



高寒草地土壤温室气体排放对放牧的响应研究进展

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摘要: 高寒草地生态系统具有独特的地理环境和气候特征,对放牧干扰十分敏感,在全球温室气体通量中贡献突出,研究高寒草地放牧对土壤温室气体排放的影响机制具有重要意义。本文总结高寒草地温室气体源/汇特征、不同放牧方式对土壤微环境和微生物群落结构的影响,发现高寒草地主要是CO₂源、CH₄汇、N₂O源。放牧通过家畜选择性采食、践踏和排泄物返还等多重机制作用于地上植物、土壤结构、温度、湿度和养分,进而影响地下微生物及温室气体通量。本文旨在为高寒草地生态系统健康发展和管理及缓解全球气候变化提供科学依据,并对未来研究方向进行展望。

关键词: 高寒草地, 放牧, 温室气体, 土壤微生物

Response of soil greenhouse gases emissions to grazing in alpine grasslands: a review

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Abstract: Due to the unique geographical environment and climate characteristics, the alpine grassland ecosystem is sensitive to grazing perturbation, contributing greatly to global greenhouse gases (GHGs) emissions. Therefore, it is significant to decipher the effect of grazing on GHGs emissions in alpine grassland. This study summarized the switch of GHGs sources or sinks and the response of soil microenvironment and microbial community structure under different grazing methods in alpine grassland. It is concluded that alpine grassland is the major CO₂ source, CH₄ sink, and N₂O source. Besides, grazing directly affects the aboveground plant, soil structure, temperature, humidity, and nutrient contents through

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selective feeding, trampling, and excreta returning of livestock, and then indirectly affects soil microorganisms and GHGs fluxes. This review provides a novel perspective for the healthy development and management of the alpine grassland ecosystem, the mitigation of global climate change in the alpine grassland.

Keywords: alpine grassland, grazing, greenhouse gases, soil microorganisms

全球变暖已成为当前科学研究的重点和热点^[1]。人类活动产生的温室气体(CO₂、CH₄和N₂O)是全球变暖的主要驱动因子,对全球增温的贡献率高达87%^[2]。高寒草地(Alpine Grassland)包括高寒草原、高寒草甸和高寒沼泽,主要分布在高纬度或高海拔、气候寒冷、冻土集中分布的地区^[3],位于中国青藏高原大部分区域、亚洲喜马拉雅山脉、苏格兰高地、斯堪的纳维亚山脉、北美洲和南美洲的美洲山脉、非洲的裂谷山脉、欧洲喀尔巴阡山脉和比利牛斯山脉和高加索山等地区^[4],具有维持土壤过程、保护生物多样性及调节土壤碳/氮源-汇平衡等重要生态服务功能^[5]。位于“世界第三极”的青藏高原高寒草地面积约为1.52×10⁶ km²,占中国草地面积的34.3%^[6],该生态系统结构简单、功能脆弱,属于典型脆弱生态系统,对全球气候变化极为敏感^[7]。放牧作为高寒草地最主要的土地利用方式,牲畜通过选择性采食、践踏和排泄影响植被群落结构、净初级生产力和土壤微环境^[8]。微生物“暗物质”作为地球各圈层之间物质循环和能量交换的重要参与者^[9],是土壤微环境的重要组成部分,对放牧扰动十分敏感,能快速反映生态系统功能和土壤质量变化^[10-11]。土壤微生物是高寒草地土壤温室气体的主要产生者,放牧会直接或间接改变土壤微生物群落结构和功能及养分循环,最终影响温室气体排放^[12]。

当前,放牧对高寒草地上植被-土壤微环境-地下微生物耦合及温室气体排放影响的研究引起了学界的极大关注^[10,13]。本文通过分析高寒草地温室气体源/汇特征和放牧对土壤理化性质、微生物和温室气体排放的影响,探讨高寒草地温室气体排放对放牧的响应机制,有助于明晰高寒草地土壤微生物

物对全球温室气体的贡献。

1 温室气体源/汇特征和产生机制

1.1 温室气体种类

1.1.1 CO₂源

土壤呼吸是陆地生态系统碳循环的重要组成部分,主要包括植物根系和微生物呼吸,产生的CO₂是土壤与大气之间的第二大碳通量,其温室效应占地球总温室效应的50%以上^[14]。土壤呼吸的细微变化会对大气CO₂浓度产生巨大影响^[15]。高寒草地生态系统因其特殊的地理环境,具有强风、低温、低CO₂含量和强光照的特点,其中,低CO₂含量使得植物很难进行光合作用,低温使植被凋落物和地下死根不易分解,并且土壤呼吸也受低温、植被凋落物量和昼夜温差限制^[16],因此高寒草地土壤中储存了大量有机碳。研究发现,土壤中大量存储的有机碳,尤其是可溶性有机碳可以使*Acidobacteria*、*Proteobacteria*、*Actinobacteria*、*Basidiomycota*和*Ascomycota*等土壤微生物活性增强,显著增加CO₂排放量^[14](表1)。高寒沼泽草地由于具有更多的植物生物量和土壤有机质,相比高寒草甸会释放更多的CO₂^[19]。综合分析已有研究发现,高寒草地主要是CO₂源^[16],例如青藏高原地区CO₂年累积排放量可达241.5–512.5 g-C/m²^[20]。放牧干扰会加速高寒草地植物生长,增加地表凋落物,增强土壤有机质腐殖化,提高土壤有机碳活性和微生物活性,加速碳循环,最终促进CO₂排放^[21](表2)。Gao等^[31]在加拿大落基山的研究表明,与非放牧相比,放牧可增加37%–51%的CO₂排放通量。此外,家畜排泄物也会促进CO₂排放,方精云等^[32]在青藏高原东北缘的研究结果表明家畜粪斑使高寒草地生态系统CO₂排放量增加0.61–3.16倍。

表 1 参与温室气体排放与吸收的微生物和基因

Table 1 Microorganisms and genes involved in the emission and absorption of greenhouse gases (GHGs)

温室气体类型 GHGs	微生物种类 Microorganism species	与 GHGs 相关的基因 Genes about GHGs	参考文献 References
CO ₂	<i>Acidobacteria</i> , <i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Basidiomycota</i> , <i>Ascomycota</i>	<i>vdh</i> , <i>vanA</i> , <i>glx</i> , <i>lip</i> , <i>aclB</i> , <i>rubisco</i> , <i>amyA</i> , <i>nplT</i> , <i>pulA</i> , <i>pectinase</i> , <i>ara_fungi</i> , <i>mannanase</i> and <i>xylA</i>	[7-8,10,14]
CH ₄	<i>Methylobacter</i> , <i>Methylosarcina</i>	<i>pmoA</i> , <i>mcrA</i> and <i>mmoX</i>	[7-8,10,17]
N ₂ O	AOB, AOA	<i>ureC</i> , <i>amoA</i> , <i>hao</i> , <i>nirK</i> , <i>nirS</i> , <i>nosZ</i> , <i>norB</i> and <i>nifH</i>	[7-8,10,18]

表 2 高寒草地温室气体种类及源汇特征

Table 2 Species and source/sink characteristics of greenhouse gases in alpine grassland

Source/Sink	Greenhouse effect	GHGs in Tibet Plateau	The reason of source/sink	Factors effect source/sink
CO ₂ source	Above 50% ^[14]	The cumulative annual emissions are 241.5–512.5 g-C/m ² ^[20]	Organic carbon promotes microbial activity ^[14]	Grazing+ ^[21]
CH ₄ sink	About 20% ^[22]	The absorption in the midwest are 60.0±7.1 μg/(m ² ·h) ^[23]	Under anaerobic conditions, CH ₄ converted by organic matter; under aerobic conditions, CH ₄ is consumed by methane-oxidizing bacteria ^[24]	Grazing– ^[17] , soil freezing/thawing+ ^[25] , rumen of ruminant livestock+ ^[26]
N ₂ O source	About 6% ^[27]	The emissions in growing season are 0.14±0.38 μg/(h·m ²) ^[23]	AOB and AOA produce N ₂ O through the process of nitrification and denitrification ^[28]	Livestock waste+ ^[29] , soil moisture– ^[30] ; soil temperature+ ^[30]

注：+：促进温室气体排放；-：抑制温室气体的排放/促进温室气体吸收

Note: +: Promoting greenhouse gas emissions; -: Curbing greenhouse gas emissions/promoting greenhouse gas absorption

1.1.2 CH₄ 汇

高寒草地 CH₄ 源汇具有不平衡性，土壤有机碳含量和土壤含水量变化是最主要的影响因素，土壤有机碳和含水率越高，土壤 CH₄ 吸收能力越强^[25]。高寒沼泽草地含有较高的土壤有机质，而且含水量高于饱和含水量，使其成为 CH₄ 源^[19]。高寒草地和高寒草甸因土壤冻融及反刍家畜瘤胃使其成为 CH₄ 源^[25]。高寒草地主要是 CH₄ 汇^[33]。在厌氧条件下，有机质被厌氧和兼性厌氧菌分解成小分子化合物(乙酸、H₂ 和 CO₂)后，再经产甲烷菌(如乙酰营养产甲烷菌)的甲基-辅酶 M 还原酶(Mcr)催化转化成 CH₄^[34]；在有氧条件下，CH₄ 经一系列氧化过程被甲烷氧化菌消耗^[24](表 2)。CH₄ 作为重要的温室气体之一，具有很强的红外吸收能力，在大气中的循环周期为 9.1 年，其增温潜势是 CO₂ 的 28 倍，对全球温室气体引起增温贡献约占 20%，综合影响仅次于 CO₂^[22]，因此，降低空气中的 CH₄ 成为减缓温室效应的有效措施。研究发现，放牧土壤中甲烷氧化菌主要属于 *Methylobacter* 和 *Methylosarcina* (I 型，

Gammaproteobacteria) 及 *Methylocystis* (II 型，*Alphaproteobacteria*) (表 1)，放牧会增加甲烷氧化菌及甲烷单加氧酶基因(*pmoA*)的丰度(约 2 倍)^[17]，PmoA 具有较高的 CH₄ 亲和力，从而使得甲烷氧化菌能够氧化空气中的 CH₄。研究显示中国青藏高原中西部地区高寒草地[60.0±7.1 μg/(m²·h)]^[23]、黄河源区高寒草甸[19.27–80.29 μg/(m²·h)]^[20]、横跨西藏多年冻土区^[35]、新疆天山放牧高寒草地[66.3–103.0 μg-C/(m²·h)]^[36]以及加拿大哥伦比亚山脉北塞尔基克山区[112 μg-C/(m²·h)]^[25]等都是 CH₄ 汇，其中位于青藏高原高寒草地的 CH₄ 吸收量占中国草地 CH₄ 吸收总量的 44%^[33]。Wei 等^[23]在青藏高原中西部的研究表明高寒草地植被生长期 CH₄ 吸收量为 0.5 g/m²。

1.1.3 N₂O 源

高寒草地是 N₂O 源。N₂O 的大气循环周期长达 150 年，不断参与大气光化学反应，间接破坏臭氧层，增温潜能是 CO₂ 的 298 倍，对全球增温贡献约为 6%^[27]。N₂O 是由有氧条件下硝化作用将铵(NH₄⁺)催化氧化成硝酸盐(NO₃⁻)和厌氧条件下反硝化作用

将硝酸盐(NO_3^-)或亚硝酸盐(NO_2^-)还原成还原态氮(NO , N_2O , N_2) 这 2 个过程产生^[28]。参与这 2 个过程的微生物主要是氨氧化细菌(Ammonia-Oxidizing Bacteria, AOB)和氨氧化古菌(Ammonia-Oxidizing Archaea, AOA)^[18](表 1, 表 2)。氨氧化是许多生态系统中的硝化限速步骤, 该步骤主要由氨单加氧酶(Ammonia Monooxygenase, AMO)和羟胺氧化酶(Hydroxylamine Oxidoreductase, HAO)调控, 其中 AMO 是由 *amoA*、*amoB* 和 *amoC* 这 3 个基因编码的蛋白亚基构成的三聚体膜结合蛋白^[37]。AOB 和 AOA 在土壤中生成 N_2O 的作用机理相似, 但二者催化 N_2O 生成的酶却不尽相同^[38]。土壤中硝化和反硝化过程一般同时进行, 但在氧气充足时主要是硝化过程产生 N_2O , 反之则是反硝化过程^[39]。土壤水分是影响硝化和反硝化作用的主要因素, 研究发现, 当土壤处于饱和含水量以下时, 因氧气充足, 硝化作用产生的 N_2O 占总排放量的 61%–98%; 处于饱和含水量以上时, 形成的厌氧环境促使反硝化作用成为 N_2O 的主要来源, 随着含水量的持续增加, N_2 成为反硝化过程的主要产物^[29]。催化 N_2O 产生的酶除 AMO 和 HAO 之外, 还包括氧化氮还原酶(Nitric Oxide Reductase, NOR)、硝酸还原酶(Naringenin, NAR)和亚硝酸还原酶(Nitrite Reductase, NIR)等^[40]。研究表明, 土壤(草地、耕地和森林等)是主要的 N_2O 来源, 约占生物圈向大气排放 N_2O 总量的 70%, 草地生态系统均为 N_2O 源^[41], 在 N_2O 总排放中的占比较大, 通常表现出比耕地和森林土壤更高的排放速率^[42]。Wei 等^[23]在青藏高原中部发现, 高寒草地生长季 N_2O 排放量是 $0.14 \pm 0.38 \mu\text{g}/(\text{h} \cdot \text{m}^2)$ 。

家畜排泄物返还是草地生态系统的天然施肥措施, 家畜将采食的 70%–95%氮返还土壤, 刺激土壤微生物生物量和活性^[26], 进而促进硝酸盐淋失和 N_2O 排放。研究显示畜圈和粪堆具有较高 N_2O 排放量, 家畜尿粪斑的 N_2O 排放量是对照样地的 3.5 倍^[43]。AOA 和 AOB 含量与排泄物中的 NO_3^- -N 和 NH_4^+ -N 浓度显著正相关, 并且 AOB 能适应更高

浓度氮的碱性环境^[8]。研究发现, 高寒草地生态系统的诸多环境因子(土壤温度、湿度和 pH)中只有土壤温度与 AOA 的生长存在相关性, 高浓度家畜尿液和粪便会降低土壤温度, 进而限制 AOA 生长^[44], 但会刺激 AOB 活性, 并显著增加 AOB 及 *amoA* (编码 AMO)、*nirK* (编码 NIR)和 *nosZ* (编码一氧化碳合成酶)基因丰度($P < 0.001$), 最终促进 N_2O 排放^[30]。

1.2 温室气体排放时间的变化规律

高寒草地温室气体排放具有明显的日/季节变化规律。温室气体日排放速率与大气温度、土壤温度和湿度变化同步^[16]。孔郑^[45]和孙步功^[20]在青藏高原黄河源区退化草地的研究表明, CO_2 最大释放速率在每日 15 时前后, 最小值在 4–7 时; CH_4 吸收通量最大值在夜晚, 最小值在 9–11 时。高寒草地土壤温室气体排放也与植物生长周期紧密相关, 并且 CO_2 排放与土壤呼吸的季节变化一致, 如 CO_2 排放量是植被生长旺盛期>返青期>枯黄期; CH_4 吸收速率是生长季>非生长季, 吸收速率与土壤水分负相关, 与土壤温度正相关^[16]。还有研究显示高寒草地不同生长期具有不同的 CH_4 源汇特性, 高寒草地在牧草返青期和生长旺盛期是 CH_4 汇, 枯黄期因土壤冻融是 CH_4 源^[46]。Li 等^[47]在天山高寒草原发现春季融雪会改变土壤水热条件, 导致微生物活性增强, 促进 N_2O 排放, N_2O 排放与表层土壤温度和含水量显著正相关($P < 0.001$), 春季融雪期 N_2O 排放占年度总排放量的 6.6%, 冬季冰冻期占 16.7%, 生长季排放占 76.7%。

2 影响温室气体排放的放牧方式

2.1 家畜种类

粪斑中高含量氮促进 N_2O 排放。虽然藏羊和牦牛这 2 种家畜放牧均可以增加高寒草地 AOA 和 AOB 丰度^[48], 但藏羊粪便通过硝化作用产生 N_2O , 牦牛粪便通过反硝化作用产生 N_2O ^[49]。与藏羊粪便相比, 牦牛粪便的 N_2O 排放量大、 CH_4 吸收量低^[50]。研究认为, 造成如上差异的原因是藏羊粪便中含有较高浓度硝化微生物作用底物 NH_4^+ -N, 而牦牛的

大粪便斑块含有较高的反硝化微生物作用底物 NO_3^- -N, 并且缺氧的斑块中心有利于厌氧反硝化微生物生长, 导致牦牛粪便主要通过反硝化作用产生 N_2O ^[51]。同时, 牦牛粪便中 NH_4^+ -N 对 AMO 上 CH_4 对应活性位点的竞争会抑制 CH_4 氧化^[52]。

2.2 放牧强度

放牧强度增加主要通过以下 3 个方面影响土壤微环境和温室气体排放(图 1^[53]): (1) 家畜过度采食会改变植被群落特征, 导致高寒草地地上生物量和土壤微生物生物量减少^[54]。(2) 家畜高强度和多频率践踏使土壤容重增加、微生物数量和生物量减少及酶活性降低^[55], 进而影响土壤微生物群落结构, 使土壤微生物由真菌为主向细菌为主转变^[56]。研究发现, 在低放牧强度下放线菌和真菌丰度最高, 而在高强度放牧条件下细菌丰度最高^[57]。(3) 高强度放牧造成家畜排泄物中的氮大量返还而刺激 AOB 活性, 并使与 N_2O 排放相关的微生物和功能基因丰

度显著增加, 促进 N_2O 排放^[30]。Xie 等^[58]研究青藏高原高寒草甸的结果表明高强度放牧使 AOB 和 AOA 丰度分别提高了 42 倍和 3.7 倍, 其原因是高强度放牧下家畜排泄物中 NO_3^- -N 和 NH_4^+ -N 返还土壤, 使得 AOA 和 AOB 作用底物增多、活性增强^[8]。

放牧强度对土壤微环境、微生物群落结构和多样性的影响最终会促进温室气体排放^[59]。例如, Du 等^[41]发现适度放牧通过增强土壤硝化作用增加年均 57.8% 和生长季 62.0% 的 N_2O 排放, 重度放牧通过采食降低土壤氮含量、增加土壤容重, 使 N_2O 排放量降低。然而有研究发现高强度放牧导致排泄物的大量返还还会促进 N_2O 排放^[58]。

2.3 围封禁牧

围封通过减少家畜对生态系统干扰, 提高地表植被覆盖度, 降低土壤温度及其变化, 减少强辐射暴露^[60], 改善土壤微生物生存环境, 增加微生物作用底物, 减少温室气体排放量^[61]。Wei 等^[60]

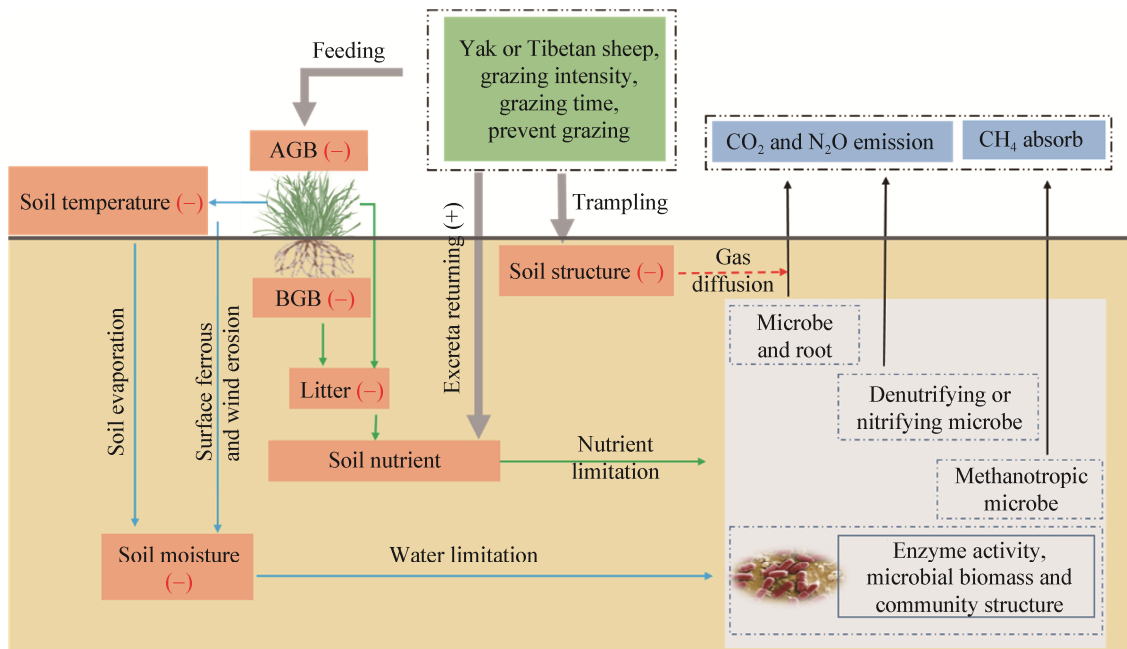


图 1 放牧对高寒草地生态系统温室气体通量的影响^[53]

Figure 1 The effects of grazing on greenhouse gases of the alpine grassland^[53]

注: -: 放牧起负作用; +: 放牧起正作用; AGB: 地上生物量; BGB: 地下生物量

Note: -: Grazing has a negative effect; +: Grazing has a positive effect; AGB: Aboveground biomass; BGB: Belowground biomass

在青藏高原北部高寒草地的研究结果显示, 围封使 CO_2 排放量减少 17.8%, CH_4 吸收量增加 33.8%。Luo 等^[62]也发现冬季围封会显著减少 CO_2 排放量约 20.1% ($P<0.05$)。围封虽然是恢复放牧退化草地的有效措施, 但长期(6 年以上)围封对土壤养分含量、地上植被生物量和多样性及土壤呼吸(微生物和根系呼吸)无显著影响^[63], 而且难以从根本上修复土壤结构, 减少温室气体排放量。综上可知, 短期围封禁牧有利于恢复轻、中度放牧退化草地, 减少温室气体排放量^[60]。

3 放牧对土壤微环境的影响

3.1 土壤

3.1.1 土壤结构

高寒草地放牧系统中家畜通过反复践踏压实表层土壤, 改变不同粒径土壤分布, 影响土壤水肥气热的供应、保持和调控能力^[64](图 1)。放牧对土壤结构的影响会阻碍植物根系延伸^[65]、降低土壤微生物呼吸速率和群落结构, 最终导致土壤 CO_2 排放速率降低、排放量减少($P<0.05$)^[66]。土壤 CH_4 吸收主要由深层土壤甲烷氧化菌群完成, 践踏增加土壤容重, 会减少 O_2 向土壤中扩散和 CH_4 向大气中扩散, 限制 CH_4 的氧化, 从而使 CH_4 吸收量减少^[60]。

3.1.2 土壤温度和湿度

土壤温度和湿度会因家畜践踏和啃食降低, 研究显示, 土壤温度和湿度与 CO_2 和 N_2O 排放呈正相关, 与 CH_4 吸收呈负相关^[67](图 1)。土壤湿度是决定高寒草地碳储量差异的主要驱动因子^[68], 土壤温度在时间和空间尺度上均影响温室气体排放^[69-70], 特别是表层土壤温湿度对温室气体排放的影响最明显^[70]。土壤湿度的增加通过刺激根系和微生物活动促进土壤呼吸, 增加温室气体排放; 土壤湿度的减少会降低微生物与有机基质接触, 导致植物根系死亡和/或失活^[71], 是土壤微生物功能基因变异的重要因素^[70]。

3.1.3 土壤养分

放牧因家畜啃食导致土壤养分含量减少, 因排

泄物返还会显著增加 NH_4^+-N 和 NO_3^--N 含量, 提高硝化和反硝化速率及促进硝酸盐淋失和 N_2O 排放^[72](图 1)。作为评价草地土壤质量和肥力的重要指标之一, 土壤养分(C、N 和 P)对维持土壤结构稳定和增强土壤恢复能力有重要作用^[26]。放牧通过影响高寒草地植物对养分的利用效率调节土壤 C、N 和 P 的生物地球化学循环, 作用于温室气体排放^[73]。研究发现, 放牧会减少高寒草地土壤有机碳和总氮含量^[73], 过度放牧因家畜采食减少了从植物凋落物向土壤输送的有机质, 导致土壤有机碳含量大大减少, 降低草地固碳能力^[74]。

3.2 土壤酶活性

土壤酶活性受土壤养分含量变化的影响较大, 围封禁牧和适度放牧有利于增强酶活性, 重度放牧抑制酶活性^[75]。土壤酶主要来自微生物, 部分来自植物和动物, 参与土壤生化反应和有机物分解^[76](图 1)。土壤酶活性是衡量微生物活性、土壤养分动态和质量变化的预警和敏感指标, 例如, 土壤纤维素酶和淀粉酶活性与土壤有机质、速效氮和地上生物量变化一致, 脲酶活性变化与之相反, 酸性磷酸酶活性与地下生物量变化一致^[77]。土壤酶活性可以快速响应放牧干扰^[78], 研究显示, 适度放牧会提高土壤 β -葡萄糖苷酶活性^[75], 而重度放牧会降低土壤 β -葡萄糖苷酶、过氧化氢酶、纤维素酶、蛋白酶、天冬酰胺酶和谷氨酰胺酶活性^[75]。家畜排泄物也会通过影响土壤理化性质和微生物区系对土壤酶活性产生明显影响^[79]。例如家畜排泄物通过提供足够的脲酶反应底物, 使其活性增强^[77]。Du 等^[80]发现围封通过向表层土壤提供微生物活性底物有机氮氮和溶解有机碳, 增强土壤主要酶(转化酶、磷酸酶、脲酶和 β -葡萄糖苷酶)活性。

3.3 放牧对土壤微生物的影响

3.3.1 微生物生物量

土壤微生物生物量碳通过对土壤胞外酶活性的影响间接驱动 CO_2 排放和 CH_4 吸收^[81]。土壤微生物生物量作为不稳定土壤有机质组成部分, 虽然只

占土壤有机质的 1%–5%，却是土壤活性的主要成分，控制着土壤养分转化，对土壤发生的细微变化反应迅速^[82]。表层土壤微生物量碳氮含量最高、受外界影响最大，土壤微生物生物量随土层深度增加而减少^[83]。放牧对土壤微生物生物量的影响较为复杂，有研究显示放牧强度增加会降低土壤微生物量^[84]，然而也有研究表明大量家畜排泄物输入和高强度放牧会刺激植物生长、增加土壤微生物生物量^[85]，且微生物生物量具有明显的夏季最大值和冬季最小值^[86]。也有研究发现，放牧与长期围封草地的土壤微生物量碳氮无显著差异^[87]。

3.3.2 微生物群落结构

放牧通过影响地上植被多样性、土壤有机碳、总氮和土壤水分含量，进而影响微生物群落组成、结构和多样性^[10-11]。研究显示高寒草地普遍呈中性偏碱，适宜细菌生长繁殖，不利于真菌生存，因此在高寒放牧草地生态系统中细菌数量最多，其次是放线菌和真菌^[88]。然而放牧强度对微生物群落结构有不同的影响，研究发现，在低放牧强度下放线菌和真菌丰度最高，而在高强度放牧条件下细菌丰度最高^[57]。适度放牧还可改变微生物生长环境，如家畜践踏促进植被凋落物进入土壤，增加土壤微生物作用底物，进而提高高寒草甸细菌群落多样性^[80]；但是过度放牧会严重降低植被生物量，改变植被群落特征，增加土壤容重和渗透阻力，并直接或间接改变草地生态系统的营养元素循环和能量转换模式，增加土壤碳氮流失，最终影响高寒草地碳氮分布格局，导致固碳能力下降，加速温室气体排放^[89]。由于高寒草地微生物群落结构与土壤有机碳($R=0.492$, $P<0.003$)、总氮($R=0.314$, $P<0.05$)和土壤水分($R=0.631$, $P<0.01$)等土壤理化性质显著正相关^[10]，因而过度放牧会显著降低细菌基因丰度和多样性指数($P<0.05$)。研究还发现青藏高原青海高寒草地放牧会显著降低微生物功能多样性^[8-11]，而且地下微生物多样性与地上植被多样性具有紧密联系($R=0.735$, $P=0.006$)^[8]，放牧通过家畜啃食减少地上生物量，降低微生物多样性。进一步研究发现放

牧会显著影响碳和氮循环基因，并从功能基因层面改变土壤微生物群落结构，例如，放牧使土壤氮矿化和硝化基因(*ureC*、*amoA* 和 *hao*)、惰性碳降解基因(*vdh*、*vanA*、*glx* 和 *lip*)丰度增加，而反硝化基因(*nirK*、*nirS*、*nosZ* 和 *norB*)、氮还原基因、氮固定(*nifH*)、氮降解基因、碳固定(*aclB* 和 *rubisco*)和活性碳降解基因(*amyA*、*nplT*、*pulA*、*pectinase*、*ara_fungi*、*mannanase* 和 *xylA*)及甲烷循环的基因(*pmoA*、*mcrA* 和 *mmoX*)的丰度降低^[7-8,10](表 1)。

4 总结与展望

本文主要综述了家畜种类(藏羊和牦牛)和放牧强度(轻度、适度和重度)对高寒草地温室气体(CO_2 、 CH_4 和 N_2O)排放的影响。高寒草地放牧生态系统是温室气体排放源。土壤微生物群落结构与土壤微环境(土壤养分、土壤容重、温度、湿度)之间存在复杂的作用关系^[68]，放牧通过采食、践踏和排泄行为影响以上土壤微环境因子，最终作用于微生物(微生物数量、生物量、群落结构和功能及酶活性等)，导致温室气体排放量增加^[8,11]。综上所述，建议在高寒草地植被生长期和生长旺盛期采取适度放牧措施的同时，在以下方面仍有待深入探索：

(1) 放牧对土壤微生物影响的研究尚处于初步阶段，关于放牧对高寒草地土壤微生物的影响机制仍存在许多问题尚待探索，如与产生/消耗温室气体相关的土壤微生物群落分布格局对放牧扰动的敏感度有何差异，以及放牧如何驱动与温室气体排放/吸收相关功能基因的变化。将新一代高通量测序技术、基因芯片(GeoChip)以及稳定性同位素标记技术应用到微生物学领域，有利于对高寒草地土壤微生物的进一步认识和研究。

(2) 目前尚不清楚高寒草地放牧如何影响地上植物和土壤微生物的耦合、互相影响及如何定量评价由此产生的温室气体对全球气候变化的贡献。开展植物根际微生物的共存网络和群体感应研究可以更好地认识和理解该机理，以及植物-微生物的互作反馈于土壤温室气体排放的分子机制。

(3) 尽管放牧对地上植被、土壤微生物及温室气体排放影响的野外原位研究在高寒草地生态系统中已取得一系列结果。在高寒草地生态系统中,放牧最先直接作用于地上植被和土壤环境,进而间接影响土壤微生物,放牧与地上植被及土壤微生物之间相互耦联、互相影响。然而现有研究多集中于对地上植被、土壤理化因子、土壤微生物等单个或2个因素对放牧的响应,而关于各因素之间的生态效应缺乏全面系统的评价。开展长期和系统的野外监测试验,从微观分子结构变化揭示温室气体排放的宏观功能过程变化,建立生态模型研究多个因素对放牧的响应及如何定量由此产生的温室气体对全球气候变化的贡献,将有利于采取有效措施减少高寒草地温室气体排放量。

REFERENCES

- [1] Guo X, Feng JJ, Shi Z, Zhou XS, Yuan MT, Tao X, Hale L, Yuan T, Wang JJ, Qin YJ, et al. Climate warming leads to divergent succession of grassland microbial communities[J]. *Nature Climate Change*, 2018, 8(9): 813-818
- [2] IPCC. Climate Change 2014 – Impacts, Adaptation and Vulnerability: Part B: Regional Aspects: Working Group II Contribution to the IPCC Fifth Assessment Report: Volume 2: Regional Aspects[M]. Cambridge: Cambridge University Press, 2014
- [3] Chu HY. Microbial communities in high latitudes and high altitudes ecosystems[J]. *Microbiology China*, 2013, 40(1): 123-136 (in Chinese)
褚海燕. 高寒生态系统微生物群落研究进展[J]. *微生物学通报*, 2013, 40(1): 123-136
- [4] Madaan S. Alpine biome: climate, location, plants and animals[Z]. 2019
- [5] Verrall B, Pickering CM. Alpine vegetation in the context of climate change: a global review of past research and future directions[J]. *Science of the Total Environment*, 2020, 748: 141344
- [6] Feng JJ, Wang C, Lei JS, Yang YF, Yan QY, Zhou XS, Tao XY, Ning DL, Yuan MM, Qin YJ, et al. Warming-induced permafrost thaw exacerbates tundra soil carbon decomposition mediated by microbial community[J]. *Microbiome*, 2020, 8(1): 3
- [7] Yang YF, Gao Y, Wang SP, Xu DP, Yu H, Wu LW, Lin QY, Hu YG, Li XZ, He ZL, et al. The microbial gene diversity along an elevation gradient of the Tibetan grassland[J]. *The ISME Journal*, 2014, 8(2): 430-440
- [8] Wang MM, Wang SP, Wu LW, Xu DP, Lin QY, Hu YG, Li XZ, Zhou JZ, Yang YF. Evaluating the lingering effect of livestock grazing on functional potentials of microbial communities in Tibetan grassland soils[J]. *Plant and Soil*, 2016, 407(1/2): 385-399
- [9] Yang YF. Dawn of microbial “Dark Matter” research[J]. *Microbiology China*, 2020, 47(9): 2683-2684 (in Chinese)
杨云锋. 微生物“暗物质”研究曙光[J]. *微生物学通报*, 2020, 47(9): 2683-2684
- [10] Yang YF, Wu LW, Lin QY, Yuan MT, Xu DP, Yu H, Hu YG, Duan JC, Li XZ, He ZL, et al. Responses of the functional structure of soil microbial community to livestock grazing in the Tibetan alpine grassland[J]. *Global Change Biology*, 2013, 19(2): 637-648
- [11] Sun X, Wang SP, Lin QY, Zhou JZ, Yang YF. Molecular ecological network analyses revealing the effects of livestock grazing on soil microbial community in the Tibetan grassland[J]. *Microbiology China*, 2015, 42(9): 1818-1831
- [12] Tveit A, Schwacke R, Svenning MM, Ulrich T. Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms[J]. *The ISME Journal*, 2013, 7(2): 299-311
- [13] Guo X, Zhou XS, Hale L, Yuan MT, Ning DL, Feng JJ, Shi Z, Li ZX, Feng B, Gao Q, et al. Climate warming accelerates temporal scaling of grassland soil microbial biodiversity[J]. *Nature Ecology & Evolution*, 2019, 3(4): 612-619
- [14] Guo N, Wang AD, Allan Degen A, Deng B, Shang ZH, Ding LM, Long RJ. Grazing exclusion increases soil CO₂ emission during the growing season in alpine meadows on the Tibetan Plateau[J]. *Atmospheric Environment*, 2018, 174: 92-98
- [15] Whitehead D, Schipper LA, Pronger J, Moinet GYK, Mudge PL, Calvelo Pereira R, Kirschbaum MUF, McNally SR, Beare MH, Camps-Arbestain M. Management practices to reduce losses or increase soil carbon stocks in temperate grazed grasslands: New Zealand as a case study[J]. *Agriculture, Ecosystems & Environment*, 2018, 265: 432-443
- [16] Zhao L, Li YN, Xu SX, Zhou HK, Gu S, Yu GR, Zhao XQ. Diurnal, seasonal and annual variation in net ecosystem CO₂ exchange of an alpine shrubland on Qinghai-Tibetan Plateau[J]. *Global Change Biology*, 2006, 12(10): 1940-1953
- [17] Li Y, Liu YW, Pan H, Hernández M, Guan XM, Wang W, Zhang QC, Luo Y, Di HJ, Xu JM. Impact of grazing on shaping abundance and composition of active methanotrophs and methane oxidation activity in a grassland soil[J]. *Biology and Fertility of Soils*, 2020, 56(6): 799-810
- [18] He D, Zhang LY, Dumont MG, He JS, Ren LJ, Chu HY. The response of methanotrophs to additions of either ammonium, nitrate or urea in alpine swamp meadow soil as revealed by stable isotope probing[J]. *FEMS Microbiology*

- Ecology, 2019, 95(7): fiz077
- [19] Li N, Wang GX, Yang Y, Gao YH, Liu GS. Plant production, and carbon and nitrogen source pools, are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau[J]. Soil Biology and Biochemistry, 2011, 43(5): 942-953
- [20] Sun BG. Study on CO₂ and CH₄ fluxes from soil-plant systems of alpine grassland under different degrees of degradation in the source area of Yellow River[D]. Lanzhou: Doctoral Dissertation of Gansu Agricultural University, 2008 (in Chinese)
孙步功. 黄河源区不同退化程度高寒草地 CO₂、CH₄ 通量研究[D]. 兰州: 甘肃农业大学博士学位论文, 2008
- [21] Chang XF, Zhu XX, Wang SP, Cui SJ, Luo CY, Zhang ZH, Wilkes A. Impacts of management practices on soil organic carbon in degraded alpine meadows on the Tibetan Plateau[J]. Biogeosciences, 2014, 11(13): 3495-3503
- [22] Kirschke S, Bousquet P, Ciais P, Saunois M, Canadell JG, Dlugokencky EJ, Bergamaschi P, Bergmann D, Blake DR, Bruhwiler L, et al. Three decades of global methane sources and sinks[J]. Nature Geoscience, 2013, 6(10): 813-823
- [23] Wei D, Xu-Ri, Liu YW, Wang YH, Wang YS. Three-year study of CO₂ efflux and CH₄/N₂O fluxes at an alpine steppe site on the central Tibetan Plateau and their responses to simulated N deposition[J]. Geoderma, 2014, 232/233/234: 88-96
- [24] Savvichev AS, Rusanov II, Kadnikov VV, Beletskii AV, Ravin NV, Pimenov NV. Microbial community composition and rates of the methane cycle microbial processes in the upper sediments of the Yamal sector of the southwestern Kara Sea[J]. Microbiology, 2018, 87(2): 238-248
- [25] Brachmann CG, Hernandez-Ramirez G, Hik DS. CH₄ uptake along a successional gradient in temperate alpine soils[J]. Biogeochemistry, 2020, 147(2): 109-123
- [26] Broucek J. Nitrous oxide production in ruminants: a review[J]. Animal Science Papers and Reports, 2018, 36(1): 5-19
- [27] Wang JY, Li YM, Bork EW, Richter GM, Eum HI, Chen CC, Shah SHH, Mezbahuddin S. Modelling spatio-temporal patterns of soil carbon and greenhouse gas emissions in grazing lands: current status and prospects[J]. Science of the Total Environment, 2020, 739: 139092
- [28] Di HJ, Cameron KC, Shen JP, Winefield CS, O'Callaghan M, Bowatte S, He JZ. Nitrification driven by bacteria and not archaea in nitrogen-rich grassland soils[J]. Nature Geoscience, 2009, 2(9): 621-624
- [29] Zhang ZX, Hua L, Yin XX, Hua LP, Gao J. Nitrous oxide emission from agricultural soil and some influence factors[J]. Journal of Capital Normal University, 2005, 26(3): 114-120 (in Chinese)
张振贤, 华璐, 尹逊霄, 滑丽萍, 高娟. 农田土壤 N₂O 的发生机制及其主要影响因素[J]. 首都师范大学学报: 自然科学版, 2005, 26(3): 114-120
- [30] Di HJ, Cameron KC, Podolyan A, Robinson A. Effect of soil moisture status and a nitrification inhibitor, dicyandiamide, on ammonia oxidizer and denitrifier growth and nitrous oxide emissions in a grassland soil[J]. Soil Biology and Biochemistry, 2014, 73: 59-68
- [31] Gao XL, Thomas BW, Beck R, Thompson DJ, Zhao ML, Willms WD, Hao XY. Long-term grazing alters soil trace gas fluxes from grasslands in the foothills of the rocky mountains, Canada[J]. Land Degradation & Development, 2018, 29(2): 292-302
- [32] Fang JY, Yang YH, Ma WH, Mohammad A, Shen HH. Ecosystem carbon stocks and their changes in China's grasslands[J]. Science China Life Sciences, 2010, 53(7): 757-765 (in Chinese)
方精云, 杨元合, 马文红, 安尼瓦尔·买买提, 沈海花. 中国草地生态系统碳库及其变化[J]. 中国科学: 生命科学, 2010, 40(7): 566-576
- [33] Wu HB, Wang XX, Ganjurjav H, Hu GZ, Qin XB, Gao QZ. Effects of increased precipitation combined with nitrogen addition and increased temperature on methane fluxes in alpine meadows of the Tibetan Plateau[J]. The Science of the Total Environment, 2020, 705: 135818
- [34] Zhang YF, Ma AZ, Zhuang GQ, Zhuang XL. The acetotrophic pathway dominates methane production in Zoige alpine wetland coexisting with hydrogenotrophic pathway[J]. Scientific Reports, 2019, 9(1): 9141
- [35] Zhang QW, Yang GB, Song YT, Kou D, Wang GQ, Zhang DY, Qin SQ, Mao C, Feng XH, Yang YH. Magnitude and drivers of potential methane oxidation and production across the Tibetan alpine permafrost region[J]. Environmental Science & Technology, 2019, 53(24): 14243-14252
- [36] Imer D, Merbold L, Eugster W, Buchmann N. Temporal and spatial variations of soil CO₂, CH₄ and N₂O fluxes at three differently managed grasslands[J]. Biogeosciences, 2013, 10(9): 5931-5945
- [37] Xiao R. Effects of long-term fertilization on the community structure diversity of prokaryotic microbes and ammonia oxidizers in the alpine meadow soil on Tibet plateau[D]. Lanzhou: Master's Thesis of Lanzhou University, 2012 (in Chinese)
肖蕊. 施肥对高寒草甸土壤中原核微生物及氨氧化菌的群落结构多样性影响研究[D]. 兰州: 兰州大学硕士学位论文, 2012
- [38] Ruser R, Schulz R. The effect of nitrification inhibitors on the nitrous oxide (N₂O) release from agricultural soils: a review[J]. Journal of Plant Nutrition and Soil Science, 2015, 178(2): 171-188
- [39] Gao XL. Study on the effect of grazing on greenhouse gas emissions in grassland soil[D]. Hohhot: Doctoral

- Dissertation of Inner Mongolia Agricultural University, 2017 (in Chinese)
 高新磊. 放牧对草原土壤温室气体排放影响的研究[D]. 呼和浩特: 内蒙古农业大学博士学位论文, 2017
- [40] Dai Y, Di HJ, Cameron KC, He JZ. Effects of nitrogen application rate and a nitrification inhibitor dicyandiamide on ammonia oxidizers and N₂O emissions in a grazed pasture soil[J]. *Science of the Total Environment*, 2013, 465: 125-135
- [41] Du YG, Cui YG, Xu XL, Liang DY, Long RJ, Cao GM. Nitrous oxide emissions from two alpine meadows in the Qinghai-Tibetan Plateau[J]. *Plant and Soil*, 2008, 311(1): 245-254
- [42] Chen H, Zhu QA, Peng CH, Wu N, Wang YF, Fang XQ, Gao YH, Zhu D, Yang G, Tian JQ, et al. The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau[J]. *Global Change Biology*, 2013, 19(10): 2940-2955
- [43] Lin XW, Wang SP, Ma XZ, Xu GP, Luo CY, Li YN, Jiang GM, Xie ZB. Fluxes of CO₂, CH₄, and N₂O in an alpine meadow affected by yak excreta on the Qinghai-Tibetan Plateau during summer grazing periods[J]. *Soil Biology and Biochemistry*, 2009, 41(4): 718-725
- [44] Peng YF, Wang GQ, Li F, Zhou GY, Yang GB, Fang K, Liu L, Qin SQ, Zhang DY, Yang YH. Soil temperature dynamics modulate N₂O flux response to multiple nitrogen additions in an alpine steppe[J]. *Journal of Geophysical Research: Biogeosciences*, 2018, 123(10): 3308-3319
- [45] Kong Z. The primary study on CO₂ and CH₄ emission from soil-plant systems of 'Black soil patch' degraded alpine meadow in the source area of Yellow River[D]. Lanzhou: Master's Thesis of Gansu Agricultural University, 2007 (in Chinese)
 孔郑. 黄河源区“黑土型”退化高寒草地 CO₂、CH₄ 排放特征研究[D]. 兰州: 甘肃农业大学硕士学位论文, 2007
- [46] Hirota M, Tang YH, Hu QW, Kato T, Hirata S, Mo WH, Cao GM, Mariko S. The potential importance of grazing to the fluxes of carbon dioxide and methane in an alpine wetland on the Qinghai-Tibetan Plateau[J]. *Atmospheric Environment*, 2005, 39(29): 5255-5259
- [47] Li KH, Gong YM, Song W, Lv JL, Chang YH, Hu YK, Tian CY, Christie P, Liu XJ. No significant nitrous oxide emissions during spring thaw under grazing and nitrogen addition in an alpine grassland[J]. *Global Change Biology*, 2012, 18(8): 2546-2554
- [48] Du YG, Shu K, Guo XW, Zhu PJ. Moderate grazing promotes grassland nitrous oxide emission by increasing ammonia-oxidizing archaea abundance on the Tibetan Plateau[J]. *Current Microbiology*, 2019, 76(5): 620-625
- [49] Cai YJ, Wang XD, Tian LL, Zhao H, Lu XY, Yan Y. The impact of excretal returns from yak and Tibetan sheep dung on nitrous oxide emissions in an alpine steppe on the Qinghai-Tibetan Plateau[J]. *Soil Biology and Biochemistry*, 2014, 76: 90-99
- [50] Yang XX, Dong QM, Chu H, Ding CX, Yu Y, Zhang CP, Zhang YF, Yang ZZ. Different responses of soil element contents and their stoichiometry (C:N:P) to yak grazing and Tibetan sheep grazing in an alpine grassland on the eastern Qinghai-Tibetan Plateau[J]. *Agriculture, Ecosystems & Environment*, 2019, 285: 106628
- [51] Holter P. Concentration of oxygen, carbon dioxide and methane in the air within dung pats[J]. *Pedobiologia*, 1991, 35: 381-386
- [52] Cai YJ, Wang XD, Ding WX, Tian LL, Zhao H, Lu XY. Potential short-term effects of yak and Tibetan sheep dung on greenhouse gas emissions in two alpine grassland soils under laboratory conditions[J]. *Biology and Fertility of Soils*, 2013, 49(8): 1215-1226
- [53] Tang SM, Wang K, Xiang YZ, Tian DS, Wang JS, Liu YS, Cao B, Guo D, Niu SL. Heavy grazing reduces grassland soil greenhouse gas fluxes: a global meta-analysis[J]. *Science of the Total Environment*, 2019, 654: 1218-1224
- [54] Derner JD, Briske DD, Boutton TW. Does grazing mediate soil carbon and nitrogen accumulation beneath C₄ perennial grasses along an environmental gradient?[J]. *Plant and Soil*, 1997, 191(2): 147-156
- [55] Gao XF, Wu CY, Han GD. Steppe soil microorganisms is impacted by the grazing and their seasonal changes[J]. *Microbiology China*, 2010, 37(8): 1117-1122 (in Chinese)
 高雪峰, 武春燕, 韩国栋. 草原土壤微生物受放牧的影响及其季节变化[J]. *微生物学通报*, 2010, 37(8): 1117-1122
- [56] Goenster-Jordan S, Ingold M, Jannoura R, Buerkert A, Joergensen RG. Soil microbial properties of subalpine steppe soils at different grazing intensities in the Chinese Altai Mountains[J]. *Scientific Reports*, 2021, 11: 1653
- [57] Zhang JX, Cao GM, Zhou DW, Zhao XQ. The rate of carbon dioxide release from alpine scrubby meadow soil under different grazing intensity[J]. *Acta Agrestia Sinica*, 2001, 9(3): 183-190 (in Chinese)
 张金霞, 曹广民, 周党卫, 赵新全. 放牧强度对高寒灌丛草甸土壤 CO₂ 释放速率的影响[J]. *草地学报*, 2001, 9(3): 183-190
- [58] Xie Z, Le Roux X, Wang CP, Gu ZK, An M, Nan HY, Chen BZ, Li F, Liu YJ, Du GZ, et al. Identifying response groups of soil nitrifiers and denitrifiers to grazing and associated soil environmental drivers in Tibetan alpine meadows[J]. *Soil Biology and Biochemistry*, 2014, 77: 89-99
- [59] Zhu XX, Luo CY, Wang SP, Zhang ZH, Cui SJ, Bao XY, Jiang LL, Li YM, Li XE, Wang Q, et al. Effects of warming, grazing/cutting and nitrogen fertilization on greenhouse gas fluxes during growing seasons in an alpine meadow on the Tibetan Plateau[J]. *Agricultural and Forest Meteorology*,

- 2015, 214/215: 506-514
- [60] Wei D, Xu R, Wang YH, Wang YS, Liu YW, Yao TD. Responses of CO₂, CH₄ and N₂O fluxes to livestock enclosure in an alpine steppe on the Tibetan Plateau, China[J]. Plant and Soil, 2012, 359(1): 45-55
- [61] Dong SK, Shang ZH, Gao JX, Boone RB. Enhancing sustainability of grassland ecosystems through ecological restoration and grazing management in an era of climate change on Qinghai-Tibetan Plateau[J]. Agriculture, Ecosystems & Environment, 2020, 287: 106684
- [62] Luo CY, Wang SP, Zhang LR, Wilkes A, Zhao L, Zhao XQ, Xu SX, Xu B. CO₂, CH₄ and N₂O fluxes in an alpine meadow on the Tibetan Plateau as affected by N-addition and grazing exclusion[J]. Nutrient Cycling in Agroecosystems, 2020, 117(1): 29-42
- [63] Zhao XX, Li YL, Xie ZM, Li P. Effects of nitrogen deposition and plant litter alteration on soil respiration in a semiarid grassland[J]. Science of the Total Environment, 2020, 740: 139634
- [64] Wei D, Zhao H, Zhang JX, Qi YH, Wang XD. Human activities alter response of alpine grasslands on Tibetan Plateau to climate change[J]. Journal of Environmental Management, 2020, 262: 110335
- [65] Sun J, Ma BB, Lu XY. Grazing enhances soil nutrient effects: trade-offs between aboveground and belowground biomass in alpine grasslands of the Tibetan Plateau[J]. Land Degradation & Development, 2018, 29(2): 337-348
- [66] Chai JL, Yu XJ, Xu CL, Xiao H, Zhang JW, Yang HL, Pan TT. Effects of yak and Tibetan sheep trampling on soil properties in the northeastern Qinghai-Tibetan Plateau[J]. Applied Soil Ecology, 2019, 144: 147-154
- [67] McSherry ME, Ritchie ME. Effects of grazing on grassland soil carbon: a global review[J]. Global Change Biology, 2013, 19(5): 1347-1357
- [68] Chu HJ, Wang SP, Yue HW, Lin QY, Hu YG, Li XZ, Zhou JZ, Yang YF. Contrasting soil microbial community functional structures in two major landscapes of the Tibetan alpine meadow[J]. MicrobiologyOpen, 2014, 3(5): 585-594
- [69] Lin XW, Wang SP, Hu YG, Luo CY, Zhang ZH, Niu HS, Xie ZB. Experimental warming increases seasonal methane uptake in an alpine meadow on the Tibetan Plateau[J]. Ecosystems, 2015, 18(2): 274-286
- [70] Yue HW, Wang MM, Wang SP, Gilbert JA, Sun X, Wu LW, Lin QY, Hu YG, Li XZ, He ZL, et al. The microbe-mediated mechanisms affecting topsoil carbon stock in Tibetan grasslands[J]. The ISME Journal, 2015, 9(9): 2012-2020
- [71] Ondier J, Okach DO, John OC, Otieno DO. Influence of rainfall amount and livestock grazing on soil respiration in a moist Kenyan savannah[J]. African Journal of Ecology, 2020, 58(1): 92-99
- [72] Tian LH, Bai YF, Wang WW, Qu GP, Deng ZH, Li RC, Zhao JX. Warm- and cold-season grazing affect plant diversity and soil carbon and nitrogen sequestration differently in Tibetan alpine swamp meadows[J]. Plant and Soil, 2021, 458(1/2): 151-164
- [73] Lu XY, Kelsey KC, Yan Y, Sun J, Wang XD, Cheng GW, Neff JC. Effects of grazing on ecosystem structure and function of alpine grasslands in Qinghai-Tibetan Plateau: a synthesis[J]. Ecosphere, 2017, 8(1): e01656
- [74] Eyles A, Coghlan G, Hardie M, Hovenden M, Bridle K. Soil carbon sequestration in cool-temperate dryland pastures: mechanisms and management options[J]. Soil Research, 2015, 53(4): 349
- [75] Sun G, Zhu-Barker X, Chen DM, Liu L, Zhang NN, Shi CG, He LP, Lei YB. Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: an implication for pasture management[J]. Plant and Soil, 2017, 416(1/2): 515-525
- [76] Xu ZC, Song YT, Wu YN, Huo GW, Wang XM, Dao RN. Effect of grazing intensities on soil enzyme activities and soil microbial biomass of *Stipa krylovii* steppe in different phenological periods[J]. Chinese Journal of Ecology, 2016, 35(8): 2022-2028 (in Chinese)
徐志超, 宋彦涛, 乌云娜, 霍光伟, 王晓朦, 道日娜. 放牧影响下克氏针茅草原不同物候期土壤酶活性与微生物生物量的变化[J]. 生态学杂志, 2016, 35(8): 2022-2028
- [77] Tan YR, Du GZ, Chen DD, Sun DS, Zhang SH, Wang XT. Impact of grazing on the activities of soil enzymes and soil nutrient factors in an alpine meadow on the Qinghai-Tibetan Plateau[J]. Journal of Lanzhou University: Natural Sciences, 2012, 48(1): 86-91 (in Chinese)
谈嫣蓉, 杜国祯, 陈懂懂, 孙大帅, 张世虎, 王向涛. 放牧对青藏高原东缘高寒草甸土壤酶活性及土壤养分的影响[J]. 兰州大学学报: 自然科学版, 2012, 48(1): 86-91
- [78] Prieto LH, Bertiller MB, Carrera AL, Olivera NL. Soil enzyme and microbial activities in a grazing ecosystem of Patagonian Monte, Argentina[J]. Geoderma, 2011, 162(3/4): 281-287
- [79] Wang LD, Wang FL, Guo CX, Han FG, Wei LY, Li FM. Review: progress of soil enzymology[J]. Soils, 2016, 48(1): 12-21 (in Chinese)
王理德, 王方琳, 郭春秀, 韩福贵, 魏林源, 李发明. 土壤酶学研究进展[J]. 土壤, 2016, 48(1): 12-21
- [80] Du CJ, Jing J, Shen Y, Liu HX, Gao YH. Short-term grazing exclusion improved topsoil conditions and plant characteristics in degraded alpine grasslands[J]. Ecological Indicators, 2020, 108: 105680
- [81] Shrestha BM, Bork EW, Chang SX, Carlyle CN, Ma ZL, Döbert TF, Kaliaskar D, Boyce MS. Adaptive multi-paddock grazing lowers soil greenhouse gas emission potential by altering extracellular enzyme activity[J]. Agronomy, 2020, 10(11): 1781
- [82] Holt JA. Grazing pressure and soil carbon, microbial

- biomass and enzyme activities in semi-arid northeastern Australia[J]. *Applied Soil Ecology*, 1997, 5(2): 143-149
- [83] Fu G, Shen ZX, Zhang XZ, Zhou YT, Zhang YJ. Response of microbial biomass to grazing in an alpine meadow along an elevation gradient on the Tibetan Plateau[J]. *European Journal of Soil Biology*, 2012, 52: 27-29
- [84] Yang ZA. A study on the responses of vegetation-soil system to grazing and nitrogen addition in an alpine meadow of Qinghai-Tibetan Plateau, China[D]. Yangling: Doctoral Dissertation of Northwest A & F University, 2017 (in Chinese)
杨振安. 青藏高原高寒草甸植被土壤系统对放牧和氮添加的响应研究[D]. 杨凌: 西北农林科技大学博士学位论文, 2017
- [85] Wang Y, Duan WX, Tu C, Washburn S, Cheng L, Hu S. Soil carbon, nitrogen and microbial dynamics of pasturelands: impacts of grazing intensity and planting systems[J]. *Pedosphere*, 2014, 24(3): 408-416
- [86] Bardgett RD, Hobbs PJ, Frostegård Å. Changes in soil fungal: bacterial biomass ratios following reductions in the intensity of management of an upland grassland[J]. *Biology and Fertility of Soils*, 1996, 22(3): 261-264
- [87] Yuan ZQ, Epstein H, Li GY. Grazing exclusion did not affect soil properties in alpine meadows in the Tibetan permafrost region[J]. *Ecological Engineering*, 2020, 147: 105657
- [88] Xun WB, Yan RR, Ren Y, Jin DY, Xiong W, Zhang GS, Cui ZL, Xin XP, Zhang RF. Grazing-induced microbiome alterations drive soil organic carbon turnover and productivity in meadow steppe[J]. *Microbiome*, 2018, 6(1): 170
- [89] Lin XW, Zhang ZH, Wang SP, Hu YG, Xu GP, Luo CY, Chang XF, Duan JC, Lin QY, Xu B, et al. Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan Plateau[J]. *Agricultural and Forest Meteorology*, 2011, 151(7): 792-802