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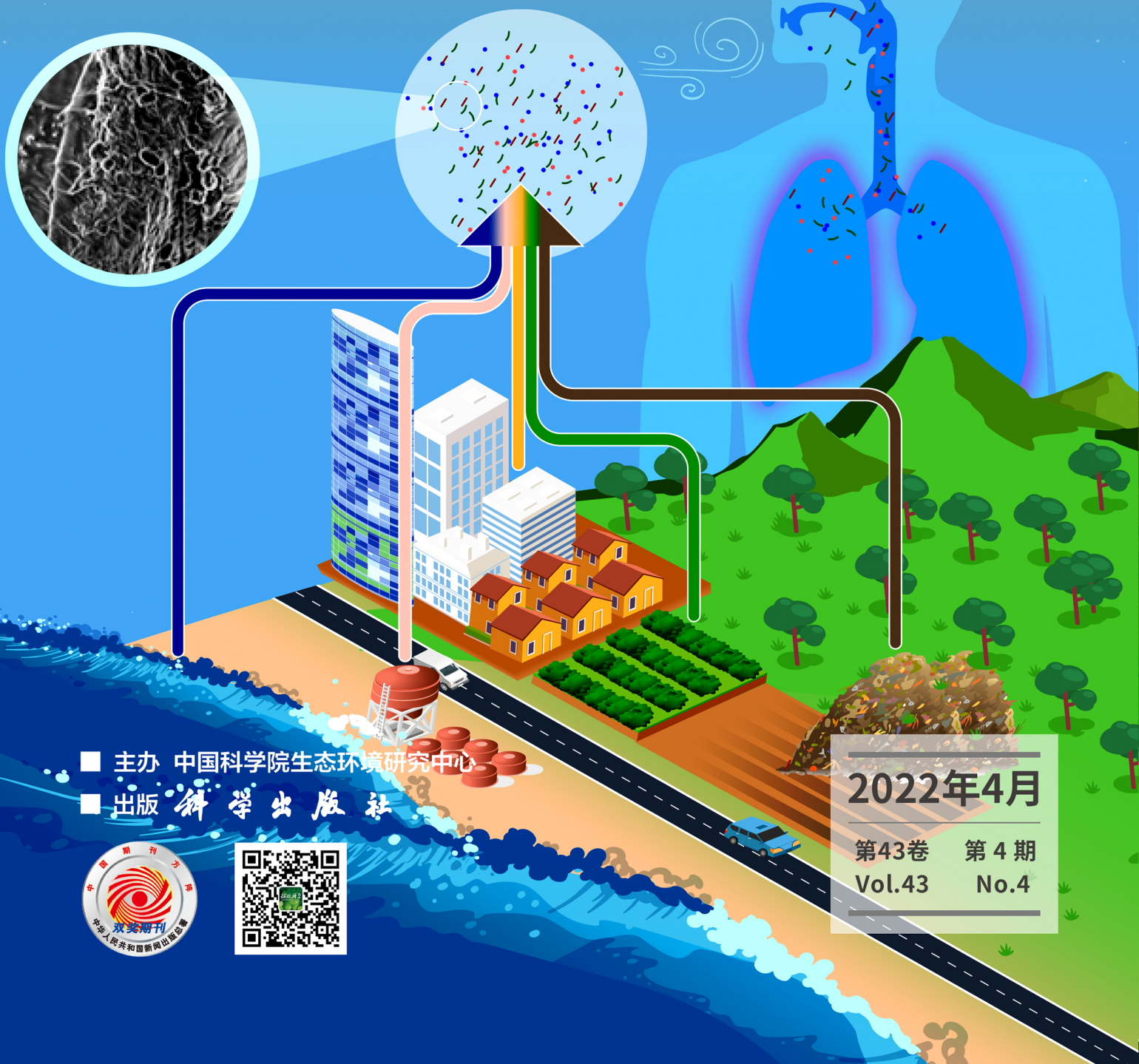
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HUANJING KEXUE

大连海岸带夏、秋季大气沉降(微)塑料的赋存特征及其表面生物膜特性

涂晨, 田媛, 刘颖, 张馨宁, 骆永明



■ 主办 中国科学院生态环境研究中心

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pH 对水稻土全程氨氧化细菌丰度和群落结构组成影响

马瑞, 赵永鹏, 王智慧, 蒋先军*

(西南大学资源环境学院, 重庆 400715)

摘要: 土壤 pH 被认为是影响 AOA 和 AOB 生态位分化的重要因子, 而最近发现的全程氨氧化细菌(Comammox *Nitrospira*)也在土壤中广泛分布, 推测 pH 可能也是影响全程氨氧化细菌生态位分化的重要因子. 选取酸性红壤和中性紫色土发育的水稻土, 采用荧光定量 PCR 及克隆测序技术, 分析了全程氨氧化细菌 Comammox *Nitrospira* clade A 和 clade B 的丰度和群落组成. 结果表明, 酸性水稻土的 Comammox clade A *amoA* 基因的丰度比中性水稻土高了 2 个数量级 ($P < 0.05$), 酸性水稻土的 Comammox clade B 的丰度也显著高于中性水稻土 ($P < 0.05$); 酸性水稻土中 Comammox clade A *amoA* 基因的丰度比 clade B 高 60 倍, 而中性水稻土中 Comammox clade A 和 clade B *amoA* 基因的丰度比约为 2, 这些结果表明土壤 pH 是影响 Comammox *Nitrospira* 丰度的重要因子. 克隆测序的结果发现中性水稻土中的 Comammox 均属于 clade A, 主要隶属于 *Nitrospira inopinata* 类群; 而未能检测到属于 clade B 的序列. 酸性水稻土中的 Comammox clade A 主要由 *Nitrospira inopinata* 和 *Nitrospira nitrosa* 类群组成, clade B 主要与土壤中发现的未培养的细菌克隆(FN395328)密切相关, 结果表明 Comammox *Nitrospira* 的群落结构也受 pH 的显著影响. 综上, pH 对土壤全程氨氧化细菌的丰度及群落结构组成有显著影响, 是影响其生态位分化的重要环境因子之一.

关键词: 土壤氮循环; 红壤; 紫色土; 单步硝化作用; 克隆测序

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Effect of pH on the Abundance and Community Structure of Comammox *Nitrospira* in Paddy Soils

MA Rui, ZHAO Yong-peng, WANG Zhi-hui, JIANG Xian-jun*

(College of Resources and Environment, Southwest University, Chongqing 400715, China)

Abstract: Soil pH is recognized as an important environmental factor in determining the niche differentiation for ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) communities. Species of comammox, a single microorganism capable of the complete oxidation of ammonia to nitrate, have recently been discovered. Metagenomic analysis and quantitative PCR showed that Comammox *Nitrospira* were found in a wide range of environments, including soil. Comammox bacteria are differentiated into one of two clades (A and B) based on the phylogeny of genes encoding the α -subunit of ammonia monooxygenase genes (*amoA*). However, all discovered Comammox *Nitrospira* strains have been isolated and cultured in aquatic ecosystems, including *N. inopinata*, *N. nitrosa*, and *N. nitrificans*, all belonging to clade A. Currently, Comammox *Nitrospira* has not been obtained from soil environments, which limits our understanding of soil Comammox *Nitrospira*. Here we hypothesized that, as AOA and AOB, the ecological site of Comammox *Nitrospira* may also be affected by pH. Therefore, soil samples with differing pH were collected, and the abundances and community structures were studied to elucidate the mechanism of pH effect on the distributions and community compositions of Comammox *Nitrospira* in soil. Quantitative PCR of comammox clade A and clade B *amoA* genes in DNA extracts were performed using QuantStudio™6 Flex Real-Time PCR Systems. The community compositions for Comammox *Nitrospira* were studied by the cloning libraries of *amoA* genes method. The results showed that the abundance of Comammox clade A *amoA* gene in acidic paddy soil was two orders of magnitude higher than that in neutral paddy soil ($P < 0.05$), and the abundance of Comammox clade B in acidic paddy soil was significantly higher than that in neutral paddy soil ($P < 0.05$); the abundance of Comammox clade A *amoA* gene in acidic paddy soil was 60 times higher than that of clade B, whereas the abundance ratio of Comammox clade A and clade B *amoA* genes in neutral paddy soil was about two times higher. These results indicated that soil pH significantly affected the abundance of Comammox *Nitrospira*. The results of cloning and sequencing showed that the Comammox in neutral paddy soil was mainly *N. inopinata*, which belonged to clade A; no strain belonging to clade B was annotated. Comammox clade A in acidic paddy soil was mainly composed of *N. inopinata* and *N. nitrosa*, and clade B was mainly uncultured bacterium (FN395328). The results indicated that soil pH was an important factor in shaping Comammox *Nitrospira* community structure. Comammox *Nitrospira* were detected in all soil samples, and Comammox clade A had a preference for acidic environments. It seemed that species from *N. nitrosa* possessed the ecological niche of low pH environments, whereas species from *N. inopinata* preferred to live in neutral environments. In conclusion, pH had a significant effect on the abundance and community structure of Comammox *Nitrospira*, which was one of the important factors affecting the niche differentiation of Comammox *Nitrospira*.

Key words: soil nitrogen cycle; red soil; purple soil; one-step nitrification; clone sequencing

硝化作用是氮素循环的重要过程^[1,2], 也是稻田土壤氮素转化的关键环节^[3]. 硝化作用的底物(铵态氮)和最终产物(硝态氮)都是微生物和农作物生长的重要来源^[4], 但是硝态氮又可以通过反硝化作用或淋洗而损失^[5,6]. 因此, 硝化作用的研究对于提高土壤氮肥利用率和减少氮素损失具有重要的意义. 传统上, 硝化作用是由氨氧化[由微生物 ammonia-oxidizing archaea (AOA) 和 ammonia-

oxidizing bacteria (AOB) 驱动] 和亚硝酸盐氧化(细菌 nitrite-oxidizing bacteria, NOB) 合作完成的两步催化过程^[7]. 然而, 在 2015 年新发现的完全氨氧化微生物——Comammox *Nitrospira* 能够通过亚硝酸直

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作者简介: 马瑞(1995~), 女, 硕士研究生, 主要研究方向为土壤微生物生态, E-mail: 1135837380@qq.com

* 通信作者, E-mail: jiangxj@swu.edu.cn

接将氨氧化为硝酸盐^[8]. 已经发现了 *Comammox Nitrospira* 属于硝化螺菌属谱系 II (*Nitrospira* Linage II), 并且有一套完整的催化硝化反应的酶, 具有氨单加氧酶(ammonia monooxygenase, AMO)、羟胺脱氢酶(hydroxylamine dehydrogenase, HAO)和亚硝酸盐氧化还原酶(nitrite oxidoreductase, NXR)^[8,9], 这表明 *Comammox Nitrospira* 既能行使如 AOA 和 AOB 的功能, 也能行使如 NOB 的功能, 这也改变了对硝化作用过程的认识^[8]. 基于 *Comammox Nitrospira amoA* 的系统发育分析, *Comammox Nitrospira* 可以分为两个进化枝, 即 *Comammox Nitrospira* 进化枝 A 和 B (clade A 和 clade B)^[8].

Comammox Nitrospira 在水产养殖系统、稻田土壤、淡水和废水处理厂等广泛分布^[10~14], *Comammox Nitrospira* 菌株都是在水生生态系统分离培养的, 包括 *Nitrospira inopinata*、*Nitrospira nitrosa* 和 *Nitrospira nitrificans*, 均属于 clade A^[9]. 目前从土壤环境中尚未获得纯菌, 这限制了人们对土壤 *Comammox Nitrospira* 的了解, 但通过宏基因组分析和定量 PCR 发现 *Comammox Nitrospira* 在土壤中分布广泛^[15], 尤其在水稻土中检测到了较高丰度的 *Comammox Nitrospira*, 甚至高于 AOB^[10]. 因此有必要对 *Comammox Nitrospira* 在水稻土中的分布进行深入研究.

土壤 pH 是影响 AOA 和 AOB 生态位分化的重要因子^[16~20], 例如专性嗜酸性 *Nitrosotalea devanattera* 的培养证明 AOA 在低 pH 土壤中生长^[21], 酸性森林土壤中高硝化作用的发生与 AOA 密切相关^[22], 而在高 pH 的农业土壤或稻田土壤中, 硝化作用是由 AOB 而非 AOA 驱动的^[23]. 此外, NOB 的群落结构组成也受土壤 pH 的影响^[24]. 基于以上分析, 本文推测土壤 pH 可能也是导致稻田土壤中 *Comammox Nitrospira* 的丰度和群落结构组成变化的主要因子. 因此, 本文选取红壤发育的水稻土(酸性水稻土)和紫色土发育的水稻土(中性水稻土)为研究对象, 利用荧光定量 PCR 和克隆测序技术分析两种不同 pH 的水稻土中 *Comammox* clade A 和 clade B *amoA* 基因的丰度和群落结构组成, 以期为进一步了解土壤全程氨氧化细菌的分布提供依据.

1 材料与方法

1.1 供试土壤

酸性红壤发育的水稻土采自湖南省农业科学院(113°04'47"E, 28°11'53"N), 该区域为亚热带季风气候, 年均气温 18.2℃, 年均降雨量 1 339.2 mm, 供

试土壤类型为红壤, 成土母质为第四纪发育红色黏土. 中性紫色土发育的水稻土采自重庆市北碚区西南大学国家紫色土土壤肥力与肥料效益检测基地(106°26'33"E, 30°26'36"N), 该区域为亚热带季风气候, 年均气温 18.2℃, 年均降雨量 1 105 mm. 供试土壤为中性紫色土, 由侏罗系沙溪庙组紫色泥岩风化的残积、坡积物发育而成的. 酸性水稻土的基本理化性质: pH 为 6.2, ω (有机质)为 13.60 g·kg⁻¹, ω (全氮)为 1.70 g·kg⁻¹, ω (NH₄⁺-N)为 6.10 mg·kg⁻¹, ω (NO₃⁻-N)为 13.60 mg·kg⁻¹. 中性水稻土的基本理化性质: pH 为 7.6, ω (有机质)为 17.55 g·kg⁻¹, ω (全氮)为 1.76 g·kg⁻¹, ω (NH₄⁺-N)为 17.77 mg·kg⁻¹, ω (NO₃⁻-N)为 13.86 mg·kg⁻¹.

1.2 土壤取样和准备

土壤样品采集于 2019 年 5 月, 使用直径为 6.5 cm 的土钻按 5 点取样法从 0~20 cm 的深度采集了土壤样品. 剔除土壤中可见植物枯枝落叶及土壤动物等杂物, 混匀. 将鲜土分成 2 份, 第 1 份储存在 -20℃ 冰箱中用于提取土壤 DNA 以及荧光定量 PCR 分析; 第 2 份是将土壤样品风干后研磨并过 2 mm 筛子, 用来测定土壤的基本理化性质, 每个土壤样品 3 次重复.

1.3 土壤基本理化性质的测定

使用 1:2.5 的土壤/蒸馏水悬浮液在 pH 计上测量土壤的 pH 值. 土壤有机质用重铬酸钾氧化法测量^[25]. 凯氏定氮法^[26]测定土壤总氮. 将 5 g 新鲜土壤悬浮在 50 mL 2 mol·L⁻¹ KCl 中来提取 NH₄⁺-N 和 NO₃⁻-N, 并使用紫外分光光度计进行浓度比色测定^[27].

1.4 提取土壤 DNA

按照 Power Soil DNA Isolation Kit (MoBio Laboratories, 美国)试剂盒的说明方法从 0.25 g 土壤样品中提取土壤总 DNA. 简而言之, 将土壤样品加到 PowerBead 管中, 使用 MO BIO 涡旋仪器以最大速度涡旋 10 min 去裂解微生物细胞, 然后洗涤 DNA 并从提供的二氧化硅旋转滤膜上洗脱以获得提取物. 在开始后续实验之前, 分别通过 NanoDrop 2000 分光光度法和 1% 琼脂糖凝胶电泳法检测土壤 DNA 的纯度和完整性.

1.5 实时荧光定量 PCR 及克隆测序

使用实时荧光定量 PCR 仪 (Quant Studio™ 6 Flex) 测定全程氨氧化细菌分支 A (clade A) 和分支 B (clade B) *amoA* 基因丰度. *Comammox* clade A 和 clade B *amoA* 功能基因的引物序列如 Pjevac 等^[10]所述. 实时荧光定量 PCR 的总反应体系为 20 μL, 具体为 DNA 模板 1 μL, 上引物、下引物以及 ROX

Reference DyeII (50 ×) 各 0.4 μL, Taq DNA 聚合酶 10 μL, 无菌水 7.8 μL, qPCR 反应扩增条件与笔者先前的描述相同^[15], 每个样品进行 3 个生物学重复. 本研究 qPCR 分析的扩增效率为 96% ~ 105%, R^2 值在 0.996 ~ 0.999 之间. 全程氨氧化细菌 clade A 和 clade B *amoA* 基因克隆测序由上海凌恩生物科技有限公司完成, 每个样品挑选 50 个阳性克隆.

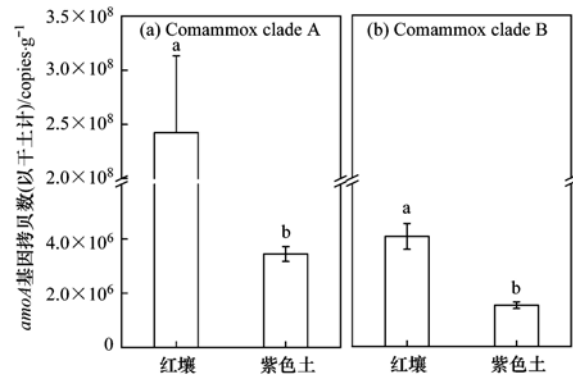
1.6 数据分析

利用 SPSS 21 软件对 Comammox clade A 和 clade B *amoA* 基因拷贝数进行统计分析. 所得 OTU 序列在 NCBI 的 GenBank 数据库进行 Blast, 获得相近的同源基因序列以及 Comammox clade A 纯菌序列; 然后使用 MEGA7 软件进行分析, 利用 NJ 法构建系统发育树.

2 结果与讨论

荧光定量 PCR 分析比较酸性水稻土和中性水稻土中 Comammox clade A 和 clade B *amoA* 基因的丰度, 研究结果显示酸性水稻土和中性水稻土 Comammox clade A *amoA* 基因的丰度(以土计)分别为 $2.48 \times 10^8 \text{ copies} \cdot \text{g}^{-1}$ 和 $3.45 \times 10^6 \text{ copies} \cdot \text{g}^{-1}$, 酸性水稻土 Comammox clade A *amoA* 基因的丰度比中性水稻土 Comammox clade A *amoA* 基因丰度高了 2 个数量级, 差异显著 [$P < 0.05$, 图 1(a)]. 酸性水稻土的 Comammox clade B *amoA* 基因的丰度(以土计)为 $4.06 \times 10^6 \text{ copies} \cdot \text{g}^{-1}$, 其丰度显著高于中性水稻土的 Comammox clade B *amoA* 基因的丰度 [$1.52 \times 10^6 \text{ copies} \cdot \text{g}^{-1}$, $P < 0.05$, 图 1(b)]. 进一步分析发现酸性水稻土中 Comammox clade A *amoA* 基因的丰度比 clade B 高 60 倍, 而中性水稻土中 Comammox clade A 和 clade B *amoA* 基因的丰度比约为 2. Hu 等^[14]报道了 300 种森林土壤样品 (pH 4.0 ~ 8.6) 中 Comammox clade A 和 clade B 的丰度, 发现 Comammox clade A 是酸性土壤 (pH < 6.0) 中最丰富的硝化细菌, 其次是 Comammox clade B. 以上研究结果说明土壤 pH 会影响水稻土中的 Comammox *Nitrospira* 不同类群的丰度.

笔者前期的研究结果发现, 在中性水稻土中 Comammox 的丰度 ($1.2 \times 10^7 \sim 7.2 \times 10^8 \text{ copies} \cdot \text{g}^{-1}$) 相较于 AOA 和 AOB 达到最高, 而且水稻土中的 Comammox 主要以 clade A 为主^[15]. Wang 等^[28]的研究利用 qPCR 法对 Comammox *amoA* 基因进行分析发现, 农业土壤中的 Comammox 的丰度范围为 $(6.45 \pm 4.31) \times 10^6 \sim (5.37 \pm 0.44) \times 10^7 \text{ copies} \cdot \text{g}^{-1}$, 其丰度低于 AOA 和 AOB, 夏季的 Comammox 对氨氧化的贡献为 3.9% ~ 19.2%, 冬季



误差线表示标准误差, $n = 3$; 不同小写字母

表示 $P < 0.05$ 水平上差异显著

图 1 不同土壤类型的水稻土的 Comammox clade A 和 clade B *amoA* 基因丰度

Fig. 1 Comammox clade A and clade B *amoA* gene abundances under different soil types

为 0.8% ~ 22.1% 其数值明显低于 AOA 和 AOB 对氨氧化的贡献 (77.8% ~ 99.2%), 这表明 Comammox 在农业土壤中广泛分布, 并且 Comammox *Nitrospira* 的丰度和生态位可能受季节的影响^[29, 30]. Li 等^[31]的研究调查了澳大利亚东部 130 种森林土壤中 Comammox *Nitrospira* 的丰度, 结果表明 AOA 的平均丰度 [$(8.97 \times 10^6 \pm 1.31 \times 10^6) \text{ copies} \cdot \text{g}^{-1}$] 显著高于 Comammox clade A [$(3.73 \times 10^6 \pm 9.62 \times 10^5) \text{ copies} \cdot \text{g}^{-1}$] 和 AOB [$(3.58 \times 10^6 \pm 1.14 \times 10^6) \text{ copies} \cdot \text{g}^{-1}$], 并且 AOA 是中等酸性土壤 (pH 5 ~ 7) 中最丰富的硝化细菌, 其次是 Comammox clade A 和 AOB, 此外通过稳定性同位素核酸探针技术研究发现普遍存在的 Comammox clade A 可能有助于森林土壤中的自养碳固定, 认为 Comammox clade A 在森林土壤中普遍存在, 可能对硝化作用有贡献, 这表明 Comammox *Nitrospira* 对较低土壤 pH 环境可能表现出较高的耐受性^[32].

同时克隆测序结果表明 Comammox 群落结构组成在酸性水稻土和中性水稻土中不完全相同 (图 2). 酸性水稻土的 Comammox clade A 系统发育分析的结果得到 12 个 OTU (图 2), 其中 OTU1 占比最高, 为 40%, 与 OTU12, OTU14、OTU8、OTU3 和 OTU18 占比的总和为 61%, 这些 OTU 均属于 *Nitrospira inopinata* cluster, 其余的 6 个 OTU 均属于 *Nitrospira nitrosa* cluster. 这表明酸性水稻土中的 Comammox 主要是由属于 clade A 的 *Nitrospira inopinata* 和 *Nitrospira nitrosa* cluster 构成的. 中性水稻土的 Comammox clade A 系统发育分析的结果得到 7 个 OTU (图 2), 并且全部落在 *Nitrospira inopinata* cluster 中, 其中 OTU4 的占比最高 (30%), 其次是 OTU1 (28%), OTU5 (26%). 中性水稻土中

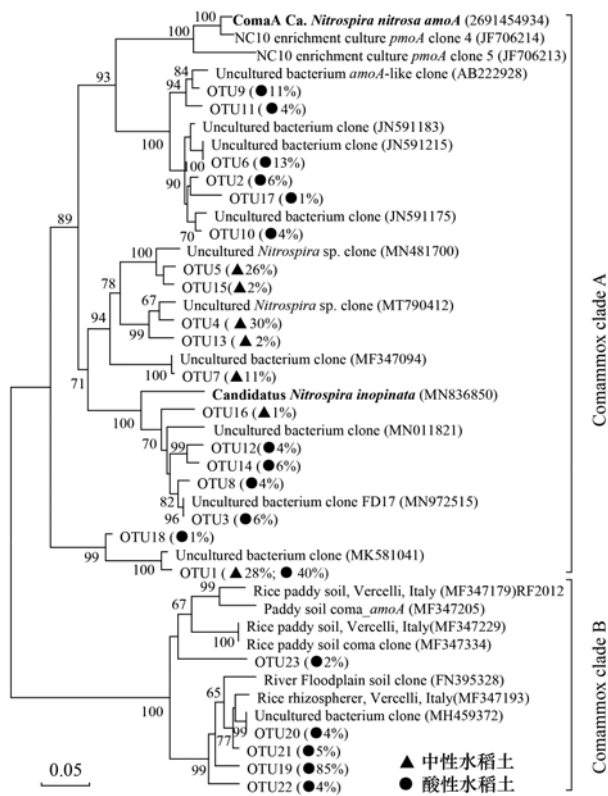


图2 不同土壤类型的水稻土的 Comammox *Nitrospira* 的群落结构组成

Fig. 2 Community compositions of Comammox *Nitrospira* under different soil types

未检测到 *Nitrospira nitrosa* cluster. 只检测到了 *Nitrospira inopinata* cluster. 笔者前期的研究利用宏基因组技术分析不同 pH 紫色土发育的旱地土壤的硝化微生物丰度和群落^[33], 结果发现 *Nitrospira inopinata* 在中性紫色土发育的旱地土壤的相对丰度达到最高, Lu 等^[29]的研究发现 *Nitrospira inopinata* 的丰度在 pH 7.53~9.17 之间与 pH 呈显著正相关关系, 这表明 *Nitrospira inopinata* 更适应在中性环境生长. 克隆测序结果发现在酸性水稻土中检测到了 *Nitrospira nitrosa*; 然而另有研究发现 *Nitrospira nitrosa* 在中性或者碱性的活性污泥样品中检测到较高的丰度^[34]. 因此, *Nitrospira nitrosa* 类群可能同时具有高和低 pH 的生态位. Comammox clade B 系统发育分析如图 2 所示, 对酸性水稻土的测序结果分析得到 5 个 OTU, 其中 OTU19 占比最高, 为 85%, 与荷兰的河漫滩土壤中获得 River Floodplain soil clone (FN395328) 序列有密切的亲缘关系^[35]. Wang 等^[36]的研究也发现我国农业土壤中 Comammox *Nitrospira* 广泛分布, 其中 Comammox clade B 的主要序列与 River Floodplain soil clone (FN395328) 有密切的亲缘关系. 本研究中酸性水稻土中有 2% 的 Comammox *Nitrospira* 群落与 Rice paddy soil, Vercelli, Italy (MF347179) 有密切亲缘关系, 该菌株

曾在意大利水稻土中发现^[8]. 此外, 在本研究发现中性水稻土中未检测到 Comammox clade B. 以上结果说明, 土壤 pH 是影响全程氨氧化细菌群落结构及生态位分化的重要因子. 此外, 在酸性水稻土中检测到两种 Comammox, 包括 *Nitrospira inopinata* 和 *Nitrospira nitrosa*, 中性水稻土中只检测到了 *Nitrospira inopinata*, 说明全程氨氧化细菌与 AOB 相似, 种群比较单一, 意味着这些物种可能是推动土壤氨氧化过程的核心微生物.

3 结论

在酸性红壤和中性紫色土发育的水稻土中均检测到了高丰度的全程氨氧化细菌 (Comammox), 这表明全程氨氧化细菌在水稻土中广泛分布. 酸性水稻土的 Comammox clade A 和 clade B *amoA* 的丰度均显著高于中性水稻土, 这意味着土壤 pH 会影响 Comammox 的丰度, 而且 clade A 比 clade B 更加适应酸性环境. 中性水稻土中的 Comammox 主要隶属于 *Nitrospira inopinata* 类群, 而 *Nitrospira nitrosa* 则可能具有低 pH 的生态位. pH 对土壤全程氨氧化细菌的丰度及群落结构组成有显著影响, 是影响其生态位分化的重要环境因子之一.

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