



# 干旱半干旱区灌丛对草本植物的促进作用研究进展

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**摘要** 植物间竞争与促进作用是调控物种、群落以及生态系统对环境变化响应的重要机制, 其中促进作用在胁迫生境发挥更重要的作用。该文从灌丛对草本植物的促进作用随水分的变化规律、发生机制以及在植被恢复中的应用3个方面, 总结了最近30年来干旱半干旱区灌丛促进作用的主要研究进展。作为预测植物间相互作用随环境胁迫程度变化的经典模式, 胁迫梯度假说(SGH)认为促进作用随环境胁迫程度的增强而增强。然而, 在以水分为主要限制因子的干旱半干旱生态系统中, SGH存在很大的不确定性, 即灌丛对草本植物的促进作用随水分的减少并不总是线性增强, 这种不确定性不仅与灌丛对土壤水分的复杂影响密切相关, 同时还受到物种特性、植物生活史阶段、研究方法、研究尺度和指标等的影响。干旱半干旱区灌丛通过调节其冠层下土壤水分、养分及微生物群落, 改善冠层内温度和辐射, 抵御取食者等的方式, 直接或间接影响其冠层下植物的存活、生长和繁殖。近年开展的去除实验结果表明, 灌木地下部分对灌丛促进作用的影响强于地上部分。灌丛促进作用被认为是退化生态系统植被恢复的有效手段, 而植被恢复成功与否受到环境胁迫程度、物种特性、植物生活史阶段和土地利用等的综合影响。在气候变化和人类活动的双重影响下, 全球干旱半干旱区面积不断扩大, 灌丛明显扩张。明确灌丛促进作用发生机制, 探索灌丛与草本植物间相互作用随干旱梯度的变化规律, 阐明灌丛对草本植物的影响, 对预测干旱半干旱区物种和生态系统对气候变化的响应具有重要意义。基于目前的研究进展和干旱半干旱区发生的气候和环境变化, 该文对未来灌丛促进作用研究提出以下展望: 1)探索利用生物指标指示环境胁迫程度和植物间相互作用; 2)明确灌木地上和地下部分在促进作用中的相对贡献, 进而阐明灌丛促进作用的发生机制; 3)探索受益物种对护卫植物的反馈作用机制; 4)综合评估护卫植物在植被恢复中的贡献; 5)加强模拟增水实验和长期定位观测研究; 6)加强促进作用与其他研究领域的结合, 如促进作用与生物入侵、灌丛化、生物多样性和生态系统功能的关系, 促进作用对气候变化的响应等。

**关键词** 护卫植物; 水分可利用性; 物种丰富度; 胁迫梯度假说; 促进作用; 植被恢复

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## Advances in the study of shrubland facilitation on herbs in arid and semi-arid regions

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### Abstract

Competition and facilitation among plants are an important part of the mechanisms regulating the responses of species, communities, and ecosystems to environmental changes. Basically, facilitation plays a more important role than competition in stress environments. The present review summarized the research progress of shrubland facilitation in arid and semi-arid regions in the past 30 years, on the aspects of trends of facilitation along a water availability gradient, mechanisms of shrubland facilitation, and the application of shrubland facilitation in vegetation restoration. As the most important empirical model that predicts the trend of plant-plant interactions along abiotic stress gradient, stress gradient hypothesis (SGH) posits that facilitation increases with increasing abiotic stress. However, SGH has been largely debated in water limiting system. Shrubland facilitation does not always increase linearly with the decreasing water availability, which is not only closely related to the complex impact of shrub on soil water, but also associates with the species identities, plant life history stages, study methods, scales and indicators. Arid shrubs could affect the survival, growth, and reproduction of its understory

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plants via ameliorating soil moisture and nutrient, mediating soil microbial community compositions, buffering extreme temperature and radiation, and resisting predators. Removal studies have shown that the effects of shrub on belowground play a stronger role than aboveground on shrubland facilitation. Shrubland facilitations are commonly considered a potential effective approach of vegetation restoration in degraded ecosystems. Whereas, the success of vegetation restoration is comprehensively affected by the abiotic stress, species identities, plant life history stages and land use. Under the dual influence of climate change and human activities, the areas of drylands and shrublands are assumed to be expanding. Thus, the studies on mechanisms of shrubland facilitation and trends of shrub-herbs interactions along drought gradient, as well as the effects of shrub on herbs, are critical for predicting the responses of species and grassland to climate change in arid and semi-arid regions. Based on the current research progresses and environmental changes in arid and semi-arid regions, the present review proposes the following issues in the future studies: 1) exploring the biological indicators to the abiotic stress and plant-plant interactions; 2) clarifying the relative contribution of shrub belowground versus aboveground on facilitation, in order to disclose the mechanisms of shrubland facilitation; 3) exploring the feedback effect of beneficiaries on facilitators; 4) assessing the comprehensive role of nurse plants on vegetation restoration; 5) popularizing the study methods of manipulative water experiments and long-term positioning observations on shrubland facilitation; and 6) addressing the study of plant facilitation on related research issues, such as the relationship between facilitation and species invasion, shrub encroachment, biodiversity and ecosystem function, and the response of facilitation to climate change.

**Key words** nurse plant; water availability; species richness; stress gradient hypothesis; facilitation; vegetation restoration

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植物间相互作用包括竞争作用和促进作用,前者也叫负相互作用,后者则为正相互作用。竞争作用是指在共享有限的生存空间和资源时,种内或种间个体对同一资源的争夺现象,通常是双向的关系。促进作用是指在植物种间或种内,施利者(护卫植物)通过改善恶劣的生存环境、增加资源的可利用性、消除潜在竞争者或抵御取食者等方式,直接或间接地促进受益者的生存、生长或者增加其丰富度,促进作用可能是单向或双向的,包括互利共生(+/+)和偏利共生(+/0和+/-)(Bertness & Callaway, 1994; Callaway, 1995, 2007; Bruno *et al.*, 2003; 张炜平等, 2013; Liancourt & Dolezal, 2021)。

竞争作用一直是生态学研究的重要领域,生态学很多经典理论都基于竞争作用,如达尔文进化论和生态位理论。与此相比,促进作用虽然早在20世纪初就被生态学家观察和记录到,然而,直到20世纪90年代初,促进作用才逐渐被越来越多的研究者所关注,经过近30年不断深入的研究,植物间促进作用已成为当今生态学研究的重要领域。有关促进作用的研究历史,国内外学者都做过详细梳理(Brooker *et al.*, 2008; 储诚进, 2010; 张炜平和王根轩, 2010; Michalet & Pugnaire, 2016; 刘泽正等,

2020)。

竞争作用和促进作用同时存在于自然界的植物群落,其净效应取决于二者的相对强度,而它们的相对强弱与环境密切相关,胁迫梯度假说(SGH)指出,随环境胁迫程度的增加,竞争作用通常减弱,而促进作用增强,前者在低胁迫环境中起主导作用,后者则在高胁迫环境发挥更重要的作用(Bertness & Callaway, 1994)。自SGH提出以来,围绕其在各类生态系统中普适性的验证成为了植物间促进作用研究的热点,大量的野外观测、控制实验、meta分析被用来验证和完善SGH(Callaway *et al.*, 2002; Callaway, 2007; Maestre *et al.*, 2009b; Malkinson & Tielbörger, 2010; He *et al.*, 2013; Soliveres *et al.*, 2015; Michalet & Pugnaire, 2016)。为准确预测促进作用随环境胁迫度的变化规律,促进作用发生机制的研究随之成为植物间相互作用研究的另一重要议题,护卫植物通过直接或间接的作用改善周围环境,从而影响受益者的生存、生长和繁殖(Maestre *et al.*, 2003; Armas & Pugnaire, 2005; Michalet *et al.*, 2015; Tirado *et al.*, 2015; Michalet & Pugnaire, 2016; Noumi *et al.*, 2016)。随着研究的不断深入,促进作用逐渐融入到生态学的重要理论中,例如,促进作用被证明是胁迫环境下物

种多样性形成与维持的重要机制(Hooper *et al.*, 2005; Kikvidze *et al.*, 2005; Butterfield *et al.*, 2013; Cavieres *et al.*, 2014, 2016; Soliveres & Maestre, 2014; Ballantyne & Pickering, 2015; Bråthen & Lortie, 2016; Michalet & Pugnaire, 2016; Pistón *et al.*, 2016; Parajuli *et al.*, 2021)。促进作用拓宽了一些物种的分布范围, 相关研究完善了一直以来基于竞争关系建立的生态位理论(Choler *et al.*, 2001; Bruno *et al.*, 2003)。对促进作用的研究修正了前期基于竞争关系提出的个体生物量与种群密度关系理论(个体生物量随种群密度的增加线性降低), 在考虑促进作用后, 个体生物量与种群密度的关系随环境胁迫的增强由单调递减变为先增后减的单峰格局, 即个体生物量最高出现在中等密度条件(Chu *et al.*, 2008)。此外, 植物间促进作用还被广泛用于退化生态系统的植被恢复(Maestre *et al.*, 2001; Gómez-Aparicio *et al.*, 2004; Padilla & Pugnaire, 2006; Gómez-Aparicio, 2009; 刘泽正等, 2020)。

对植物间促进作用的系统研究, 最早始于盐沼地生态系统(Bertness, 1991; Bertness & Shumway, 1993; Bertness & Hacker, 1994), 后来逐步扩展到以垫状植物作为护卫植物的高山生态系统(Cavieres *et al.*, 2006, 2016; Butterfield *et al.*, 2013; Pugnaire *et al.*, 2015)和以灌木作为护卫植物的干旱半干旱生态系统(Pugnaire *et al.*, 1996; Moro *et al.*, 1997a; Michalet *et al.*, 2015; Noumi *et al.*, 2016; Zhang *et al.*, 2018a)。在气候变化和人类活动的影响下, 干旱半干旱区生态系统正发生着剧烈变化, 灌丛作为干旱半干旱区重要的植被类型, 其促进作用对生态系统-气候变化响应关系及生态系统功能的体现具有重要影响。然而, 干旱半干旱区灌丛促进作用的发生机制, 尤其是灌丛对草本植物的促进作用沿水分梯度的变化, 目前还没有较为统一的结论。此外, 灌丛在植被恢复中的作用也尚未得到全面的评估和运用。本文从灌丛对草本植物的促进作用随水分的变化规律、灌丛促进作用的发生机制以及灌丛促进作用在植被恢复中的应用等方面总结了最近30年来的主要研究进展, 并在此基础上提出了未来研究中需深入探索的问题。

## 1 灌丛促进作用随水分的变化规律

植物间竞争和促进作用的强度与环境密切相关,

作为植物间相互作用随环境胁迫程度变化研究中影响最深远的预测模型, SGH得到了大量野外数据的验证(Pugnaire & Luque, 2001; Callaway *et al.*, 2002; Holzapfel *et al.*, 2006; Armas *et al.*, 2011; Ziffer-Berger *et al.*, 2014; Lortie *et al.*, 2016)。然而越来越多的研究发现植物间促进作用随环境胁迫增强并不总是线性增强, 这种不确定性在干旱半干旱生态系统尤为明显(Tielbörger & Kadmon, 2000; Maestre & Cortina, 2004; Maestre *et al.*, 2005, 2006, 2009b; Lortie & Callaway, 2006; Michalet *et al.*, 2006; Holmgren & Scheffer, 2010; Liancourt *et al.*, 2017; O'Brien *et al.*, 2017; Zhang *et al.*, 2018b; Berdugo *et al.*, 2019)。例如, 在以色列Negev沙漠, 灌木对一年生草本植物密度和种子数的促进作用随降水量的减少而减弱, 原因是在极度干旱的年份(年降水量38 mm), 灌木冠层的截流作用导致其下草本植物遭受严重水分胁迫, 而在湿润年份, 水分不是主要限制因子, 灌木对微气候的改善发挥了较强的促进作用(Tielbörger & Kadmon, 2000)。在西班牙半干旱区, 随降水量的减少, 豆科灌木*Retama sphaerocarpa*对其冠层下草本植物生物量和物种丰富度的影响由促进作用转为竞争作用(O'Brien *et al.*, 2017)。在中国巴丹吉林沙漠, 沙拐枣(*Calligonum mongolicum*)对其冠层下草本植物的促进作用随夏季降水量的减少转为中性作用, 原因是灌丛对土壤水分的促进作用随夏季降水量的减少而减弱(Zhang *et al.*, 2018a)。

促进作用发挥的关键是护卫植物能改善受益者存活或生长的限制因子, 水分作为干旱半干旱区植物存活和生长的主要限制因子(Liancourt *et al.*, 2005; Báez *et al.*, 2013), 灌丛对水分的影响复杂多变, 这可能是造成灌丛与草本植物间相互作用沿水分梯度较难预测的重要原因。干旱半干旱区灌木能通过根系提水作用将深层土壤水分转移到浅层土壤, 提高浅层土壤的水分含量(Richards & Caldwell, 1987; Prieto *et al.*, 2011)。灌木遮阴能减弱蒸散发, 进而提高土壤含水量(Liu *et al.*, 2021)。然而, 灌木的截流和竞争等作用可能会对土壤水分产生负作用(Tielbörger & Kadmon, 2000; Darrouzet-Nardi *et al.*, 2006; Hamerlynck *et al.*, 2011)。Butterfield等(2016)模拟了美国西部灌丛内外土壤含水量的动态变化, 基于多年平均值时, 灌丛对土壤水分的促进作用随干旱增强而减弱, 而在极端干旱或湿润年份, 灌丛

对土壤水分的影响随干旱增强呈单峰格局, 研究指出灌丛对土壤水分的影响与降水、蒸发以及蒸腾速率的相对强弱密切相关。

随着研究的不断深入, 学者们普遍认识到灌丛与草本植物间相互作用不仅受水分的影响, 还与物种特性、植物生活史阶段以及环境胁迫类型等密切相关(He *et al.*, 2013; Soliveres *et al.*, 2014; Zhang *et al.*, 2016; Losapio *et al.*, 2018; Chaieb *et al.*, 2021; Parajuli *et al.*, 2021), 例如, 在巴西东北部半干旱地区, 矮灌木 *Poincianella microphylla* 对冠层下草本物种始终表现为促进作用, 而 *Cnidocolus quercifolius* 和 *Mimosa tenuiflora* 的促进作用随草本物种的生长逐渐转变为中性或竞争作用(Paterno *et al.*, 2016)。在印度北部地区, 变色锦鸡儿(*Caragana versicolor*)对禾草类和直立生长的物种发挥促进作用, 而对匍匐生长的物种更多地表现为竞争作用(Iyengar *et al.*, 2017)。在西班牙东南部, 岩蔷薇属灌木 *Cistus clusii* 对针茅属植物 *Stipa tenacissima* 的促进作用随针茅的成熟而减弱, 原因是成熟针茅获取限制性资源即水分的能力增强(Armas & Pugnaire, 2005)。此外, 研究方法、研究水平和指标选取的不同, 也会影响灌丛与草本植物间相互作用的结果(Maestre *et al.*, 2009b; Soliveres *et al.*, 2015; Iyengar *et al.*, 2017), 例如, Maestre等(2005)对1970–2004年间干旱半干旱区植物间相互作用研究案例进行了综合分析, 发现护卫植物对受益者的存活和生长普遍表现出中性作用, 而对受益者密度和繁殖而言, 在干旱胁迫较低的生境中表现为促进作用, 在干旱胁迫较高的生境则表现为竞争作用。Liancourt等(2017)在印度西北部拉克地区的研究发现, 随海拔降低(干旱增强), 变色锦鸡儿对草本植物的促进作用在群落水平呈现单峰格局, 而对优势伴生种低株披碱草(*Elymus jacquemontii*)和驼绒藜属植物 *Krascheninnikovia pungens* 的促进作用随海拔降低而增强。Metz和Tielbörger (2016)利用空间梯度法(沿降水梯度设置调查样点)、时间法(研究样点连续9年监测)和控制实验法(通过截留和增水设置干旱梯度)比较了以色列蔷薇科灌木 *Sarcopoterium spinosum* 对其冠层下草本植物的影响, 发现不同研究方法的结果并不一致: 模拟增雨和干旱处理条件下, 灌木对草本植物生物量和存活率无显著影响; 空间梯度法的结果表明灌

木对草本植物生物量的促进作用随干旱增强而增强, 但对存活率无显著影响; 时间法结果表明随干旱增强, 灌木对草本植物存活率和生物量的竞争作用增强。Maestre等(2009b)给出了一系列环境胁迫类型(包括资源胁迫如水、光照和养分, 以及非资源胁迫如温度、风和盐碱度)和物种特性(胁迫忍耐种和竞争性物种)组合下, 植物间相互作用随环境胁迫程度变化的趋势, 例如当护卫植物和受益者分别是竞争性物种和胁迫忍耐种时, 更容易出现SGH预测的结果; 而当相互作用的物种具有相似的竞争性或胁迫忍耐生活史性状, 且胁迫梯度受资源因子驱动时, 相互作用的两个物种在胁迫梯度的两端都会出现竞争作用。

在植物间相互作用研究中, 定量描述环境胁迫程度是准确预测相互作用随环境胁迫变化的关键(Callaway, 2007)。在实际研究中, 环境胁迫因子并不总是显而易见的, 物理环境的胁迫并不等于植物的生理胁迫, 因为植物往往能通过调节物候期、生物量分配、器官性状等的方式来适应干旱环境, 其对干旱的响应也并非线性的(Padilla & Pugnaire, 2007; de Dios Miranda *et al.*, 2009; Padilla *et al.*, 2009a; Malkinson & Tielbörger, 2010; Soliveres *et al.*, 2015; Xie *et al.*, 2015; Wei *et al.*, 2016)。例如, Wei等(2016)发现内蒙古毛乌素沙地黑沙蒿(*Artemisia ordosica*)通过改变冠层水平氮分配和叶片结构性状的策略来适应更干旱的环境。促进作用只有在物理环境偏离物种生态幅时才会体现(Liancourt *et al.*, 2005, 2017; Wang *et al.*, 2008; He *et al.*, 2016; Liancourt & Dolezal, 2021), 因此, 在定义和度量胁迫程度时, 要充分考虑护卫植物和受益者对胁迫环境的进化适应性, 这是因为, 在护卫植物分布的边界, 物种可能因不适应当地环境而受到较强的胁迫, 此时护卫植物对环境改善作用会减弱, 促进作用就可能在极度胁迫环境下失效或转为竞争作用(Michalet *et al.*, 2006; Maestre *et al.*, 2009b; Schöb *et al.*, 2013)。相反, 如果护卫植物能很好地适应当地气候环境, 促进作用就可能随环境胁迫增强而线性增加(Holzappel *et al.*, 2006; Armas *et al.*, 2011)。一项基于喜马拉雅干旱山区垫状植物与草本植物间相互作用的研究发现, 水分可利用性是驱动该地区植物间相互作用的主要因子, 叶碳稳定同位素比值( $\delta^{13}\text{C}$ )和基于卫星遥感数据的归一化植被指数(NDVI)能

很好地指示植物间相互作用的变化, 提出了利用生物因子指示环境胁迫程度和种间关系变化的新思路(Ale *et al.*, 2018a, 2018b)。

## 2 灌丛促进作用的发生机制

干旱半干旱区灌丛促进作用影响着其冠层下草本植物的物种丰富度和生长, 灌丛促进作用是干旱半干旱生态系统物种多样性形成与维持的重要驱动因子, 主要有如下3个机制。首先, 由于灌木对微环境的改善作用, 其冠层下物种丰富度往往高于冠层外(Holzappel *et al.*, 2006; Pistón *et al.*, 2016; Iyengar *et al.*, 2017; Zhang *et al.*, 2018a; Parajuli *et al.*, 2021)。其次, 由于灌木提供的异质环境, 使得灌木冠层内外物种组成存在差异, 一些物种只在灌木冠层下或冠层外出现, 进而提高了群落水平的物种丰富度(Armas *et al.*, 2011; Ballantyne & Pickering, 2015; Madrigal-González *et al.*, 2016; Liancourt *et al.*, 2017; Han *et al.*, 2021)。另一方面, 共存的灌木物种塑造了不同的微环境, 进而庇护不同物种在其冠层下存活(Paterno *et al.*, 2016; Pistón *et al.*, 2016)。护卫植物提高群落水平物种丰富度这一结论, 在以垫状植物为护卫植物的高山生态系统也得到了证实(Cavieres *et al.*, 2014, 2016)。此外, 灌木对其冠层下物种的种子萌发、幼苗存活及生长同样发挥着促进作用(Valiente-Banuet & Ezcurra, 1991; Armas & Pugnaire, 2005; Barchuk *et al.*, 2005; Armas *et al.*, 2011; Zhang *et al.*, 2018a, 2018b)。受益者对护卫植物的反馈作用是评估共存物种长期进化方向和群落动态的重要依据(Armas & Pugnaire, 2005; Michalet *et al.*, 2016), 目前有关草本植物对灌木的反馈作用鲜有报道。Armas和Pugnaire (2005)在西班牙东南部开展的岩

蔷薇属灌木 *Cistus clusii* 和针茅属植物 *Stipa tenacissima* 的去除实验发现, 针茅幼苗对护卫灌木表现为中性作用, 针茅成熟以后, 其获取限制性资源的能力增强, 对护卫灌木表现为竞争作用。Iyengar等(2017)对印度北部豆科灌木变色锦鸡儿开展的去除冠层下草本植物的研究发现, 草本植物的去除提高了灌木下一年的开花数。

干旱半干旱区灌木往往通过增加其冠层下土壤水分、提高土壤养分、减弱辐射、降低温度和抵御动物取食等方式发挥促进作用(图1)。干旱半干旱区灌丛能通过遮阴减弱辐射和降低温度, 有效保护冠层下物种免受强辐射和极端温度的伤害(Valiente-Banuet & Ezcurra, 1991; Maestre *et al.*, 2001; Holmgren *et al.*, 2012; Pistón *et al.*, 2016)。灌丛还能抵御捕食者, 尤其是带刺的灌木物种, 能有效地保护草本物种免受或少受食草动物的取食(Rebollo *et al.*, 2002; Tirado *et al.*, 2015; Lortie *et al.*, 2016; Xie *et al.*, 2017)。例如, 在喜马拉雅山区的Langtang河谷, 研究发现有棱小檗(*Berberis angulosa*)因其对牲畜取食的抵御, 灌丛内物种丰富度显著高于灌丛外, 一些适口性较好且不耐取食的物种如多星韭(*Allium wallichii*)、野燕麦(*Avena fatua*)和云梅花草(*Parnassia nubicola*)等仅在有棱小檗冠层下出现(Parajuli *et al.*, 2021)。

土壤水分和养分是干旱半干旱区植物存活和生长的主要限制因子, 二者深刻影响着灌丛与草本植物间的相互作用。干旱灌丛通常能发挥“肥岛效应”, 提高冠层下土壤养分含量, 从而促进其下植物的生长(Pugnaire *et al.*, 1996; Wezel *et al.*, 2000; Maestre *et al.*, 2001; Hortal *et al.*, 2013; Noumi *et al.*, 2016; Zhang *et al.*, 2018b; Cai *et al.*, 2020)。灌丛对土壤养分

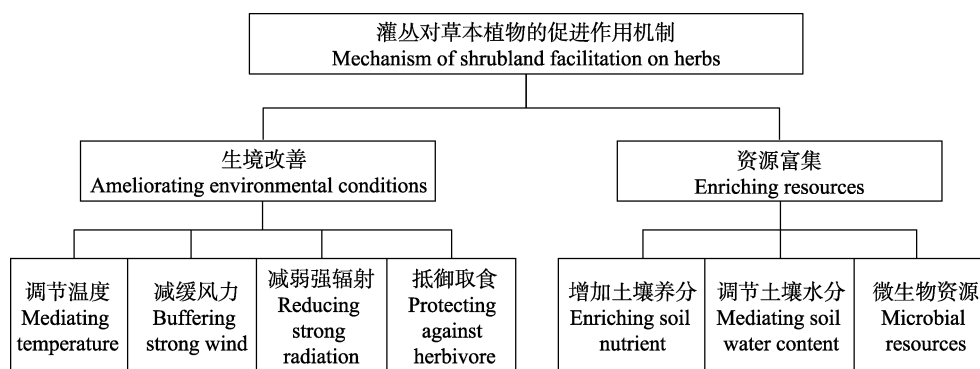


图1 干旱半干旱区灌丛对草本植物的促进作用机制框架图。

Fig. 1 Frame diagram depicting the mechanism of shrubland facilitation on herbs in arid and semi-arid regions.

的改善作用在冠层下的不同位置可能存在差异, 研究发现西班牙东南部豆科灌木 *Retama sphaerocarpa* 冠层中心的土壤有机质和氮含量高于冠层边缘, 而介于冠层中心与边缘地带之间的土壤矿化速率和有机质分解速率最高(Moro *et al.*, 1997a, 1997b)。作为干旱半干旱区典型的优势灌木物种, 豆科灌木对土壤养分和草本植物的促进作用还与根瘤菌的共生固氮作用密切相关(Ouyang *et al.*, 2016; Zhang *et al.*, 2016; Dovrat *et al.*, 2018; Dovrat & Sheffer, 2019), 豆科灌木能显著提高其冠层下土壤氮含量(Pugnaire *et al.*, 1996; Zhang *et al.*, 2011; Saixiyala *et al.*, 2017)。土壤微生物在灌丛促进作用中的重要性近年备受关注(Wang *et al.*, 2018; Pugnaire *et al.*, 2019; Yu *et al.*, 2021), 例如, Hortal等(2013)发现西班牙干旱区豆科植物 *Retama sphaerocarpa* 灌层内外土壤微生物多样性无显著差异, 但灌木冠层下土壤微生物活性、生物量以及和高碳利用效率和固氮等功能相关的类群数量明显高于冠层外。Xie等(2021)发现内蒙古狭叶锦鸡儿(*Caragana stenophylla*)灌层下土壤线虫以及细菌、真菌群落多样性高于灌层外, 灌木的存在直接提高其下土壤线虫和细菌群落多样性, 而灌木通过提高土壤养分的方式间接促进土壤真菌生长。总的来说, 干旱半干旱区灌丛通过影响其冠层下土壤微生物的丰度、组成和活性, 进而增强土壤养分矿化速率, 改善土壤物理结构, 释放化学信号影响植物物候和功能性状, 增强植物防御取食和病原体的能力, 发挥菌根真菌的补偿作用等, 最终影响灌木冠层下的草本植物(Maestre *et al.*, 2009a; Hortal *et al.*, 2013; Rodríguez-Echeverría *et al.*, 2016)。

灌木与其冠层下草本植物间的相互作用通常是灌木对微环境改善后的综合体现, 学者们普遍采用比较冠层内外各环境要素差异的方法来探究灌木发挥促进作用的机制(Ziffer-Berger *et al.*, 2014; Zhang *et al.*, 2018a), 与此相比, 去除实验能定量比较灌木地上(冠层)和地下(土壤)部分对草本植物的相对影响(Maestre *et al.*, 2003; Armas & Pugnaire, 2005; Michalet *et al.*, 2015; Tirado *et al.*, 2015; Wang *et al.*, 2017)。在青藏高原东北部开展的金露梅(*Potentilla fruticosa*)去除实验发现, 灌木地上和地下部分对草本物种丰富度的影响分别表现为竞争和中性作用, 净效应表现为竞争作用, 并且不同物种受灌木地上

和地下及净效应的影响不同, 进而导致灌木下物种组成存在差异(Wang *et al.*, 2017)。在突尼斯干旱半干旱区, 灌木去除实验的结果发现, 灌木地下部分对草本植物表现为促进作用, 冠层表现为竞争或中性作用, 且随干旱增强, 地下部分的促进作用减弱, 冠层的竞争作用则增强, 因为随干旱增强, 灌木对土壤水分的影响逐渐减弱(Noumi *et al.*, 2016; Chaieb *et al.*, 2021)。Lozano等(2020)通过土块互移实验发现西班牙半干旱区豆科灌木 *Retama sphaerocarpa* 冠幅大小和土壤性质对草本植物群落结构的影响是相互独立的, 土壤性质(土壤水分、温度、氮含量和团聚体结构)决定冠层下草本植物的物种组成, 而冠幅大小造成的微气候差异深刻影响着灌层内外的草本植物群落地上生物量和物种丰富度。由此可见, 地下部分(包括土壤养分和土壤微生物)在灌丛与草本植物的相互作用中发挥着重要作用。然而, 目前开展的地下部分对灌丛促进作用沿水分梯度变化的影响的研究还较少, 这可能是今后探索灌丛促进作用沿干旱梯度变化规律研究中值得关注的重点。

### 3 灌丛促进作用在植被恢复中的应用

退化生态系统的植被恢复是生态修复中的重要措施, 在干旱半干旱区的退化生态系统, 植被恢复常常受到水分可利用性、极端温度和土壤养分等的限制(Hoover *et al.*, 2020; Shackelford *et al.*, 2021)。灌木能改善其冠层下土壤和微气候等条件, 促进相邻物种的存活和生长, 因此被广泛用于干旱半干旱区退化生态系统的植被恢复(Maestre *et al.*, 2001; Young *et al.*, 2005; Padilla & Pugnaire, 2006; Gómez-Aparicio, 2009; Michalet & Pugnaire, 2016; Ibáñez & Rodríguez, 2020; 刘泽正等, 2020)。例如, 在摩洛哥半干旱地区, 先锋灌木 *Lavandula stoechas* 改变了土壤微生物群落组成并促成丛枝菌根真菌群落建成, 进而促进 *Cupressus atlantica* 幼苗的生长(Duponnois *et al.*, 2011)。在内蒙古高原, 成熟的狭叶锦鸡儿通过改善微生境和防止食草动物取食的方式促进种内幼苗建成(Xie *et al.*, 2017)。在塞浦路斯地中海气候的干旱半干旱区, 深根系灌木 *Ziziphus lotus* 能显著提高在其附近生长的 *Thymbra capitata* 种群密度(Constantinou *et al.*, 2021)。

值得注意的是, 植被恢复成功与否受到环境胁

迫程度、护卫植物和目标恢复物种的物种特性和植物生活史阶段以及土地利用等的综合影响。例如, 在西班牙东南部, Gómez-Aparicio等(2004)比较了16种护卫灌木对目标恢复物种幼苗存活和生长随海拔和坡向的变化, 发现促进作用的强度因护卫灌木和目标恢复物种的物种差异而有所不同, 并且表现出在高海拔强于低海拔、在阴坡强于阳坡的生境差异。Padilla等(2009b)比较了用于干旱生态系统植被恢复的14种灌木在浇水和对照处理下的幼苗成活率, 结果发现: 处于演替中期的物种, 如无叶植物*Ephedra fragilis*和C<sub>4</sub>植物*Salsola oppositifolia*和豆科植物*Coronilla juncea*、*Genista umbellata*和*Retama sphaerocarpa*的存活率远远高于处于演替后期的物种, 且在不浇水处理下, 演替中期的物种存活率高于演替后期的物种, 研究指出处于演替中期的物种更有利于干旱区植被恢复。Padilla和Pugnaire (2009)在西班牙干旱半干旱区的研究发现, 豆科灌木*Retama sphaerocarpa*对其冠层下*Olea europaea*幼树成活率表现为促进作用, 而对*Pistacia lentiscus*和*Ziziphus lotus*幼树成活率分别表现为中性和竞争作用。植物生活史阶段对植被恢复的影响主要表现为: 在植被恢复前期, 护卫植物对目标物种发挥促进作用, 随着目标物种种群的建立, 对资源的需求随之增多, 护卫植物和目标物种的关系就可能从促进转为中性或竞争, 导致植被恢复的失败(Miriti, 2006; Suding, 2011; Yang *et al.*, 2014)。放牧是干旱半干旱区灌丛化草原最主要的土地利用方式, 研究发现内蒙古小叶锦鸡儿(*Caragana microphylla*)灌丛对土壤养分的促进作用随放牧强度增强呈单峰格局, 即在轻度放牧条件下灌丛对土壤养分促进作用最强, 促进作用在过度放牧条件下失效(Cai *et al.*, 2020)。因此, 在植被恢复过程中, 要充分考虑促进和竞争作用的潜在影响, 准确评估促进作用在植被恢复过程中的贡献, 所选择的护卫植物要最大程度避免与目标物种竞争有限的资源, 从而有效促进目标物种的建立和生长(Padilla & Pugnaire, 2006; Ibáñez & Rodríguez, 2020)。

## 4 展望

干旱半干旱区占全球陆地面积的1/4, 而自20世纪70年代以来, 全球干旱区的面积扩大了2倍以上(Dai *et al.*, 2004; Dai, 2011)。近百年来, 干旱半干旱

区气温升高幅度明显高于其他地区(Huang *et al.*, 2012), 气温的持续升高导致干旱半干旱区气候呈现明显的暖干化趋势(IPCC, 2013)。在气候变化和人类活动的共同影响下, 全球大部分干旱半干旱区都发生了灌木密度、盖度或分布面积增加的灌丛化现象(Knapp *et al.*, 2008; Maestre *et al.*, 2009a; Eldridge *et al.*, 2011; Loydi *et al.*, 2013), 研究表明, 过去150年里全球草原大约10%–20%的地区发生了灌丛化(van Auken, 2009), 豆科灌木是灌丛化物种中占比最高的类群(Eldridge *et al.*, 2011)。干旱半干旱区发生的气候变化和灌丛化无疑对区域生态系统结构和功能产生重要影响, 因此, 准确评估灌丛在干旱生态系统中的作用是预测干旱半干旱区物种和生态系统对气候变化的响应, 以及制定干旱生态系统管理和实施生态安全屏障建设工程的关键。我国干旱半干旱区分布面积广, 灌丛和草原是干旱半干旱区重要的生态系统类型, 近年来, 学者们针对我国内蒙古高原以锦鸡儿属灌木为主的灌丛(Zhang *et al.*, 2011, 2018a, 2018b; Xie *et al.*, 2017, 2021; Liu *et al.*, 2021)以及青藏高原东部金露梅灌丛(Xu *et al.*, 2010; Wang *et al.*, 2017, 2018, 2019, 2021)的促进作用开展了较为详细的研究。青藏高原中西部是典型的高寒干旱半干旱区, 灌丛化草原广泛分布, 生态环境脆弱, 目前尚未见到该地区有关灌丛促进作用的相关报道, 因此, 加强推进灌丛促进作用相关研究, 对于青藏高原生态安全屏障建设以及区域植被恢复无疑具有重要的理论和实践意义。

经过近30年的研究, 植物间促进作用已成为生态学研究的重要组成部分。基于现有认识, 我们对未来植物间促进作用, 尤其是干旱半干旱区灌丛促进作用提出以下值得关注的研究内容。

### 4.1 环境胁迫程度的量化

在以水分为主要限制因子的生态系统, 促进作用随水分可利用性的变化模式一直是植物间相互作用研究中颇具争议的问题。其中, 干旱梯度的准确量化是预测灌木与草本植物间相互作用随水分变化的关键, 利用生物指标指示环境胁迫程度和种间关系是今后研究中值得深入探讨的问题(Ale *et al.*, 2018a, 2018b)。

### 4.2 明确地下部分对灌丛促进作用的相对贡献

近年来开展的几项去除实验均发现灌木地下部分对灌丛促进作用的贡献强于灌木冠层的作用, 表



明灌木对地下过程如土壤条件的改善作用可能强于灌木冠层对微气候的调节作用。灌木地下部分发挥的促进作用与灌木对土壤养分的改善以及土壤微生物群落的影响密切相关(Michalet & Pugnaire, 2016; Chaieb *et al.*, 2021), 然而, 目前灌木地下部分对促进作用的贡献尚未得到全面评估, 加强相关研究是准确评估干旱半干旱区灌丛促进作用发生机制以及预测灌丛与草本植物间相互作用随环境变化规律的关键。

#### 4.3 探索受益者对护卫植物的反馈作用机制

目前, 大量研究已证实护卫植物对其相邻植物的存活和生长普遍发挥着促进作用, 而有关受益物种对护卫植物的反馈研究鲜有报道, 受益物种对护卫植物的影响可能表现为竞争或促进作用。研究发现禾草类植物对高山地区的垫状护卫植物(Michalet *et al.*, 2016)以及干旱半干旱区的护卫灌木(Armas & Pugnaire, 2005)都表现出竞争作用, 原因是与其他类群植物相比, 禾草类对根的投资更多, 且从土壤获取资源的能力更强。在祁连山地区的研究发现杂类草和豆科植物对护卫植物囊种草(*Thylacospermum caespitosum*)果实的形成有促进作用, 这可能与杂类草能吸引更多传粉者有关(Michalet *et al.*, 2016)。由此可见, 受益者对护卫植物的反馈作用可能受不同植物功能群的调节, 加强相关研究进而明确植物间相互作用及其机制是评估物种间长期进化关系的重要依据。

#### 4.4 综合评估促进作用在植被恢复中的贡献

护卫植物对微环境和相邻植物群落有明显促进作用, 因此, 人为种植护卫植物进而发挥其促进作用被认为是潜在的用于开展退化生态系统植被恢复的有效手段。然而, 护卫植物的促进作用还与环境胁迫程度、物种特性以及土地利用方式等密切相关, 在实际的应用中应综合考虑各方面影响因素, 预先评估促进作用在植被恢复中的贡献。

#### 4.5 加强模拟增水实验和长期定位观测研究

环境因子的变化会改变植物间促进与竞争之间的平衡(O'Brien *et al.*, 2017), 模拟增水实验为检测竞争与促进作用转变的阈值提供了理想实验平台, 但鲜有相关研究报道。此外, 有关不同植物物种间促进作用的研究大量集中在沿自然环境梯度如海拔和经度、纬度的调查, 然而在较大的环境梯度上, 护卫植物和相邻植物群落的物种组成都可能发生变化

(Liancourt *et al.*, 2017; Zhang *et al.*, 2018b), 使得很难了解促进作用的改变在多大程度上受到物种更替的影响, 而结合长期的定位观测将有助于排除这一不确定因素。

#### 4.6 促进作用与其他研究领域的结合

未来应加强促进作用与生态学其他研究领域的结合, 如促进作用与生物入侵、灌丛化、生物多样性和生态系统功能的关系研究(Soliveres *et al.*, 2015; Wang *et al.*, 2021)。特别是在气候变化背景下, 作为调节物种及生态系统对环境变化的重要机制, 促进作用能否增强生态系统弹性和稳定性, 增强抵御气候变化的能力(Brooker, 2006; Anthelme *et al.*, 2014; Pugnaire *et al.*, 2021), 这些都是在今后的研究中值得关注的议题。

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