

木本植物多度在草原和稀树干草原中增加的研究进展

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摘要:木本植物多度在草原和稀树干草原中增加已经成为全球范围普遍发生的现象。为揭示这一现象发生的原因,从放牧和气候变化与木本植物多度增加的关系、木本植物多度增加过程中的正反馈作用以及木本植物侵入的关键阶段——幼苗的补充和定居,这三个方面综述了目前的研究结果。强调放牧和气候变化之间的相互共同作用,可能引发了木本植物向草原和稀树干草原中的入侵;而生物引起的正反馈作用则进一步促进了木本植物的扩展。从生态系统干扰的角度,讨论了木本植物多度增加机制的复杂性,并指出木本植物幼苗补充和定居的连续性和间断性两种方式,对于草原和稀树干草原木本植物多度增加的贡献。

关键词:放牧; 气候变化; 木本植物多度; 正反馈作用; 幼苗补充和定居

Increased abundance of woody plants in grasslands and savannas

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Abstract: Abundance of woody plants has increased substantially in grasslands and savannas worldwide. To explain these phenomena, this paper reviews the three aspects of the related research results, including relationships between grazing or/and climate change and the increased abundance of woody plants, roles of positive feedback in increasing abundance of woody plants, and the recruitment and establishment of seedling of woody plants, which is considered the critical stage for woody plant invasion into the vegetation. It is emphasized that grazing, combined with climate changes, may trigger the encroachment of woody plants into these types of vegetation, and that biological positive feedbacks promote the increase of woody plant abundance within the vegetation. From a view of disturbances in ecosystems, we discuss the complexity of mechanisms for the increased abundance of woody plant, and indicate the contributions of episodic and continuous recruitment and establishment of seedling to woody plant expansion in the vegetation.

Key words: grazing; climate change; abundance of woody plants; positive feedback; recruitment and establishment of seedling

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木本植物多度(abundance)在草原和稀树干草原中的增加,已经成为全球范围普遍发生的现象^[1-4]。随着木本植物的扩展(expansion),多年生草本植被被木本植物植被所取代^[5-10],草原或稀树干草原转变为灌木地或林地。全球陆地总面积的大约40%是由于旱、半干旱地区的稀树干草原、灌木地和草原生态系统构成,因此,土地植被覆盖的这种变化,不仅影响到这些地区植被的组成和外貌,而且将潜在影响到区域以至于全球尺度上生态系统生物地化循环过程^[4,11,12]。因此,木本植物多度在草原和稀树干草原生态系统中增加成为全球变化生态学(global change ecology)研究的重要领域之一。

我国内蒙古锡林河流域位于典型草原区,在长期的过度放牧下,典型草原的旱生灌木小叶锦鸡儿(*Caragana microphylla*)分布的增加,已经导致了草原灌丛化现象^[13-17]。小叶锦鸡儿灌丛化草原的出现成为锡林河流域典型草原退化的一大景观标志^[18,19]。张宏等^[20]综述了国外对半干旱草原灌丛化与土壤异质性关系的研究进展。这表明在我国草原生态学领域的研究中,开始关注到草原生态系统放牧退化中的灌丛化现象。

在全球气候变化和人类活动特别是过度放牧的双重影响下,木本植物的多度在草原和稀树干草原增加与许多因素有关:气候变化和历史时期CO₂浓度变化、火烧方式、啮齿类动物种群和家畜放牧,在植被的这种变化中都被作为推动力^[4,7,21-23]。

本文从放牧和气候与木本植物多度增加的关系、木本植物增加过程中的正反馈作用以及木本植物侵入的关键阶段—幼苗的补充和定居,这三个方面对木本植物多度在草原和稀树干草原中增加的研究进展进行了综述,强调了放牧和气候变化的共同作用引发草原和稀树干草原中木本植物多度的增加,各种正反馈作用促进木本植物多度的进一步增加,最终使草原和稀树干草原成为灌木地或林地。

1 家畜放牧和气候变化与木本植物多度增加的关系

放牧常常被作为引起木本植物多度增加的首要因素。放牧或家畜的引入与木本植物多度增加的相关性已经得到确认^[24-27]。尽管火烧频率很低,受保护而未被放牧的稀树干草原仍然能够维持,而邻近的放牧地却转变为林地,这是放牧促进木本植物多度增加的具有说服力的证据。

家畜放牧的直接、间接效应包括:对禾草偏好性利用、土壤理化性质的变化、木本植物种子的散播以及火烧强度和频率减少,这些都明显影响到木本植物的种群动态,一般促进了木本植物种子产生和幼苗定居并延长了其寿命^[2]。

家畜放牧引起草原退化,啮齿类动物的活动随之增强^[24,28,29],可燃物减少使得火烧受到抑制^[5],这与木本植物多度的增加关系密切。长期高强度放牧使得纤细可燃物数量维持减少,导致火烧频率和强度的降低^[30-32],这将使已定居但受到抑制的木本植物如mesquite (*Prosopis glandulosa*)生长增加,通过种子繁殖补充种群数量,引起木本植物在草原中扩张^[33]。对于能够在致密草皮上定居的木本植物如mesquite^[6],与放牧相联系的火烧频率、强度降低是其多度增加的首要因素^[30,31,34]。

放牧对于草原和稀树干草原中木本植物多度的影响是在特定的气候背景下发生的,因此放牧在其中的作用必然与气候变化情况密切相关。

放牧和干旱的共同作用使草本植物盖度减少,随之引起灌木mesquite向草原中侵入^[1,35]。放牧也影响到大气湿度和降水的变化^[36,37],这也与木本植物多度增加有关。特别是降水的增加促进了木本植物的种子生产以及幼苗大量定居的间断性(episodic)发生^[38-40]。

放牧和气候对木本植物定居的影响是同时存在的^[1,35,39]。Grover和Musick^[1]推断:在18世纪后期美国西南部两种灌木creosotebush (*Larrea tridentata*)和mesquite多度显著增加,这与过度放牧和对多年生草本植物生长不利的干旱发生是密切相关的。干旱和放牧的共同作用,通过减少草本植物盖度和产生新的定居地点,随后的降水增加将大大加速灌木的侵入和定居过程^[41-44]。

气候与放牧的直接、间接的相互作用很可能影响到木本植物侵入的速率和动态^[35,39,45]。例如,有利于木本植物定居的偶发的短期气候事件可能促进草本植物生产而增加了可燃物,从而提高火烧发生的可能

性^[46]。火烧直接抑制木本植物生长和定居,当放牧减少了纤细可燃物数量的维持时,木本植物侵入将会迅速发生^[47]。

放牧压力的增强和与降水季节性变化的相互作用,比仅仅提高放牧压力或仅改变降水方式,更能减少植被盖度,增加地表土壤对侵蚀的敏感性^[1]。多年生禾草盖度减少引起土壤侵蚀,这使原为植被覆盖的地表裸露,裸地的出现常常有利于灌木的定居。

适口性差的木本植物的侵入显示了气候和放牧的潜在相互作用,干旱发生或家畜放牧单独不足以引起稀树干草原向林地的转变,植被的变化是二者共同作用的结果^[48]。

2 引起木本植物多度增加的正反馈作用

如果说放牧和气候变化的协同作用引发了木本植物多度的增加,那么木本植物定居后土壤资源的空间异质性增强,则通过生物引起的正反馈作用促使更多的木本植物定居^[8]。

在美国西南部稀树干草原中,持续的强度放牧使多年生草本植物生长受到抑制,来自多年生草本植物的凋落物和养分也相应减少;裸地面积增加的促进了更温暖、更干燥的小气候和土壤侵蚀的发生^[49]。因为缺乏足够可燃物用于引燃或火势蔓延,火烧彻底被消除^[30,31]。这时,适口性差的具有固氮能力的灌木种,由于能够适应更严酷的小气候和养分贫瘠环境而定居;一旦定居生长将促进木本植物的进一步侵入^[50~52],这时即使放牧压力减轻,木本植物定居仍然能够进行,而生物引起的正反馈作用的存在,维持或提高了稀树干草原中木本植物的多度^[1]。

美国西南部草原向灌木地转变被认为是稳定态之间的一种交替过程^[8,53]。当草本植被占据优势的稳定态发生变化,即使在短期时间内,灌木侵入也将发生,而正反馈作用将使这一过程得以持续进行。

Grover 和 Musick 总结了有助于两种灌木 creosotebush 和 mesquite 定居与维持的、与生物和土壤因素有关的正反馈作用,提出灌木向美国西南部草原侵入的概念模型^[1]。这两种灌木的定居,将产生不利于多年生草本植物生长的环境,尤其是土壤状况变化,将促使土壤侵蚀的发生和随后灌木的定居。灌木种向草原的侵入,导致生态系统植物物种组成、外貌、优势度和植被盖度的空间分布的显著变化^[28,53,54]。草原向灌木地的转变涉及到一些物理因子如灌丛间地表温度和水分蒸发率的改变,还有植被分布对于生物地化过程的影响^[8,42,55]。

在干旱和半干旱区生态系统中,灌木下土壤生物地化循环速率高于灌丛间土壤中的速率,这导致氮素等养分的富集^[54~57]。养分在灌木周围富集而在灌丛之间土壤的相对贫瘠化,使得多年生禾草在灌木之间区域的更难以恢复,但却使侵入的灌木得以存在和维持^[8]。还有一些生物引起的反馈作用涉及动物种类组成和其食物生境的变化。小的啮齿类动物种群数量在 creosotebush 和 mesquite 灌木地中增加^[24,29],它们的采食减少禾草盖度或散播灌木种子,从而促进灌木的侵入^[29]。

植被组成、外貌和空间分布的变化能够改变地面能量收支的几个构成组分,从而对局部和区域尺度的气候产生了影响^[58~60]。灌木侵入引起植被的空间分布、冠层结构的变化,这些变化决定着草原向灌木地转变中地面能量收支情况。优势植被外貌的变化引起地表与气候潜在相互作用^[1]。植被盖度减少和土壤裸露能够通过地表温度升高,导致区域性的气候效应^[61],反过来可能促进灌木在草原生态系统中的扩展。

3 木本植物幼苗的补充和定居

对于具有潜在长寿命和定居后低死亡率的木本植物,幼苗补充和定居使种群更新得以实现,成为其生活史最关键的阶段^[62]。家畜放牧的各种直接与间接效应相互起作用,促进木本植物幼苗在禾草群落中定居^[63]。伴随长期放牧植物物种组成的变化、草本植物密度以及地上、地下生物量的减少,为草原中木本植物幼苗定居提供了条件^[64]。

在半干旱草原木本植物侵入研究中,集中于幼苗定居阶段的放牧模拟实验表明:与去叶相联系的禾草生物量减少,导致其竞争能力的减弱,从而促进木本植物幼苗的定居^[65~68]。这也得到野外观察证据的支持^[69~71]。草本植物的存在因而减少木本植物出现、生长和存活^[70,72,73]。

草本植物对木本植物幼苗补充、定居发生影响是通过对水分的竞争机制实现的。草本植物与灌木 mesquite 幼苗的竞争发生于地下部分^[74],由于优先向根系发育分配资源,禾草对灌木幼苗的竞争排除最小

化,并使幼苗得到更深土壤层更稳定的水分供应。类似机制似乎也能够引起 *Pinus radiata*^[75] 和 oaks (*Quercus* spp.) 的幼苗在半干旱稀树草原^[15,70] 和高草草原^[76] 定居;相反,如果木本植物幼苗根系不能够扩展达到草本植物根系分布区以下深度,土壤干旱的发生将抑制其定居^[72,78]。对水分利用的模拟试验表明:木本植物幼苗的定居,在缺乏草本植物的时期或地点出现,或出现在二者的根系能够长时期共存的地点,最后通过延长根系来摆脱来自草本植物对水分的竞争^[78]。

但在美国得克萨斯稀树干草原研究表明:当放牧已经大大改变了植被的组成和生物量、以至于灌木 mesquite 幼苗定居的速率和方式,并不受草原植物生物量的限制,而是受种子散播的控制^[7]。

因此,草本植被对木本植物侵入过程的影响程度是可变的,其中存在除了水分的竞争的其它机制,它们能够以复杂方式发挥作用影响其萌发和定居^[79-81]。

4 讨论

干扰被认为是一种生物性或非生物性的作用力,它们引起对生态系统扰动和胁迫^[82]。放牧作为一种对生态系统的综合性干扰,常常与气候变化共同影响到生态系统的变化。在许多情形下,很难确定气候变化正常变动范围与引起生态系统变化的干扰程度之间的对应性^[45,83-86]。由于植被的变化明显滞后于气候变迁,因此难以界定正常气候变动范围与放牧引起干扰的程度^[48]。由于放牧干扰叠加于地形和土壤异质性以及气候变动的背景之上,结果使长期适应于特定地点土壤和气候状况的植物物种,在特定干扰体系下具有竞争优势,而当干扰体系发生变化时将处于从属地位、甚至趋于灭绝。放牧干扰和气候变化之间的相互作用能够缓解或加剧生态系统的变化,在适宜的气候状况下,放牧的影响可能被弱化;而气候处于极端状况时,放牧的影响可能被增强^[48]。因此,与家畜放牧相联系的草原衰退性的变化,在高于平均降水量的年份可能被缓解,而在低于平均降水量年份被增强^[45,87-89]。气候变化和未预期的极端天气事件与放牧之间的相互作用,引起不同植物种群的增长或衰退,导致多年生禾草与木本植物之间平衡关系的变化^[90]。

因此,对于草原和稀树干草原中木本植物多度增加,这一全球性的普遍发生现象的影响而言,家畜放牧和气候变化共同作用,并非总是在单一方向上变化,与生物因素和土壤因素相关反馈作用的存在,增强了木本植物多度增加机制的复杂性。

在干旱和半干旱区植被动态的研究中,事件驱动(event-driven)或间断性过程的作用都得到重视^[91]。在一些干旱和半干旱生态系统中,木本植物例如灌木 Mesquite 定居的发生可能是罕有的,只是出现于降水量异常丰沛的年份^[38,39,90,92,93];但在另一些干旱和半干旱生态系统中,灌木的连续补充对于其种群的更新而言,要比事件-驱动的间断性补充更加重要^[94]。通过模拟放牧、土壤湿度和禾草竞争三者之间相互作用,对于草原中灌木 mesquite 幼苗出现和短期存活的影响,结果表明:幼苗的定居并非是短期间断性^[95]。对于草原和稀树干草原中木本植物多度的增加,其幼苗的补充和定居存在着连续性和间断性两种方式,在不同的群落状况和环境条件下有着各自不同的贡献。

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