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微生物驱动土壤矿物结合态有机碳的形成

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摘要 矿物结合态有机碳(mineral-associated organic carbon, MAOC)是土壤中重要的稳定态有机碳, 其含量和动态决定着土壤碳库组成和容量, 显著影响全球气候格局. 植物和微生物是MAOC形成的两个主要途径, 其来源和贡献一直存在很大的争议, 特别是在不同生态系统中, 植物和微生物对MAOC形成的相对贡献和控制因素可能存在较大的不确定性, 对这些问题认知的不足阻碍了土壤可持续管理战略的实施. 本研究选取中国区域尺度的旱地(n=24)、水田(n=19)和林地(n=21)表层土壤(0~20 cm), 基于矿物结合态有机质(mineral-associated organic matter, MAOM)中的氨基糖和木质素酚的分析, 揭示了MAOC中微生物和植物源的贡献及其驱动因子. 结果显示, 在旱地、水田和林地土壤MAOC中, 植物来源碳分别贡献了44.5%、50.1%和49.3%, 微生物残体碳分别贡献了44.2%、40.4%和41.0%, 其中真菌氨基葡萄糖/细菌胞壁酸比相似(10.6、10.0和11.5, P>0.05). 这些结果表明, 微生物残体碳在MAOC中具有相似的稳定性, 矿物结合改变了土壤有机碳(soil organic carbon, SOC)的组成, 可以在很大程度上抵抗土地利用变化对SOC分解的影响. 在所有生态系统中, MAOC的形成主要由微生物活动调控. 与旱地生态系统相比, 水田的环境胁迫导致微生物分解能力受到限制, 林地中较高的植物输入量因微生物分解能力有限使植物残留相对富集, 土壤稳定碳库以植物源碳为主. 高黏粉粒含量和高年平均温度(mean annual temperature, MAT)有利于MAOC中植物源碳的相对富集, 而低土壤pH和低MAT使微生物源碳的贡献增加. 研究结果对于调整和完善农业土壤管理策略, 增加土壤碳储量及减少碳排放, 实现土壤碳中和目标具有重要意义.

关键词 矿物结合态有机碳, 微生物残体碳, 植物源碳, 氨基糖, 木质素酚

土壤有机碳(soil organic carbon, SOC)是最大的陆地碳库, 1 m深度的土壤约含1500 Pg C, 对全球碳循环有着至关重要的作用[1,2]. 在全球矿质土壤中, 约有65%的有机碳与具有较大比表面积和较高活性的土壤矿物结合, 形成矿物结合态有机碳(mineral-associated organic carbon, MAOC)[3,4]. 这些矿物结合态有机碳相对稳定, 不易分解, 在土壤中存留时间长, 它们推动土壤团聚体的形成, 调控土壤中的一系列物理、化学和生物学过程, 决定着陆地和海洋生态系统中有机碳的长期储存[5,6]. 最新的研究表明, 全球土壤MAOC的总量约为840~1540 Pg C, 占SOC的34%~51%[4]. MAOC作为大气CO_2的重要源和汇, 在影响和缓解全球气候变化中扮演着重要的角色[7]. 了解MAOC的组成及形成过程已成为理解土壤碳动态和减缓气候变化的关键[8,9].

MAOC的主要成分为多糖、脂质和蛋白质, 其中多糖和脂质分别占MAOC的18%~52%和3%~45%, 酰

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胺态含氮化合物(蛋白质、肽)占10%~40%，木质素在10%以下[10,11]. 除木质素完全来源于植物外，其他化合物可能来源于植物或微生物[12]. 前者是完整或部分氧化的植物化合物直接掺入MAOC(植物来源的MAOC)，后者是植物来源的碳经微生物同化和生物合成，微生物产物掺入MAOC(微生物来源的MAOC)[13,14]. 基于氨基糖和木质素等生物标志物[15,16]，对土壤有机碳来源的研究表明，全球不同生态系统土壤中微生物残体碳占SOC的比例为30%~80%[9,17,18]. 近年来，微生物对稳定土壤有机碳库的贡献得到了广泛的认可，越来越多的学者认为微生物来源的有机碳可能主导MAOC的形成[19~21]. 然而，最近的研究显示，植物来源的有机碳占SOC的20%~70%，其对SOC的直接贡献可能与微生物不相上下[9]. 尤其是在MAOC中，脂类、木质素和糖类等植物源生物分子可能占有相当的份额，并在稳定有机碳的形成和积累过程中发挥重要作用[18,22]，然而这方面的工作还很欠缺.

综上所述，土壤矿物结合态等稳定有机碳的形成与来源还有很大的争议，特别是基于大尺度不同生态系统的系统研究还很少，诸多问题有待厘清. 为此，我们采集了中国东部地区从南到北跨度约4200 km的旱地、水田和林地土壤共64个，测定了MAOC中氨基糖和木质素的含量，在大尺度上系统探讨了不同生态系统土壤MAOC中植物和微生物来源有机碳的相对贡献，通过相关性分析、随机森林回归(random forest regression, RF)、方差分解分析(variance partition analysis, VPA)和结构方程模型(structural equation modeling, SEM)等，探讨了调控MAOC形成积累的环境因素和土壤特性及可能的机制. 我们提出以下科学假设: 植物对MAOC的贡献比微生物更大，尤其是植物生物量输入较多的森林土壤.

1 实验

(ⅰ) 土壤采集. 在中国东部的25个地区(18.7°~47.5°N，105.5°~126.9°E)共采集了64个土壤的表层(0~20 cm)样品，包括19个水田、24个旱地和21个林地样品. 年平均温度(mean annual temperature, MAT)为2.2~24.6°C，年平均降雨量(mean annual precipitation, MAP)为412~1691 mm(https://www.worldclim.org). 每个采样点随机选取3个1 m×1 m的样方，用5 cm的土钻从每个样方0~20 cm深度随机采集3个土芯. 然后将3个土芯混合，以等比例均质混匀为一个复合样品. 所有的新鲜土壤样品在采集后立即置于冰盒中保存并及时运回实验室，一部分保存于–20°C冰箱中备用. 另一部分土样风干，去除可见的石子、植物组织和有机碎片后，通过2 mm筛进行后续测定.

(ⅱ) 土壤理化性质测定. 土壤pH用pH计(FiveEasy Plus, Mettler-Toledo, 瑞士)测定(土水比为1:2.5). 土壤颗粒组成和比表面积(specific surface area, SSA)采用激光粒度仪(Mastersizer 3000, Malvern Co., 英国)测定. 土壤微生物生物量碳(microbial biomass C, MBC)利用氯仿熏蒸法提取，碳/氮元素分析仪(Vario PYRO cube, Elementar, Hanau, 德国)测定.

土壤活性金属氧化物采用DCB(dithionite-citrate-bicarbonate)方法提取[23]，利用电感耦合等离子体发射光谱(inductively coupled plasma-optical emission spectrometry, ICP-OES, VISTA-MPX, Varian Co., 美国)测定活性铁(Fe_d)、铝(Al_d)、锰(Mn_d)、硅(Si_d)、钾(K_d)、钙(Ca_d)和镁(Mg_d). 土壤层状硅酸盐矿物组成通过X射线衍射仪分析(Bruker D8 Advance, Cu Kα，管压40 kV，管流40 mA，扫描速度10 D/min，扫描范围3°~35°).

(ⅲ) 土壤密度和粒径分级. 通过密度和粒径分离方法获取土壤矿物结合态有机质(mineral-associated organic matter, MAOM). 称取过2 mm筛的自然风干的土壤样品10.00 g于100 mL离心管中，加入30 mL密度为1.60 g/cm^{3}的NaI溶液[24]，220 r/min振荡3 h，水平静置24 h后，分离上层游离态颗粒有机质(free particulate organic matter, fPOM). 对剩余的沉淀液进行超声处理，能量输入为175 J/mL. 4000 g离心10 min后，分离上层悬浮的闭蓄态颗粒有机质(occluded particulate organic matter, oPOM). 剩余残渣用蒸馏水洗涤至溶液的电导率小于50 μS，以去除过量的盐[25]. 最后，对残渣进行湿筛，得到矿物结合态有机质(MAOM, <53 μm)，40°C烘干，称重. 利用元素分析仪(Vario PYRO cube, Elementar, Hanau, 德国)测定MAOM中碳和氮的含量[26].

(ⅳ) 木质素酚分析. 采用碱性氧化铜氧化水解-气相色谱法测定木质素的含量[27]. 称取0.5 g土壤样品于20 mL聚四氟乙烯反应罐内，加入0.1 g CuO粉末、0.1 g六水合硫酸亚铁铵和15 mL 2 mol/L的NaOH溶液，170°C加热2.5 h. 冷却后加入0.4 mL内标溶液，离心，调节pH至1，静置后再次离心. 利用乙酸乙酯萃取上清液中有机相，45°C旋转蒸发至小于2 mL，N_2吹干. 加入200 μL吡啶溶解，然后加入50 μL三氟乙酰胺(BSTFA)，70°C加热30 min进行衍生化，生成三甲基硅基(TMS)衍

生物. GC 2010 Plus气相色谱仪(Shimadzu Co., 日本)测定衍生后的样品. MAOC中植物来源有机碳的贡献P根据式(1)计算[28]:

$$P = \frac{\left(\frac{V}{33\%} + \frac{S}{90\%} + C\right)}{8\% \times MAOC} \times 100\%, \quad (1)$$

式中, V为香草基类(vanillyl)在MAOC中的含量(mg kg^{-1} MAOC); S为丁香基类(syringyl)在MAOC中的含量(mg kg^{-1} MAOC); C为肉桂基类(cinnamyl)在MAOC中的含量(mg kg^{-1} MAOC).

(v) 氨基糖分析. 利用盐酸水解-气相色谱法测定氨基糖含量. 称取含0.3 mg N的土壤样品置于水解瓶中, 加入10 mL 6 mol/L的HCl, 充满N_2后在105°C下水解8 h. 加入100 μL的肌醇(内标1), 过滤后旋转蒸发至干燥, 残渣溶解后用0.2 mol/L KOH调节pH至6.6~6.8, 离心去除沉淀. 上清液干燥后用3 mL无水甲醇溶解, 再次离心, 上清液用N_2吹干. 干燥物溶于1 mL超纯水中, 加入100 μL *N*-甲基氨基葡萄糖(内标2), 再次冷冻干燥. 加入衍生试剂, 75~80°C条件下加热30~40 min. 加入1 mL乙酸酐, 再次加热20~30 min. 冷却后加入1.5 mL的二氯甲烷, 振荡后加入1 mL 1 mol/L的HCl. 以同样的方式用去离子水提取有机相3~5次, 用N_2吹干. 溶于乙酸乙酯:正己烷混合液(v:v=1:1). 使用GC 2010 Plus气相色谱仪测定4种氨基糖, 即氨基葡萄糖(glucosamine, GlcN)、氨基半乳糖(galactosamine, GalN)、甘露糖胺(mannosamine, ManN)和胞壁酸(muramic acid, MurA)的总和为总氨基糖含量. 使用式(2)和(3)分别计算真菌和细菌残体碳的含量(mg g^{-1} soil):

$$\text{细菌残体碳} = \text{MurA} \times 45, \quad (2)$$

$$\text{真菌残体碳} = (\text{GlcN} / 179.17 - 2 \times \text{MurA} / 251.23) \times 179.17 \times 9, \quad (3)$$

其中, 179.17和251.23分别是GlcN和MurA的分子量; 45是从MurA到细菌残体碳的转换因子, 9是GlcN到真菌残体碳的转化因子[29,30].

(vi) 数据分析. 首先利用Shapiro-Wilk检验数据是否满足正态分布. 对于正态分布的数据采用单因素方差分析(analysis of variance, ANOVA)Duncan方法, 对于非正态分布的数据利用Kruskal-Wallis检验, 以比较不同生态系统中的土壤性质、氨基糖和木质素酚含量的差异. 采用Pearson相关性分析评估气候和土壤性质与氨基糖以及木质素酚含量之间的相关性, 对不满足正态分布的数据进行对数处理以增强数据的正态性. 使用SPSS 26.0进行统计分析, 使用Origin 2021进行绘图. 使用R 4.2.2中的"vegan"包和"randomForest"包完成方差分解分析和随机森林回归(random forest regression, RF), 利用SPSSPRO实现结构方程模型. 为了优化模型和减少变量, 在进行结构方程模型分析前, 分组对变量进行主成分分析(principal component analysis, PCA).

2 结果

2.1 MAOM中木质素酚和氨基糖的分布

不同生态系统土壤矿物结合态有机碳中木质素酚的含量为15.1~55.3 mg g^{-1} MAOC(图1), 水田和林地土壤大致相当, 旱地土壤低9.9%~11.2%. 旱地和水田土壤MAOM中的木质素主要由V型酚(24.7%~60.3%)和S型酚(23.8%~53.2%)构成, 而林地土壤以V型酚为主(31.0%~70.8%), 其次是S(13.4%~44.5%)和C型酚(11.0%~34.6%).

通常采用V型和S型酚的酸醛比((Ad/Al)v和(Ad/Al)s)来评估木质素的降解特征, 其比值越大, 表示木质素的氧化程度越高[31]. 相比于林地, 水田土壤MAOC中的木质素酚表现出较低的(Ad/Al)s(0.3~1.3). 此外, 随着水田土壤MAOC含量的降低和木质素酚浓度的增加, (Ad/Al)v和(Ad/Al)s均增加(P<0.05, 图S1).

所有土壤样本MAOC中的氨基糖含量范围为29.4~103.4 mg g^{-1} MAOC(图1(e)), 旱地、水田和林地土壤之间的差异不显著(P>0.05). 不同土地利用类型之间, 真菌氨基葡萄糖和细菌胞壁酸的含量以及真菌/细菌生物标志物比均没有显著差异(P>0.05, 图1(g)~(i)).

我们使用木质素酚和氨基糖两种生物标志物, 估算了植物和微生物来源的MAOC(图2). 所有土壤MAOC中植物源碳的含量范围为0.4~10.4 mg g^{-1}(图2(a)), 其中水田土壤最高, 分别比旱地和林地土壤高51.9%和35.6%(P<0.05). 旱地、水田和林地土壤中植物源MAOC的贡献分别为18.9%~68.9%、23.4%~68.1%和24.3%~69.1%(图2(c)).

相比之下, 所有土壤MAOC中微生物残体碳的含量为1.1~12.1 mg g^{-1}(图2(b)). 其中, 真菌残体碳的含量为0.5~6.9 mg g^{-1}(图S2(a)), 细菌残体碳的含量为0.4~5.4 mg g^{-1}(图S2(b)). 不同生态系统土壤中, 微生物源MAOC的含量、真菌和细菌残体碳的贡献, 以及真

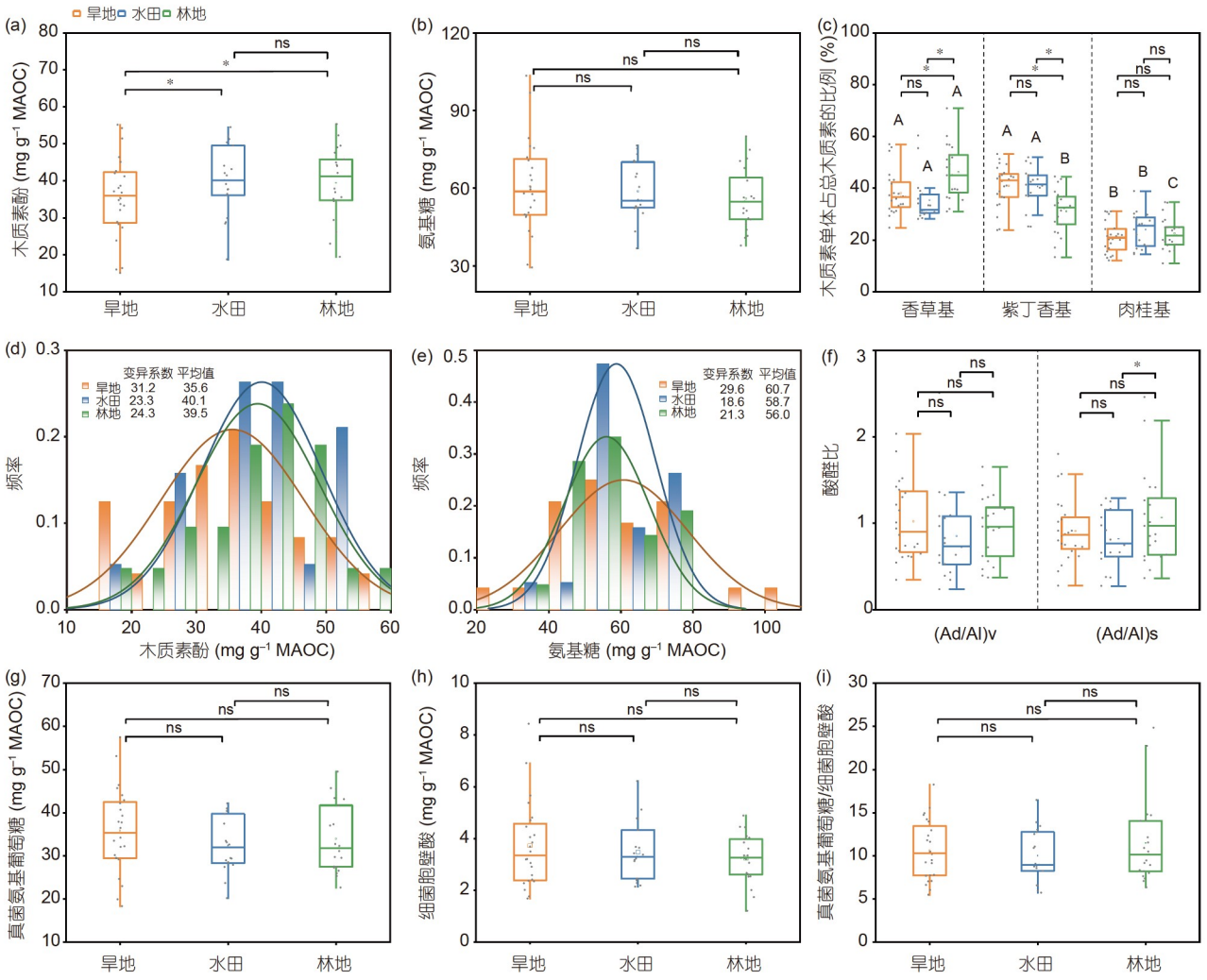


图 1 (网络版彩色)旱地、水田和林地土壤MAOC中木质素酚和氨基糖的分布特征. (a) 木质素酚含量; (b) 氨基糖含量; (c) 木质素酚中V、S和C单体的比例; (d) 木质素酚分布频率; (e) 氨基糖分布频率; (f) V和S单体木质素酚的酸醛比((Ad/Al)v和(Ad/Al)s); (g) 真菌氨基葡萄糖含量; (h) 细菌胞壁酸含量; (i) 真菌氨基葡萄糖/细菌胞壁酸比. ns表示不同生态系统之间无显著差异(P>0.05), *表示不同生态系统之间存在显著差异(P<0.05); (c)中不同大写字母表示同一生态中V、S和C单体之间存在显著差异(P<0.05)

Figure 1 (Color online) Distribution pattern of lignin phenols and amino sugars in upland, paddy, and forest soils MAOC. (a) Content of lignin phenols; (b) content of amino sugars; (c) ratio of V, S, and C monomers in lignin phenols; (d) distribution frequency of lignin phenols; (e) distribution frequency of amino sugars; (f) acid/aldehyde ratio of V and S monomers in lignin phenols ((Ad/Al)v and (Ad/Al)s); (g) content of fungal glucosamine; (h) content of bacterial muramic acid; (i) ratio of fungal glucosamine to bacterial muramic acid. ns indicates no significant difference between different ecosystems (P>0.05). * signifies significant differences between different ecosystems (P<0.05). Different lowercase letters in (c) represent significant differences among V, S, and C monomers within the same ecosystem (P<0.05)

菌/细菌残体碳比率等均没有显著差异(P>0.05, 图S3). 旱地、水田和林地土壤中微生物源MAOC的占比分别为23%~70%、26%~57%和29%~55%(图2(c)).

2.2 MAOC中木质素酚和氨基糖与土壤性质和环境因子的关联分析

基于随机森林回归(RF), 我们采用气候条件、土壤物理化学和生物特性等26个变量, 分别解释了旱地、水田和林地土壤MAOM中木质素酚总方差的23%、27%和42%, 以及氨基糖总方差的33%、61%和66%(图3). 结果发现, 控制旱地、水田和林地土壤MAOC中木质素酚含量的最重要因素是真菌残体, 氨基糖的积累主要取决于土壤pH. 为了比较气候、土壤特性和微生物对MAOC积累的重要性, 我们对4个类别

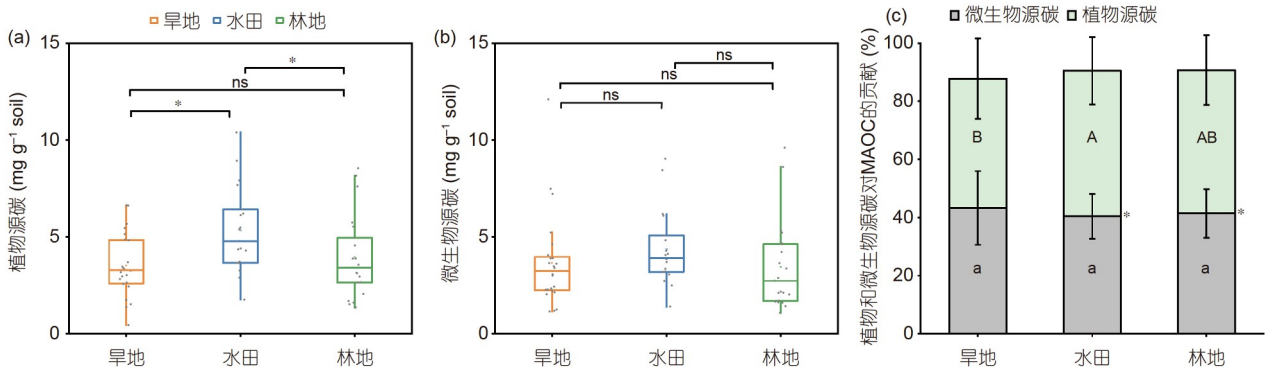


图 2 (网络版彩色)旱地、水田和林地土壤MAOC中植物(a)和微生物源碳(b)的含量以及植物和微生物源碳对MAOC的贡献(c). (a), (b) ns表示不同生态系统之间无显著差异(P>0.05); *表示不同生态系统之间存在显著差异(P<0.05). (c) 不同大写字母表示MAOC中植物源碳的贡献在生态系统之间存在显著差异(P<0.05); *表示同一生态系统中植物和微生物源碳对MAOC的贡献存在显著差异(P<0.05)

Figure 2 (Color online) The content of plant-derived (a) and microbial-derived C (b) in MAOC, and the contributions of plant- and microbial-derived C to MAOC (c) of upland, paddy, and forest soils. (a), (b) "ns" indicates no significant difference between different ecosystems (P>0.05); * signifies significant differences between different ecosystems (P<0.05). (c) Different uppercase letters represent significant differences in the contributions of plant-derived C to MAOC between ecosystems (P<0.05); * indicates significant differences in the contributions of plant- and microbial-derived C to MAOC within the same ecosystem (P<0.05)

的环境因素进行了方差分解分析(VPA, 图4). 为了消除数据之间的共线性, 我们选取了4个类别环境因素中的代表性因子, 以微生物生物量碳代表微生物生物量, 真菌氨基葡萄糖/细菌胞壁酸表示微生物残体组成. 结果表明, 旱地、水田和林地土壤中, 微生物生物量和残体组成可以解释MAOC的最多变化, 分别解释了42%、34%和28%的方差.

我们还使用了相关性分析和结构方程模型(SEM)描述木质素酚类和氨基糖与主要环境变量之间的复杂相互作用(图S4和5). 结果表明, 较高的MAT有利于旱地和林地MAOM中木质素酚的积累(P<0.05), 林地中氨基糖则与蒙脱石和C/N比呈正相关(P<0.05). 基于SEM, 不同生态系统中的活性矿物、层状硅酸盐、土壤pH、微生物生物量碳、黏粒和粉粒, 通过直接和间接影响MAOC中的木质素酚和氨基糖, 进而促进MAOC的积累. 值得注意的是, 氨基糖对MAOC的总效应大于木质素酚, 微生物源碳对MAOC形成的作用大于植物源碳.

3 讨论

土壤矿物结合态有机碳是土壤中最稳定的有机碳形态之一, 占比很高, 以往对其来源从未进行细致和有效的区分. 我们率先在区域尺度上, 提供了不同生态系统土壤的MAOM中植物和微生物来源碳贡献的直接证据. 旱地土壤MAOM中植物和微生物源碳的贡献相似(P>0.05), 分别为44.5%和44.2%, 而水田和林地中植物源碳的贡献(50.1%和49.3%)大于微生物源碳的贡献(40.4%和41.0%)(P<0.05, 图2(c)). 本研究中, 水田和林地土壤MAOM中微生物残体碳的比例高于之前报道的平均值(38.6%)[9], 与水田全土中有机碳主要来源于植物(33%~54%), 微生物来源碳占比较低(28%~36%)的结果相似[28]. 这可能是由于水田土壤中氧气的限制导致微生物的活性降低, 代谢合成能力减弱, 微生物残体的形成受到抑制, 使更多的植物残体得以保留. 对林地土壤而言, 其较高的植物生物量的输入, 部分持久性植物残体(如木质素)分解非常缓慢, 导致它们相对于微生物残体积累更多[32].

我们发现, 不同利用类型土壤中, MAOC中微生物残体碳的贡献相似(P>0.05, 图2(c)), 这与全土的研究结果不同, 耕地和草地全土中微生物残体碳对SOC的贡献比森林土壤的高20%[17,30]. 这说明, 土壤中有机碳的保存和稳定性更多地受到微生物转化和矿物结合的影响, 而不是决定于输入的有机物来源. 微生物残体由真菌和细菌残体组成, 细菌胞壁酸是比真菌氨基葡萄糖更容易分解的生物标志物[33,34]. 本研究表明, 旱地、水田和林地生态系统中MAOC具有相似的真菌氨基葡萄糖/细菌胞壁酸比(10.6、10.0和11.5), 显示微生物残体碳在MAOM中具有相似的稳定性(图1(i)). 而全土中微生物残体的组成(真菌/细菌生物标志物)却因生态系统类型而异[28,30]. 这进一步说明, 矿物结合改变了SOC的组成, 可以在很大程度上抵抗土地利用变化对SOC分

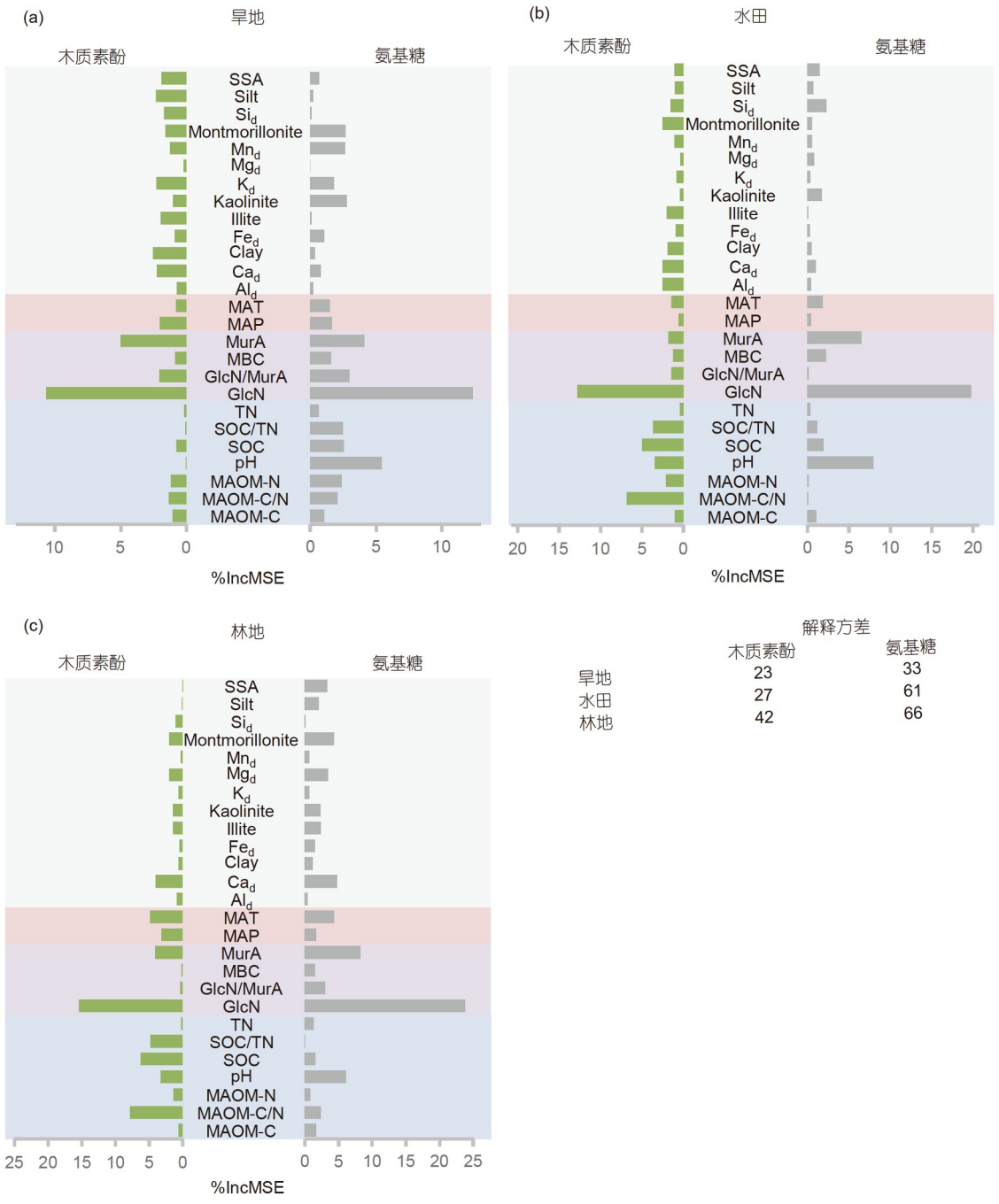


图 3 (网络版彩色)随机森林预测环境因子对旱地(a)、水田(b)和林地(c)土壤MAOC中木质素酚和氨基糖的相对重要性. SSA: 比表面积; Clay: 黏粒; Silt: 粉粒; Kaolinite: 高岭石; Montmorillonite: 蒙脱石; Illite: 伊利石; Fe_d、Al_d、Ca_d、K_d、Mg_d、Mn_d、Si_d: DCB提取的活性铁、铝、钙、钾、镁、锰、硅; MAT: 年平均温度; MAP: 年平均降水量; MBC: 微生物生物量碳; MurA: 细菌胞壁酸; GlcN: 真菌氨基葡萄糖; GlcN/MurA: 真菌氨基葡萄糖/细菌胞壁酸比; TN: 总氮; SOC: 土壤有机碳; SOC/TN: 土壤有机碳/总氮比; MAOM-C: 矿物结合态有机碳; MAOM-N: 矿物结合态总氮; MAOM-C/N: 矿物结合态有机碳/矿物结合态总氮比

Figure 3 (Color online) The relative importance of environmental factors for lignin phenols and amino sugars in MAOC of upland (a), paddy (b), and forest (c) soils by using RF analysis. SSA: Specific surface area; Fe_d, Al_d, Ca_d, K_d, Mg_d, Mn_d, and Sid: Active Fe, Al, Ca, K, Mg, Mn, and Si; MAT: Mean annual temperature; MAP: Mean annual precipitation; MBC: Microbial biomass C; MurA: Bacterial muramic acid; GlcN: Fungal glucosamine; GlcN/MurA: Fungal glucosamine/Bacterial muramic acid ratio; TN: Total nitrogen; SOC: Soil organic C; SOC/TN: Soil organic C/total nitrogen ratio; MAOM-C: Mineral-associated organic C; MAOM-N: Mineral-associated organic nitrogen; MAOM-C/N: Mineral-associated organic C/mineral-associated organic nitrogen ratio

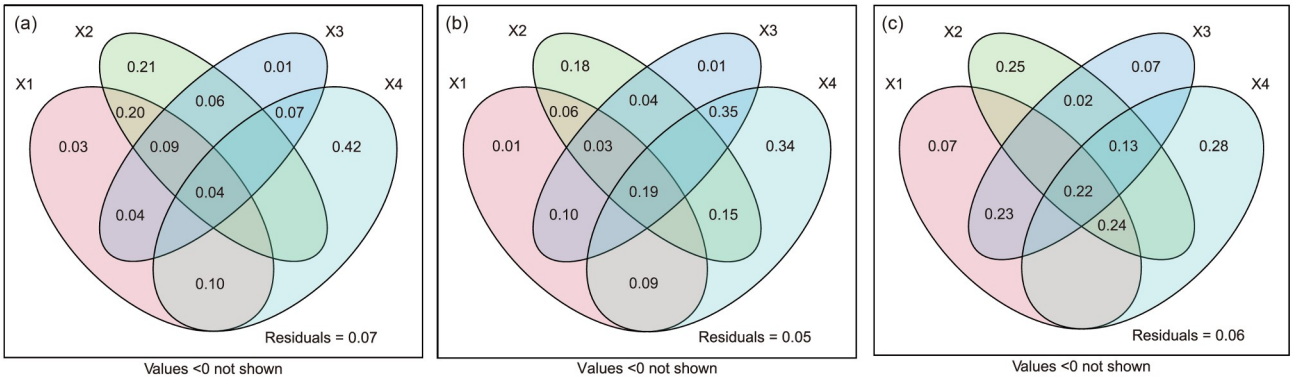


图 4 (网络版彩色)旱地(a)、水田(b)和林地(c)土壤MAOC的方差分解分析(variance partition analysis, VPA)结果. X1: 气候因子(年平均温度和年平均降水量); X2: 矿物因素(活性铁、活性铝、高岭石、蒙脱石、伊利石、黏粒和粉粒); X3: 土壤性质(碳氮比和pH); X4: 微生物参数(微生物生物量和残体组成)

Figure 4 (Color online) VPA for MAOC in upland (a), paddy (b), and forest (c) soils. X1: Climatic factors (mean annual temperature and mean annual precipitation); X2: Mineral factors (active Fe, active Al, kaolinite, montmorillonite, illite, clay, and silt); X3: Soil properties (C/N ratio and pH); X4: Microbial parameters (microbial biomass and community composition)

解的影响.

水田土壤MAOC中植物源碳的贡献比旱地的高5.6%, 意味着其具有比旱地更有效的植物源碳封存(图2(c)). 这主要是因为水田土壤环境限制了微生物的分解能力, 还可能与旱地土壤较干燥, 溶解和淋溶作用弱, 可溶性有机碳被矿物的直接吸附和共沉淀较少有关[35]. 水田和林地土壤MAOC中较高比例的植物源碳还与其组成和分解特点有关. 就木质素酚的组成而言, 林地土壤MAOC中的木质素含有46.3%的V型酚, 而旱地仅含有38.1%的V型酚. 水田中木质素酚的C/V比(0.8)高于旱地(0.6)和林地(0.5), S/V比(1.3)高于林地(0.8), (Ad/Al)s比(0.8)低于林地(1.1)(图S5和2(c), (f)). V型酚的分解时间一般更长, 且更容易与矿物表面结合[36]. 此外, $(Ad/Al)_v$和$(Ad/Al)_S$比例的增加反映了木质素侧链氧化程度的提高, 而C/V和S/V比例的降低表明微生物转化阶段的增加[37]. 可见, 水田和林地土壤的环境更有利于难降解的植物源有机碳与矿物的结合, 并最终在土壤中积累.

基于多种分析和统计方法的研究显示(图3和S4), 真菌残体是影响不同生态系统土壤MAOM中木质素酚含量的主要因素, 揭示了微生物合成代谢对MAOC中植物源碳的积累具有重要的调控作用. 这表明, 虽然MAOC中植物源有机碳占比超过微生物源, 但其主要的驱动力是微生物代谢活动. 而且, 氨基糖对MAOC的总效应大于木质素酚, 意味着微生物源有机物比植物源有机物在调控和促进MAOC的积累中可能更为重要. 基于此, 我们提出, MAOC的形成主要由微生物代谢驱动, 调控作用因生态系统类型而异(图6). 其次是矿物因素, 黏粉粒主要通过增加植物源碳促使MAOC的积累, 可溶性植物小分子和经微生物胞外酶分解后的植物残体与矿物的吸附而成为土壤的稳定态碳. 在气候因素中, MAT是控制MAOC组成和积累的重要因素, 这不同于POC, 其积累主要受MAP的调控[38]. 这可能是因为降水对有机碳的分布和积累更多地影响植被生长和有机物的输入, 对有机碳的长期稳定性影响较小. pH也是调控MAOC的重要因素, 较高的pH不利于真菌生长, 真菌来源有机碳减少, 导致MAOC中的微生物残体碳含量下降, 这与影响总SOC积累的趋势一致[28,30].

4 结论

我们率先提供了大陆尺度旱地、水田和林地土壤稳定碳库中植物和微生物源碳贡献的直接定量证据, 水田和林地土壤MAOC中以植物源碳为主, 微生物对MAOC的贡献不因生态系统类型而异. MAOC的形成主要由微生物代谢驱动, 调控作用因生态系统类型而异, 其次是矿物组成, 以及年均温和土壤pH. 农业土壤可以通过施肥和排灌等措施, 调节土壤微生物活性, 增加微生物残体, 促进土壤稳定碳库的形成, 达到土壤固碳减排的目的, 为实现碳达峰、碳中和(“双碳”)目标作出贡献.

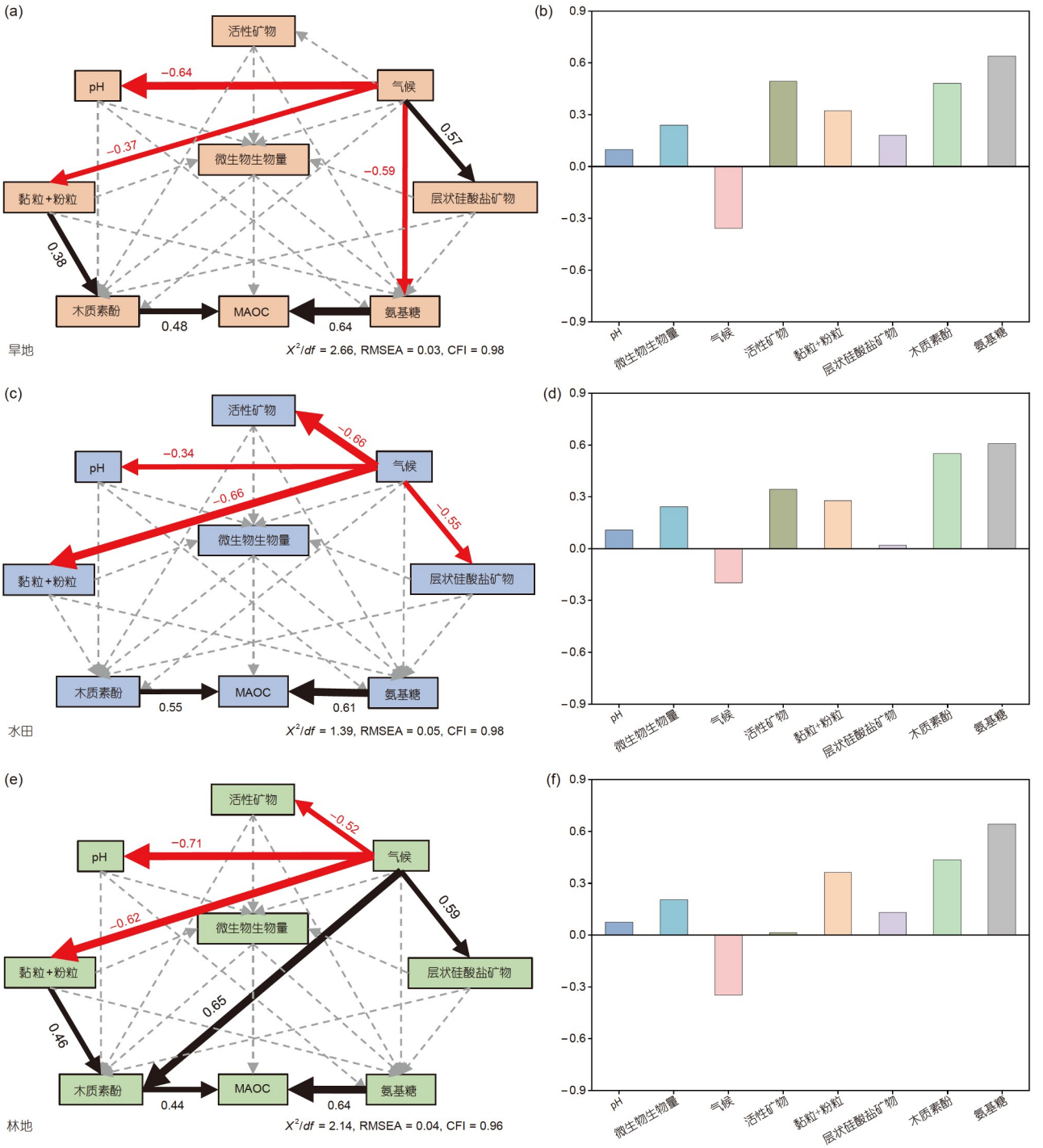


图 5 (网络版彩色)结构方程模型(structural equation modeling, SEM)显示气候因素(MAT和MAP)、土壤性质、木质素酚和氨基糖对旱地(a, b)、水田(c, d)和林地(e, f)土壤MAOC的影响. 土壤性质包括黏粒+粉粒、活性矿物(铁、铝、钙、钾、镁、锰和硅)、层状硅酸盐(高岭石、蒙脱石和伊利石)、微生物生物量(MBC)和pH. 箭头旁边的数字是标准化路径系数(仅显示有效路径系数, P<0.05); 箭头宽度表示标准化路径系数的强度. 黑线表示正路径系数, 红线表示负路径系数

Figure 5 (Color online) SEM shows the effects of climate factors (MAT, MAP), soil properties, lignin phenols and amino sugars on MAOC in upland (a, b), paddy (c, d) and forest soils (e, f). Soil properties include clay + silt, reactive minerals (Fe_d, Al_d, Ca_d, K_d, Mg_d, Mn_d, Si_d), phyllosilicates (kaolinite, montmorillonite, illite), microbial biomass (MBC), and pH. The number next to the arrow is the standardized path coefficient (only significant path coefficients are shown, P<0.05), and the width of the arrow indicates the strength of the standardized path coefficient. Black and red lines represent positive and negative path coefficients, respectively

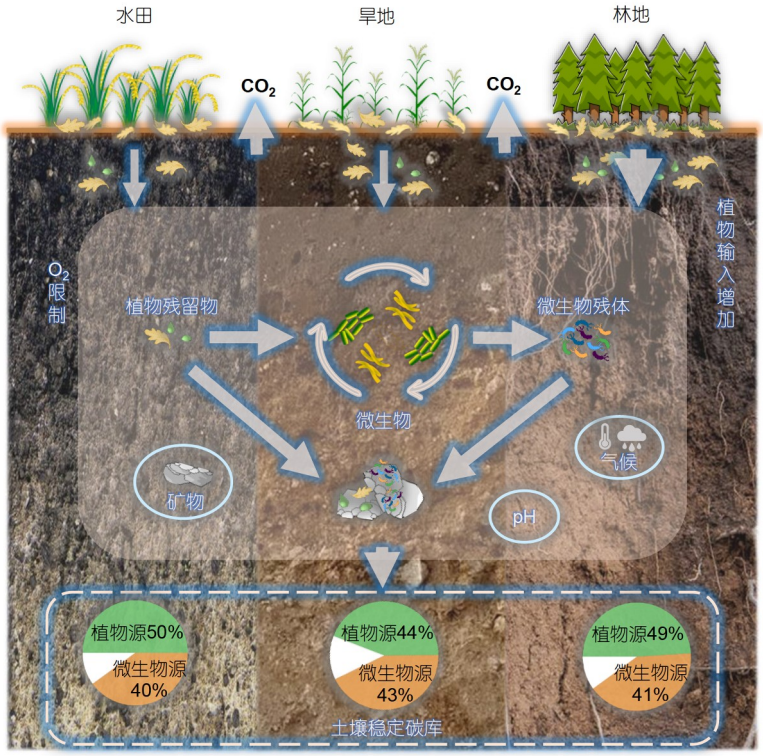


图 6 (网络版彩色)微生物对不同生态系统土壤MAOC的调控模式
Figure 6 (Color online) Microbial regulation patterns of MAOC in different ecosystems

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补充材料

图S1 (Ad/Al)v和(Ad/Al)s与MAOC和木质素酚的相关性
图S2 旱地、水田和林地土壤MAOC中真菌和细菌残体碳的含量
图S3 旱地、水田和林地土壤MAOC中真菌和细菌残体碳对MAOC的贡献及真菌/细菌残体碳比
图S4 旱地、水田和林地土壤MAOC中木质素酚和氨基糖的相关性分析
图S5 木质素酚单体比率

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Summary for “微生物驱动土壤矿物结合态有机碳的形成”

Microorganisms drive the formation of mineral-associated organic carbon in soils

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Soil stores the largest amount of carbon in terrestrial ecosystem with ~1500 Pg C at the 1m soil depth which plays a crucial role in regulating greenhouse gas emission and global climate change. As the stable organic carbon pool in soils, mineral-associated organic carbon (MAOC) determines the composition, capacity and cycling of soil C. The sources and formation of MAOC, particularly from plants and microorganisms, have long been a subject of debate. Recently, it is widely believed that microbial-derived organic carbon may dominate the preservation of soil organic carbon (SOC) particularly the formation of MAOC. However, a number of evidences have also suggested the important contribution of plant derived organic carbon to MAOC. Plant derived biomolecules such as lipid, lignin and carbohydrate may account for a remarkable proportion of MAOC, making a vital contribution to the accumulation and stabilization of soil organic carbon. However, to date, there is a considerable uncertainty regarding the relative contributions and controlling factors of plant- and microbial-derived MAOC across different ecosystems which hinders the implementation of sustainable soil management strategies. In this study, we are the first to provide empirical evidences on the contribution of plant and microbial derived carbon to MAOC in soils of different ecosystems at a large scale. Surface soils (0−20 cm) were collected from uplands (n=24), paddy fields (n=19), and forest soils (n=21) in eastern China ranging from 18°N to 47°N, and the contributions and driving factors of microbial and plant-derived MAOC were scrutinized based on the analysis of amino sugars and lignin phenols. Correlation analysis, random forest (RF) analysis, variance partition analysis (VPA) and structural equation modeling (SEM) were employed to disentangle the environmental factors and soil attributes regulating the formation and accumulation of MAOC and the possible mechanisms. The major scientific hypothesis is that the contribution of plant-derived C to MAOC is greater than that of microbial-derived, especially for forest soils which have larger plant biomass input. Our results show that microbial necromass C accounts for 44.2%, 40.4%, and 41.0% of MAOC in upland, paddy field, and forest soils, while plant-derived MAOC makes up 44.5%, 50.1%, and 49.3% respectively. Plant-derived carbon was found to be the main source of MAOC in paddy and forest soils, while the contribution of microbial-derived C was insignificant among different ecosystems. Similar values are found for the fungal glucosamine/bacterial muramic acid ratios (10.6, 10.0, and 11.5, P>0.05) in MAOC. These observations suggest that microbial necromass C tends to be constant in MAOC for various ecosystems, and OC associated with minerals alters the composition of SOC, which is highly resistant to decomposition under varying land utilizations. We discovered that fungal necromass is the main factor affecting lignin phenol content in all ecosystems, indicating the vital roles of microbial anabolism in driving the accumulation of plant-derived carbon in MAOC. The higher proportions of plant-derived C in the stable C pool for paddy and forest soils are assigned to the environmental stress and larger input of plant residues in the two ecosystems, respectively. High clay and silt content and mean annual temperature (MAT) are conducive to the enrichment of plant-derived C in MAOC, while low soil pH and MAT avail the accumulation of microbial-derived C. The findings obtained from this work are of great significance for understanding the responses and stability of SOC to soil managements so as to increase soil C storage and reduce C emissions, and achieve C neutrality goals. Agricultural soils hold great promise in carbon sequestration and the formation of stable carbon pool through various management strategies to regulate soil microbial activity and increase the accumulation of microbial residues.

mineral-associated organic carbon, microbial necromass C, plant-derived C, amino sugar, lignin phenol

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