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草地植物生产力主要影响因素研究综述

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摘要:草地是全球分布面积最大的陆地生态系统,植物初级生产力是反映草地功能的重要指标。从植物种多样性、资源有效性、放牧、退化草地恢复和气候变化等方面较系统综述了影响草地植物生产力的关键要素和驱动力。大量研究表明,植物多样性与生产力的关系尚未有一致的结论,依据试验地点、起始状态甚至度量指标不同而不同;特别是资源有效性调节着生产力水平并对植物多样性和生产力关系产生显著影响;放牧改变了植物群落特征和养分有效性进而影响生产力的形成过程,也改变了资源有效性-植物多样性-生产力之间的关系;对于退化生态系统,在退化草地恢复过程中植物与土壤资源有效性的互作效应对植物生产力的变化起着关键作用;而在未来气候变化特别是增温对植物生产力的影响因地点和生态系统的不同而异,但多数研究结果显示增温提高了草地植物生产力。与国外其它草地分布区相比,国内的相关研究不仅在数量上明显不足,更重要是欠缺机理上的深入研究。在放牧和未来气候变化背景下如何维持和提高草地生产力,如何加速退化草地生态系统的恢复,进而实现生态安全建设和经济社会协调发展,是我国当前急需解决的理论和实践问题。

关键词:物种多样性;资源有效性;放牧;退化草地恢复;气候变化;草地生产力

Factors affecting plant primary productivity of grasslands: a review

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Abstract: Grassland is the largest distribution area of terrestrial ecosystems on the earth. The plant net primary production (NPP) is an important indicator to reflect the function of the grassland ecosystems. Some research results are reviewed about the effects of plant species diversity, resource availability, grazing, restoration of degraded grassland and climate change on NPP of grassland ecosystems in the paper. These researches show that (1) there are inconsistent conclusions about the relationship between plant diversity and NPP which depends on experimental site, starting status and indicators measured; most of the studies find their "single peak" relationship due to compensation effect of different plant resource utilization niche. However, some studies report that they arepositive and negative relationships when NPP is relatively low and high, respectively. there are many mechanisms to explain their negative correlations including the hypotheses of disturbance, competition and resources availability. (2) Resource availability determines NPP and modifies the relationship between it and plant diversity. Some researches show that there is an interactive effect on NPP between different resources. Improving the level of a limiting resource may reduce its use efficiency, but it may improve the use efficiency of other resources.Nutrient additions improve the productivity of the grassland, while it reduces plant diversity. (3) Grazing affects NPP through changing plant composition and resource availability. Heavy grazing reduces soil nitrogen (N) mineralization rate and NPP, while moderate grazing increases them. In particular, moderate grazing enhances plant diversity due to

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increase of grassland heterogeneity. (4) Availability of nutrient resources and feedback of plants to it play key roles on NPP in the restoration of degraded grasslands. With the increasing of root biomass, root C / N ratio and the amount of microbial C and soil carbon pool, the net N mineralization rates and N bioavailability rapidly decline during the processes of the restoration. Plant-soil interaction manifestes as negative feedback, which in turn limites the further improvement of plant productivity. NPP may increase with restoration of the degraded grasslands, , whereas maximum NPP occurs in the middle or late stages of the restoration. NPP will decline at the late stage of the restoration if there is no disturbance or grazing.(5) Most of experimental warming studies show that there are inconsistent effects of warming on NPP and plant diversity which varies with the different locations and grassland ecosystems due to differences of resource availability and grazing/clipping. In general, the impacts of warming on underground NPP is larger than on aboveground NPP. These results above suggest that they may be easy for the maintenance of the low NPP level through plant diversity conservation and for improving NPP through increasing the availability of nutrient resources, However, how to maintain a high NPP level for long-term without compromising other ecological functions, such as plant diversity loss, is more challenges for us. Compared to international researches in the field, limited data can be available in China now. In particular, there are lacks in the processes and mechanisms of affecting plant primary productivity for grassland ecosystems in China. Therefore, understanding how grazing with future climate change affects plant primary productivity and recovery of degraded grassland ecosystems is a key knowledge to realize the ecological security and sustainable development of economy and society.

Key Words: species diversity; resource availability; grazing; degraded grassland restoration; climate change; plant primary productivity

草地是全球分布面积最大的陆地生态系统,约占陆地面积的三分之一[1]。草地具有重要的生态和社会功能[2],为人类提供了许多产品[3]和生态服务[4],其中,植物初级生产力是反映草地功能的重要指标[5-6]。许多研究表明,影响植物生产力的因素很多,在较大的地理尺度上气候等环境因子(如气温、降水和土壤类型等)是决定植物生产力的关键因子[7-11],而在较小的地理单元上,生物和资源有效性等可能是植物生产力大小的主导因子[12]。随着环境条件的改善,生产力逐渐增加[8]。但是不同的生态系统在不同的时期,其生产力对于环境变化的响应程度有很大的差异[9]。这些可以归结于生物与环境相互作用模式的差异[10]。这可能是目前众多研究结论不一致甚至相左的原因[11]。特别是影响草地植物生产力的众多因素相互交织在一起,共同影响着生产力水平,而目前的大多数研究主要集中在某一个单一的因子上,因此对于这些众多因子是否存在互作效应或者是否存在可加性缺乏深入的研究。本文通过对影响草地植物生产力的主要因素或过程的有关研究进展进行扼要综述,在此基础上提出存在的可能问题和建议,希望对我国相关研究提供一些有益的借鉴和参考。

1 植物多样性对生产力的影响

自20世纪70年代以来,国内外已经开展了大量有关植物多样性与植物生产力之间关系的研究,到目前为止仍然没有得出一致性的结论[13-14]。尽管一些研究支持了高植物多样性导致了高生产力的假设[6,14-19],但更多研究似乎发现两者呈“单峰型”关系[20],也有研究认为没有显著关系[20-22]或者认为“单峰型”不是主要关系[13]。许多研究认为多样性提高生产力的基本假设是因为不同植物对资源利用的生态位补偿效应引起的,特别认为植物根系深度多样性对生产力的影响更大[18]。这些综述性文章对产生这些不同结果的原因进行了分析,主要包括:(1)用于研究草地植物多样性-生产力关系的许多试验都是破坏性的(如起始状态为人为翻耕后的裸地)或人为地控制试验(如人种播种控制物种数或均匀度等),而不是在自然状态下进行的。事实上,这些实验所用物种数有限、且隐含了一种演替过程,由此得出的植物多样性-生产力间的关系会随时间而变化[23];(2)研究的空间尺度不同造成的[24-25],在小尺度上(如某一个地点或单个试验)的结果往往与大尺度的结果不尽相同,这也是许多发现两者间有正相

关、负相关或没有关系的原因,其实决定生产力的因素很多,不完是多样性决定的[22,26];(3)在过去的许多综述性文章中,忽略了一些具体的观测方法或指标(如用盖度、NDVI 等生产力的代用指标),包含了一些无效的数据,所以得出来的结果有很大偏差[27]。普遍认为在生产力相对较低时,多样性与生产力正相关;而在生产力相对较高时,多样性与生产力负相关[13]。对于负相关阶段的机理目前还没有明确的定论,引起的争议较多,包括干扰、竞争和资源等假说[13]。因此,目前有关对植物多样性-生产力关系的机理更多地停留在一些假设上(如资源比率变化以及生态位补偿假设等),而缺乏一些直接的试验证据;特别是缺乏在自然状态下对不同草地生态系统和演替阶段过程中两者关系变化的机理研究,如根系的空间分布及其多样性如何影响生产力水平还知之甚少,严重制约了人们对通过植物多样性保护进而维持和提高植物生产力水平的理解和应用。

2　资源有效性对植物生产力的影响

一些经验证据表明,资源有效性控制着植物多样性和生产力水平[22],因此,可以通过调控资源有效性达到提高多样性与生产力的目的[10,28-31]。由于植物在不同资源的利用能力方面存在"折衷",因此提高一种限制性资源的供应水平可能会降低植物对该资源的利用效率,但会改善植物对另一资源的利用效率及植物生产力[32]。在干旱半干旱草地,水分是植物生长的主要限制因子,只有在湿润年份施肥(N)才能有效提高植物生产力[10,33-34],而且 N 的利用效率随着灌溉增加而增加、但随着 N 施肥量增加而降低[34]。水分利用效率与初级生产力和生物量分配紧密相关[35]。研究表明,水分利用效率随降雨量增加而降低,但随土壤 N 有效性增加而增加[10,34,36],在养分等胁迫消除以后植物水分利用效率将达到最大值[35]。因此,对于干旱半干旱草地而言,水分和土壤 N 的有效性对初级生产力形成存在交互作用[34,36-37]。资源供应状况改变对生产力和多样性的影响不同,养分添加提高了草地的生产力,但降低了植物多样性[10,31,34]。与添加某一种限制性的资源相比(如 N)[10],添加多种限制性资源(如 N 和 P)使得植物多样性的丧失更多[31,38],有人认为 N 的作用通常比 P 的作用更大[31,39]或一样大[40]。总之,最大限制性资源水平的提高会促进生产上力的发展,其它限制性资源水平的提高是否对生产力有促进作用取决于与最大限制性资源的交互作用。因此,对于天然草地而言,能否通过限制性资源的添加特别是平衡施肥达到同时维持较高的植物多样性和生产力水平,亟待深入研究。

3　放牧对生产力的影响

放牧通过选择性的采食、践踏和粪尿归还等过程而对草地产生了综合性的影响,包括改变了植物生产力及影响生产力形成过程中的诸多因子,如植物种类组成与多样性、土壤 C/N 库大小及土壤养分(如 N)的有效性等,特别是过度放牧对上述各个方面几乎都产生了显著的负面效应[33,41-45]。不同放牧强度对土壤 N 有效性的影响随生长季节而变化。总体上,在生长早期中度以上的放牧提高了土壤 N 的矿化速率,但生长盛期和非生长季都降低了土壤 N 的矿化速率,因此不利于植物生产[46]。然而,适度放牧提高了土壤 N 可利用性[47],则有利于维持草地植物多样性和生产力水平[41-42,48-51],甚至产生补偿性生产[42,45]。有研究表明放牧提高了草地的异质性,从而增加植物多样性[52-53],特别是不同放牧家畜的混牧有利于草地植物多样性的维持[49,54]。最近的许多研究表明,就生产力、牧草品质、凋落物量、抗旱性以及可恢复性等方面而言,当放牧强度超过中度以上都会造成内蒙古典型草原这些生产-生态指标的下降[45,55-58]。因此,与禁牧相比,适度放牧既可以获得畜产品生产,又可以维持甚至提高草地的生态功能,包括提高生产力。因此,如何确定不同草地生态系统适宜的放牧率水平仍将是放牧生态学的关键科学问题,这里,生产力应该是主要指标但不应该是唯一指标,必须考虑生态系统的其他功能,特别是生物多样性的维持和土壤质量的提高等方面。

4　退化草地恢复对植物生产力的影响

在生态系统恢复过程中,自然状态下净初级生产是提高土壤有机质累积的主要来源[59-60],而土壤有机质增加又会改变其植物生产性能,即植物生产-土壤性质之间存在反馈作用[61-62],在退化草地恢复过程中这种植物与土壤资源有效性的互作效应对植物生产力的变化起着关键作用[59,62-63]。一旦从退化

状态开始恢复,土壤的 C、N 储量便从低水平的状态向高水平的状态演替并最终达到当地生态系统顶级状态的稳定水平[59,64-65]。在此过程中,随着根系生物量、根系中的 C/N 比、微生物 C 量以及土壤碳库的增加,土壤净 N 矿化速率和 N 的生物有效性快速下降[66],植物-土壤的互作表现为负反馈,从而反过来限制了植物生产力的进一步提高[59]。Baer 等[63]的研究证实,在退化草地的 8a 恢复过程中,施 N 肥显著提高了生产力,同时该研究也看到生态系统的其它功能都没有受到施 N 肥的影响。在内蒙古退化草场恢复过程中,由于物种组成的变化,施 N 肥仅在湿润年份提高了地上初级生产力,但对地下生产力没有显著影响,因而即使施用 N 肥,土壤 C、N 库也没有能够快速恢复到先前的水平[33]。草地在恢复初期生产力逐渐提高,在恢复的中后期达到最大。如果没有干扰和放牧,恢复后期生产力会下降。因此,如何利用恢复过程中植物-土壤的反馈关系,通过针对性的干扰措施来设计和加速恢复进程,是未来恢复生态学的重点研究内容之一。

5 气候变化对植物生产力的影响

尽管许多研究表明,增温直接促进了冻原植物生长和物种组成的变化、延长了植物生长季[58,67-69]、以及间接增加了土壤 N 有效性[29,70],但到目前为止,增温对土壤 N 的有效性和植物生产力的影响仍然没有一致的结论,因地点和生态系统的不同而异[67-68,71-75]。总体而言,增温对地下生产力的影响大于对地上生产力的影响,显著提高了地上和地下总生产力[75]。有研究表明,只有在土壤 N 有效性和水分不是制约因子时,增温才提高了植物生产力[74-75]。放牧作为天然草地的主要利用方式之一,在放牧条件下,放牧与增温的互作效应对草地植物生产力、物种组成和土壤养分有效性产生了显著影响,放牧甚至改变了群落组成对增温的反应模式[76-78]。由于土壤 N 的有效性对生产力的影响随物种组成变化而不同[31,33,63],因此,在放牧条件下,未来增温对不同草地植物多样性和生产力等生态过程的影响仍然存在很大的不确定性,目前这方面的研究很少。Klein 等[76,79]利用 OTC 试验研究表明,增温而不是刈割降低了植物多样性和生产力,特别是降低了禾草的比例、增加了阔叶草的比例,因此,刈割可以缓解增温对高寒草甸的负面影响。然而,通过 6a 红外增温和放牧试验研究表明,增温和放牧都提高了凋落物和粪便的分解速率[47,66],增加了土壤水溶液中 DOC 的含量[66]。与 Klein[76,79]等的研究结果不同,发现增温对植物多样性影响不大,但提高了高寒草甸植物地上生产力达 40%左右,但放牧降低了地上生产力对增温的反应程度[78]。特别是发现了是过度放牧而不是增温导致了高寒草甸的退化,因为增温提高了禾草和豆科牧草的比例[78]。因此,放牧与增温对不同草地生态系统的各自影响及其可能的互作效应的程度及其过程,将是未来气候变化生态学的关键研究内容之一,也是认识气候变化对草地生态系统的影响、发展适应性的管理措施的核心内容之一。

6 存在的科学和实践问题

综上所述,尽管国内外对影响草地植物生产力的主要影响因素进行了深入研究,但与国外其它草地分布区相比,国内这方面的研究不仅在研究数量上明显不足,更重要是欠缺机理上的深入研究。因此,在放牧和未来气候变化背景下如何维持和提高草地生产力,如何加速退化草地生态系统的恢复,进而实现生态安全建设和经济社会协调发展,是当前急需解决的理论和实践问题。为此,提出草地植物生产力研究存在以下一些科学问题及其基本假设(图 1)。

1)资源有效性-植物多样性-生产力三者间的关系

假设在低资源有效性下植物多样性对生产力的维持有正效应;然而,由于不同植物对资源有效性改变的反应不同,根据现有多数研究发现,自然状态下(不放牧)资源有效性的提高将降低植物多样性,但提高了生产力,由此可推论在资源有效性高的状况下,植物多样性与生产力呈负相关;由于植物多样性降低,高资源有效性不能长期维持高生产力,从而对其它生态功能产生负面影响。

2)适度放牧-植物多样性-生产力三者间的关系

根据已有多数研究发现,在自然状态下(即资源有效性低的情况下),适度放牧提高了植物多样性和生产力;然而,当资源有效性提高时,由于适度放牧部分抑制了对资源获取能力强的植物生长(容易被

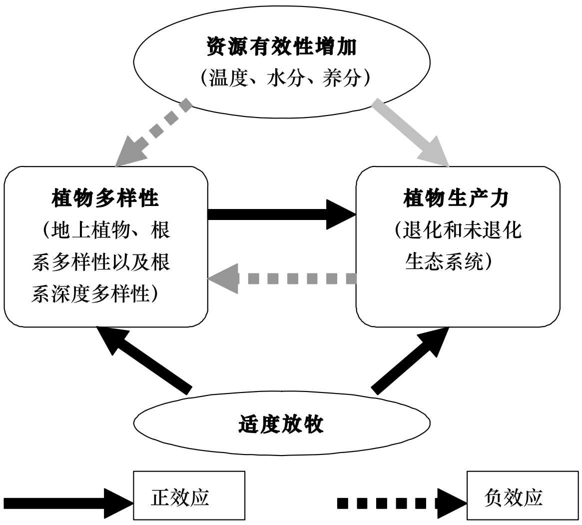

图 1　草地生态系统植物多样性与生产力之间的关系对适度放牧和资源有效性变化的响应示意图

Fig. 1　The relationship between plant diversity and productivity response to changes in moderate grazing and resources availability in grassland ecosystem

黑颜色箭头表示适度放牧效应;灰颜色箭头表示资源有效性效应

采食),从而能继续维持或提高植物多样性和生产力。因此,在提高资源有效性的同时进行适度放牧,仍然可以同时维持较高的植物多样性和生产力水平。

因此,低水平生产力的维持(如靠现有的植物多样性水平就可以维持)和提高(如提高资源有效性等)可能相对比较容易,而怎样长期维持高水平的生产力、同时又不损害其它生态功能,则比较困难。

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