

狼毒扩张的微生物生态学研究进展



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摘要: 狼毒 *Stellera chamaejasme* 扩张已成为毒草型退化草原治理过程中一个不可忽视的问题, 严重影响着草原的生态安全和畜牧业的可持续发展, 当前关于狼毒在退化草原扩张机制方面的研究引起了国内学者的广泛关注。随着测序技术和生物信息学分析技术的快速发展, 对狼毒相关微生物方面的研究不断深入, 并揭示出狼毒与土壤微生物以及与自身内生菌之间的相互作用是其在退化草原成功扩张的重要机制之一。该文对狼毒相关土壤微生物和内生菌生态学方面的研究进展进行综述, 并对微生物在狼毒的种间竞争、凋落物分解、植物-土壤反馈作用过程中的潜在作用进行探讨, 最后对利用宏组学技术开展狼毒功能菌群挖掘与利用的前景进行展望, 以期从植物-微生物互作角度了解这种重要毒害草的扩张机制, 为挖掘狼毒微生物资源和开发狼毒生态防控新方法提供参考依据。

关键词: 狼毒; 土壤微生物; 植物内生菌; 植物-微生物互作; 扩张机制

Advances in the study on microbial ecology associated with *Stellera chamaejasme* expansion

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Abstract: The expansion of *Stellera chamaejasme* has become a significant issue in the management of degraded grasslands dominated by poisonous weeds, which poses a serious threat to the ecological security of grassland and the sustainable development of animal husbandry. Current research on the mechanism of expansion of *S. chamaejasme* in degraded grassland has attracted widespread attention among domestic scholars. With the rapid development of sequencing technology and bioinformatic analysis, the application of high-throughput sequencing technology over the past decade has significantly advanced microorganism-associated research on *S. chamaejasme*. Exploring the interactions between *S. chamaejasme* and soil microorganisms, as well as with its own endophytes, has become a crucial aspect for revealing its successful expansion. In this paper, the research progress in the ecology of *S. chamaejasme*-associated soil microorganisms and endophytes were reviewed, with an aim to understand the importance of plant-microbe interactions in this important poisonous weed. This paper also suggested the potential role of microorganisms in interspecific competition, litter decomposition, and plant-soil feedback processes of *S. chamaejasme*, and discusses the prospects of using metagenomic techniques to ex-

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plore and utilize the functional microbiota of *S. chamaejasme*. Such work can provide a theoretical basis for the exploration of *S. chamaejasme* microbial resources and development of new approaches for ecological control of *S. chamaejasme*.

Key words: *Stellera chamaejasme*; soil microorganism; plant endophyte; plant-microorganism interactions; spreading mechanism

狼毒 *Stellera chamaejasme* 是瑞香科狼毒属的多年生草本植物,在我国天然草原广泛分布(郭丽珠和王塑,2018)。狼毒全株有毒,以根的毒性最大,但家畜一般不主动采食,却常在早春草料匮乏时因误食而中毒。狼毒通常是草原群落中的伴生种,在草原退化初期不会大量扩张;但随着草原退化程度加剧,草原群落中的优势物种逐渐被狼毒取代,在一些严重退化草原上形成以狼毒为主的单优群落景观。当前,狼毒扩张已成为毒草型退化草原治理过程中一个不可忽视的问题,不仅导致草原生产力降低、草群质量变差,而且严重影响着草原的生态安全和畜牧业的可持续发展(王文婷等,2019)。

随着狼毒种群在退化草原的扩张问题日益凸显,我国学者陆续对狼毒的分布与危害(郭丽珠和王塑,2018)、生物学特征(Zhang B et al., 2021; Hu et al., 2022)、抗逆生理(Liu et al., 2020)、种群特征(邢福等,2005; Guo et al., 2021)、化感作用(Cheng et al., 2022; Chen et al., 2023)以及防控措施(宋梅玲等,2018)等开展了大量研究,极大地丰富了我国天然草地主要毒害草狼毒的研究。此外,微生物对狼毒在退化草原的快速扩张也发挥了重要作用(Ma et al., 2020; Zhang Y et al., 2021; Hu et al., 2023)。随着测序技术和生物信息学分析技术的迅猛发展,对狼毒相关微生物的研究不断深入,主要涉及2大类:一是土壤微生物,二是植物内生菌。

1 狼毒扩张的土壤微生物生态学机制

微生物在土壤的各种生态活动中扮演着重要角色,对植物的生长和健康影响深远。狼毒与土壤微生物之间的相互作用关系深刻影响着狼毒的适应性和竞争力,在其扩张过程中发挥着重要作用(Sun et al., 2009)。狼毒定殖与否(He et al., 2019)及其种群密度(Cheng et al., 2022; Hu et al., 2023)和株丛大小(汪睿等,2023)均能够明显改变土壤微生物的生物量、群落组成、多样性以及功能菌群,特别是显著影响了土壤氮有效性及氮循环过程(Sun et al., 2009; Ma et al., 2020)。

1.1 狼毒扩张对土壤微生物生物量的影响

狼毒扩张显著影响了土壤微生物的生物量。孙庚(2008)研究发现,无论在平地还是在阳坡,狼毒斑块表土的微生物生物量碳、生物量氮和生物量磷都高于无狼毒土壤。同时,无论是在典型草原(河北省沽源县)还是高寒草甸(青海省海晏县),狼毒生长区土壤微生物的生物量碳、生物量氮、生物量磷均显著高于邻近狼毒未生长区土壤(安冬云,2015)。此外,随着狼毒种群密度增加,土壤微生物生物量碳、生物量氮也显著增加(Hu et al., 2023)。然而,也有研究发现狼毒生长对土壤生物量碳及生物量氮均无显著影响(王亚楠,2022)。总体而言,狼毒扩张可以提高土壤微生物生物量,推测相关原因主要涉及2个方面:一方面可能是狼毒根系分泌出更多有机酸和碳水化合物,刺激了土壤微生物的生长和繁殖;另一方面则归因于狼毒凋落物数量与质量的改变(孙庚,2008),土壤有机质增加,土壤微生物生物量碳、生物量氮和生物量磷的质量分数亦随之升高,最终导致土壤酶活性、微生物功能及养分循环发生改变。

1.2 狼毒扩张对土壤微生物群落的影响

1.2.1 狼毒定殖对土壤细菌组成和多样性的影响

狼毒定殖后虽然没有改变定殖地土壤的优势细菌门组成,但其相对丰度发生了明显变化。在区域尺度上,放线菌门、变形菌门、厚壁菌门均是青藏高原和内蒙古高原狼毒根际土壤和非根际土壤的优势细菌门,但厚壁菌门的相对丰度在非根际土壤中显著增加(孟慧珍,2022)。此外,青藏高原狼毒根际土壤细菌的Chao 1多样性指数显著高于非根际土壤细菌,而内蒙古高原狼毒根际土壤和非根际土壤的细菌Chao 1多样性指数接近(孟慧珍,2022)。Cui et al.(2015)通过可培养方法比较了青藏高原狼毒根际土壤和非根际土壤在狼毒4个生长阶段之间细菌群落组成的差异,发现厚壁菌门和放线菌门是狼毒所有生长阶段均存在的优势菌门,且狼毒开花期和结果期的根际土壤细菌群落多样性均高于非根际土壤细菌。

1.2.2 狼毒定殖对土壤真菌组成和多样性的影响

同样,狼毒定殖后也没有改变定殖地土壤的优

势真菌门组成,但其相对丰度发生了明显变化。子囊菌门、担子菌门、接合菌门和球囊菌门是青海省祁连县狼毒定殖地和非定殖地土壤中最主要的真菌群落组成,但子囊菌门、接合菌门及球囊菌门的相对丰度在狼毒定殖后发生了显著变化;而且非定殖地土壤中的真菌操作分类单元(operational taxonomic unit, OTU)数量和物种丰富度指数显著高于定殖地土壤(He et al., 2019)。在区域尺度上,子囊菌门、担子菌门、被孢霉门是青藏高原高寒草甸和内蒙古高原典型草原狼毒根际土壤和非根际土壤中相对丰度排名前三的真菌门,约占所有菌群的90%,然而狼毒根际土壤和非根际土壤的真菌多样性并无显著差异(孟慧珍,2022)。

1.2.3 不同种群密度狼毒对土壤微生物群落的影响

随着狼毒种群密度或盖度的增加,不同草地类型中狼毒扩张引起的微生物种类和多样性发生不同的变化。担子菌门是高寒草甸(甘肃省武威市)无狼毒样地土壤中的优势真菌门,子囊菌门是狼毒盖度为25.13%、52.63%和89.69%样地土壤中的优势真菌门,然而不同狼毒盖度样地土壤之间的细菌组成差异并不明显,优势细菌门均为变形菌门;且土壤中真菌和细菌的丰富度及多样性会随着狼毒盖度的增加而增加(Cheng et al., 2022)。在四川省康定市高寒草原,土壤优势细菌门随着狼毒扩张程度的增加而发生了变化,其中狼毒重度扩张下土壤中放线菌门和变形菌门的相对丰度显著增加,中度扩张下土壤厚壁菌门的相对丰度最高(Hu et al., 2023)。在内蒙古自治区西乌珠穆沁旗典型草原,土壤细菌中的放线菌门和Gemmatimonadota的相对丰度随着狼毒盖度增加呈现上升趋势,而拟杆菌门的相对丰度下降;子囊菌门、被孢霉门和担子菌门是土壤真菌群落中的优势菌门,但子囊菌门和被孢霉门的相对丰度仅在狼毒重度盖度下发生明显增加和降低的趋势(Yang et al., 2024)。土壤细菌和真菌对狼毒扩张程度的响应不一致,其中细菌多样性先增加后下降,而真菌多样性先下降后上升,且相较于细菌群落,真菌群落对狼毒扩张程度更敏感(Yang et al., 2024)。

1.3 狼毒扩张对土壤微生物功能菌群的影响

狼毒扩张改变了土壤氮素形态及有效性(表1),而土壤氮转化过程中功能菌群的差异是其影响土壤氮有效性的重要机制(McLeod et al., 2016)。目前,学者主要研究了狼毒定殖后土壤氮转化过程中的氨氧化菌群(孙天舒,2013;Ma et al., 2020)和固氮菌群(Zhang Y et al., 2021)。氨氧化作用是硝

化作用的第一步,也是限速步骤,其主要驱动者是氨氧化细菌(ammonia-oxidizing bacteria, AOB)和氨氧化古菌(ammonia-oxidizing archaea, AOA)(贺纪正和张丽梅,2013)。孙天舒(2013)研究发现科尔沁草地上狼毒种群扩张主要造成土壤中AOB发生变化;而在青藏高原高寒草甸上,以狼毒为优势种的草甸土壤中AOB的丰度较以老芒麦*Elymus nutans*为优势种的草甸土壤显著降低,且狼毒生长土壤的硝化速率也较低(Ma et al., 2020)。此外,土壤中的氮水平与固氮菌群的大小和组成有关(Ribeiro et al., 2017),狼毒定殖科尔沁草地后土壤中氮含量以及固氮菌群中*Bradyrhizobium*和*Desulfuromonas*的相对丰度变化显著(Zhang Y et al., 2021)。Yang et al. (2024)对氮循环相关基因的绝对丰度进行定量分析,发现除*amoB*基因的相对丰度在狼毒种群不同盖度土壤之间没有显著差异外,其余氮循环相关基因的相对丰度均随着狼毒种群盖度增加呈现先降后升的趋势。同时,狼毒扩张可能也会改变土壤其他元素储量和循环过程,但相关研究较少。

狼毒对土壤真菌的影响研究主要集中在丛枝菌根真菌及植物病原菌方面。He et al.(2019)研究表明在青海省祁连县狼毒定殖地土壤中丛枝菌根真菌的相对丰度显著低于非定殖地土壤,且在更大尺度上及在不同草原类型土壤中也得到了相似的结果(孟慧珍,2022; Meng et al., 2024)。然而Zhang RH et al.(2023)通过盆栽试验证实,随着狼毒密度的增加,土壤中丛枝菌根真菌的相对丰度降低,共同种植的羊草*Leymus chinensis*体内丛枝菌根真菌的相对丰度则增加。He et al.(2019)研究发现青海省祁连县狼毒定殖地土壤中植物病原菌的丰度更高;但孟慧珍(2022)在更大尺度上的研究结果则不同,表明这种趋势不具备普遍性,随着样点分布的变化差异较大。

2 狼毒扩张的内生菌生态学机制

植物内生菌作为宿主植物的共生功能体,在调节植物生长发育、促进植物养分吸收、影响植物健康和病害防御、提高植物对环境胁迫适应性、增强植物在生态系统中的竞争和适应能力等方面扮演着关键角色(Trivedi et al., 2020; 2022)。有研究表明,狼毒植株拥有丰富的内生细菌(Jiang et al., 2022)和内生真菌(Tang et al., 2023),其中包含具有促生功能的内生菌,推测其与狼毒在退化草原上的强竞争力有关。此外,在狼毒植株不同组织部位(Jin et al.,

2014; 2015)和不同物候期(Jin et al., 2013)植株中的微生物群落构成与多样性也不同。部分内生真菌可以亲自参与宿主植物成分的降解(杨国栋,2009)以

及产生宿主植物含有的相同或相似的次级代谢产物,这将为综合防治狼毒和开发微生物生防资源提供新思路。

表1 狼毒生长对土壤氮素的影响

Table 1 Effect of *Stellera chamaejasme* growth on soil nitrogen

研究地点 Study site	草原类型 Grassland type	采样部位 Sampling position	土层深度 Depth of soil layer/cm	氮形态 Nitrogen form				参考文献 Reference
				总氮 Total nitrogen	硝态氮 Nitrate nitrogen	铵态氮 Ammonium	有效氮 Available nitrogen	
四川省松潘县 Songpan County, Sichuan Province	高寒草甸 Alpine meadow	斑块土 Soil in patch soil	0~15 15~30	↑ * ↑ *	↑ * ↑ *	NS	-	孙庚,2008 Sun, 2008
内蒙古自治区翁牛特旗 Ongniud Banner, Inner Mongolia	荒漠草原 Desert grassland	扩散区土 Soil in expansion area	0~10 10~30	↑ ↑ *	↑ ↓	↑ ↑	-	孙天舒,2013 Sun, 2013
青海省海晏县 Haiyan County, Qinghai Province	高寒草甸 Alpine meadow	生长区土 Soil in growth area	0~30	-	-	-	↑ *	安冬云,2015 An, 2015
河北省沽源县 Guyuan County, Hebei Province	典型草原 Typical grassland	生长区土 Soil in growth area	0~30	-	-	-	NS	安冬云,2015 An, 2015
青海省祁连县 Qilian County, Qinghai Province	高寒草甸 Alpine meadow	生长区土 Soil in growth area	0~20	↓ *	-	-	-	He et al., 2019
内蒙古自治区海拉尔区 Hailar District, Inner Mongolia	草甸草原 Meadow grassland	样方土 Soil in sampling plot	0~10	NS	-	-	NS	崔雪,2020 Cui, 2020
内蒙古自治区翁牛特旗 Ongniud Banner, Inner Mongolia	荒漠草原 Desert grassland	样方土 Soil in sampling plot	0~15	↑ *	↑ *	↓ *	-	Zhang Y et al., 2021
内蒙古高原7个样点 Seven sample sites in Inner Mongolia Plateau	高寒草甸 Alpine meadow	生长区土 Soil in growth area	0~15	NS	NS	NS	-	孟慧珍,2022 Meng, 2022
青藏高原19个样点 19 sample sites in Qinghai-Tibet Plateau	典型草原 Typical grassland	生长区土 Soil in growth area	0~15	↑ *	NS	↑ *	-	孟慧珍,2022 Meng, 2022
内蒙古自治区鄂温克自治旗 Ewenki Autonomous Banner, Inner Mongolia	草甸草原 Meadow grassland	斑块土 Soil in patch soil	0~5	NS	-	-	-	陈晨,2022 Chen, 2022
甘肃省天祝县 Tianzhu County, Gansu Province	高寒草甸 Alpine meadow	根际土 Rhizosphere soil	-	↑ *	-	-	↑ *	程济南,2022 Cheng, 2022
内蒙古自治区海拉尔区 Hailar District, Inner Mongolia	草甸草原 Meadow grassland	斑块土 Soil in patch soil	0~10	NS	-	-	NS	王亚楠,2022 Wang, 2022
河北省沽源县 Guyuan County, Hebei Province	典型草原 Typical grassland	斑块土 Soil in patch soil	0~10	NS	-	-	NS	王亚楠,2022 Wang, 2022
四川省雅江县 Yajiang County, Sichuan Province	高寒草甸 Alpine meadow	斑块土 Soil in patch soil	0~10	NS	-	-	NS	王亚楠,2022 Wang, 2022
四川省红原县 Hongyuan County, Sichuan Province	高寒草甸 Alpine meadow	斑块土 Soil in patch soil	0~10	NS	-	-	NS	王亚楠,2022 Wang, 2022
西藏自治区那曲县 Naqu County, Xizang Autonomous Region	高寒草甸 Alpine meadow	斑块土 Soil in patch soil	0~10	NS	-	-	↑ *	王亚楠,2022 Wang, 2022
四川省康定县 Kangding County, Sichuan Province	高寒草甸 Alpine meadow	根际土 Rhizosphere soil	0~20	↓ *	-	-	↓ *	Hu et al., 2023
内蒙古自治区西乌珠穆沁旗 Xi Ujimqin Banner, Inner Mongolia	典型草原 Typical grassland	样方土 Soil in sampling plot	0~10	NS	NS	↑ *	-	Yang et al., 2024

若研究中设计了不同狼毒盖度,则主要比较狼毒盖度最大时与无狼毒时的土壤氮含量差异。↑表示含量增加,↓表示含量减少,*表示差异显著,NS表示无显著差异,-表示该研究未测量此指标。If different coverage was designed in the study, the main focus would be on comparing the difference in soil nitrogen content between the maximum *S. chamaejasme* coverage and the absence of *S. chamaejasme*. ↑ indicates an increase in content, ↓ indicates a decrease in content, * indicates significant difference, NS indicates no significant difference, - indicates this indicator was not measured in the study.

目前,基于培养基分离、分子鉴定方法(Jin et al., 2013)以及高通量测序技术(Jin et al., 2015; Cheng et al., 2022)均已证实子囊菌门是狼毒不同组织部位(茎、叶、根)内生真菌的优势菌门,且其根部的内生真菌物种丰富度及多样性最高。其中可培养的优势菌属是枝孢属 *Cladosporium* 和青霉属 *Penicillium* 而免培养的优势属是 *Apotrichum* 和 *Athelopsis*(Tang et al., 2023)。进一步通过促生功能试验发现从狼毒中分离得到的菌株有91.30%具有解磷、产生生长素和铁载体能力,其中黑曲霉菌 *Aspergillus niger* 菌株 STL3G74 显示出最佳的促生性能(Tang et al., 2023)。另外,狼毒茎叶中的黄酮类和香豆素类成分能够被其内生真菌曲霉菌属的C1-Y7-4菌株降解(杨国栋,2009;潘翠,2012),而且狼毒植株中还含有可以合成黄酮类物质的内生真菌(王欢,2016)。

狼毒的内生细菌同样丰富,不同组织部位内生菌群的结构和优势菌存在差异(表2)。Jin et al.(2014)研究发现85%的狼毒根、茎、叶样品中内生

细菌为厚壁菌门、变形菌门和放线菌门,其中变形菌门是根内优势细菌,而厚壁菌门则是叶和茎中的优势菌。假单胞菌 *Pseudomonas* 是狼毒根内的优势菌,其中筛选出的菌株 ST3CS3 能显著促进宿主植物生长,进而推测高丰度的假单胞菌可能与狼毒较强的竞争力有关(Jiang et al., 2022)。内生菌定殖除了对组织部位有选择性外,还受宿主生长区域环境的影响。从不同采样地以及不同海拔地区采集的狼毒,其根内的优势菌门均为变形菌门和放线菌门(Jin et al., 2018;程济南等,2022)。对狼毒内生放线菌群落结构和抗菌活性进一步研究发现,根部分离的菌株数量最多,茎、叶部分离的居中,花部分离的最少,其中链霉菌属 *Streptomyces* 为主要优势放线菌群,且分离出的大部分代表菌株对西瓜枯萎病病原真菌尖孢镰刀菌 *Fusarium oxysporum*、黄瓜炭疽病病原真菌瓜类刺盘孢菌 *Colletotrichum orbicular* 和玉米弯孢病病原真菌月状弯孢菌 *Curvularia lunata* 这3种病原真菌均有抗性(廖敏等,2016)。

表2 狼毒内生菌相关研究的统计

Table 2 Statistics on research on endophyte in *Stellera chamaejasme*

内生菌类型 Endophyte	组织部位 Tissue	微生物检测方法 Microbial detection method	采样地点 Sample site	参考文献 Reference
内生真菌 Endophytic fungi	茎、叶、花、根 Stem, leaf, flower, root	培养法 Culture method	陕西省太白县 Taibai County, Shaanxi Province	杨国栋,2009 Yang, 2009
	茎、叶、花 Stem, leaf, flower	培养法 Culture method	甘肃省肃南县、天祝县,青海省门源县,山西省阳城县,陕西省旬邑县 Sunan, Tianzhu counties, Gansu Province; Menyuan County, Qinghai Province; Yangcheng County, Shanxi Province; Xunyi County, Shaanxi Province	潘翠,2012 Pan, 2012
	茎、叶、根 Stem, leaf, root	培养法+分子鉴定 Culture method+molecular identification	甘肃省渝中区 Yuzhong District, Gansu Province	Jin et al., 2013
	茎、叶、根 Stem, leaf, root	高通量测序 High throughput sequencing	甘肃省岷县 Min County, Gansu Province	Jin et al., 2015
	根 Root	高通量测序 High throughput sequencing	甘肃省祁连山 Qilian Mountain, Gansu Province	程济南,2022 Cheng, 2022
	地上部分、地下部分 Aboveground part, belowground part	培养法+高通量测序 Culture method+high throughput sequencing	云南省香格里拉县 Shangri-La County, Yunnan Province	Tang et al., 2023
内生细菌 Endophytic bacteria	茎、叶、根 Stem, leaf, root	高通量测序 High throughput sequencing	甘肃省渝中区 Yuzhong District, Gansu Province	Jin et al., 2014
	根 Root	高通量测序 High throughput sequencing	西藏地区不同海拔梯度样地 Sample sites at different altitudes in Xizang	Jin et al., 2018
	根 Root	高通量测序 High throughput sequencing	甘肃省祁连山 Qilian Mountain, Gansu Province	程济南,2022 Cheng, 2022
	地上部分、地下部分 Aboveground part, belowground part	培养法+高通量测序 Culture method+high throughput sequencing	云南省香格里拉县 Shangri-La County, Yunnan Province	Jiang et al., 2022
内生放线菌 Endophytic actinomycetes	茎、叶、花、根 Stem, leaf, flower, root	培养法 Culture method	四川省阿坝区6个样点 Six sample sites in Aba Prefecture, Sichuan Province	廖敏等,2016 Liao et al., 2016

3 展望

本文从土壤微生物和植物内生菌2个方面归纳整理了近10年来在我国不同区域开展的狼毒微生物相关研究,分析了狼毒-微生物互作关系的研究现状,总结了狼毒扩张的不同微生物机制。然而,功能真菌丛枝菌根真菌与狼毒生长的关系、微生物在狼毒凋落物分解过程中发挥的作用、化感物质-微生物-狼毒三者之间的关系、以及新技术在挖掘功能菌群对狼毒的防控或微生物资源开发方面的应用等内容是今后仍需关注的研究方向。

3.1 验证功能真菌丛枝菌根真菌与狼毒扩张的关系
狼毒虽为我国本地物种,但其大范围的传播及扩张,与入侵物种的传播机制存在相同之处。渐崩共生假说是生物入侵的一种重要假说,即非菌根植物的入侵降低了入侵地丛枝菌根真菌的丰富度,从而使那些强烈依赖丛枝菌根的当地植物种在与入侵的非菌根植物竞争过程中受到排挤,最终导致外来种的入侵和定殖(Vogelsang & Bever, 2009; Pinzone et al., 2018)。狼毒是否通过调节丛枝菌根真菌使其地下微生物与其他物种间的共生关系逐渐崩溃进而实现扩张,以及该作用过程是通过狼毒根系分泌物直接调控(Zhu et al., 2020)或是通过地上部分分解后间接调控均需要进一步研究。

3.2 探索微生物在狼毒凋落物分解过程中的作用

狼毒扩张后显著改变了土壤氮有效性及氮循环过程(Sun et al., 2009; Ma et al., 2020),而土壤氮循环通常与凋落物的分解和养分释放有关。微生物群落是凋落物分解的“引擎”,驱动着凋落物中有机物质的降解和养分的释放过程(Zhang WP et al., 2023)。狼毒植株叶片含氮量高(Guo LZ et al., 2022)、凋落物产量大且质量高(Sun et al., 2009),因此推测狼毒凋落物可能通过微生物作用将氮素转化迁移到土壤中,而土壤中的可利用养分及微生物又对狼毒生长起到显著的反馈作用,有利于其进一步扩张。但是当前对狼毒凋落物的研究甚少,仅有报道描述了青藏高原东缘高寒草甸狼毒凋落物的分解动态(Sun et al., 2009)以及狼毒凋落物对羊草生长的影响(Guo Q et al., 2022),而微生物在狼毒凋落物分解过程中的功能与作用尚不清楚,今后可以开展更多工作来探究它们在生态系统物质循环和能量流动中的具体角色,以及它们如何影响狼毒分布和草原退化的生态过程。

3.3 深入化感物质介导的植物土壤反馈机制

植物通过根系分泌物和凋落物分解同时从地下和地上向土壤释放化学物质,从而塑造植物生长微环境。狼毒残体(凋落物)分解已被证明是狼毒释放化感物质的一条途径(王慧,2011),但当前多数研究主要聚焦于狼毒根系分泌物(Cheng et al., 2022; Hu et al., 2023),对狼毒凋落物分解产物中化感物质成分及变化规律了解甚少。最近有研究表明土壤微生物区系与植物地下部分的化学作用在介导植物-土壤反馈作用方面扮演着重要角色(Delory et al., 2024)。明确土壤微生物与土壤代谢物在介导植物-土壤互作中的交互作用,有助于解决植物-土壤反馈作用中一些难以解释的变化,进而提高对反馈效应强度和方向的预测能力。狼毒凋落物化感物质的研究是狼毒土壤代谢物研究的重要内容,在今后的研究中也应重视化感物质介导的植物-土壤反馈作用对狼毒在退化草地扩张的贡献。

3.4 利用宏组学进行狼毒-微生物互作机制研究

宏基因组、宏转录组、宏蛋白组以及宏代谢组等是微生物群落研究中广泛使用的组学技术。其中,宏基因组可用于解析菌群的功能性问题,宏转录组(李莹等,2021)、宏蛋白质组(Abiraami et al., 2020)和宏代谢组(Chevrette et al., 2022)则可用于揭示不同理化环境条件下菌群准备发挥什么功能、正在发挥什么功能、已经发挥了什么功能(黄佳城等,2022)。将这些组学技术有效地结合起来,有助于构建整个微生物群落组成、功能、相互作用关系的图谱。当前,狼毒相关微生物的研究主要利用高通量测序技术揭示微生物的构成及多样性,对功能菌群的研究仍处于起步阶段。虽然目前宏组学分析技术仍存在一些局限性,且测序费用昂贵,但系统认识微生物群落与其功能,挖掘新的微生物菌种对狼毒进行生物防控或用于微生物资源开发,这将是未来狼毒相关微生物生态学研究的新方向。

3.5 挖掘与利用狼毒微生物组资源

植物微生物基因组被称为植物的“第二基因组”,在调节植物生长发育、促进植物营养吸收、提高植物病害防御能力以及环境胁迫适应性等方面均发挥着重要作用(曾青等,2023)。近10多年对狼毒植株不同部位微生物组的组成、多样性以及功能等都有了初步认识,但距其精准应用还有很长的路要走,特别是合成功能菌群的应用。目前,人工合成的功能微生物菌群在抵御有害生物入侵、控制土壤病害和增加植物生物量等方面已经发挥了重要作用(冀

宇等,2016),因此利用狼毒微生物构建合成菌群在促进植物生产、减少化肥农药使用等方面具有广阔的应用前景。

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