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放牧影响草地凋落物分解研究进展

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摘要:放牧是草地生态系统的主要土地利用方式之一, 能够通过改变土壤环境、土壤生物与非生物因素、凋落物质量与产量调控草地凋落物分解, 进而影响草地生态系统养分循环和能量流动, 但放牧如何影响草地凋落物分解过程及其微生物机制仍缺乏统一认识。本研究利用文献计量分析, 回顾了放牧影响草地凋落物分解的历史发展并剖析了各阶段热点研究内容, 从土壤环境(水分、温度、容重、光照、pH等)、微生物活动(群落结构、养分、主场效应)、凋落物质量(植物群落结构、植物多样性、凋落物质量)等多个方面阐释了放牧影响草地凋落物分解的研究进展与不足, 并进一步总结放牧导致的草地凋落物分解变化对养分循环的影响。基于上述分析, 提出未来重点研究方向: 1) 加强长期放牧强度控制试验联网建设; 2) 亟须查明放牧条件下不同径级根系凋落物分解机制; 3) 探明放牧对混合凋落物分解的影响机理; 4) 以植物—凋落物—土壤环境—微生物为整体, 系统阐释放牧影响凋落物分解的关键过程及机制; 5) 综合考虑放牧与全球变化要素对凋落物分解过程的协同影响。以期为深入探讨全球变化对草地凋落物分解的影响, 以及草地生态系统服务功能的维持机制与可持续发展提供科学依据。

关键词:放牧; 草地生态系统; 凋落物分解; 土壤微生物; 凋落物质量; 养分循环

Progress in research on the effects of grazing on grassland litter decomposition

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Abstract: Grazing, as one of the major land-use types in grassland ecosystems, regulates litter decomposition through altering the soil environment, biotic and abiotic factors, and litter quantity and quality, thus affecting nutrient cycling and energy flow. However, there is still much to learn about how grazing affects litter decomposition in grasslands and the microbial mechanisms related to this process. In this study, we conducted a bibliometric analysis and literature review to provide an overview of research on grazing and its effects on litter decomposition. The progress and deficiencies of research on the effects of grazing on litter decomposition in grasslands were clarified from three aspects, i. e., the soil environment (e. g., soil moisture, soil temperature, bulk density, light, and pH), microbial activity (e. g., community structure, nutrients, and home-field advantage), and litter quality (plant community structure, plant diversity, and litter quality). We summarized the results of studies on the effects of

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grazing-induced changes in litter decomposition on nutrient cycling. On the basis of our findings, we propose several future research directions: 1) Construct a network of long-term experiments in which grazing intensity is manipulated; 2) Explore the mechanisms by which grazing affects the litter decomposition of roots with varying diameters; 3) Determine the effects of grazing on mixed-species litter decomposition; 4) Identify the key processes and mechanisms by which grazing affects litter decomposition from a systematic perspective that integrates plant-litter-soil and environment-microorganisms; and 5) Determine the synergistic effects of grazing and global change on litter decomposition. This study provides a scientific basis for understanding how global change will affect litter decomposition and the mechanisms underlying the maintenance and sustainable development of ecosystem services in grasslands.

Key words: grazing; grassland ecosystem; litter decomposition; soil microorganism; litter quality; nutrient cycling

草地是陆地重要生态系统之一,约占地球陆地面积的 40%,维持着 20%~30% 的陆地生产力^[1-2]。草地储存了超过 10% 的全球陆地生物量碳与 10%~30% 土壤有机碳,提供了全球 30%~50% 的畜产品^[3],在全球变化、碳氮及养分循环、畜牧业发展等方面具有重要作用,且在实现“碳达峰,碳中和”战略目标方面具有巨大潜力。放牧是草地生态系统主要土地利用方式之一^[3],合理的放牧强度与方式能够保障草畜平衡,维持草地健康、稳定及可持续发展。此外,凋落物作为地上与地下生态系统连接的关键枢纽^[4],约 50%~99% 的地上净初级生产力会变成凋落物并进入土壤食物链^[5],因而其分解速率在一定程度上决定着土壤有机质形成、养分矿化速率和陆地生态系统碳平衡^[6],并最终影响着养分循环和能量流动。近年来,关于放牧影响凋落物分解过程及其对养分循环、生态系统功能等影响已有大量研究,但由于时空异质性与多重研究手段等问题,当前对放牧影响草地凋落物分解的认识尚不系统。本研究详细梳理了放牧与草地凋落物分解的相关研究进展,提出未来的发展方向,以期为实现草地资源合理开发与可持续利用提供科学依据。

1 基于文献计量的研究发展态势分析

1.1 历史发展

本研究以放牧与草地凋落物为研究对象,运用文献计量学的方法,利用 Web of Science(WOS)、Scopus 和 CNKI 数据库对 1950—2021 年期间全球草地生态系统放牧与凋落物相关研究的中英文文章进行检索(参见:文献计量分析检索式),共检索到文献 4190 篇(WOS:2849 篇,Scopus:1196 篇,CNKI:265 篇,其中 120 篇重复),并利用 CiteSpace 5.8.R3 对文献进行关键词频次统计、关键词共现和引用突变分析。

文献计量分析检索式:

WOS 数据库文献计量分析检索式:“TS=(grazing) or TS=(livestock)” and “TS=(litter)” and “TS=(grassland) or TS=(steppe) or TS=(meadow) or TS=(savanna) or TS=(pasture)”。

Scopus 数据库文献计量分析检索式:“TITLE-ABS-KEY("grazing") or TITLE-ABS-KEY("livestock")” and “TITLE-ABS-KEY("litter")” and “TITLE-ABS-KEY("grassland") or TITLE-ABS-KEY("steppe") or TITLE-ABS-KEY("meadow") or TITLE-ABS-KEY("savanna") or TITLE-ABS-KEY("pasture)”。

CNKI 数据库文献计量分析检索式:“SU%='放牧'” and “SU%='凋落物'” and “SU%='草地' or SU%='草原' or SU%='草甸' or SU%='疏林草原' or SU%='牧场'”。

总体上,放牧影响草地凋落物分解大致可以分为 4 个阶段(图 1)。

20 世纪 70 年代以前,草地凋落物研究主要关注放牧条件下土壤属性、土壤微气候对凋落物覆盖和分布动态的响应,进而影响植物生长、根系分布动态、微生物活动等。

自 20 世纪 70 年代以来,生态学家开始着重探索放牧条件下凋落物对草地生态系统过程和功能的影响,侧重于凋落物养分对土壤属性、植被生产力和群落多样性的影响,以及植被与分解者子系统(decomposer subsystem)对凋落物养分动态的响应。该阶段重要进展主要是发现放牧通过动物的啃食行为影响植物的补偿生长机制,调节凋落物生物量,并影响凋落物与植物生长的互作,最终调控向分解者子系统的能量流动。

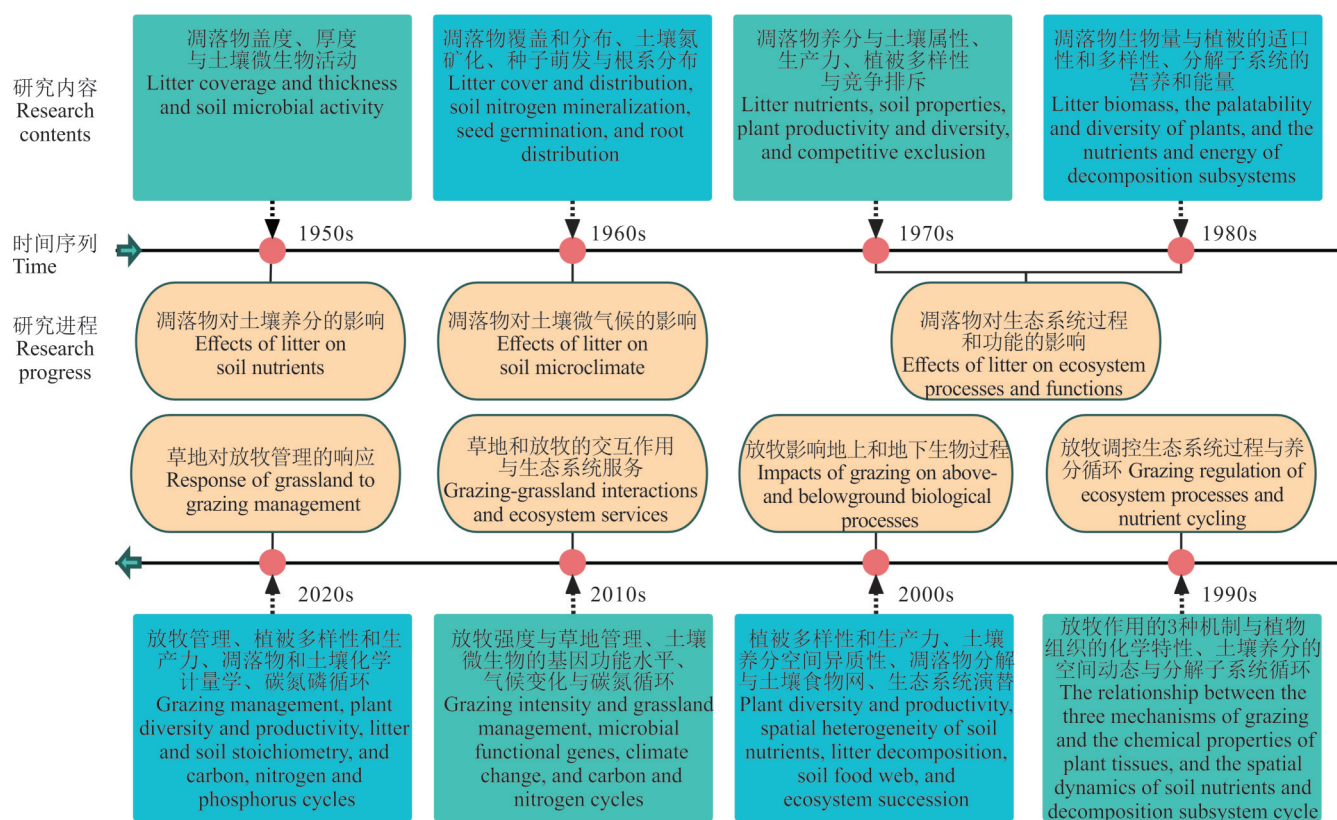


图1 放牧影响草地凋落物的不同研究阶段

Fig. 1 Different research stages for the effects of grazing on grassland litter

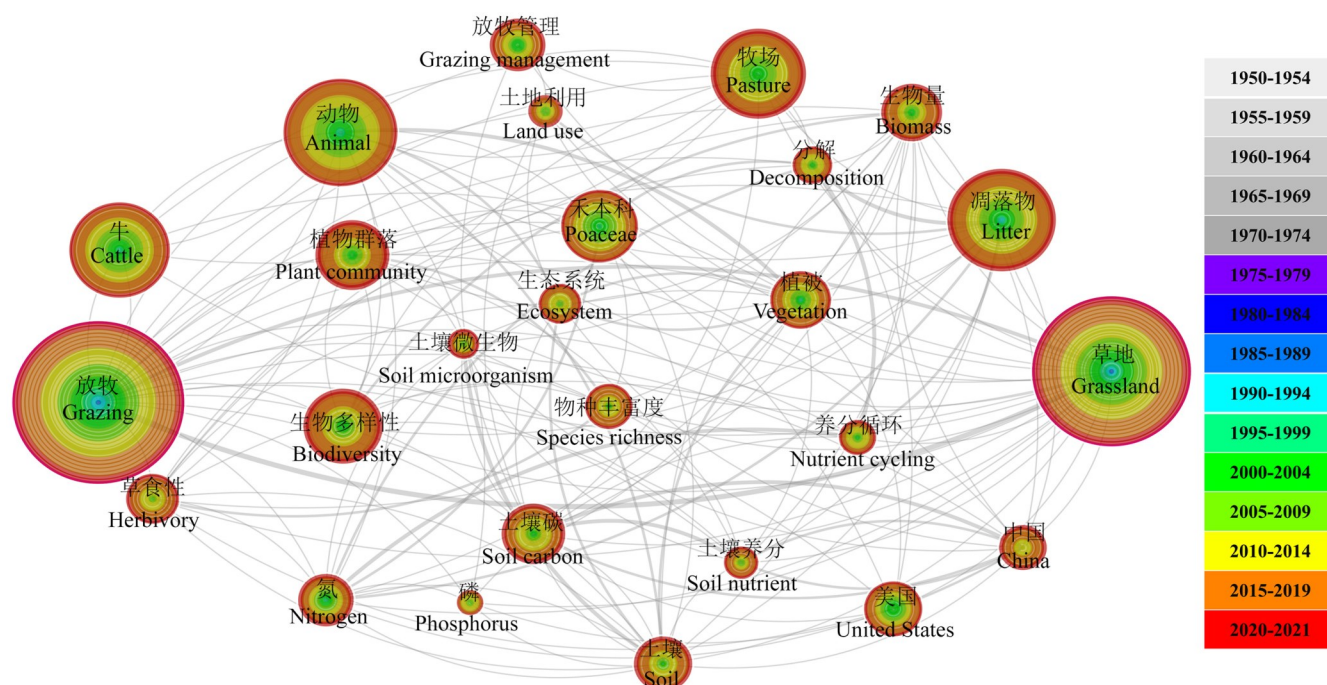


图2 放牧与草地凋落物的热点关键词共现网络可视化

Fig. 2 Co-occurrence networks of hot keywords for grazing effects on litter in grasslands

图中圆圈越大代表关键词出现的频率越高, 圆圈间的连线越粗代表关联越大 (即共同出现次数越多)。The larger circle means the higher frequency of a keyword, and the thicker line represents the higher correlation among keywords.

20 世纪 90 年代后,研究重点逐渐由地表凋落物分布转向地下分解者子系统中的微生物活动和分布,通过研究凋落物分解动态探索放牧对地上和地下联系、生态系统过程和功能、养分循环的调控机制。主要发现凋落物分解速率作为植物生命周期的建立和再生阶段、植物对环境和生态系统响应等生态过程的预测因子,植物响应放牧通过调控分解者食物网影响着生态系统功能和养分循环^[7]。

2010 年以后,草地生态系统响应放牧管理和放牧强度成为草地生态学的研究重点,而土壤微生物的功能基因和胞外酶活性是深入了解放牧影响草地凋落物分解及其对生物地球化学循环影响的重要手段。

1.2 研究现状

通过 CiteSpace 共生网络分析(图 2)、关键词聚类(表 1)与突变分析(表 2)发现,放牧与草地凋落物在近 70 年内主要集中在土壤属性与生物地球化学循环、放牧管理及生物多样性等方面对放牧干扰的响应研究。中国和美国是该领域最为活跃的两个国家,中国更多关注的是放牧条件下草地生物多样性与凋落物分解和土壤养分的关系,而美国则主要关注食草动物的草食性与草地生物多样性的联系(图 2)。从时间序列上来看(表 2),20 世纪主要集中于美国和亚洲的草地放牧和火灾制度关联,此后逐步倾向于凋落物分解导致的土壤化学属性变化对养分循环的影响,而近年来则更关注于高山地区(如青藏高原)放牧对土壤微生物、植物—土壤互作及凋落物分解的影响。

表 1 1950–2021 年间草地生态系统放牧与凋落物方向 SCI 文章中出现频次最多的前 40 个关键词

Table 1 Top 40 keywords with the highest frequency in SCI articles of grazing and litter on grassland ecosystem during 1950–2021

序号 No.	关键词 Key words	频次 Frequency	序号 No.	关键词 Key words	频次 Frequency
1	放牧 Grazing	392	21	物种丰富度 Species richness	75
2	草地 Grassland	357	22	物种多样性 Species diversity	75
3	动物界 Animalia	249	23	土壤碳 Soil carbon	71
4	牧场 Pasture	217	24	养分循环 Nutrient cycling	67
5	凋落物 Litter	182	25	磷 Phosphorus	63
6	禾本科 Poaceae	158	26	非人类的 Nonhuman	62
7	土壤 Soil	124	27	畜牧 Livestock	62
8	生物区系 Biome	123	28	大草原 Steppe	60
9	氮 Nitrogen	108	29	碳 Carbon	60
10	美国 United States	103	30	土壤有机质 Soil organic matter	60
11	中国 China	101	31	羊 Sheep	58
12	生物多样性 Biodiversity	101	32	农业 Agriculture	56
13	牛 Cattle	95	33	碳固定 Carbon sequestration	54
14	放牧管理 Grazing management	87	34	土壤氮 Soil nitrogen	53
15	绵羊 <i>Ovis aries</i>	87	35	家牛 <i>Bos taurus</i>	53
16	生态系统 Ecosystem	86	36	牧草 Forage	52
17	植物群落 Plant community	86	37	放牧压力 Grazing pressure	52
18	草食性 Herbivory	85	38	叶凋落物 Leaf litter	50
19	植被 Vegetation	84	39	火 Fire	49
20	分解 Decomposition	83	40	生理学 Physiology	44

2 相关研究的重要进展

凋落物分解是地上一地下生物地球化学循环的重要过程,其分解过程包括:淋溶、粉碎和代谢^[1],但实质是微生物在凋落物酶和土壤酶系统作用下的酶解过程,主要是 1) 通过微生物作用于木质素、纤维素与其他化合物的矿化和腐殖化;以及 2) 可溶性化合物浸出到土壤中,伴随着碳氮逐渐矿化^[8]。凋落物分解是植物养分供给的重要

表2 1950–2021年间草地生态系统放牧与凋落物方向SCI文章关键词突变检测

Table 2 Keywords burst detection of SCI articles of grazing and litter in grassland ecosystems during 1950–2021

关键词 Key words	强度 Strength	开始 Begin	结束 End	1950–2021
羊 Sheep	5.16	1975	2004	
家牛 <i>B. taurus</i>	23.93	1980	2009	
放牧 Grazing	13.47	1985	2004	
亚洲 Asia	6.05	1985	2009	
草地 Grassland	5.88	1985	1999	
火 Fire	4.38	1985	1999	
苔藓植物门 Bryophyta	4.33	1985	2014	
美国 USA	7.78	1990	1999	
澳大利亚 Australia	7.34	1990	2009	
动物界 Animalia	16.02	1995	2009	
美国 United States	8.69	1995	2004	
热带草原 Savanna	5.92	1995	2004	
欧亚大陆 Eurasia	14.93	2000	2009	
北美 North America	14.11	2000	2009	
澳大拉西亚 Australasia	10.20	2000	2009	
世界 World	8.93	2000	2009	
欧洲 Europe	8.91	2000	2009	
三叶草 <i>Trifolium</i>	6.49	2000	2009	
远东 Far East	5.34	2000	2009	
降解 Degradation	5.13	2000	2009	
东半球 Eastern hemisphere	5.10	2000	2009	
山羊 <i>Capra hircus</i>	4.85	2000	2009	
撒哈拉以南非洲 Sub Saharan Africa	4.85	2000	2009	
非洲 Africa	4.54	2000	2009	
哺乳动物 Mammalia	4.35	2000	2014	
禾本科 Poaceae	6.89	2005	2009	
南美 South America	5.42	2005	2009	
植物营养体 Phytoma	5.20	2010	2014	
化学 Chemistry	4.75	2010	2019	
优势 Dominance	4.71	2010	2014	
植被 Vegetation	4.69	2010	2019	
动物 Animal	4.52	2010	2019	
微生物群落 Microbial community	6.52	2015	2021	
牛科动物 Bovine	5.00	2015	2019	
土壤有机碳 Soil organic carbon	4.73	2015	2021	
青藏高原 Qinghai–Tibet Plateau	4.72	2015	2021	
土壤植被互作 Soil vegetation interaction	4.72	2015	2021	
保护 Conservation	4.68	2015	2019	
草本植物 Herb	4.65	2015	2019	
高山环境 Alpine environment	4.43	2015	2021	

来源,尤其是优势植物的凋落物周转驱动着生态系统碳氮循环^[9],其分解速率不仅影响草地生产力,也影响养分循环速率。放牧影响凋落物分解主要涉及3个机制:啃食、排泄物归还与踩踏^[10],通过改变土壤环境、微生物活动、凋落物质量等因素^[1],进而影响凋落物被微生物矿化的生物过程。放牧通过选择性啃食改变群落物种优势度,降低植被对光的种间竞争作用而间接改变群落结构和组成,踩踏和排泄物会影响土壤、根系和微生物等地下群落结构和功能,改变凋落物分解速率,进而影响生态系统养分循环^[11]。本研究分别从土壤环境、微生物活动、凋落物质量等三方面综述草地凋落物分解如何响应放牧及其对养分循环的影响。

2.1 土壤环境

放牧通过改变土壤环境条件主要影响凋落物分解的早期阶段(以可溶性化合物的淋溶为主)^[12-13],啃食和踩踏行为主要通过影响土壤水分、温度、容重等微气候条件影响微生物活动^[14],排泄物通过改变土壤碳氮含量、pH等直接影响微生物活动^[15],进而影响凋落物分解过程与速率^[16-17]。

放牧导致的短期土壤增温可通过促进微生物活动^[18]和胞外酶活性加快凋落物分解^[19-20];长期则通过改变微生物的物种丰富度和群落结构、植物的物种组成和群落结构影响凋落物分解^[16,21]。放牧既能通过动物的踩踏降低根系和苔藓层的分布深度而增加土壤温度^[22],也能通过啃食降低植被覆盖度和凋落物层的厚度增加光照^[23],进而增加土壤温度^[24]。适宜温度有助于微生物生长^[25],促进微生物利用凋落物碳,加速凋落物分解^[26]。

凋落物分解与土壤水分具有紧密联系^[27],水分可以通过改变可溶性组分的淋溶量^[28]、调控凋落物间的物质转移,影响微生物群落结构与胞外酶活性,进而影响凋落物分解^[16,29]。动物排泄物中的水分可以加速高质量凋落物的氮淋溶^[30]。动物啃食行为能够降低植被盖度,减少植物蒸腾,增加土壤水分^[4,16],进而可能加速凋落物分解。动物踩踏会增加土壤容重^[31],不仅会降低土壤孔隙度和水分渗透,增加土壤水分蒸发^[32],也会降低土壤微生物氧气的可利用性与微生物呼吸速率,进而抑制凋落物分解^[10]。放牧也能增加土壤理化性质的空间异质性,对同一覆盖类型的放牧区和未放牧区进行比较发现,踩踏路径下未放牧区水分含量高于放牧区^[33]。此外,放牧也会通过影响土壤pH影响凋落物分解。例如,低pH的土壤条件会降低微生物生物量^[2],在凋落物分解初期增加真菌与细菌比值,抑制凋落物分解^[34],而在分解后期促进真菌对难降解有机物的分解^[31]。但是,放牧强度对土壤pH的影响具有很大不确定性(增加^[2,31]、降低^[35]、无影响^[36]),未来还应加强放牧条件下土壤pH变化对凋落物分解的影响研究。

放牧通过动物啃食行为降低植物盖度,进而增加光的穿透与反射至土壤表面^[16,37]。短期而言,放牧导致的光照增加可以通过增加土壤温度促进微生物活动,加速凋落物分解^[4,11,38];长期而言,太阳辐射的增加能影响凋落物质量与微生物群落特征,进而影响凋落物分解速率^[38]。例如,在半干旱系统中,光降解是凋落物分解的主要调控因素,紫外线和可见光辐射不仅可以促进木质素的光降解,还可以通过降低有机化合物(如可溶性有机质)的稳定性加速凋落物分解^[6,38]。然而,放牧导致的光降解调控凋落物分解相关的研究目前鲜有发现,未来需要加强这方面的试验证据与研究。

2.2 微生物活动

土壤微生物群落与凋落物分解速率有着直接关联^[4],特别是分解、矿化、吸收等过程^[39]。草地生态系统的营养决定分解者的丰富度,短期放牧通过啃食和排泄将植物碳移除或改变其组成,导致微生物生物量显著减少^[40],进而可能抑制凋落物分解;在长时间尺度上,放牧改变植物生产力、植物群落组成与结构、凋落物质量、土壤养分可利用性以及土壤条件,调控微生物群落和结构组成^[39],从而影响凋落物分解^[41]。

放牧通过啃食减少凋落物生物量并增加进入土壤的叶片碎片,也能通过排泄物归还对草地土壤养分产生影响^[15,37],这为微生物提供更易利用的养分资源^[42],促使凋落物分解^[43]。例如,排泄物通过促进细菌的生长^[44]和定殖^[30],进而促进细菌降解凋落物中的纤维素和半纤维素^[45]。由于微生物在土壤表层最活跃,放牧通过踩踏还会产生凋落物分解的位置效应(position effect):即埋在土壤表层中的凋落物分解得最快,土壤表面的分解速率次之,而立枯凋落物分解速率最慢^[46]。大型动物的踩踏不仅会增强植物残体的物理解析^[47],也会增加分配到地下食物网的植物碎片,增加输入到土壤中的碳和营养物质,促进植物根部的生长,同时增加细菌、真菌和丛枝菌根真菌丰度,从而促进凋落物分解^[10]。但是,也有研究表明放牧通过啃食可能会减少根系碳分配^[48],降低土壤微生物生物

量与细菌多样性^[49],减弱凋落物分解^[31]。

放牧强度和放牧历时也能通过影响微生物活动调控凋落物分解。例如,适度放牧能大幅提升土壤微生物丰度和活性,提高土壤呼吸、土壤氮的净矿化作用和净硝化作用^[31],从而对凋落物分解产生积极的影响。过度放牧能够促使以真菌为主的温带草原生态系统转变为以细菌为主的生态系统^[50],但与真菌相比,细菌对于凋落物分解前期的调控作用更强^[51]。此外,长期放牧能够通过改变根冠比和根系生物量而影响微生物活动,从而改变凋落物分解速率。动物长期啃食会使植物合成更多碳水化合物以促进植物补偿生长^[22],但可能减少根系生物量与碳分配^[24,48],降低微生物丰度,进而减慢凋落物分解^[52];相反,长期踩踏和排泄物积累则能增加根系分泌物和生物量^[10,48],刺激土壤微生物呼吸和活动^[7,53-54],加快凋落物分解。

植物凋落物分解具有“主场优势”(home-field advantage, HFA^[55-56]),表明其主场(即原始栖息地)的植物凋落物分解率高于其原始栖息地以外的场地。HFA效应体现了微生物与土壤环境条件的互作,在主场领域的微生物群落更适应和更有效地分解局地的凋落物^[57]。放牧通过改变土壤微生物群落影响HFA效应主要有两条途径^[41]:1)促进分解者对主场中具有金属元素的抗性化合物的分解;2)提升少数特定土壤微生物的主场地位,这类微生物能够快速降解低质量(即碳氮比高和木质素与氮比高)的凋落物^[58]。HFA效应通常与某些特定优势真菌的存在密切相关^[41]。在凋落物分解的后期阶段,分解过程主要由能够分泌特定木质素降解酶的真菌群落控制^[51,59]。放牧能够导致某些植物产生耐牧性,形成难降解化合物浓度高(如木质素)的凋落物,同时放牧引起的土壤微气候与真菌群落组成的改变,最终会加速难降解化合物(如木质素^[51])的分解^[38],这会增强HFA效应对凋落物分解的影响^[41]。放牧通过啃食增加木质素的光降解^[6],也将促进HFA效应。然而,部分试验不支持放牧影响凋落物分解的HFA效应^[43,57],未来研究工作中应加强关注这方面的试验结果。

2.3 凋落物质量

凋落物质量(如可溶性碳、氮、磷、纤维素、半纤维素、木质素等及相关比值^[60-63])是影响凋落物分解的重要因素^[12,43],高质量凋落物(即碳、氮浓度高、碳氮比低、木质素浓度低)比低质量凋落物分解更快^[43,63-64]。试验表明放牧和增温对凋落物质量(碳、氮、半纤维素、纤维素、木质素、碳氮比等)没有显著影响^[16]。但是,更多的试验结果表明放牧能够通过影响土壤环境条件与植物—土壤反馈效应影响植物群落结构和植物养分含量,改变凋落物质量,从而影响凋落物分解^[29,65]。在资源丰富环境条件下,适度放牧通过增加植物根分泌物刺激土壤微生物活动,排泄物能提高土壤氮的可利用性,土壤营养浓度的增加有利于微生物的氮矿化过程、促进根对矿物质氮的吸收^[7,54],增加根系凋落物的氮浓度^[10,37],从而产生积极的反馈。啃食也可能引起植物将氮向地下部分转移,形成低质量的叶片凋落物(即叶片碳氮比高)阻碍分解^[66]。

草地生态系统的生产力差异对放牧的响应表现为高生产力促进、低生产力抑制凋落物分解^[37]。在生产力高的草地生态系统中,刈割和啃食促使植物补偿生长的营养再分配,导致形成的新生组织比成熟组织具有更高的氮浓度^[54]。由于营养物质被高度吸收,放牧可能在增加凋落物氮含量的同时降低半纤维素浓度、碳与氮、木质素与氮、纤维素与氮和半纤维素与氮的比值,这在一定程度上可提高凋落物质量^[66],促进凋落物分解^[67]。因此,放牧能维持养分吸收率较高的优势、耐牧或适口植物的高生长和高再生率^[37],并巩固其优势地位^[61,68],提高凋落物质量^[37]。然而,在低生产力的草地生态系统中,动物的选择性取食也可能促进非适口物种的优势^[43],形成大量低质量凋落物,限制微生物活动,进而抑制凋落物分解^[52]。

放牧强度、放牧历时以及放牧类型能够通过调控凋落物质量影响凋落物分解。在轻度放牧区,凋落物碳、氮浓度、碳氮比和生物量随地上植物生物量的增加而增加^[4,31],而长期重度放牧会导致植物叶片变小,进而增加凋落物的可分解性^[69]。过度放牧比轻度放牧区的排泄物输入多、凋落物质量高^[37]。连续放牧导致凋落物碳、氮浓度下降,碳氮比增加,而轮牧能够增加碳浓度以促进微生物分解^[39]。禁牧也能显著增加碳浓度和碳氮比^[70],但长期禁牧会降低植物养分含量、凋落物质量和分解速率^[57]。单种动物放牧会降低凋落物氮浓度,直接或间接抑制凋落物分解;而混合放牧则能提高凋落物质量,促进凋落物分解,并且分解后期的分解速率差异受混合放牧动物体型和取食偏好性的差异影响^[64]。

由于物种间的养分浓度存在差异,放牧通过改变植物群落结构和物种组成,影响凋落物质量^[71]和凋落物可分解性^[61]。放牧通过啃食(促进凋落物或叶片的掉落)、踩踏和排泄改变土壤条件^[10],促进耐牧植物、适口植物物种的生长^[43,61];同时,食草动物唾液中的植物生长刺激物通过促进植物的补偿生长效应^[72]改变植物的物种丰度和叶片组织结构,并间接改变草地的物种组成和功能^[68],这些放牧导致的植物群落的改变会影响凋落物质量及分解。在草地生态系统中,1) 短期内觅食选择性的差异(如高营养低纤维浓度的植物)可引起植物组织的短期生态生理变化、植物的能量模式和营养分配模式变化^[52],通过影响群落内植物间竞争互作模式,改变植物的物种丰富度和形态结构,最终改变进入土壤的凋落物质量,进而影响凋落物分解^[43];2) 长期放牧则通过改变植被群落组成的异质性(即斑块,短植被斑块以易被动物啃食的高质量耐牧植物为主,而高植被斑块是以不易被食草动物啃食的低质量植物为主)^[24,69],增加非适口植物或耐牧植物的丰富度^[73],改变凋落物数量和质量^[10,31],增加或降低凋落物的可分解性^[37,41]。在放牧条件下,物种密度与覆盖度低的植物功能群中凋落物分解较慢,而在物种多样性高的植物功能群中凋落物分解较快^[4]。养分转移假说认为微生物优先以高氮凋落物为食^[74],凋落物可分解性的差异促进其混合物间氮养分的转移,提高难降解凋落物的质量^[59,75];混合凋落物可能产生非加性效应促进凋落物分解^[76],即混合凋落物通过调节微生物活动和资源利用效率以及凋落物分解的微气候条件促进凋落物分解^[77]。植物多样性可以通过缓解土壤微生物群落间的相互竞争,进而影响凋落物分解^[9]。例如,真菌间争夺相似食物资源产生拮抗作用会抑制凋落物分解,而食物资源多样性能够促进真菌驱动凋落物间的养分转移并加速凋落物分解^[59]。

2.4 放牧导致的凋落物分解变化对养分循环的影响

凋落物分解是涉及有机物质分解和养分循环的关键过程^[78],影响植物生产力、物种组成、碳储量及养分含量^[79]。放牧影响养分循环主要是通过转移植物养分到排泄物和影响凋落物分解^[7,61]。动物啃食植物会形成比凋落物更易分解的排泄物,加速养分释放,促进养分循环^[50,80];但植物更多的是以凋落物形式进入土壤^[81]。因此,放牧引起的凋落物分解变化对草地生态系统养分循环至关重要。

放牧通过改变土壤微气候条件、植被群落组成和凋落物质量影响凋落物分解,进而影响养分循环^[61];特别是动物啃食适口植物可以改变植物多样性^[9]和群落结构、凋落物质量,能够改变进入土壤的植物碎片数量和类型,影响微生物活动^[54],从而影响凋落物分解动态和养分循环^[82-83]。动物啃食行为可以加速养分循环^[23,80,84];1) 在高生产力系统中,维持高再生率、高质量耐牧植物的优势地位;2) 选择性取食导致非禾本类植物增加^[85]、禾本类减少^[61],并加速非禾本类凋落物的分解^[62]。相反,动物啃食也能够抑制养分循环^[62];1) 在低生产力系统中,促进低质量物种在群落中逐渐取得优势地位;2) 选择性取食高质量的固氮豆科植物或高生长率、高生产力的植物,减少高氮浓度叶片碎片和凋落物进入土壤,这会减缓凋落物分解并减弱氮循环^[23,86-87]。踩踏通过改变土壤孔隙度、土壤水分、土壤容重、氧气浓度、团聚体、盐碱度等土壤环境,同时增加分解者与凋落物的接触^[88],改变凋落物养分被释放的时间,进而影响养分循环^[10,89]。动物排泄物通过为微生物提供可利用的碳、氮资源,加速凋落物分解和养分循环^[43]。例如,大量的氮从排泄物转移到分解中的凋落物,可以通过缩短固氮时间,从而促进低质量凋落物中纤维素、半纤维素降解和高质量凋落物中氮、磷释放,进而加速碳循环和养分循环^[30]。长期适度放牧通过选择耐牧基因型的禾本植物,影响凋落物分解及养分循环^[43],或通过选择适合降解耐牧凋落物的微生物,加速养分循环^[71];过度放牧则会抑制凋落物的形成与分解,进而抑制养分循环^[4,90-91]。尽管放牧通过影响凋落物分解而改变养分循环(加速^[43]、抑制^[92]、无明显影响^[68,93]),但目前的试验证据及其机制仍不明晰,未来需要通过野外控制试验、室内控制试验、大数据分析等方式系统阐释其机理过程。

3 总结与展望

放牧通过动物的啃食、踩踏和排泄 3 种机制改变土壤微环境、土壤微生物(群落结构和胞外酶活性)和凋落物质量(群落组成和化学计量特征),进而影响凋落物分解过程与养分循环过程(图 3)。为了全面解析放牧影响草地凋落物分解过程,未来研究工作应加强以下几个方面:1) 放牧强度控制试验较少且持续时间短,导致无法准确评估凋落物分解对放牧强度的响应,未来应加强各方合作且基于统一的试验方法进行研究;2) 大多研究仅关注地上植物凋落物,极其缺乏根系分解研究,根系凋落物对土壤碳的贡献远远大于地上部分,未来应加强放牧条件

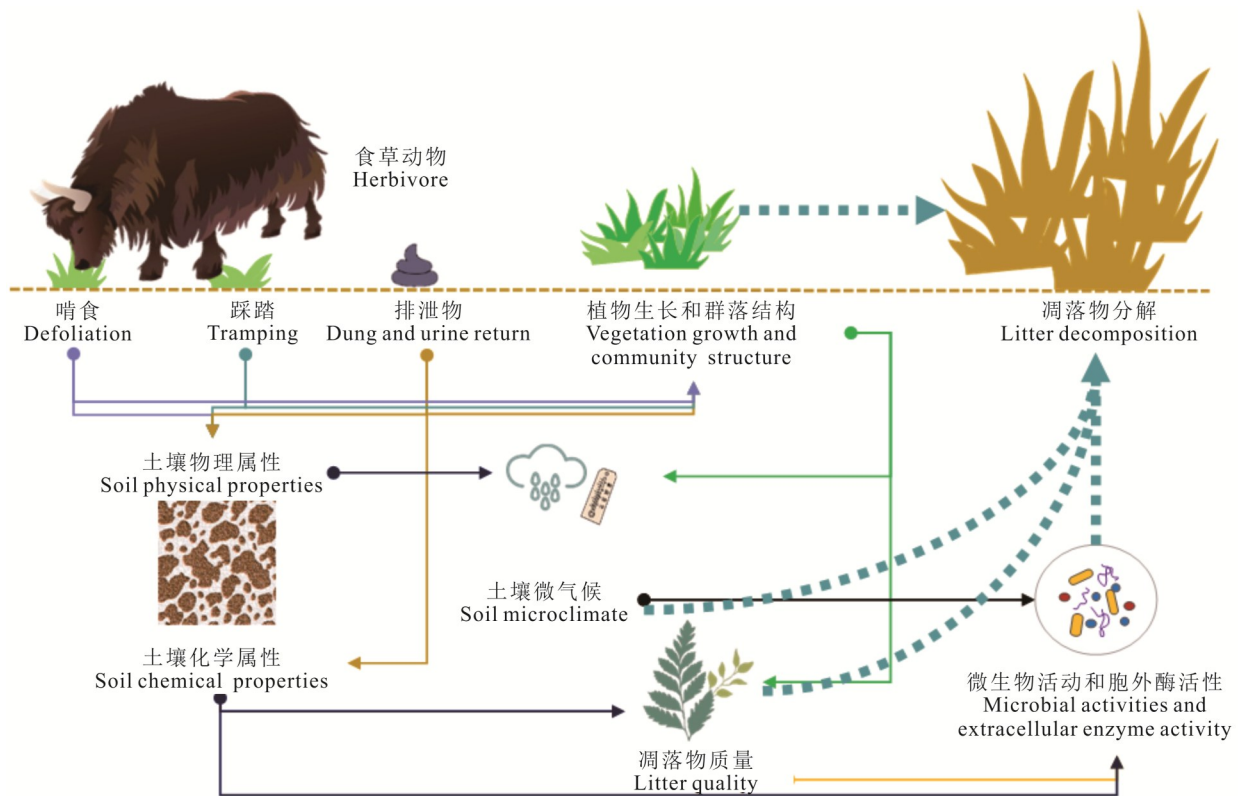


图3 放牧影响凋落物分解概念图

Fig. 3 The conceptual diagram of grazing effects on litter decomposition

下不同径级根系凋落物分解研究;3) 缺乏放牧影响混合凋落物的分解效应,整合单物种与混合物种的分解动态能够加深对放牧影响生物多样性—凋落物分解关系的认知;4) 需要综合考虑植物—凋落物—土壤环境—微生物之间的相互关系,可为系统性理解放牧影响凋落物分解的关键过程及机制提供重要思路;5) 广泛分布的草地生态系统不可能仅受到放牧单一驱动力的影响,同时还会受到诸如气候变暖、降水格局改变、氮沉降增加等其他因素的影响,综合考虑放牧与全球变化要素对凋落物分解过程的协同影响是未来研究工作的重点与趋势。

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