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不同放牧强度对内蒙古荒漠草原藻结皮特征的影响

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摘要:藻结皮是荒漠草原重要的生物结皮类型,作为重要的“生态工程师”,在固土、保水、抗风蚀和碳氮固存方面作用显著。然而,关于不同放牧强度对荒漠草原藻结皮特征影响的研究相对较少。本研究依托内蒙古四子王旗荒漠草原长期放牧试验平台(2004年—至今),探究了不同放牧强度对藻结皮特征的影响及关键驱动因子。本研究测定了不同放牧强度下藻结皮的盖度、厚度、叶绿素a含量以及相关土壤理化性质。结果显示,随着放牧强度的增加,藻结皮盖度、厚度和叶绿素a含量均显著降低($P<0.05$)。结构方程模型进一步揭示了驱动藻结皮变化的关键土壤因子,其中土壤速效氮是影响藻结皮特征的最关键因子。本研究表明,中度和重度放牧显著抑制了荒漠草原藻结皮的生长,其中与藻结皮特征变化最相关的关键因子是土壤容重、毛管持水量和土壤速效氮。为维持藻结皮在荒漠草原生态系统中的生态作用,严格控制放牧强度至关重要,长期高强度放牧将导致其严重退化。

关键词:荒漠草原;藻结皮;放牧强度;土壤理化性质

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The Influence of Different Grazing Intensities on the Characteristics of Algal Crusts in the Desert Steppe of Inner Mongolia

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Abstract: Algal crusts represent a crucial type of biological soil crust in desert grasslands and serve as an important significant “ecological engineer”. They play a vital role in soil stabilization, water retention, wind erosion resistance, and carbon and nitrogen sequestration. However, researches on the effects of different grazing intensities on the characteristics of algal crusts in desert grasslands remains relatively limited. Based on a long-term grazing experiment platform (2004-present) in the desert grassland of Siziwang Banner, Inner Mongolia, in this study we investigated the impacts of varying grazing intensities on the algal crusts characteristics and identified the key driving factors. We measured the coverage, thickness, chlorophyll-a content of algal crusts, as well as related soil physicochemical properties under different grazing intensities. The results showed that as grazing intensity increased, the coverage, thickness, and chlorophyll-a content of algal crusts significantly decreased ($P<0.05$). Structural equation modeling further revealed the key soil factors driving changes in algal crusts, among which soil available nitrogen was the most critical factor influencing characteristics of algal crusts. This study demonstrated that moderate and heavy grazing significantly inhibited the growth of algal

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crusts in desert grasslands, with soil bulk density, capillary water holding capacity, and soil available nitrogen were the most closely related factors to the changes in algal crusts characteristics. To maintain the ecological functions of algal crusts in desert grassland ecosystems, it is essential to strictly control grazing intensity, as long-term high-intensity grazing will lead to their severe degradation.

Key words: Desert steppe; Algal crusts; Grazing intensity; Soil physical and chemical properties

生物结皮是由藻类、地衣和苔藓等非维管束植物和真菌、细菌等土壤微生物,通过菌丝体、假根系和分泌物与土壤颗粒胶结形成的有机复合物^[1]。藻结皮作为生物结皮的初始阶段,主要由藻类、土壤微生物与土壤颗粒相互作用形成^[2],是地衣结皮和藓结皮形成的先决条件^[3],广泛分布于干旱半干旱地区。生物结皮被称为“荒漠生态系统工程师”,藻结皮作为生物结皮的初始阶段也发挥着重要的作用^[4]。藻结皮能有效附着于土壤表面,维持土壤湿度、减少地表水分蒸发,从而有效保持土壤水分^[5]。同时,藻结皮还能够改善土壤结构,显著增强土壤的抗侵蚀能力^[6]。有研究表明^[7],蓝藻结皮能显著提高地表稳定性,有效抑制风蚀,大幅降低土壤风蚀程度。此外,藻结皮还能吸收空气中的二氧化碳,增加碳、氮固存,减少温室气体排放,具有重要的生态功能^[8]。因为这些特性,藻结皮在干旱生境中扮演着先锋拓殖角色^[9],其在荒漠化草地生态恢复方面的应用备受关注。然而藻结皮对外界干扰十分敏感,放牧干扰是草地系统中最常见的干扰形式^[10]。藻结皮抵抗家畜践踏等干扰的能力较弱,放牧践踏直接导致藻结皮受损,被破坏后藻结皮的恢复需要较长时间^[11]。Belnap在美国犹他州冷沙漠的研究表明^[12],完全破坏的藻结皮恢复到未受干扰状态至少需要30~40年,而其生态功能的完全恢复所需要的时间可能更长。放牧干扰会明显抑制藻结皮的发育^[13],使藻结皮难以正常生长和扩展,在科尔沁沙地的研究^[14]中,受放牧干扰区域的藻结皮发育程度远低于未受干扰区域。然而,在黄土丘陵区的一项研究表明^[15],在模拟轻度放牧情况下藻结皮盖度相比较于对照增加了。Concostrinazubiri等^[16]的研究发现,长期放牧干扰显著降低了藻结皮的物种丰富度。鉴于藻结皮在干旱半干旱区分布广泛且具有独特的生态功能,其独特的生态地位已引起国内外研究人员的广泛关注,然而关于不同放牧强度对荒漠草原藻结皮特征影响的研究相对较少。

藻结皮的拓殖和生长受多种因子影响,主要是土壤环境因子。有研究表明^[17],高pH值会抑制蓝

藻活性,进而影响蓝藻结皮的生长。有研究发现土壤粒径是影响藻结皮拓殖的重要因子^[18]。Bullard等^[19]研究发现蓝藻结皮对土壤水分反应迅速,在土壤水分更高的环境下表现出更高水平的光合作用。Zhao等^[20]研究发现土壤养分含量与蓝藻结皮的生长呈正相关。相反,土壤环境胁迫会显著抑制藻结皮的生长,Lan等^[21]研究发现在干旱胁迫下蓝藻结皮的代谢活动显著降低。也有研究发现土壤盐胁迫显著影响藻结皮的生物量^[22]。尽管如此,藻结皮具有独特的生理机制来适应恶劣环境,Xu等^[23]研究发现荒漠蓝藻能通过启动多种适应策略的综合调节机制,包括胞外多糖、脱水响应蛋白、抗氧化剂的合成,以及C/N等营养物质代谢和细胞膜流动性的调节等以增强应激耐受能力。

荒漠草原位于干旱半干旱区,生态环境脆弱,对气候变化和人为活动干扰都极为敏感^[24]。放牧作为该草原最主要的利用方式之一,对草地生态系统影响显著,不仅作用于植被结构和功能,还影响土壤结构稳定性、养分状况及生态系统循环过程^[25]。本研究以四子王旗荒漠草原的藻结皮为研究对象,测定分析了不同放牧强度下藻结皮的盖度、厚度、生物量及相关土壤理化性质,旨在探讨藻结皮的特征变化及其与土壤环境因子的关系,试图回答以下科学问题:(1)藻结皮特征在不同放牧强度下是怎么变化的?(2)放牧情况下影响藻结皮特征变化的关键土壤环境因子是什么?为荒漠草原藻结皮生态管理提供科学依据。

1 材料与方法

1.1 研究区概况

本研究区位于中国内蒙古四子王旗荒漠草原(41°46′43.6″N, 111°53′41.7″E,海拔1450 m)。该地区干旱少雨,年平均气温4.15℃,年平均降水量229 mm,建群植物为短花针茅(*Stipa breviflora*),优势植物有无芒隐子草(*Cleistogenes songorica*)和冷蒿(*Artemisia frigida*)^[26],土壤类型为砂壤土。

放牧试验平台于2004年建立,采用完全随机区组试验设计,基于Wei等人^[27]的研究结果,设4个放牧强度,对照(Control, CK)、轻度放牧(Light grazing, LG)、中度放牧(Moderate grazing, MG)和重度放牧(Heavy grazing, HG),载畜率分别为0, 0.91, 1.82和2.71只羊·ha⁻¹·a⁻¹。每个处理3次重复,共12个样地(每个小区面积为4.4 ha)。在每年的6月1日—11月30日,使用两岁的蒙古羯羊进行放牧管理,每三年更换一次羊群。每日放牧时间为上午6:00—下午6:00,并确保提供充足的水源和盐分。

1.2 样品取样和处理

于2024年8月在四子王旗采集藻结皮及相应下层土壤样品。每个样地各选取4个面积为50 cm×50 cm的样方,在样方内用酒精消毒过的金属铲子采集藻结皮(表层土1~2 cm)及其下层土壤(结皮下层2~5 cm),结皮层和结皮下层土壤完全分离,去除石块、枯落物等杂质后用无菌密封袋封装。每个藻结皮样品由颜色、形态等外观一致的3个藻结皮混合组成,其相应下层土壤则混合成一个土壤样品,藻结皮样品和土壤样品分开装取。每个样地各取4个藻结皮样品和土壤样品,共取2组96个样品。

藻结皮样品用冰袋保存后运到实验室,测定相关特征。土壤样品用冰袋保存运到实验室,一份于-80℃保存、备用,另一份在室温自然风干后用于测定相关土壤理化性质。此外,在每个样方内随机使用环刀(100 cm³,高5 cm,直径5.05 cm)收集1个结皮下层土壤样品(0~5 cm),用于水文特征的相关指标测定。



图1 样地藻结皮照片

Fig. 1 Photos of algal crusts in the sample plots

1.3 样品测定及方法

1.3.1 藻结皮特征测定 采用样方法对藻结皮盖度进行了目测统计。藻结皮厚度使用游标卡尺测定。藻结皮生物量用叶绿素a含量来反映,测定方

法^[28]:在避光条件下用研钵研磨藻结皮,使藻体分离。准确称取(2±0.01) g磨碎样品于试管中,加入10 mL二甲基亚砜,置于65℃恒温水浴锅中避光萃取1 h,萃取液经滤纸过滤后,收集上清液。在665 nm和750 nm波长处测定上清液的吸光值,然后向上清液中加5滴1 mol·L⁻¹ HCl,酸化10 min后再次于波长665 nm和750 nm处测定吸光值。叶绿素a含量的计算公式为:

$$Chla = 26.73 \times [(E_{665} - E_{750}) - (A_{665} - A_{750})] \times \frac{V}{M}$$

式中:Chla为测定的叶绿素a含量(mg·g⁻¹);E₆₆₅和E₇₅₀分别为萃取液酸化前于波长665 nm和750 nm处的吸光值;A₆₆₅和A₇₅₀分别为萃取液酸化后于波长665 nm和750 nm处的吸光值;V为萃取液体积(mL);M为土样质量(g)。

1.3.2 土壤理化性质测定 土壤pH值:称取自然风干土壤10 g置于烧杯内,加入50 mL蒸馏水,搅拌两分钟后静置半小时,然后使用pH值计测定。

土壤容重(Soil bulk density, BD)、毛管持水量(Capillary capacity, CC):用定水头法^[29]测定。取下环刀上盖,将环刀(有网孔和滤纸一端向下)放入盆中。向盆中注水至环刀上沿,放置12小时,称取此时环刀与饱和土壤的总重记为W₁₀将环刀移至覆有5 cm厚干砂的盆中静置12小时,称取此时环刀与土壤的总重记为W₂₀继续将环刀在覆有干砂的盆中放置3~5天,称取此时环刀与土壤的总重记为W₃₀将环刀放入烘箱,在105℃烘干至恒重,称重记为W₄₀去除环刀内土壤,称取空环刀的重量记为W₅₀计算公式为:

$$BD = \frac{W_4 - W_5}{V}$$

$$CC = \frac{W_2 - W_4}{W_4 - W_5}$$

式中:V是环刀的体积。

土壤速效磷使用碳酸氢钠浸提法测定^[30]。土壤有机碳使用重铬酸钾-外加热法测定^[31]。土壤速效氮使用碱解扩散法测定^[32]。

1.4 数据处理

数据统计分析使用SPSS 23软件,图表绘制使用Origin 2024软件。采用单因素方差分析评估放牧强度对藻结皮特征和土壤理化性质的影响。绘制相关性热图分析藻结皮特征与土壤理化性质之间的相关性。最后,使用Amos软件生成结构方程模型(SEM)。

2 结果与分析

2.1 不同放牧强度下藻结皮的特征变化

不同放牧强度处理下藻结皮的特征表现出的差异(图2)。与CK处理相比,藻结皮盖度在不同放牧强度处理下分别减少了32.10%,52.64%,71.86%,其随着放牧强度的增加而显著降低($P<0.05$)(图2a)。藻结皮厚度在不同放牧强度处理下

分别为4.29,4.15,3.49和3.34 mm,其中CK和LG处理下藻结皮厚度无显著变化,MG和HG处理下藻结皮厚度显著小于CK和LG处理($P<0.05$)(图2b)。在不同放牧强度处理下藻结皮叶绿素a含量分别为23.01,18.80,10.16和10.19 $\text{mg}\cdot\text{g}^{-1}$,随着放牧强度增加藻结皮叶绿素a含量显著降低($P<0.05$),其中MG和HG处理下藻结皮叶绿素a含量相比CK处理显著降低($P<0.05$)(图2c)。

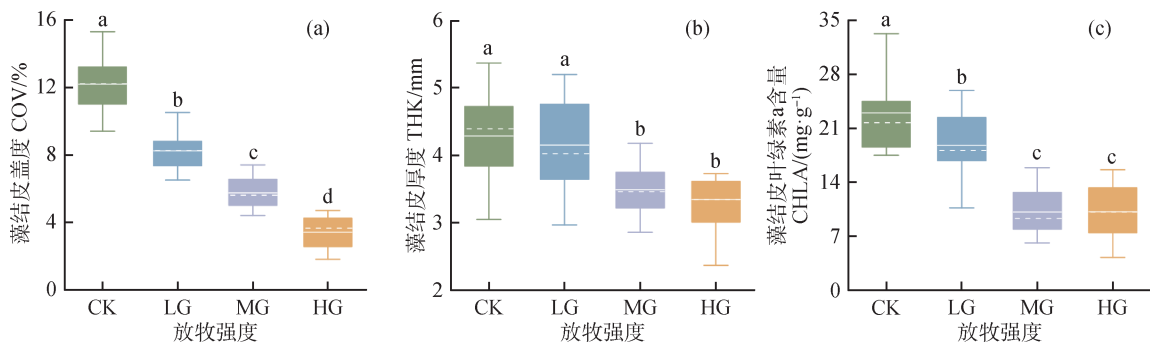


图2 不同放牧强度下藻结皮特征变化

Fig. 2 Characterization of algal crust variations under different grazing intensities

注:CK,对照;LG,轻度放牧;MG,中度放牧;HG,重度放牧。不同字母表示差异显著($P<0.05$)

Note: CK, control; LG, light grazing; MG, moderate grazing; HG, heavy grazing. Different letters indicate significant differences ($P<0.05$)

2.2 不同放牧强度下土壤理化性质的变化

在不同放牧强度处理下的土壤pH值分别为6.99,7.20,7.13和7.21。在LG, MG, HG处理下的土壤pH值无显著变化,且都显著大于CK处理($P<0.05$)(图3a)。相比CK处理, LG, MG和HG处理下土壤容重分别增加了1.48%,7.41%,4.44%,其中MG处理下土壤容重显著大于CK和LG处理($P<0.05$),MG和HG处理下土壤容重无显著变化(图3b)。毛管持水量随着放牧强度的增加而减少,其中MG处理下毛管持水量显著低于CK和LG处理($P<0.05$)(图3c)。土壤速效磷含量分别为13.62,11.78,11.30和8.25 $\text{mg}\cdot\text{kg}^{-1}$,HG处理下土壤速效磷含量最小且显著小于其他放牧强度处理($P<0.05$)(图3d)。随着放牧强度的变化,土壤有机碳含量无显著变化(图3e)。随着放牧强度的增加土壤速效氮含量显著降低($P<0.05$),分别为12.92,11.93,11.07和10.16 $\text{mg}\cdot\text{kg}^{-1}$,相较于CK处理,在其他放牧处理下土壤速效氮含量分别降低了7.66%,14.32%,21.36%(图3f)。

2.3 藻结皮特征和土壤理化性质之间的关系

由图4可知,藻结皮盖度与毛管持水量、土壤速

效磷、土壤速效氮含量有显著正相关关系($P<0.05$),与土壤pH值、土壤容重有显著负相关关系($P<0.05$)。藻结皮厚度与毛管持水量、土壤速效氮含量有显著正相关关系($P<0.05$)。藻结皮叶绿素a含量与毛管持水量、土壤速效磷、土壤速效氮含量有显著正相关关系($P<0.05$),与土壤容重有显著负相关关系($P<0.05$)。

2.4 放牧处理下影响藻结皮特征的关键因子

结构方程模型(SEM)显示,影响藻结皮特征变化的关键因子是土壤容重、毛管持水量和土壤速效氮。放牧强度通过增加土壤容重、降低毛管持水量和土壤速效氮对藻结皮盖度产生显著的负面影响,总负间接效应分别为0.02,0.07和0.70($P<0.05$)(图5)。同时,放牧强度通过减少效应值为0.21的土壤速效氮对藻结皮厚度产生显著的间接负面影响($P<0.05$)(图5)。放牧强度通过增加土壤容重、降低毛管持水量和土壤速效氮对藻结皮叶绿素a含量产生显著的负面影响,总负间接效应分别为0.09,0.13和0.20($P<0.05$)(图5)。放牧对藻结皮特征也有直接效应,总负直接效应分别为0.86和0.60($P<0.05$)(图5)。

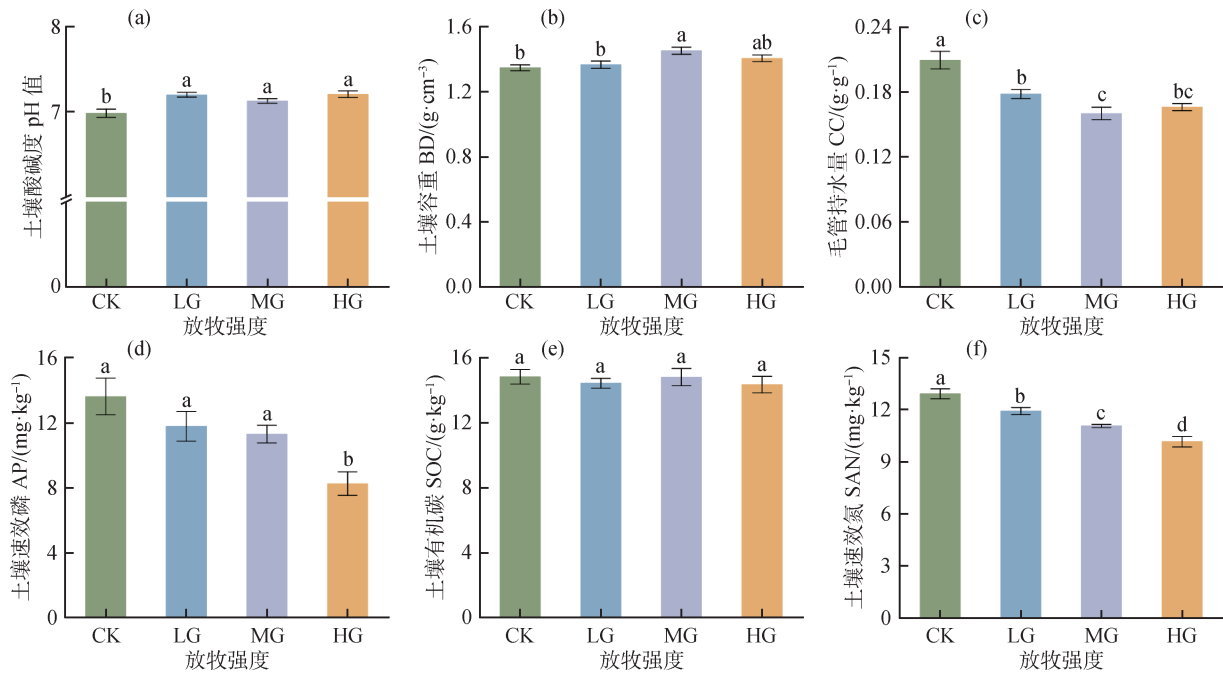


图3 不同放牧强度下土壤理化性质变化

Fig. 3 Changes in soil physical and chemical properties under different grazing intensities

注:CK,对照;LG,轻度放牧;MG,中度放牧;HG,重度放牧。不同字母表示差异显著($P < 0.05$)

Note: CK, control; LG, light grazing; MG, moderate grazing; HG, heavy grazing. Different letters indicate significant differences ($P < 0.05$)

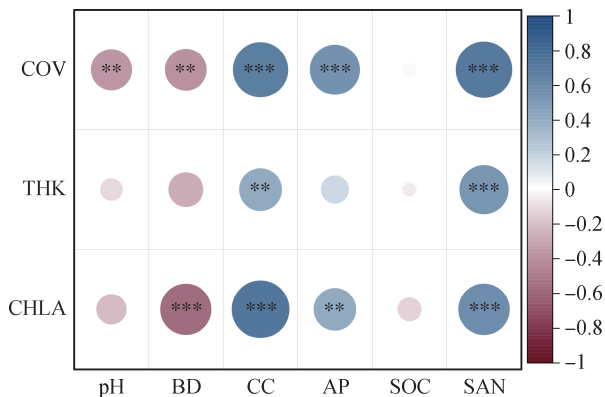


图4 藻结皮特征和土壤理化性质之间的相关性热图

Fig. 4 Heatmap of the correlation between algal crust characteristics and soil physical and chemical properties

注:图中颜色越蓝正相关性越强,颜色越红负相关性越强。COV,藻结皮盖度;THK,藻结皮厚度;CHLA,藻结皮叶绿素a含量;pH,土壤酸碱度;BD,土壤容重;CC,毛管持水量;AP,土壤速效磷;SOC,土壤有机碳;SAN,土壤速效氮。*表示 $P < 0.05$,**表示 $P < 0.01$,***表示 $P < 0.001$

Note: In the figure, darker blue indicates a stronger positive correlation, while darker red indicates a stronger negative correlation. COV, algal crust coverage; THK, algal crust thickness; CHLA, chlorophyll a content of algal crust; pH, soil pH; BD, soil bulk density; CC, capillary capacity; AP, soil available phosphorus; SOC, soil organic carbon; SAN, soil available nitrogen. * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$

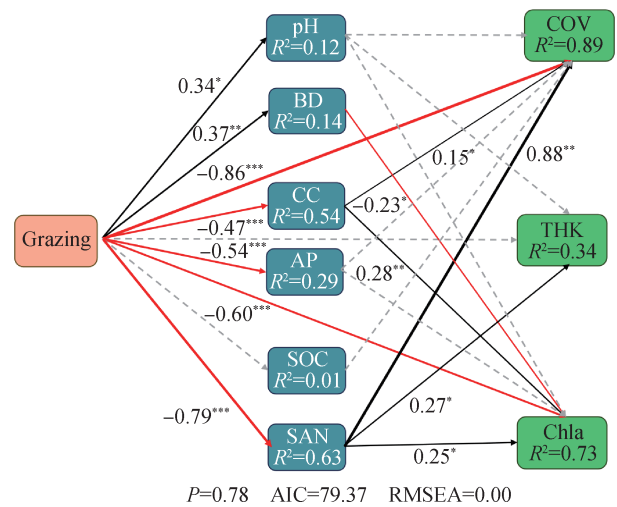


图5 放牧影响藻结皮特征的结构方程模型

Fig. 5 Structural equation modeling of grazing effects on algal crust characteristics

注:Grazing,放牧处理;COV,藻结皮盖度;THK,藻结皮厚度;CHLA,藻结皮叶绿素a含量;pH,土壤酸碱度;BD,土壤容重;CC,毛管持水量;AP,土壤速效磷;SOC,土壤有机碳;SAN,土壤速效氮。*表示 $P < 0.05$,**表示 $P < 0.01$,***表示 $P < 0.001$

Note: Grazing, grazing treatment; COV, algal crust coverage; THK, algal crust thickness; CHLA, chlorophyll a content of algal crust; pH, soil pH; BD, soil bulk density; CC, capillary capacity; AP, soil available phosphorus; SOC, soil organic carbon; SAN, soil available nitrogen. * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$

3 讨论

3.1 不同放牧强度对藻结皮特征的影响

本研究中不同放牧强度处理下藻结皮特征发生显著差异。随放牧强度的增加,藻结皮盖度呈显著下降的趋势,在重度放牧的情况下藻结皮盖度最低。藻结皮作为附着于地表的薄层结构(通常仅1~2 mm至数厘米厚),其物理结构脆弱,对机械压力极为敏感,放牧活动可能会导致藻结皮被踩碎、剥离或完全移除^[33]。Belnap等人^[12]的研究表明,家畜践踏是导致藻结皮盖度损失的最主要原因。本研究结果与在科尔沁沙地的研究^[14]一致,即受放牧干扰区域的藻结皮盖度显著低于未受干扰区域。本研究中藻结皮厚度在对照处理和轻度放牧处理下无显著差异,在中度放牧和重度放牧处理下显著小于轻度放牧。在轻度放牧处理下,藻结皮可能通过其内在藻丝体的调整或局部的恢复维持了其垂直维度的结构完整性^[34]。然而,一旦达到中度放牧和重度放牧强度处理,藻结皮厚度即发生显著下降。同时过度放牧也会造成土壤养分的流失,导致土壤养分贫瘠^[25],不利于藻类的生长和藻结皮的增厚。本研究中藻结皮叶绿素a含量随着放牧强度的增加而不断降低,在中度放牧和重度放牧处理下无显著变化。过度放牧会使土壤过度紧实,孔隙度减小,土壤通气性和透水性变差,限制了藻类的生长,导致藻结皮叶绿素a含量下降^[35]。过度放牧也会导致土壤养分流失^[25],影响藻类对养分的吸收和利用,进而影响藻结皮叶绿素a的合成。本研究中毛管持水量与藻结皮叶绿素a含量显著正相关。张丙昌等人^[36]的研究发现,随着施水量的增加,藻结皮生物量显著增加,本研究观察到的结果与张丙昌等的研究结果一致。

3.2 放牧条件下影响藻结皮特征的关键因子

本研究通过相关性分析和结构方程模型探索了不同放牧强度下驱动藻结皮特征变化的关键因子,结构方程模型分析显示影响藻结皮的关键因子是土壤容重、毛管持水量和土壤速效氮。放牧强度通过改变这些土壤环境因子,对藻结皮产生间接的负面影响,同时放牧活动本身对藻结皮也会产生直接的负面影响。随着放牧强度增加,土壤容重显著增加,这可能与放牧家畜的反复践踏导致土壤压实紧密相关^[37]。一方面放牧直接导致的家畜践踏极易破坏藻结皮的结构,导致其盖度和生物量下降^[38]。另一方

面,压实后的土壤表面通气性变差、水分入渗受阻,阻碍了藻类的拓殖,从而抑制了新藻结皮的形成和原有结皮的恢复,导致盖度降低^[15]。结构方程模型还显示,土壤容重通过降低毛管持水量间接对藻结皮盖度产生负面影响。有研究显示在水分充足时,蓝藻结皮能快速扩张结皮结构^[34]。在本研究中,放牧导致土壤容重增加,进而导致毛管持水量减少,抑制了藻结皮盖度的增加。此外,毛管持水量随放牧强度增加而降低,且与藻结皮的盖度、厚度和叶绿素a含量均呈显著正相关。结构方程模型结果进一步证实,放牧通过降低毛管持水量对藻结皮盖度和叶绿素a含量产生了显著的间接负效应。毛管持水量是衡量土壤保持有效水分能力的关键指标^[39]。有研究显示其下降主要归因于放牧践踏导致的土壤容重增加^[40]。在干旱半干旱的荒漠草原,水分是最主要的限制因子,藻结皮中的生理活动高度依赖有限的土壤水分^[41]。较低的毛管持水量严重限制了藻类的生长,最终表现为生物量降低、盖度、厚度下降。赵燕翘等人^[42]的研究也强调了水分是荒漠藻结皮生长发育的关键影响因素。氮素是生命必需营养元素,也是草地系统生产力的体现^[43]。有研究显示放牧显著降低了土壤氮含量^[44],随着放牧强度的增加土壤氮含量整体也呈下降趋势^[45],这与本研究结果一致。本研究中,土壤速效氮含量随放牧强度增加而显著降低,并且与藻结皮的盖度、厚度和叶绿素a含量均呈显著正相关关系。结构方程模型结果表明,在所有考察的土壤因子中,土壤速效氮对藻结皮特征的影响路径效应值最大,因此土壤速效氮是影响藻结皮特征指标的最关键因子,且放牧主要通过减少土壤速效氮对藻结皮产生负面影响。氮素是藻类合成蛋白质、叶绿素和核酸等关键物质的必需元素,土壤速效氮的匮乏直接限制了藻类的生长,导致叶绿素a含量降低、生物量下降。

4 结论

本研究结果表明,随着放牧强度的增加,藻结皮盖度、厚度和叶绿素a含量显著降低,在重度放牧情况下藻结皮严重退化。放牧主要通过增加土壤容重、降低毛管持水量和土壤速效氮含量,进而抑制藻结皮盖度、厚度和叶绿素a含量。因此,为维护荒漠草原藻结皮的生态功能,需控制草地的放牧强度,长期高强度放牧会导致藻结皮严重退化。

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