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围封禁牧对小叶锦鸡儿灌丛化草原群落组成和结构的影响

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摘要:典型草原向灌丛化草原的转变是过度放牧引起的重要结果之一。为研究内蒙古地区小叶锦鸡儿灌丛化草原对围封禁牧的响应,在内蒙古锡林郭勒典型草原退化区选取小叶锦鸡儿成片分布的典型地段,自2003年,分别设置禁牧样区和放牧样区。于2008—2011年连续四年调查禁牧样区小叶锦鸡儿种群生长和生理生化指标及灌丛间群落基本特征,并将2011年禁牧样区与放牧样区小叶锦鸡儿种群与灌丛间群落进行比较。结果显示:(1)围封后小叶锦鸡儿种群开始衰退,主要体现在种群盖度的降低和叶片氮磷含量(特别是磷含量)有所降低,而个体构件生长状况无显著差异;(2)灌丛间群落的物种组成随围封年限增加发生显著变化;禁牧后1年生植物逐渐退出群落,多年生丛生禾草重要值随围封年限增加而显著增加,即围封禁牧对小叶锦鸡儿灌丛化草原的群落恢复有积极作用;(3)小叶锦鸡儿种群盖度与多年生丛生禾草的重要值显著负相关,说明两者之间存在竞争关系,推测多年生丛生禾草的竞争是禁牧后小叶锦鸡儿衰退的重要原因。

关键词:小叶锦鸡儿;群落组成;禁牧;多年生丛生禾草;恢复

Effects of grazing exclusion on the composition and structure of steppe communities dominated by *Caragana microphylla*

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Abstract: Grassland ecosystem is one of the most important terrestrial ecosystems in the world which may impose an impact upon global environmental change. The dynamics of a grassland ecosystem can be affected by disturbance in terms of promoting community succession and changing community structure. Among the disturbing factors, grazing is considered one of the key factors which affect both above- and below-ground processes in the ecosystem. One of the most prominent consequences of overgrazing is the transformation of grassland to shrub-land. In order to protect grassland ecosystem and restore vegetation productivity, a number of measures have been put into practice, among which fencing an area to exclude livestock is often considered to be a simple but effective way. The aim of the present study was to explore the response of the *Caragana microphylla*-dominated community to fencing and to predict when the degraded community would restore to its normal status after grazing exclusion. The study site was located in Xilingol degraded grassland of Inner Mongolia, China. Long-time grazing resulted in the expansion of *C. microphylla* populations in this site, and we set different treatments since 2003. Animals were excluded by fencing in the plot of grazing exclusion (EG), while the grazing intensity was controlled at 3 sheep/hm² in the plot of grazing (G). The two plots were adjacent and had similar environment until 2003. We investigated the growth and physiological traits of *C. microphylla* and the basic characteristics of the herbaceous

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communities, and compared the temporal changes in plot EG after 5—8 years of fencing and the spatial differences between these two plots after eight years of different utilization regimes. We analyzed the response of the traits of *C. microphylla* and the composition of herbaceous community to grazing and fencing, and also the relationship between the cover of *C. microphylla* and the ‘Importance Value’ of different functional groups. (1) The coverage of *C. microphylla* decreased in the plot EG during the four years while the morphological traits showed no significant variation, indicating that *C. microphylla* population declined after grazing exclusion. The decline of *C. microphylla* reflected a decrease of population coverage instead of the growth status of individual modules. Moreover, leaf nitrogen and phosphorus content, especially the latter, decreased after grazing exclusion, which might be associated with the decline of *C. microphylla* population. (2) Herbaceous community composition showed significant change after eight years of grazing exclusion. Annuals disappeared from the community, while the Important Value of perennial bunch grasses increased significantly in the plot EG both in temporal and spatial comparison. The change of community structure indicated that grazing exclusion had a positive effect on the restoration of *C. microphylla*-dominated grassland. (3) The coverage of *C. microphylla* decreased with the increasing Importance Value of perennial bunch grasses, indicating that there existed a competition between *C. microphylla* and the perennial bunch grasses. The decline of *C. microphylla* population might be caused by the expansion of well-grown perennial bunch grasses. It is suggested that grazing exclusion impose an effect on the restoration of *C. microphylla*-dominated community, but re-establishment of the typical steppe with climax community needs at least eight years; in other words, the restoration of *C. microphylla*-dominated grassland to its original status is a long-term process.

Key Words: *Caragana microphylla*; community composition; grazing exclusion; perennial bunch grass; restoration

内蒙古典型草原是欧亚草原生态系统的代表性组成部分之一,在区域生态环境与社会经济方面起着重要作用^[1],但近几十年来,随着过度放牧与全球气候变化,内蒙古草原退化严重,约70%的草原地区处于退化状态^[2-3]。草原退化的重要后果之一是典型草原向灌丛化草原转变^[4],世界范围内许多干旱草原生态系统发生了明显的多年生禾草盖度降低与木本灌木盖度增加的现象^[5],在内蒙古典型草原区,多年生灌木物种小叶锦鸡儿种群扩展,盖度增大,也已成为了普遍现象,表现为典型草原灌丛化加重^[6]。

为保护草原生态系统与恢复植被生产力,一系列措施被投入实践,例如围封、重新播种和/或肥料的使用^[7]。其中,设置围栏禁牧因其简单有效,在近几十年中广泛应用于全世界的草原保护^[8-9]。对于去除放牧干扰后小叶锦鸡儿(*Caragana microphylla*)灌丛化草原能否恢复,不同学者间意见并不一致。有学者指出小叶锦鸡儿灌丛化草原具有显著次生性质,属于非气候性顶级群落,在去除干扰后可以恢复原貌;小叶锦鸡儿是退化草原恢复演替过程中的消退种,随着恢复演替的进行,在群落中的作用将逐年降低^[10-11]。但也有学者认为典型草原与灌丛化草原之间的转变存在阈值,仅仅去除放牧干扰,不能使小

叶锦鸡儿灌丛化草原恢复原貌^[12]。本文通过在小叶锦鸡儿灌丛化草原内设置持续放牧样区和围封禁牧样区,研究了两种利用方式对草原群落组成和结构的影响,并重点探讨了小叶锦鸡儿种群与灌丛间植物群落在围封禁牧后的动态变化,即从空间与时间两方面展开研究,以探究围封禁牧后小叶锦鸡儿灌丛化草原能否恢复,从而为内蒙古退化草原生态系统的恢复提供一定的理论基础和实验证据。

1 实验方法

1.1 研究区域概况

研究区域位于内蒙古锡林郭勒典型草原区,气候属半干旱草原气候,年降水量240 mm左右,主要集中于6—8月份,年平均气温2.7 °C,最冷月(1月)平均气温为-21.0 °C,最热月(7月)平均气温为23.3 °C,年日照时数2950 h左右,无霜期约为110 d,土壤类型为栗钙土。近几十年由于过度放牧,草原退化严重,草本层盖度减少,多年生禾草优势度下降,小叶锦鸡儿分布逐渐增加。于2003年,在小叶锦鸡儿灌丛化草原选取典型样地(北纬43°52'30"—43°52'33",东经116°22'38"—116°22'53"),设置禁牧样区(EG)和放牧样区(G),两样区间仅以围栏隔开,在

不同处理前具有原生群落和生境的一致性。其中,放牧样区的放牧强度为每公顷3只羊,为中等放牧强度。该样地在2003年前一直处于自由放牧状态,草地发生明显退化,灌丛化严重。

1.2 研究方法

1.2.1 小叶锦鸡儿性状测定

2008—2011年7月底,在禁牧样区内作5个40 m×20 m的小叶锦鸡儿分布样方,调查小叶锦鸡儿种群盖度,并在样区内随机选取25株样本株以进行植物性状测定:每株样本株选择5个具有代表性的当年枝,测定复叶数与中部复叶面积,样品于80℃烘箱中烘干48 h至恒重,测定当年枝总干重、叶干重。其中2009—2011年,还测定了叶片的比叶重和氮磷含量,每样本株选择5片向阳、年轻而充分展开的叶片,将贴有复叶的A4纸扫描,用PHOTOSHOP计算复叶面积,揭下叶片后于80℃烘箱中烘干48 h至恒重,测定复叶质量,计算得到比叶重(复叶质量/复叶面积),所得叶片磨碎后用于测定叶片氮磷含量,氮含量的测定采用半微量凯氏定氮法,磷含量的测定采用钼锑抗比色法,根据叶片质量和面积可以分别得到以面积和质量为单位的叶片氮磷含量。

2011年7月底,在放牧样区内对小叶锦鸡儿种群进行相同的观测研究。样品采集与测定方法均参照Cornelissen等^[13]

1.2.2 小叶锦鸡儿灌丛间群落调查

2008—2011年8月中旬,在禁牧样区采用常规1 m×1 m样方法调查植物群落特征,在小叶锦鸡儿灌丛间(即样方内不包含小叶锦鸡儿)随机选择,调查植物种类并测定植株高度、密度,并按物种剪取植物地上部,分别装入信封,带回实验室80℃烘干至恒重,称重,测定地上部分生物量,计算各个物种以及各功能群^[14](多年生根茎禾草、多年生丛生禾草、多年生杂类草、灌木和半灌、1年生植物与多年生禾草)的重要值:

重要值=(相对高度+相对密度+相对地上生物量)/3

2011年8月中旬,在放牧样区内进行相同的观测研究。

1.3 数据分析

计算禁牧样区不同功能群重要值和小叶锦鸡儿盖度对围封的响应比(response ratio),即禁牧样区对应年份该性状/2008年该性状,响应比常用来判断性

状对各种环境因子的响应,在实际应用中,常以其自然对数的形式显示,正值代表环境因子对该性状存在促进作用,负值代表环境因子对该性状存在抑制作用,绝对值越大,说明作用越强^[15-16]。

利用单因素方差分析分析不同年份间禁牧样区小叶锦鸡儿植物性状与群落特征的差异;利用t检验分析不同样区内小叶锦鸡儿种群和群落特征(2011年测定)的差异显著性;对小叶锦鸡儿盖度与各功能群重要值间的关系分别按禁牧样区年间数据和不同样区同年数据进行汇总,作Spearman秩相关分析。以上数据分析均在SPSS13.0中完成,分析结果以EXCEL 2003作图。

2 结果

2.1 小叶锦鸡儿植株性状变化

不同处理8a后,禁牧样区小叶锦鸡儿盖度(0.042)显著小于放牧样区(0.088)(P=0.007);禁牧样区内小叶锦鸡儿种群盖度响应比呈负值,随围封年限增加而明显降低(图1),即样区间及围封禁牧年际动态都说明小叶锦鸡儿种群在围封禁牧后开始衰退。

禁牧样区与放牧样区间除复叶数以外各项形态指标均不存在显著差异;禁牧样区内当年枝形态性状在年际间存在显著差异,但并没有明显趋势(表1)。禁牧样区单位质量叶磷含量显著小于放牧样区;禁牧样区内小叶锦鸡儿叶片氮磷营养含量均有随围封年限增加而显著减小的趋势,特别是单位面积的氮磷含量(表2)。

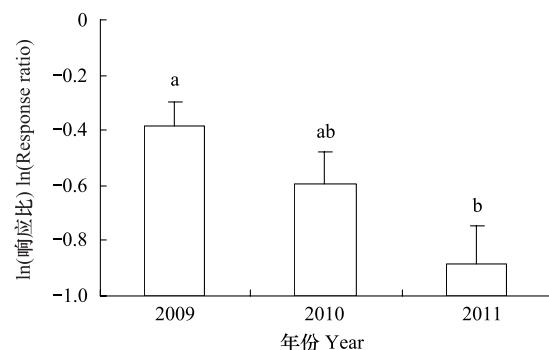


图1 禁牧样区不同年份小叶锦鸡儿盖度响应比

Fig.1 The response ratio of coverage of *Caragana microphylla* in plot grazing exclusion (EG) in different years (Means±SE)

不同字母表示年际差异显著(P<0.05)

表1 小叶锦鸡儿当年枝形态性状

Table 1 Morphological traits of first-year shoots of *Caragana microphylla* (Means \pm SE)

性状 Trait	禁牧样区 plot grazing exclusion (EG)				放牧样区 Plot grazing (G) 2011
	2008	2009	2010	2011	
每枝总干重 Dry weight per shoot/g	1.48 \pm 0.09b	0.38 \pm 0.08c	1.94 \pm 0.10a	0.45 \pm 0.04c	0.46 \pm 0.02
每枝叶片干重 Leaf dry weight per shoot/g	0.99 \pm 0.07a	0.25 \pm 0.05b	1.14 \pm 0.06a	0.32 \pm 0.02b	0.31 \pm 0.02
当年枝长 Shoot length/cm	27.60 \pm 0.82b	8.00 \pm 1.08d	34.05 \pm 0.97a	12.82 \pm 0.41c	13.95 \pm 0.48
每枝复叶数 Compound leaves number per shoot	25.75 \pm 1.28a	13.63 \pm 1.40b	26.01 \pm 1.21a	15.44 \pm 0.67b	18.44 \pm 0.70 *
复叶面积 Compound leaf area/cm ²	7.92 \pm 0.71a	3.54 \pm 0.37c	7.02 \pm 0.37a	4.90 \pm 0.32b	4.52 \pm 0.19

同一行数据内不同字母表示年际差异显著, * 表示不同样区间差异显著($P<0.05$)

表2 小叶锦鸡儿叶氮磷含量与比叶重

Table 2 Leaf nitrogen and phosphorus contents and leaf mass area of *Caragana microphylla* (Means \pm SE)

性状 Trait	禁牧样区 plot EG			放牧样区 plot G 2011
	2009	2011	2011	
单位质量叶氮含量/(mg/g)	29.33 \pm 0.85a	29.48 \pm 0.48a	26.43 \pm 0.75b	25.56 \pm 0.96
Leaf nitrogen content per unit mass				
单位面积叶氮含量/(g/m ²)	4.15 \pm 0.18a	3.39 \pm 0.08b	2.18 \pm 0.08c	1.97 \pm 0.10
Leaf nitrogen content per unit area				
单位质量叶磷含量/(mg/g)	1.72 \pm 0.04	1.65 \pm 0.07	1.62 \pm 0.05	1.82 \pm 0.04 *
Leaf phosphorus content per unit mas				
单位面积叶磷含量/(g/m ²)	0.24 \pm 0.007a	0.19 \pm 0.006b	0.13 \pm 0.005c	0.14 \pm 0.003
Leaf phosphorus content per unit area				
比叶重 Leaf mass area (g/m ²)	141.10 \pm 3.80a	114.96 \pm 2.17b	82.56 \pm 2.15c	76.62 \pm 1.82

同一行数据内不同字母表示年际差异显著, * 表示不同样区间差异显著($P<0.05$)

2.2 小叶锦鸡儿灌丛间草本植物群落结构特征与物种组成变化

禁牧样区内灌丛间植物地上生物量显著高于放牧样区;而禁牧样区内灌丛间植物地上生物量与密度在年际间波动较大,没有显著的变化趋势(图2)。

不同处理8a后,稗草、狗尾草、猪毛菜、灰绿藜等在放牧样区均有分布,与其在禁牧样区已经基本消失的状况有所不同,对于不同植物功能群,多年生丛生禾草在禁牧样区优势显著高于放牧样区,多年生杂类草和1年生植物则相反(表3);在禁牧样区,草本群落的物种组成随围封年限增加发生了显著变化:多年生根茎禾草、多年生丛生禾草与多年生杂类草在群落中重要值随围封年限增加均有所增加,其中多年生根茎禾草与丛生禾草变化趋势一致,不过多年生根茎禾草年际差异不显著,1年生植物随围封年限增加逐渐退出群落,而灌木和半灌木在小叶锦鸡儿灌丛间仅有零星分布(图3,表3)。

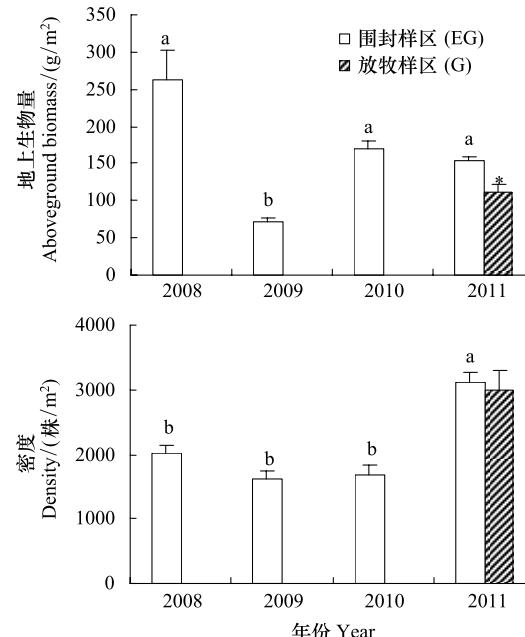


图2 草本群落地上生物量与密度

Fig.2 The herbaceous community aboveground biomass and density (Means \pm SE)

不同字母表示年际差异显著, * 表示不同样区间差异显著($P<0.05$)

表3 主要物种及各功能群重要值

Table 3 The importance values of different main species and functional groups

物种 Species	禁牧样区 plot EG				放牧样区 plot G 2011
	2008	2009	2010	2011	
多年生根茎禾草 Perennial rhizome grasses	0.108±0.028	0.180±0.028	0.163±0.025	0.189±0.032	0.197±0.026
羊草 <i>Leymus chinensis</i>	0.108±0.028	0.180±0.028	0.163±0.025	0.189±0.032	0.197±0.026
多年生丛生禾草 Perennial bunch grasses	0.405±0.036b	0.535±0.032ab	0.517±0.028ab	0.612±0.047a	0.321±0.049 *
大针茅 <i>Stipa grandis</i>	0.139±0.018b	0.204±0.042ab	0.248±0.021a	0.215±0.023ab	0.011±0.008 *
克氏针茅 <i>Stipa krylovii</i>	0.047±0.014	—	—	—	0.119±0.036 *
糙隐子草 <i>Cleistogenes squarosa</i>	0.199±0.034c	0.315±0.046ab	0.262±0.026bc	0.383±0.030a	0.189±0.043 *
羽茅 <i>Achnatherum sibiricum</i>	0.021±0.013	0.016±0.016	0.007±0.007	0.014±0.008	0.002±0.002
多年生杂类草 Perennial forbs	0.134±0.019b	0.230±0.017a	0.174±0.016ab	0.198±0.020ab	0.311±0.040 *
苔草 <i>Carex korshinskyi</i>	0.087±0.020b	0.204±0.026a	0.078±0.011b	0.133±0.017b	0.251±0.039 *
细叶韭 <i>Allium tenuissimum</i>	0.029±0.008	0.023±0.014	0.020±0.004	0.030±0.007	0.012±0.004 *
糙苏 <i>Phlomis umbrosa</i>	0.010±0.006bc	0.001±0.001c	0.058±0.013a	0.029±0.008ab	0.013±0.005
1年生植物 Annuals	0.353±0.024a	0.040±0.012c	0.144±0.017b	0.001±0.001c	0.171±0.020 *
灰绿藜 <i>Chenopodium glaucum</i>	0.044±0.009	—	0.074±0.015	—	0.006±0.003 *
轴藜 <i>Axyris amaranthoides</i>	0.048±0.012a	—	0.010±0.004b	—	0.020±0.004 *
猪毛菜 <i>Salsola collina</i>	0.261±0.019a	0.040±0.012b	0.057±0.012b	—	0.018±0.003 *
稗草 <i>Echinochloa crusgalli</i>	—	—	—	—	0.053±0.014 *
狗尾草 <i>Setaria viridis</i>	—	—	—	0.001±0.001	0.050±0.012 *
灌木和半灌木 Shrubs and semi-shrubs	—	0.014±0.014	0.001±0.001	—	—
冷蒿 <i>Artemisia frigida</i>	—	0.014±0.014	—	—	—
胡枝子 <i>Lespedeza bicolor</i>	—	—	0.001±0.001	—	—

同一行数据内不同字母表示年际差异显著, * 表示不同样区间差异显著($P<0.05$)

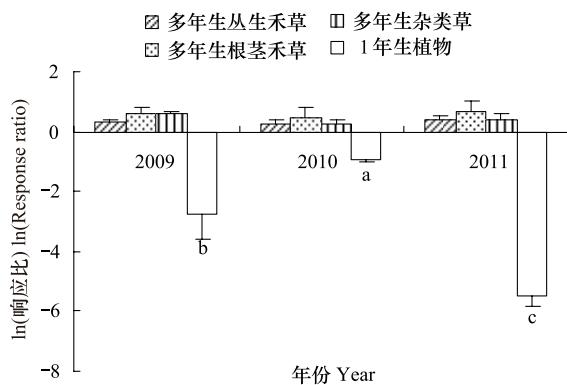


图3 不同年份各功能群重要值响应比

Fig.3 The response ratio of important value of different functional groups in different years (Means±SE).

不同字母表示年际差异显著($P<0.05$)

2.3 小叶锦鸡儿种群盖度与各功能群重要值关系

小叶锦鸡儿种群盖度与各功能群重要值呈现出不同的关系，并且根据禁牧样区年间数据和不同样区同一年数据分别进行分析，趋势完全一致：小叶锦鸡

儿种群盖度与多年生丛生禾草显著负相关，呈现此消彼长的关系，说明两者间可能存在竞争关系；与一年生植物显著正相关，说明伴随着小叶锦鸡儿的衰退，1年生植物也逐渐退出群落；与多年生根茎禾草和多年生杂类草间没有显著的相关关系(图4)。

3 结论和讨论

本研究发现，无论是禁牧样区年际比较，还是采取不同利用方式8a后禁牧样区与放牧样区间的比较均显示，围封禁牧后小叶锦鸡儿盖度降低，灌丛间草本植物群落结构发生变化，多年生丛生禾草比例增加，这说明去除放牧干扰可以促进小叶锦鸡儿灌丛化草原向典型草原的恢复。已有研究表明，小叶锦鸡儿灌丛可以改善退化草原土壤环境，减缓风蚀水蚀，妨碍牲畜采食，对草本植物有一定的保护作用，并能成为重要的牧草种子库，为其在灌丛下定居与发育提供可能，从而有利于牧压减轻后牧草迅速

由灌丛内部和边缘向灌丛外发展^[17-18]。在退化草原的恢复过程中,邵新庆等^[19]认为豆科植物在恢复早期能改善提高土壤养分,同时一年生先锋植物在恢复早期对群落恢复贡献较大,本研究也发现围封禁牧5年后一年生植物在群落中比例较高,小叶锦鸡儿灌丛的沃岛效应和一年生植物的枯落物为其它植物的定居创造了稳定的土壤环境。随后,多年生禾

草随围封年限增加在群落中的比例增加,这与已有研究结果一致,因为围封措施去除了家畜的选择性取食,有利于禾草与其它物种的竞争^[20]。在多年生禾草中大针茅和糙隐子草的增加最为明显,前者具有较深的根系,在资源利用方面存在优势,而后者是牲畜喜食的类型,禁牧后得以迅速扩张^[21]。

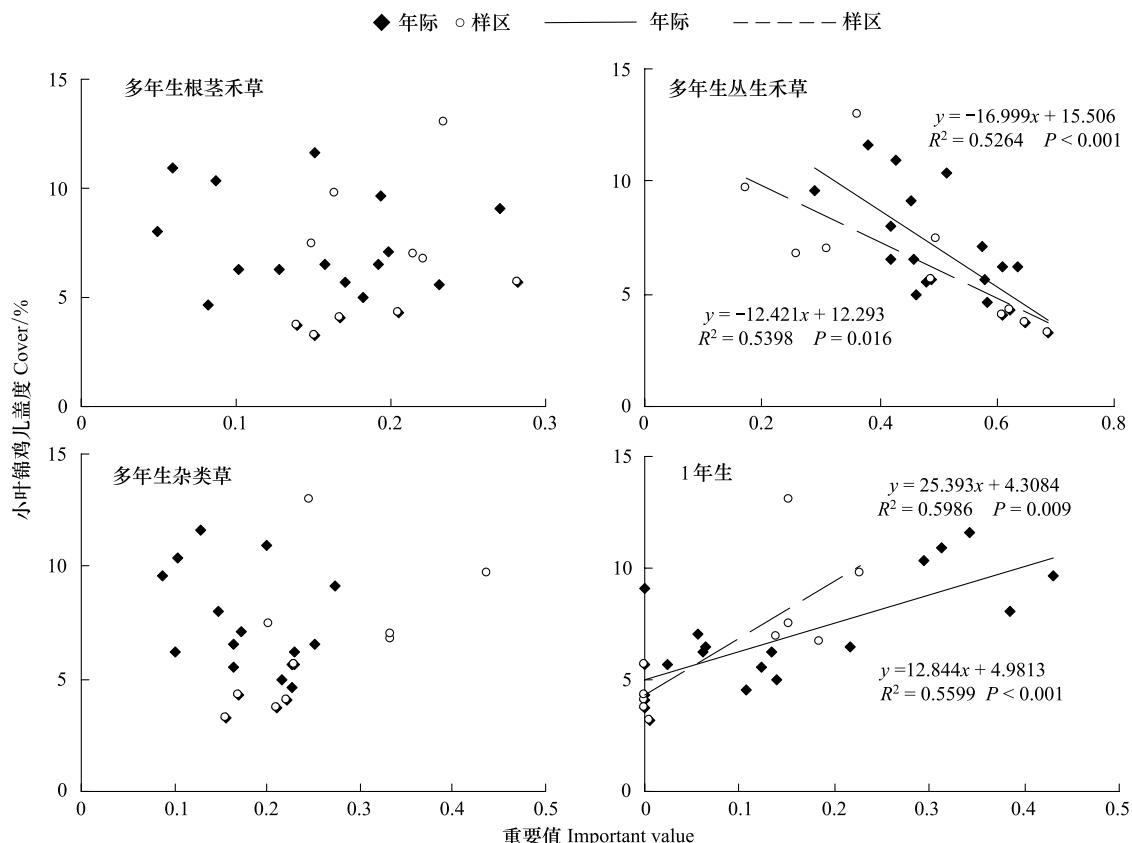


图4 小叶锦鸡儿盖度与各功能群重要值关系

Fig.4 The relationship between the coverage of *Caragana microphylla* and important values of different functional groups
 $n=20$ for years analysis and 10 for plots analysis, respectively

小叶锦鸡儿盖度降低可能是由于禾草与其竞争造成的,本研究中小叶锦鸡儿盖度与多年生丛生禾草在群落中的重要值呈显著负相关,在另一研究中也曾发现小叶锦鸡儿生长状况与草本层(特别是禾草)生物量呈负相关^[22],这与草本植物的竞争会对灌木生长造成负面影响的结论一致^[23-24]。另外,小叶锦鸡儿是构件生物,部分构件死亡衰退不代表全株的死亡,因而本研究发现小叶锦鸡儿的衰退体现在盖度的降低上,而并不体现在当年枝生长状况的变化上。基于小叶锦鸡儿这一特性,灌丛化草原内小叶锦鸡儿的退出需要长时间去除放牧干扰才能实

现。裴浩等^[25]也指出小叶锦鸡儿建群的片段演替速率较慢,它的发展与衰退是一个较长的动态过程。Valone等^[26]指出时间尺度在草原与灌丛化草原间的转换方面十分重要,对于灌丛化草原,多年生禾草对去除放牧作出响应需要至少20a的时间。本研究也发现,围封8a后,小叶锦鸡儿在样区内仍然占据一定生境,而灌丛间的草本植物群落优势种为糙隐子草,属于典型草原植物群落退化演替序列中度退化时期的优势种或主要伴生种^[27],这说明小叶锦鸡儿建群的灌丛化草原要恢复到羊草或大针茅占优势的顶级群落需要很长的时间。

除了盖度以外,禁牧样区内小叶锦鸡儿单位叶面积的氮磷含量随围封年限增加而减少的趋势显著,而以单位面积表现的性状在生理角度上十分重要,因为光合作用等生理进程中的步骤,如光能截获和二氧化碳扩散等是通过单位叶表面积通量发生的^[28]。氮是光合作用相关蛋白(特别是 Rubp 酶)的重要组成成分,最大光合速率经常与叶氮含量正相关^[29];而生长速率假说(growth rate hypothesis, GRH)指出,生长依赖于富含磷的核糖体驱动的蛋白质合成,磷含量与植物生长速率关系密切^[30]。较低的氮磷含量可能伴随着较低的光合能力与生长速率,叶片氮磷含量的减少可能也与小叶锦鸡儿在禁牧后的衰退有关。另外,禁牧样区小叶锦鸡儿叶片磷含量显著小于放牧样区,而氮含量差异不显著,叶片磷含量可能与小叶锦鸡儿的衰退关系更密切。对于小叶锦鸡儿来说,虽然当年枝生长状况尚未体现出显著差异,但小叶锦鸡儿叶片氮磷含量的减少可能预示了未来部分构件甚至全株在围封禁牧后的衰亡,这种推测是否成立需要进一步研究。

综上所述,本研究发现小叶锦鸡儿灌丛化草原在围封8a后有所恢复:灌丛间草本植物群落物种组成发生了显著变化,多年生丛生禾草逐渐占据优势,1年生植物逐渐退出群落;小叶锦鸡儿种群发生衰退,主要体现于盖度的降低上,并与多年生丛生禾草重要值的上升密切相关,说明禾草与小叶锦鸡儿的竞争可能是导致其在禁牧后发生衰退的原因。本文认为去除放牧干扰后,小叶锦鸡儿灌丛化草原可以恢复,但要恢复到以羊草和大针茅建群的典型草原,还需要更长的时间,故而是一个长期的过程,有待进一步的长期观测。

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