放牧对草地生态系统磷循环调控机制的研究进展与展望

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摘要 放牧是全球范围内草地生态系统最主要和最直接的利用方式. 磷(P)是植物生长所必需的大量元素, 同时也是草地初级生产力的关键限制性养分元素, 广泛参与植物的光合、呼吸等重要代谢过程. 放牧通过直接和间接作用影响草地植物和土壤各组分P含量和P库, 进而通过正负两种反馈影响生态系统的P循环. 目前, 国内外有关放牧对草地P循环的影响机制, 特别是P循环的生物学过程和机制尚不十分清楚. 本文总结了有关放牧对植物和土壤各组分P含量及P库的影响及其机制, 并对该领域的几个重要研究方向和亟待回答的科学问题进行了展望. 未来研究中需要重点关注的问题包括: (1) 土壤微生物量P组成沿不同放牧强度的变化, 以及放牧对土壤微生物P源和汇的影响机制; (2) 放牧如何影响土壤磷酸酶的活性(磷酸单酯酶、磷酸二酯酶、三磷酸单酯水解酶等)进而调控土壤中P的矿化过程; (3) 放牧如何调控P在植物-土壤-微生物系统中的转化过程; (4) 采用分子生物学和组学的手段, 揭示土壤微生物在P循环及生态系统功能中的作用, 以及放牧如何影响植物和根际微生物, 进而调控生态系统P循环; (5) 不同放牧强度如何影响植物多样性、菌根真菌多样性及两者之间的关系, 进而影响植物对P的吸收和利用, 以及地上和地下生物量P库; (6) 不同家畜种类的食性差异及其对磷循环的影响机制; (7) 其他植食动物(野生食草动物、植食昆虫、啮齿动物、蚯蚓、植食性线虫等)在草地生态系统P循环中的作用; (8) 不同放牧强度如何调控生态系统各营养级组分的N:P化学计量关系, 进而影响N、P循环之间的耦合关系.

关键词 放牧生态系统, 磷循环, 磷含量, 磷库, N:P比, 磷限制

草地是陆地生态系统的重要组成部分, 世界草地总面积为52.5亿公顷, 约占地球陆地总面积的40.5%(不包括格陵兰岛和南极)^[1]. 放牧是全球范围内草地生态系统最主要和最直接的利用方式, 对生态系统功能和服务的维持具有重要的调控作用^[2]. 据统计, 由于长期超载放牧我国草地90%发生了不同程度的退化, 其中重度退化草地比例达60%左右^[3]. 过度放牧引起的草地退化使生态系统功能(如初级生产力、养分循环等)和服

务(如水土保持、碳固持)显著降低^[4,5]. 磷(P)作为植物生长和繁殖的必需元素, 广泛参与有机体的光合和呼吸等代谢过程, 同时也是组成DNA、RNA、ATP等生物分子以及细胞核和细胞膜的关键元素, 在生态系统物质循环和能量流动过程中起到了重要作用^[6].

生态系统养分循环包括生态系统的养分输入和输出以及养分元素在生态系统内生物(植物、微生物和消费者)和非生物组分之间的移动^[7]. 陆地生态系统中,

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植被生产力通常受N、P或两者共同限制, N、P循环之间的耦合关系非常密切^[7]. 近年来, 生态系统氮(N)循环受到了广泛的重视, 研究人员开展了大量的研究工作. 然而, 同N循环相比, P循环的研究相对较少, 尤其是放牧对草地P循环影响的研究十分有限^[8]. 例如, 早期研究认为, 水分和氮是干旱、半干旱地区生态系统初级生产力的主要限制因子^[9,10], 但近年来一些研究发现, P似乎比N对初级生产力的限制作用更强^[8]. 大量研究表明, 施肥、氮沉降、种植固氮植物等人类活动的加剧, 加速了陆地生态系统的N循环^[7,11], 使土壤中的N的含量及其有效性增加^[12], 进而使P的相对限制性增加^[8,13,14]. 然而, 与N循环不同, P循环属于相对封闭的沉积型循环, 其周转时间为 $10^7 \sim 10^8$ 年. 在成土过程中, 土壤中的P会随着植物的利用和人类的开采而不断消耗. 因此, 从某种意义上讲P属于地球上的不可再生资源, P必将取代N成为植物生长和生态系统功能和服务维持的主要限制因子^[8,15]. 目前, 由于不合理的开发和利用已经造成P资源的相对枯竭, 据初步估计在21世纪中叶地球上50%的廉价P将被耗竭^[16].

草地生态系统中, 放牧主要通过采食、践踏和粪尿返还等方式影响养分循环过程^[17~22]. 在较短的时间尺度, 磷循环主要发生在生态系统内植物、动物和土壤组分之间, 植物、动物和土壤微生物的生理生态过程控制着磷在土壤和生物体内的移动和形态转化^[7]. 目前已有的研究主要集中在放牧对草地土壤和植物P含量及P库的影响, 结果存在较大差异, 影响机制尚不十分清楚(图1). 为此, 本研究在查阅相关文献的基础上, 从三个方面对已有的研究进行总结, 并对未来研究重点进行展望: (1) 放牧对草地生态系统P元素内外循环

的影响; (2) 从土壤P的垂直分布、输入与输出、土壤侵蚀和空间异质性四个方面讨论放牧对土壤P含量和P库的影响; (3) 放牧对不同组织水平(个体、物种、植物功能群、群落)植物P含量和P库的影响机制; (4) 草地磷循环研究展望.

1 放牧对草地生态系统磷元素内外循环的影响

植物在生长发育过程中所需的P主要来源于土壤, 但同C、N等元素相比, 土壤中的P含量很低, 仅占土壤总质量的0.02%~0.2%^[23]. 我国土壤P含量为 $0.17 \sim 1.11 \text{ g kg}^{-1}$, 受成土母质的影响我国北方草地属于严重缺P地区, 土壤中的P绝大部分以无效P的形式存在, 土壤有机质是生态系统最主要的P库^[24,25].

草地生态系统中, P的输入方式主要包括大气干沉降^[26]、母质风化^[27]和降水^[28], 输出方式主要包括地表径流^[29]、风蚀^[30,31]和淋溶^[32]等途径. 在放牧系统中, 畜产品的N、P输出往往是不可忽视的重要途径^[17,18]. 生态系统中, P最初都来源于岩石矿物的风化作用, 但该过程十分缓慢, 一般通过风化作用进入生态系统的P为 $0.05 \sim 1.0 \text{ kg hm}^{-2} \text{ a}^{-1}$, 有些地区可以达到 $5.0 \text{ kg hm}^{-2} \text{ a}^{-1}$. 风化速率通常与土壤母质、气候、地形、植被覆盖等非生物和生物因素有关, 生态系统中土壤风化主要是风而非水的作用^[27]. 在干旱、半干旱草原, 水分是主要的限制因子, 因此通过降雨、淋溶的方式输入和输出生态系统的P均相对较少, 而大气干沉降和风蚀是影响草地生态系统P输入和输出的关键因子^[30,33~35]. 研究表明, 干沉降和风蚀往往是同时发生的, 因此土壤P的输入和输出也同时发生, 它们共同受植被覆盖度和高

图1 放牧对草地生态系统磷循环影响的概念图

Figure 1 A conceptual diagram for the influence of grazing on P cycle in grassland ecosystems

度^[26]、地形^[31]、放牧强度等^[36]因素影响。例如,内蒙古草原由于春季受到风的强烈影响,干沉降可达 $7 \text{ kg P ha}^{-1} \text{ a}^{-1}$ ^[37],有些地区甚至可以达到 $9 \text{ kg P ha}^{-1} \text{ a}^{-1}$ ^[38],其中放牧强度起到关键的调控作用,甚至可以改变土壤沉降或侵蚀的方向^[30]。Zhou等人^[39]对全球443篇文献进行Meta分析发现,草地生态系统中P的输入和输出量分别为 $0.001\sim 13.9$ 和 $0.001\sim 12.7 \text{ kg P ha}^{-1}$,二者的变化范围大致相同。He等人^[40]进一步研究发现,在全球尺度上,放牧显著增加了植物叶片、茎、根系、凋落物P库,使土壤P库增加3.6%。

放牧对P在生态系统内循环的影响主要表现为:(1)改变植物群落的物种组成,植物与菌根真菌之间的互惠共生关系,影响植物对土壤P的吸收利用,以及植物对P的重吸收^[41-45]; (2)改变群落生物量的大小及其在地上/地下部分的分配比例、凋落物的数量和质量,以及放牧家畜的粪尿返还,影响土壤P的输入和家畜生物量输出,进而影响生态系统各组分P库的大小以及P循环速率^[17,41,43,46]; (3)改变小气候、光的有效性和土壤水分状况,影响土壤微生物活性,进而影响土壤有机质的矿化和P循环^[6,47-49]。近期研究发现,干湿交替增加了土壤P的有效性,有利于干旱忍耐型植物对P的利用^[50]; (4)改变生态系统中植物-土壤动物-土壤微生物之间调控与反馈关系、养分限制和养分平衡^[15,51],特别是P与C、N的化学计量关系,以及P循环与C、N循环之间的耦合关系^[14,52-54]。

2 放牧对土壤磷的影响

2.1 放牧对土壤磷含量垂直分布的影响

土壤P缺乏是我国北方草原面临的共性问题。汪卫卫^[55]对松嫩草地的研究发现,没有放牧的草地,土壤全磷的垂直分布格局呈先降低后增加的趋势,表层土壤的全P含量为 0.27 g kg^{-1} ,最小值出现在70 cm土层,全P含量仅为 0.08 g kg^{-1} ;放牧条件下,只有重度放牧会降低土壤表层全P含量,轻度和中度放牧的草地土壤P含量随土层深度的增加而降低。李香真^[56]对内蒙古羊草草原的研究发现,放牧使0~100 cm的土壤P储量降低了21%,P储量随土层深度增加而降低。李耀等人^[57]对内蒙古典型草原的研究也得出了类似的结果,不同土层中全P含量均表现为禁牧>自由放牧>轮牧,在不同利用方式中P含量均随土层深度增加而降低。郭颖^[58]对青藏高原不同植被类型土壤表层全P含量的研究表明,全P

含量为 $0.12\sim 1.11 \text{ g kg}^{-1}$,草地、高寒草甸和高山草原的土壤全P含量一般随土层深度的增加而降低。尽管放牧对不同草地类型土壤P含量和P库的影响目前仍然没有一致性的结论,但放牧通过改变风蚀、水蚀、凋落物、植物根系分布、粪尿返还等,影响表层土壤微生物活性以及植物和微生物对P的吸收和周转^[59,60],进而影响表层土壤的P含量和P库。特别是长期重度放牧,使表层土壤的风蚀和水蚀增加,凋落物显著降低,植物根系分布浅层化,粪尿返还量显著增加^[26,41,46,61]。

放牧草地中,受植物残体、放牧家畜粪尿返还以及土壤有机质长期积累的影响,土壤有效P(如Olsen P)含量一般随土层深度的增加而显著降低^[62]。家畜排泄出的P绝大部分以粪便的形式存在,其P含量远远高于饲草中的P含量。例如,绵羊粪便中的全P含量为 8 g kg^{-1} ,牛粪便中的全P含量为 5.5 g kg^{-1} ;同时,新鲜粪便中的P含量显著高于干燥粪便中P含量^[63]。粪便中的P大约20%为植物可以利用的无机态P,而粪便中的有机态P则需要经过微生物分解后才能缓慢地被植物利用^[63,64]。Baron等人^[46]对人工草地的研究发现,由于家畜的粪尿返还作用,放牧显著增加了表层土壤的可提取P含量(extractable P concentration),0~15 cm土壤的可提取P含量在重度放牧下最高,中度放牧下次之,轻度放牧下最低。因此,重度放牧下,家畜的粪便返还增加了P的流动,进而加速了表层土壤的P循环。

2.2 放牧对土壤磷含量及磷输入和输出的影响

在放牧系统中,家畜对草地的利用驱动着物质循环和能量流动,放牧通过采食、粪尿排泄以及畜产品的输出等方式改变了植物-土壤的反馈作用,对土壤产生正、负两种反馈机制影响土壤P含量。一些研究发现,围栏禁牧阻止了家畜采食,减少了能量和养分从生态系统的输出,增加了土壤的P含量。在物质输出方面,由于植物固定了大量养分,禁牧可以有效减少物质和能量从土壤-植物系统到消费者的输出^[65],而放牧家畜以皮、毛、肉、奶、粪尿等形式将N、P输出生态系统^[17,18],持续高强度的放牧增加了P的输出量和输出速率,降低了土壤P含量及其P储量。在物质输入方面,放牧通过改变输入系统的凋落物数量和质量进而减缓了养分循环^[19]。许多研究表明,在干旱、半干旱草原,放牧对地上生物量和地下生物量均有显著的负效应^[41,52,61,66]。一些研究发现,放牧改变了植物群落结构和物种组成^[5,41,67],显著降低了地上生物量的养分含

量^[68],进而对凋落物和根系分解产生抑制作用,减缓了P返还生态系统的数量和速率.放牧还可以通过植物-土壤-家畜间的正反馈作用增加土壤的磷含量.研究表明,放牧系统中,家畜从生态系统中获取P,但家畜未能同化吸收的养分绝大部分都以粪尿的形式返还土壤^[17,69].由于P的移动性差,被固定后很少向土壤深层迁移,家畜排泄后P又重新与土壤中的Fe、Al、Ca等元素结合形成难溶性络合物,或吸附于土壤胶体中^[8],使P在土壤表层中富集,增加了土壤表层的P含量.李香真^[56]研究认为,放牧家畜的践踏作用使表层土壤容重增加,限制了水分和养分的垂直移动,动物排泄物的输入使表层土壤速效养分增加.这些因素使根系向土壤表层分配的比例增加,表现为根系浅层化现象,因此表层土壤的有机碳、磷在一定的阶段内可以维持原有水平或高于原有水平^[56].进一步研究发现,尽管在干旱、半干旱地区,适度放牧增加了植物群落地上生物量^[70]和养分含量^[71],促进了土壤-植物间的正反馈作用^[19],而且适度的践踏可以加速凋落物的破碎化,减少凋落物的现存量,增加分解的表面积^[72],加速P返还生态系统的速率.

风蚀不仅破坏土壤的结构,对草地初级生产力维持具有负面影响,同时也是引起草地退化的主要机制^[31,73].在放牧系统中,土壤侵蚀是导致表层土壤P含量发生变化的主要因素^[35].放牧主要通过家畜采食影响植被盖度和高度,进而改变土壤风蚀和水蚀过程.由于受到风的强烈影响,我国北方地区土壤风蚀和干沉降往往是同时发生的,这两个过程很难分开^[26],放牧强度对这两个过程起到关键的调控作用,甚至可改变其方向^[30].在放牧强度较低或禁牧状态下,群落具有较高的植被高度和盖度,增加了地表的粗糙度,这不仅可以有效地减少风蚀引起土壤侵蚀,而且能够截获风沙中高养分含量的土壤细砂.但重度放牧破坏了土壤团粒结构和土壤结皮,降低了植被高度和盖度,造成了严重的地表裸露,同时增加了近地面的风速,这些因素都会加剧风蚀作用,使土壤表层由养分含量低的粗砂组成,降低了土壤P含量.Li等人^[74]从能量角度解释了植被盖度和群落结构对风蚀和土壤养分流失的影响,他们发现,当植被盖度较低时,发生土壤侵蚀的风速阈值会降低.这是由于当土壤颗粒跃移过程发生后,已经发生移动的土壤颗粒将部分能量转移到土壤表层颗粒,有效地降低了阈值风速.同时,植被盖度降低特别是草本植物盖度的降低,使植被对风的动力衰减作用降低,导致

表层土壤风蚀加剧.另外,凋落物输入减少和丧失使土壤含水量降低,导致表土对风蚀的敏感性增加^[74].因此,过度放牧引起的植被盖度降低、群落物种组成改变(如多年生禾草被一年生杂类草替代)、凋落物减少,是导致干旱和半干旱草原表层土壤风蚀加剧、生态系统P净输出增加的主要原因.

一些学者认为,放牧在短时间内对土壤P含量的影响不大,而造成其含量差异的主要因素可能是空间异质性^[75-77].家畜通过粪尿排泄、践踏和选择性采食等方式改变土壤的空间异质性,但目前有关放牧对土壤空间异质性的影响仍没有一致的结论^[75-79].一些研究认为,家畜的粪尿排泄对土壤养分的空间分布有直接的作用^[77,80].例如,绵羊为了避免牧草被粪尿污染通常会在相对固定的区域排泄,因此在排泄物相对集中的区域形成粪斑和尿斑^[81],植物可利用的N、P在这些斑块的土壤表层富集,增加了土壤养分的空间异质性.同时,家畜的践踏作用直接或间接地改变了土壤的理化性质和植被的分布格局,进而影响土壤N、P的空间异质性.适度的践踏通常可以增加土壤的空间异质性,而重度践踏则降低异质性^[82].家畜的选择性采食对土壤养分(如N、P)空间异质性的影响具有复杂性,表现为采食作用既可能增加也可能降低土壤养分的空间异质性.家畜的选择性采食减少了可食牧草的盖度和高度,造成不同强度的采食斑块,形成了“肥岛效应”(island of fertility)^[79,83,84],增加了土壤养分的空间异质性^[76].但如果家畜采食降低群落中非优势物种的多度,使优势物种分布更均匀,这可能造成土壤空间格局的同质性^[85].然而,Burke等人^[79]对美国矮草草原的研究发现,地形是影响土壤空间变异的主要因素,而放牧和物种则几乎没有影响.Kölbl等人^[31]对内蒙古典型草原研究发现,放牧强烈影响着景观尺度上地形控制的土壤颗粒迁移过程,并对地上生物量和与生物量相关的土壤特性具有强烈的影响.上述研究表明,长期放牧可能通过选择性采食、践踏、粪尿排泄等方式改变不同土壤斑块的生物、物理和化学属性,进而影响斑块尺度的P含量和P循环.

3 放牧对植物地上生物量磷含量和磷库的影响

草地生态系统中,植物群落的养分含量受气候、土壤、物种组成和放牧等生物和非生物因素的影响^[41,86-88].据最新估算,我国草地生物量P储量为3.31

Tg, 植物叶片平均P含量为 1.27 g kg^{-1} (95%的置信区间为 $0.82\sim 1.98 \text{ g kg}^{-1}$), 根系平均P含量为 0.69 g kg^{-1} (95%的置信区间为 $0.42\sim 1.13 \text{ g kg}^{-1}$), 叶片N:P平均为 $12.7^{[89]}$. 研究表明, 放牧通过改变草地生态系统的结构和功能来影响养分循环^[18,41,90]. 例如, 放牧会改变群落的物种组成和多样性^[90], 物种的相对多度和P含量、P输入与输出等影响植物P含量和地上生物量P库^[17,18,41,70,91], 进而影响生态系统P循环.

3.1 放牧对植物个体和物种水平磷含量及磷库的影响

植物的资源利用策略、养分权衡分配、表型可塑性等都会影响其P含量和P库, 放牧对植物的形态、物候和生理等多方面具有重要的影响^[41,71,92]. Li等人^[93]研究了放牧对羊草(*Leymus chinensis*)养分分配和个体大小的影响发现, 放牧显著增加了羊草茎和叶的P含量, 但降低了其叶茎比和个体P库, 二者间存在显著的负相关. 这表明放牧改变了羊草个体水平P含量与P库之间的权衡关系, 使养分更多地分配给光合器官, 导致了羊草的矮小化. 生长稀释假说认为, 如果叶生物量的累积增加大于养分获取量的增加, 养分含量将下降^[94]. 放牧系统中, 家畜采食养分含量高的叶片组织, 植物为了完成其生活史, 将更多的养分分配给叶片, 增加了叶片的P含量. 但在没有放牧的群落中, 植物生物量的增加导致了P的稀释作用. 植物在无牧和放牧条件下养分分配策略的改变, 反映了草原植物同草食动物长期协同进化过程中形成的植物个体水平上生长与维持之间的权衡. 在物候方面, 可食牧草被家畜采食后的再生, 延迟了植物的物候, 而幼嫩组织的P含量显著高于成熟组织^[68]. 在物种水平, 近期研究发现, 长期自由放牧使典型草原群落中具有高比根长、高细根比例、根鞘酸性磷酸酯酶活性高的物种多度增加, 这些物种具有较高的P获取能力^[95]. Smith等人^[96]研究发现, 具有较低比根面积和较高根系P含量的物种, 其根系分解速率更快. 因此, 放牧引起的物种组成改变将影响植物群落水平P的吸收利用和周转, 以及P与碳、氮之间耦合关系.

3.2 放牧对植物功能群水平磷含量和磷库的影响

植物功能群(plant functional group)通常是指对特定或相同环境因子的改变具有相同响应, 在生态系统中起相似作用的一类物种的组合. 植物功能群的变化对生态系统功能和服务具有重要影响^[90,97]. Zheng等

人^[71]对内蒙古锡林河流域的研究发现, 放牧对植物C、N、P含量的影响随着组织水平的增加而增加(物种-功能群-群落), 放牧改变了不同植物功能群的相对生物量和P含量, 进而影响了植物群落地上生物量P库. 在植物功能群组成中, 一、二年生植物属于资源获取型策略(acquisitive resource-use strategy), 为了完成其生活史, 放牧后这类植物将更多的N、P分配给地上组织; 多年生丛生禾草则属于资源保守型策略(conservative resource-use strategy), 由于其适口性较差, 降低了被家畜的采食, 因此其叶片N、P含量变化不显著; 多年生根茎型禾草属于中旱生植物, 具有较高的适口性和耐牧性, 放牧后幼嫩器官取代了衰老器官, 增加了N、P向叶片的分配; 多年生杂类草在资源利用方式、放牧耐受性等方面都介于一、二年生植物和多年生丛生禾草之间, 其对放牧的响应比较温和. Bai等人^[41]在蒙古高原草原样带调查中也发现了类似的结论, 放牧引起植物功能群组成的改变是生态化学计量关系和生态系统功能发生变化的主要机制. 尽管放牧对草甸草原、典型草原和荒漠草原不同植物功能群的影响大小和方向并不完全一致, 但放牧降低了这三类草原群落的地上生物量和凋落物P库, 增加了草甸草原和典型草原地下生物量P库, 降低了荒漠草原地下生物量P库. 对于草甸草原, 放牧增加了地上生物量N:P比. 这些结果表明, 长期放牧加速了草甸草原的N、P循环, 但可能减缓了典型草原和荒漠草原的P循环, 进而改变了N、P循环之间的耦合关系.

3.3 放牧对植物群落水平磷含量和磷库的影响

在群落水平上, 放牧主要通过促进和抑制养分循环两个相反的机制影响植物的P含量和P循环. 促进养分循环假说(accelerating nutrient cycling hypothesis)认为, 家畜采食促进了养分含量高的耐牧物种的损失, 这些物种可以通过快速吸收养分、提高相对生长率来进行补偿性生长, 同时具有较高的组织养分含量, 这些变化会引起凋落物分解和养分周转加快, 进而促进养分循环^[20,21]. 而抑制养分循环假说(decelerating nutrient cycling hypothesis)则认为, 家畜优先采食养分含量高的植物, 使木质素含量高、养分含量低、适口性差的物种的优势度增加, 进而使凋落物分解速度降低, 减缓了养分的周转和循环速率^[98]. Sitters等人^[99]研究发现, 放牧促进了北极冻原生态系统的N循环, 但增加了生物量的P限制. 目前, 大量的研究已经从资源有效性、凋

落物分解以及植物-土壤反馈等角度证实了放牧对植物群落P含量或P库有正、负两种效应^[17,41,68,100-103]。

放牧除了改变植物群落水平的平均P含量外,还可以通过改变地上生物量,进而影响生物量P库。尽管有关放牧对地上生物量的影响目前仍存在很大的争议,但我国草地连续多年的放牧控制实验表明,在干旱、半干旱草原,中度和重度放牧对地上生物量均表现为负效应^[41,54,67,104,105]。这些结果与放牧优化假说相悖,这一方面可能与目前草地持续较高的放牧强度有关,另一方面放牧能否促进植物生长主要与资源有效性有关。在水分条件较好、养分利用率高、竞争低和早期放牧的条件下,植物会对放牧产生超补偿效应;而在水分条件差、养分有效性低、竞争强的环境下,植物对放牧产生等补偿或欠补偿效应^[106]。我国的干旱、半干旱草原,放牧历史悠久,水分和养分有效性共同限制了放牧对植物生长的促进作用,因而长期放牧降低了群落地上生物量P库,特别是大部分的家畜粪尿滞留在畜圈内,不能返还到草地,加上畜产品的输出,加剧了生态系统水平的P输出。

4 放牧对植物根系磷含量和磷库的影响

4.1 放牧对根系形态和生理特征以及植物与丛枝菌根真菌共生关系的影响

根系不仅为植物地上部分的生长提供了水分和N、P等养分,同时根系是植物重要的养分库,植物光合作用固定的碳60%以上被分配到地下根系中^[61],因此根系动态对生态系统碳循环和养分循环具有重要的调节作用^[66]。Bardgett等人^[103]认为,在较短的时间尺度家畜采食改变了植物根系分泌物和碳的分配模式,在较长的时间尺度放牧改变了植物的根系生物量及其形态,二者共同影响了植物根系的P含量和P库动态。植物可以通过与丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)共生^[107,108],也可以通过改变自身形态特征^[61,109,110]来提高其养分吸收能力。研究表明,植物所需90%的P来自AMF^[111],AMF在土壤中形成广泛的菌丝网,能够有效地获取P,供给宿主植物^[112]。碳限制假说认为,长期放牧减少了养分向地下部分的分配,降低了AMF的丰富度^[113]。在资源相对丰富的条件下,放牧增加了AMF的菌根侵染率及其频度,维持了更高的生物多样性和地上生产力;反之,放牧则降低了菌根侵染率和频度,对多样性和生产力有一定的负效应^[114,115]。

同时,AMF的菌丝长度与放牧后资源有效性及土壤理化性质有很强的相关性^[45]。在生理上,植物可以通过增加表皮细胞质膜和P的亲和力以及释放有机酸、根系分泌物等活化P,增加P的吸收效率,特别是在石灰质土壤中,酸化有利于释放Ca-P化合物中的P^[116]。

根系形态(根系直径、根毛长度等)对植物吸收和利用P具有至关重要的作用^[117]。周艳松等人^[118]对内蒙古半干旱草原大针茅根系构型的研究发现,根系分叉数、根表面积和总根长是影响大针茅根系对放牧响应的主要指标,随着放牧强度的增加,大针茅根系趋于小型化,根表面积减少,植物为了更好地适应环境会分叉产生新的侧根吸收养分和水分。此外,重度放牧降低了羊草的总根长、根表面积、根尖数等根系性状,抑制了根系的吸收作用^[119]。

4.2 放牧对根系生物量和地下生物量磷库的影响

代谢理论和植物生物量分配理论可以解释放牧后根系生物量的变化^[120,121]。放牧通过改变植物光合产物向地上和地下器官的分配,使根系生物量及其占总生物量的比例发生变化,进而影响地下生物量P库和生态系统P循环。研究表明,放牧对草地地下生物量的影响主要与气候条件、放牧强度、放牧时间和土壤条件有关。在干旱、半干旱地区,大部分研究认为,放牧对根系生物量有显著的负效应^[61,66,71,122]。Gao等人^[61]对半干旱典型草原的研究发现,同不放牧的围封群落相比,放牧显著降低了群落地下总生物量、活根生物量和净地下初级生产力,但对根系周转速率没有显著影响。其中,重度放牧使群落地下总生物量降低了37%,活根生物量降低了56%,地下净初级生产力降低了36%。Yan等人^[104]基于全国草地的Meta分析表明,同全球草地的均值相比,放牧对我国草地地下生物量具有很大的负效应,这种负效应主要来源于重度放牧草地。这表明,重度放牧对地下生物量P库具有负效应。放牧降低了植物地上生物量,导致光合产物更多地分配给植物地上器官,促进其补偿性生长,导致植物以牺牲地下部分为代价^[123]。此外,由于家畜的选择性采食,重度放牧降低了禾本科植物的丰富度,改变了物种共存,进而改变了地下生物量^[124]及其P库。上述研究表明,长期过度放牧引起的根系生物量(包括活根和死根)对土壤有机质的输入减少,可能会降低土壤微生物的活性,如酸性和碱性磷酸单酯酶(phosphomonoesterase)活性,导致土壤有机P矿化速率的降低,进而减缓生态系统P循环。但也有一

含量随不同放牧强度的变化,以及放牧对土壤微生物P源和汇的影响机制^[130]; (2) 放牧如何影响土壤磷酸酶的活性,包括磷酸单酯酶(phosphomonoesterases)、磷酸二酯酶(phosphodiesterases)、三磷酸单酯水解酶(triphosphoric monoester hydrolases)及作用于含磷酰基酸酐和P-N键的酶类,进而调控土壤中P的矿化过程^[131]; (3) 放牧如何调控P在植物-土壤-微生物系统中的转化过程,包括:植物和微生物对P的吸收,植物根系和微生物分泌物引起的土壤固相中无机P(H_3PO_4 、 H_2PO_4^- 、 HPO_4^{2-} 和 PO_4^{3-})的释放,植物残体向土壤中释放的无机P,以及微生物和有机质矿化引起的无机P释放等^[132]; (4) 采用分子生物学和组学的手段在多大程度上能够帮助我们深入理解土壤微生物在P循环及生态系统功能中的重要作

用,以及放牧如何影响植物和根际微生物,进而调控生态系统P循环的生物过程^[133]; (5) 不同放牧强度如何影响植物多样性、AMF多样性及两者之间的关系,进而影响植物对P的吸收和利用,以及地上和地下生物量P库; (6) 已有研究中,放牧家畜类型比较单一^[17],未来研究中应关注不同家畜种类的食性差异对P循环的影响机制; (7) 其他植食动物,包括野生食草动物(如黄羊、藏羚羊)、植食昆虫(如蝗虫)、啮齿动物、蚯蚓、植食性线虫等在草地生态系统P循环中的作用^[134,135]; (8) 多数情况下,草地生态系统中N和P循环是耦合在一起的^[60,127]. 因此,不同放牧强度如何调控生态系统各营养级组分的N:P化学计量关系,进而影响N和P循环之间的耦合关系,也是未来研究中的一个新的增长点.

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Summary for “放牧对草地生态系统磷循环调控机制的研究进展与展望”

Grazing regulation of phosphorus cycling in grassland ecosystems: Advances and prospects

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Grassland ecosystems, which cover a total area of 52.5 million square kilometers and account for 40.5% of the global land surface, are the largest biomes in the world. Grazing is the most dominant and direct land use type in grasslands and a predominant driver regulating multiple ecosystem functions and services, such as primary production, nitrogen (N) and phosphorus (P) cycling, carbon sequestration, forage and food production, and water and soil erosion control etc. Many studies have demonstrated that primary production of grasslands is often limited by water, N and P availability, which interact with grazing to influence the maintenance of ecosystem functions and services. However, compared with numerous studies on the effects of grazing on N cycling and plant water use, fewer studies have explored how grazing influence P cycling of grasslands, particularly the internal cycling of P among main pools within ecosystems. Here we reviewed the advances in grazing effects on soil and plant P pools and biological processes of P cycling. Our review is mainly focused on: (1) Grazing effects on internal and external cycles of P in grassland ecosystems; (2) grazing effects on soil P vertical distribution, and P inputs and outputs mediated by soil erosion and spatial heterogeneity; and (3) mechanisms underlying grazing-induced changes in plant P content and P pools across different levels of organization (individual, species, functional group and community). Finally, we proposed a unified framework synthesizing the influence of grazing on P pools and key biological processes of P cycling in grassland ecosystems. We also proposed eight key questions that need to be addressed in future studies: (1) How do the dominant P forms (e.g., nucleic acids, phospholipids, cytoplasmic inorganic P, cytoplasmic organic P, and polyphosphate) and concentration within soil microbial biomass vary with grazing intensity? How does the role of microorganisms as sink and source of P change with increasing grazing intensity? (2) How does grazing affect enzyme activities, including phosphomonoesterases, phosphodiesterases, triphosphoric monoester hydrolases, and enzymes acting on phosphoryl-containing anhydrides and on P–N bonds, and thereby P mineralization in soil? (3) How does grazing regulate the biological processes of P transformation in plant-soil-microbial P cycle? (4) To what degree molecular approaches and omics analyses can improve our understanding of the important role of plants and rhizosphere microorganisms in P cycling? (5) How does grazing affect the relationship between plant diversity and arbuscular mycorrhizal fungi (AMF) diversity, and thereby plant P uptake and utilization? (6) How do grazing animals differ in their effects on the pools and pathways of P cycling due to the interspecific differences in diet and foraging preference? (7) How do other herbivores in terms of grasshoppers, rodents, earthworms, and plant feeding nematodes influence the biological processes of P cycling? (8) How does grazing affect the N:P stoichiometry of key ecosystem compartments, and hence the coupled N and P cycles.

grazing system, phosphorus (P) cycling, P content, P pool, N:P ratio, P limitation

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