calcium ammonium nitrate | 青贮玉米 Silage corn | 表面撒施 Surface broadcast | 沙壤土 Sandy loam | 180 | 90 | 0.7 | 0.4 | [97] |

47%～58%，AOB 对 $N_2O$ 的贡献可以忽略。因此，在施入或添加外源铵态氮造成 $NH_3$ 浓度较高时，AOB 主导了硝化作用的进行，而当 $NH_3$ 主要来源于土壤的矿化作用时 AOA 是硝化作用过程进行的主要执行者。同时，长期向土壤中添加不同形态的氮素也会显著影响硝化微生物基因丰度。Zhou 等[106]在连续进行 44 年施肥试验的草地土壤中发现，添加有机氮显著增加了 AOA 的 *amoA* 基因拷贝数，而 AOB 的 *amoA* 基因拷贝数在添加无机氮的处理中出现增加，且 AOA/AOB 比值随有机氮添加量的增加而增大。Ai 等[107]在农田土壤中也发现，长期施用氮肥 (尿素) 能显著增加土壤硝化潜势和 AOB 的种群丰度，而施用有机肥增加了 AOA 的种群丰度。这可能与 AOA 优先氧化有机氮 (来源于有机肥或土壤有机质) 矿化出来的氨有关，特别是在氨氧化速率超过矿化速率时，AOA 对氨具有很高的亲和性[108]。而对于反硝化作用过程来说，增加土壤中 $NO_3^-$通常会造成 $N_2O/N_2$ 比值升高[109]，这主要是由于 $NO_3^-$作为末端电子受体 (terminal electron acceptor，TEA) 会被优先利用，且高 $NO_3^-$含量也会抑制 $N_2O$ 还原酶活性[110]。

### 2.2 碳源

土壤碳源含量主要受耕作、有机肥投入、根系分泌物和作物残渣投入 (如秸秆) 等因素影响。Badagliacca 等[111]研究发现，免耕措施下 $N_2O$ 排放显著高于传统耕作，这可能与免耕增加土壤有效性碳含量有关[112]。有机肥的施用显著增加土壤反硝化潜势。这主要是因为田间施用有机肥或其他有机物料后显著增加了土壤异养微生物的呼吸，同时有机物料中有效性碳为反硝化微生物提供了电子供体，促进了反硝化作用的发生。在植物根系根区内可通过根际沉积作用向根际土壤分泌一些低分子量碳的化合物，如糖类、有机酸和氨基酸等[113]。这些低分子量有机物极易分解，结合土壤根系的呼吸作用，造成根际土壤 $N_2O$ 产生量高于非根际土壤[114-115]。Giles 等[116]对不同低分子量有机物研究发现，葡萄糖、谷氨酰胺和柠檬酸均显著增加 $N_2$ 的释放，且柠檬酸与葡萄糖和谷氨酰胺相比显著降低了 $N_2O$ 的排放。

目前，秸秆还田被认为是增加土壤肥力、提高土壤健康的农田管理措施之一。秸秆施入后主要通过影响土壤碳、氮有效性及土壤通气性进而间接影响 $N_2O$ 排放。Kravchenko 等[117]研究发现，多数情况下秸秆施入可提高土壤 $N_2O$ 排放，并抵消土壤碳储存的气候效益。如在设施菜田土壤中，田间施用玉米秸秆能够显著增加 $N_2O$ 通量排放[118]；在小麦–玉米轮作的粮田种植体系，小麦秸秆施用后可显著增加玉米季 $N_2O$ 排放量[119]。秸秆还田在不同农田土壤土地利用方式下对 $N_2O$ 排放的影响也不一致。Shan 等发现秸秆还田在休耕地、旱地土壤中显著增加 $N_2O$ 排放，而在稻田中 $N_2O$ 排放显著降低[120]。与施用有机肥相比，通过秸秆深施可显著降低小麦季土壤 $N_2O$ 排放量[121]。Li 等[122]通过$^{15}N$ 示踪技术直接证明了作物秸秆施用后在不同水分条件下反硝化过程是土壤 $N_2O$ 排放的主导途径。然而，作物秸秆施用后并未发现土壤的反硝化微生物数量出现明显增加。Philippot 等[123]研究发现，短期添加小麦秸秆对土壤反硝化菌基因丰度影响有限。同时，短期添加小麦、油菜和苜蓿秸秆也没有改变反硝化菌的数量，其反硝化作用与反硝化菌群落丰度呈解耦关系，与呼吸作用显著相关[124]。作物秸秆碳氮比是影响氮素释放的重要因子，可调控土壤氮素的固定和释放[125]。一般认为，高碳氮比植物残体施入土壤后可增加氮素固持进而有利于土壤肥力的提高，而低碳氮比植物残体会增加 $N_2O$ 的排放[120, 126]。Chen 等[14]利用大样本分析发现，作物秸秆碳氮比 $< 45$ 时对土壤 $N_2O$ 排放有显著正效应，而在碳氮比 $> 100$ 时略有负效应。同时，作物秸秆对土壤 $N_2O$ 排放的影响与土壤理化性质，特别是土壤水分和质地紧密相关。如，在低碳氮比土壤中施入动物有机肥可导致 $N_2O$ 排放量增加[127]，而在高土壤碳氮比下，氮素气态损失主要以 $N_2$ 为主[128]。类似地，增加土壤有效性碳与硝态氮的比例可促进 $N_2O$ 还原为 $N_2$[129]。此外，大多数研究已证实，土壤施用生物炭能够显著减少 $N_2O$ 的排放[130-131]，这主要与生物炭和土壤性质以及它们的交互效应有关。生物炭可通过改变土壤物理 (气体扩散、团聚体、保水性等)、化学 (pH、Eh、有效性有机和矿质态氮、溶解性有机碳等) 以及生物学性质 (微生物种群结构、微生物量及活性、与氮循环相关酶活性等) 影响 $N_2O$ 的排放[132]。如生物炭通常具有高 C/N 比，并含有小分子量有机化合物，其多孔的结构适宜微生物生长并利于土壤氮素的固定，进而减少氮素有效性，降低土壤 $N_2O$ 的排放。同时，具有碱性特性的生物炭可用来改良酸性土壤，提高土壤 pH。相关研究也已证实，生物炭可增加土壤微生物 *nosZ* 基因丰度，进而促进 $N_2O$ 的还原[133-134]。

### 2.3 水分含量

土壤水分是环境驱动力中最重要的因素之一[8]。水分影响土壤微生物细胞代谢活性和养分的运输[135]，对硝化和反硝化作用过程具有决定性影响[136]。在土

壤水分饱和区或淹水条件下，高土壤水分含量阻碍气体扩散，使土壤形成嫌气环境，增加土壤反硝化潜势和速率。同时，在该条件下，硝化作用进行得较为缓慢，参与反应的硝化微生物在植物根系周围的氧化区域具有较高活性[137]。在土壤水分非饱和区，其易于硝化作用的进行，该水分条件下反硝化作用主要发生在土壤团聚体和土壤微域环境中[138]。以土壤孔隙含水量 (WFPS) 作为判定 $N_2O$ 主要来源的指标已有大量研究。一般认为，硝化作用在 30%～60% WFPS 下是产生 $N_2O$ 的主要来源，而在土壤水分含量高于 70% 时 $N_2O$ 主要源于反硝化过程[138]。然而，在以硝化过程为主导的土壤环境中，$N_2O$ 的排放总量远低于以反硝化过程主导的土壤环境[34]。土壤灌水后 $N_2O$ 含量迅速增加主要是反硝化作用的结果[139]。农田土壤玉米播种灌水后 WFPS 由 20% 迅速增加至 80%，其产生的 $N_2O$ 剧烈排放可能主要来源于反硝化作用过程[140]。设施菜田土壤 $N_2O$ 排放主要集中在基施有机肥并灌水后的 1 周内，$N_2O$ 排放也主要受反硝化作用影响[119]。此外，施用有机肥并灌水显著增加了分子态氮 ($N_2$) 的损失[141]。

水分含量影响土壤硝化和反硝化微生物的活性。Uchida 等[142]发现在土壤淹水后的几小时内 (3 h)，反硝化基因 (*nirK*，*nirS*，*nosZ*) 在 mRNA 水平 0—1 cm 土层土壤中显著增加并达到峰值，也就是说当水分含量造成土壤氧气浓度发生改变时，反硝化细菌会迅速做出反应以适应新的环境条件，表明降雨或灌溉后导致 $N_2O$ 排放峰的出现与反硝化过程有关。与此类似的是，Riya 等[143]研究表明，在土壤淹水消失前 48 h 添加 $NH_4^+$后，*amoA* 的 mRNA 拷贝数在 5—10 mm 土层土壤中虽有增加，但不显著，而 *nirK* 的 mRNA 转录水平在淹水消失 6 h 后急剧增加。然而，与上述观点不同的是，Theodorakopoulos 等[144]发现，随着土壤 WFPS 上升，并未发现在 0—10 cm 土层土壤中反硝化基因转录数 (mRNA) 增加，而显著增加了细菌 *amoA* 的转录数，且其与 $N_2O$ 排放呈极显著正相关，这可能与土壤中低氧气含量和铵态氮有效性增加有关。

## 2.4　氧气

土壤氧气含量是驱动生物地球化学循环的关键因素之一，也是影响硝化作用和反硝化作用对 $N_2O$ 排放相对贡献的决定因子之一[145]。在自然生态系统中，空气对流和气体扩散影响土壤中的氧气含量；同时，异养微生物呼吸作用或微生物耗氧分解以及硝化作用的发生也会减少土壤氧气浓度[146]。Groffman 等[147]认为土壤“热点”(hot spots) 的形成主要是因为水分含量的提高和有机肥施用后增加了土壤有效性碳氮的富集，进而影响了氧气浓度在土壤中分布。在氧气受限而有效性碳充裕的土壤环境下，其“热点”区域 $N_2O$ 的排放以反硝化作用为主导途径。氧气浓度在土壤中的非均质性分布，也是导致 $N_2O$ 产生或排放出现差异性的重要原因[148]。

氧气浓度影响硝化、反硝化作用对 $N_2O$ 排放的贡献。Khakil 等研究发现，在低氧浓度下 (0.35 kPa) 反硝化作用是产生 $N_2O$ 排放的主导途径。随土壤厌氧环境的形成，硝化作用对 $N_2O$ 排放的贡献明显下降[148]。Zhu 等[34]研究发现，在低氧条件下氨氧化和硝化细菌的反硝化作用是产生 $N_2O$ 的主要来源。其中，在 0.5% 和 3%(体积比) 氧浓度下，硝化细菌的反硝化作用对 $N_2O$ 排放的贡献为 34%～66%。这可能主要是由于在低氧条件下，氨氧化细菌 (AOB) 的群落组成发生改变，一些 AOB 物种能够进行反硝化作用，如亚硝化单胞菌和类亚硝化单胞菌在低氧条件下丰富度增加，同时异养反硝化作用对 $N_2O$ 的贡献量主要受氧气和有效性碳含量的影响[149]。需要注意的是，部分硝化微生物在利用亚硝酸盐而不是氧气作为电子受体时，氧气仍是氨氧化过程反应发生所不可缺少的条件[137]。

## 2.5　土壤 pH

土壤 pH 可直接通过影响生物[150]和非生物学过程调控 $N_2O$ 的排放。pH 也能够改变土壤底物有效性，如低 pH 会降低土壤矿质氮和有机碳的可利用性进而间接影响 $N_2O$ 排放[151]。大样本分析证实，降低土壤 pH 会增加 $N_2O$ 排放[152]。Sun 等[153]发现，在草原和森林土壤中 $N_2O/N_2$ 比值随土壤 pH 下降而升高。在我国农田土壤中，由于过量施用氮肥，土壤 pH 明显下降[154]，或将大幅度增加 $N_2O$ 排放。

硝化作用过程对土壤 pH 的响应可能较为敏感，这主要与 pH 影响 $NH_3$ 有效性 (AMO 的底物) 有关 [$NH_3(aq) + H^+(aq) \Leftrightarrow NH_4^+(aq)$；$pK_a = 9.25$，25℃][155]。每改变 1 个 pH 单位 $NH_3$ 浓度的变化将近 10 倍[156]。硝化速率通常随土壤 pH 的增加而上升[157-158]，其培养的硝化细菌最适 pH 范围为 7.5～8.0[157]。对于氨氧化微生物而言，增加土壤 pH 可以增加氨氧化古菌 (AOA) *amoA* 基因丰度，而对氨氧化细菌 (AOB) *amoA* 基因丰度没有影响，甚至有些减少[159-160]，但也有人认为土壤 pH 增加可以提高 AOB 的丰度，而对 AOA 没

有影响[161-162]。大量研究发现酸性土壤硝化作用的主要贡献者为 AOA[163-165]，这与 AOA 在酸性条件下对 $NH_3$ 具有较高的亲和力有关[166]。研究表明，pH 与硝化细菌的反硝化过程产生的 $N_2O$ 呈正相关关系，而与反硝化作用产生的 $N_2O$ 呈负相关[167]。Cheng 等[168]研究发现，好氧条件下，当土壤 pH 约低于 4.4 时反硝化作用主导 $N_2O$ 的产生，降低土壤 pH 能够显著增加反硝化作用对 $N_2O$ 的贡献，这可能与真菌反硝化有关[169-171]。曹文超等[129]在菜田土壤中研究发现，增加土壤 pH 会提高土壤反硝化速率，并促进 $N_2O$ 还原为 $N_2$，这与 Richardson 等[81]发现的结果相一致，即在碱性环境下，反硝化主要产物为 $N_2$，$N_2O$ 产生量较少。原因主要是低 pH 会干扰反硝化过程中 $N_2O$ 还原酶组装 (*nosZ* 基因的表达)，降低酶的活性[27, 172]，导致反硝化作用 $N_2O$ 排放量增加和 $N_2O/(N_2O + N_2)$ 比值增大。此外，土壤 pH 也会显著影响非生物学过程对 $N_2O$ 的贡献[66]。如羟胺 ($NH_2OH$) 在 pH 低于 5.95 条件下以较游离 $NH_2OH$ 更稳定的质子化形态 ($NH_3OH^+$) 存在，导致其有效性降低，进而减少了 $N_2O$ 排放。

### 2.6　温度

在全球气候变暖的大背景下，温度对 $N_2O$ 排放的影响十分重要。在高纬度地区，土壤温度是影响 $N_2O$ 排放的主要因子。如在我国三江平原地区不同施氮处理条件下土壤温度可解释 $N_2O$ 排放 16%～33% 的变异[173]。温度可直接和间接影响土壤 $N_2O$ 排放。直接调控主要表现在对土壤微生物生长和酶活性的影响，如降低土壤温度能够抑制土壤生物活性，进而减少 $N_2O$ 产生[174]。其间接调控主要是通过微生物活动改变土壤氧气和有效性碳的含量[175-176]。此外，氧气在土壤溶液中的溶解和释放也受温度的间接影响[177]。

温度影响土壤微生物反应活性，进而影响 $N_2O$ 排放。对于氨氧化微生物而言，与 20℃ 相比，AOB 和 AOA 的生长在 30℃ 和 40℃ 下均受到抑制[59]。Maag 和 Vinther[174]发现提高土壤温度可降低硝化作用对 $N_2O$ 的贡献，而增加反硝化过程 $N_2O$ 的产生量。Davidson 等[177]也发现，随土壤温度提高，反硝化作用产生的 $N_2O$ 排放量增加。这可能是因为升温后增加了微生物的呼吸作用，造成土壤微域氧气亏缺，为反硝化微生物活动创造了厌氧条件[178]，同时升温也增加了土壤反硝化活性[179]。许多研究表明，当土壤温度在 10～35℃ 时，每升高 10℃，土壤反硝化的活性可提高 1.5～3.0 倍[180-181]。类似地，Saleh-Lakha 等利用 *Pseudomonas mandelii* 进行液体培养发现，其在 10～30℃ 范围内反硝化作用活性随温度的上升而增加[182]。对于施用有机肥后的碱性土壤而言，提高土壤温度显著增加 $N_2O$ 排放，同时，与仅施用化学氮肥处理相比，有机肥施入增加了反硝化作用对 $N_2O$ 总排放量的贡献。这可能与提高温度后显著增加了反硝化 *nirS* 基因丰度有关[183]。然而，在酸性土壤中研究发现，30℃ 时施用有机肥处理的 *nirK* 基因丰度显著增加，而 *nirS* 在该温度下迅速降低[59]。

### 2.7　其他因素

土壤 $N_2O$ 排放随大气 $CO_2$ 浓度的增加而增加[184-185]。这可能与增加土壤反硝化作用对 $N_2O$ 的贡献有关。一方面，大气 $CO_2$ 浓度升高后减少了植物地上部 (如叶片) 的蒸腾作用，进而使土壤含水量增加；另一方面，高 $CO_2$ 浓度促进了植物地下部有效性碳的分配，如增加根系分泌物的释放等。二者均有益于反硝化作用的进行[184]。但也有研究认为 $N_2O$ 排放增加是由于硝化作用贡献增加的结果[186]。此外，$CO_2$ 浓度提高后，真菌的活动使草地土壤 $N_2O$ 排放潜势增加了 49%，同时，$CO_2$ 浓度升高显著增加真菌基因丰度和真菌与细菌拷贝数比例[187]。

土壤结构也是影响 $N_2O$ 排放的重要因素之一，其主要影响土壤通气性和气体扩散，进而影响 $N_2O$ 的产生[188-189]。在农田土壤中，机械化操作导致土壤压实可造成土壤 $N_2O$ 排放量增加[190]。土壤动物活动也会影响 $N_2O$ 排放[191]。如大样本分析表明土壤大型动物蚯蚓活动增加 $N_2O$ 排放量达 42%[192]。Zhu 等研究发现蚯蚓和弹尾虫二者显著增加土壤 $N_2O$ 排放量[193]。除蚯蚓外，在许多生态系统中，蚂蚁生活所形成的蚁丘土壤是 $CO_2$ 排放的“热点”区域[194-195]。近年已有研究表明，蚁丘土壤 $N_2O$ 产生量显著高于相邻自然土壤，这主要是由于蚂蚁活动增加了土壤碳氮和粘粒的含量[196]。此外，不同蚁群种类形成的蚁丘土壤对 $N_2O$ 和 $CO_2$ 排放也有差异[177]。

## 3　农田土壤水肥管理对 $N_2O$ 排放的综合影响

农田土壤 $N_2O$ 的产生和消耗本质上是土壤碳、氮、氧等因子综合作用的结果，而田间水、碳、氮的管理措施是影响这些环境因子变化的主要因素 (图 2)。综合田间土壤 $N_2O$ 通量监测结果，$N_2O$ 峰值排放阶

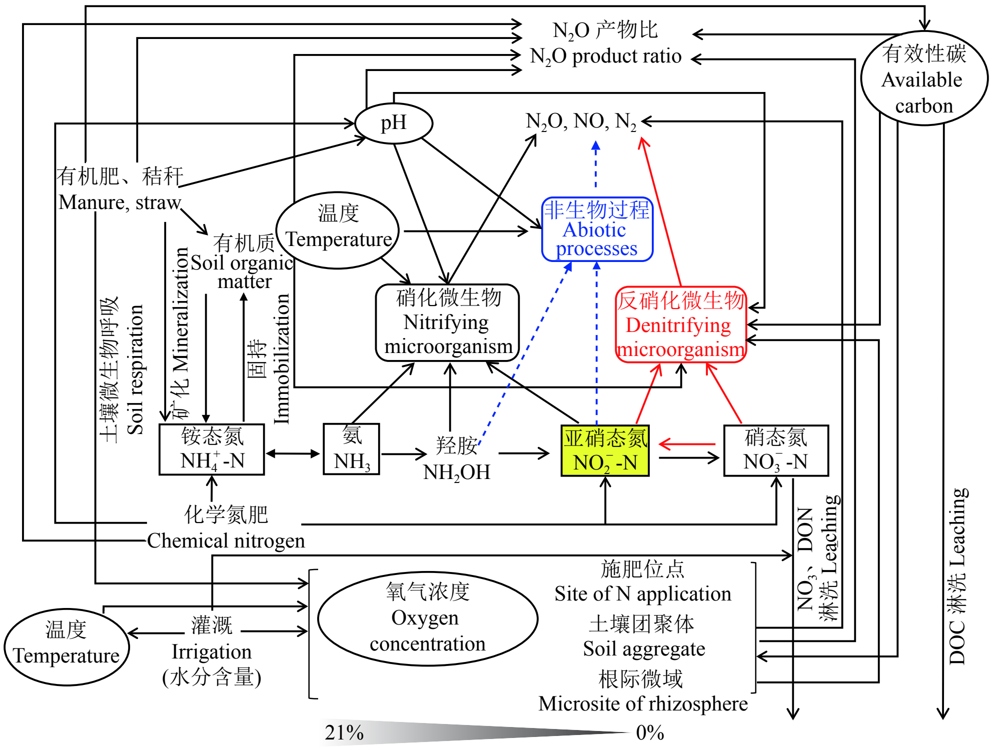

**图 2 农田土壤主要调控因子对 N$_2$O 排放综合影响的概念图**

**Fig. 2 Conceptual diagram of comprehensive influences of main regulatory factors on N$_2$O emissions in soils**

段是其排放的关键，该时期 N$_2$O 累积排放量约占全年农田排放量的 50% 左右[197-198]。

在农田土壤水肥管理中，有机肥施入和灌水是造成 N$_2$O 剧烈排放的主要诱因。以设施菜田土壤种植体系为例，有机肥极大地促进土壤中异养微生物的呼吸作用，显著降低土壤孔隙中氧气浓度；同时大量灌水降低了土壤相对气体扩散系数 (RD)，造成土壤出现低氧甚至厌氧的土体环境，尤其在土壤施肥位点、土壤团聚体及根际微域等区域中更易形成，这为反硝化微生物活动提供了厌氧条件。此外，土壤有机氮或有机肥矿化形成 NH$_4^+$后，硝化作用对土壤氧气的消耗也有贡献 ($NH_3 + 2O_2 \rightarrow NO_3^- + H_2O + H^+$)。有机肥施入土壤后为反硝化微生物提供了其所需的有效性碳，保障了反硝化作用过程发生所需的能源。值得注意的是，与大田土壤相比，设施菜田土壤硝态氮含量已不是反硝化过程发生的限制因子，因此，在其施用有机肥导致土壤有效性碳含量增加的短期时间内，将极大地促进以反硝化作用过程为主导途径的 N$_2$O 峰值排放。

在土壤含水量较低 (质量含水量 25% 左右) 条件下，铵态氮肥施入可增加硝化作用过程 N$_2$O 的排放，但其整体排放系数较低 (1% 左右)，且长期施用铵态氮肥会造成土壤酸化。土壤 pH 值的改变又将影响土壤微生物种群结构的变化。以氨氧化微生物细菌 (AOB) 和古菌 (AOA) 为例，由于它们在不同的土壤环境条件下占据不同的生态位[199-201]，其对土壤 pH 值的响应也不相同。一般认为，AOB 在中性、碱性和高氮素投入的条件下是驱动硝化过程进行的主体，而 AOA 在酸性的自然生态系统中更能发挥作用[202]。同时，对于反硝化微生物来说，低 pH 阻碍 N$_2$O 还原酶的形成[203]，导致 N$_2$O 产物比值增加。值得注意的是，非生物学过程在低 pH 土壤中对 N$_2$O 的贡献不可忽略，特别是在过量施肥导致土壤出现 NO$_2^-$累积时，非生物学过程对 N$_2$O 排放的贡献更加明显。此外，温度也是影响农田土壤 N$_2$O 排放的重要因子，在全球气候变暖的大背景下会受到更多关注。在农田土壤水肥管理措施中，硝化抑制剂、缓控释肥等高效施氮 (见 2.1 部分) 和间歇灌溉等技术的应用，有利于农田土壤 N$_2$O 的减排。

## 4 结论与展望

综上所述，虽然土壤 N$_2$O 产生途径有反硝化、硝化、硝化细菌的反硝化和硝化–反硝化耦合、真菌反硝化、化学反硝化，以及硝酸异化还原为铵等，但就一般农田土壤而言，生物反硝化过程或许仍然

是 $N_2O$ 产生的主要途径。支持这一观点的依据既表现在环境因子和管理措施对农田土壤 $N_2O$ 排放的影响机理方面，而且也有分子生物学的证据。而硝化细菌的反硝化、硝化–反硝化耦合过程等，实质上也是生物反硝化过程的一部分。硝化过程本身对农田土壤 $N_2O$ 排放的直接贡献较小，在许多情况下可能仅仅是背景排放。然而，由于硝化过程为生物反硝化和化学反硝化提供了底物，特别是中间产物 $NO_2^-$的释放，其对 $N_2O$ 排放具有很大的间接贡献。此外，真菌反硝化和化学反硝化在酸性土壤以及 DNRA 过程在高有机质和厌氧的土壤环境中，也对土壤 $N_2O$ 排放具有不可忽视的重要作用。合理管理有机肥和水分，辅之以硝化抑制剂的利用[204-205]，可在很大程度上减少农田土壤 $N_2O$ 排放。

目前人们对农田土壤 $N_2O$ 的产生和消耗方面的认识还面临诸多挑战。主要表现在：首先，农田土壤 $N_2O$ 排放主要来自于自然降水后，特别是施肥后立即灌水而产生的排放峰。在这一阶段的 $N_2O$ 产生和消耗过程进行深入研究，对农田土壤 $N_2O$ 减排措施的提出具有重要意义。其次，降低土壤反硝化过程 $N_2O/N_2$ 的产物比，是 $N_2O$ 减排的有效措施之一。为此，需要深入了解环境因子和调控措施对反硝化产物比的影响及其机理，以便为通过降低产物比实现 $N_2O$ 减排提供依据。再者，加强对 $N_2O$ 还原过程及其影响因素的了解，也具有重要意义。最后，在寻找与 $N_2O$ 排放有关的关键微生物方面人们遇到了很大挑战，这与反硝化微生物功能类群的广谱性和生理类型的多样性有密切关系，相信随着分子生物学和基因芯片技术的发展，这一问题能够逐步得到解决。与此同时，综合利用新技术方法，如平面光极技术[148]、Robot 自动培养技术[206]、氦环境培养—气体同步直接测定技术[207]、宏基因组测序技术等进一步探究土壤物理、化学和生物学因素对氮素转化过程、$N_2O$ 关键位点排放及关联微生物多样性的影响，构建氮素平衡和相关 $N_2O$ 排放模型，可进一步为 $N_2O$ 排放机制及相关影响因素提供理论依据。此外，通过对反硝化过程中 $N_2O/N_2$ 产物比产生规律及其影响因素的深入了解，将为利用田间 $N_2O$ 监测数据定量估算氮的反硝化损失提供一种新的途径。

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